The Sharamurunian rodent fauna in the Erlian Basin, Nei Mongol, China Postprint

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Date: 2022-11-25T00:00:00+00:00

Abstract

New middle Eocene rodent fossils discovered from the lower part of the Shara Murun Formation of Ula Usu, Erlian Basin, Nei Mongol, China, the classical locality of Sharamurunian mammalian fauna, were identified as 9 separate species (the ctenodactyloids Yuomys cavioides, Gobiomys neimongolensis, G. exiguus, and G. asiaticus, the dipodids Allosminthus uniconjugatus and Primisminthus shanghenus, the cricetid Pappocricetodon rencunensis, the ischyromyid Hulgana cf. H. ertnia, and the cylindrodontid Proardynomys ulausuensis) belonging to 7 genera, 4 families, and 1 superfamily of Rodentia. The Ula Usu rodent assemblage shares a high degree of similarity with that from the "Lower Red" beds of the Erden Obo, and they both represent the typical Sharamurunian rodent assemblages found in northern China. The Sharamurunian rodent fauna in the Erlian Basin is analyzed by the minimum number of individuals based on the rodent materials from the lower part of the Shara Murun Formation in the Ula Usu and the "Lower Red" beds of the Erden Obo. In the Sharamurunian rodent fauna of the Erlian Basin, ctenodactyloids are the most dominant elements, and dipodids and cricetids follow next in prevalence. By analyzing the evolution of the rodent species richness in the Erlian Basin, the rodent faunas show a transformation from a ctenodactyloid dominant assemblage to a cricetid-dipodid dominant one in chronological order. The Sharamurunian rodent fauna from the Erlian Basin differs from that of the Yuanqu Basin and the differences in the rodent assemblages may be a response to the differences between the regional environments.

Full Text

Preamble

The Sharamurunian Rodent Fauna in the Erlian Basin, Nei Mongol, China

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Abstract

New middle Eocene rodent fossils discovered from the lower part of the Shara Murun Formation at Ula Usu, Erlian Basin, Nei Mongol, China—the classical locality of the Sharamurunian mammalian fauna—were identified as nine separate species belonging to seven genera, four families, and one superfamily of Rodentia. These include the ctenodactyloids *Yuomys cavioides*, *Gobiomys neimongolensis*, *G. exiguus*, and *G. asiaticus*; the dipodids *Allosminthus uniconjugatus* and *Primisminthus shanghenus*; the cricetid *Pappocricetodon rencunensis*; the ischyromyid *Hulgana* cf. *H. ertnia*; and the cylindrodontid *Proardynomys ulausuensis*. The Ula Usu rodent assemblage shares a high degree of similarity with that from the "Lower Red" beds of Erden Obo, and together they represent the typical Sharamurunian rodent assemblages found in northern China. The Sharamurunian rodent fauna in the Erlian Basin was analyzed using the minimum number of individuals based on rodent materials from the lower part of the Shara Murun Formation at Ula Usu and the "Lower Red" beds of Erden Obo. In the Sharamurunian rodent fauna of the Erlian Basin, ctenodactyloids are the most dominant elements, followed by dipodids and cricetids. Analysis of rodent species richness evolution in the Erlian Basin reveals a transformation from ctenodactyloid-dominant assemblages to cricetid-dipodid-dominant ones in chronological order. The Sharamurunian rodent fauna from the Erlian Basin differs from that of the Yuanqu Basin, and these differences in rodent assemblages likely reflect regional environmental variations.

Key words: Nei Mongol, Erlian Basin, Ula Usu, Sharamurunian, rodent fauna

Citation: Li Q, Li Q, in press. The Sharamurunian rodent fauna in the Erlian Basin, Nei Mongol, China. *Vertebrata PalAsiatica*.

1 Introduction

Following the principle of North American Land Mammal Ages (NALMA), Romer (1966) proposed several related Asian Paleogene Land Mammal Ages (APLMA) based on mammalian faunas from different stratigraphic levels. Most of the APLMA proposed by Romer were derived from selected Paleogene mammal faunas found in the Erlian Basin, Nei Mongol, such as the Arshantan, Irdinmanhan, and Sharamurunian. Subsequent researchers revised the nomenclature and re-estimated the ages of these land mammal ages (Li and Ting, 1983;

Woodburne et al., 1987; Tong et al., 1995; Wang, 1997a, b).

The type locality of the Sharamurunian fauna is Ula Usu in the Erlian Basin, Nei Mongol. In the Sharamurunian mammalian fauna, perissodactyls were the most predominant group, while artiodactyls became increasingly diversified and ruminants first appeared (Wang et al., 2007). However, studies on Sharamurunian rodent fossils at Ula Usu—the classical locality of the Sharamurunian mammal fauna—were very limited. Only Li (1975) reported a few specimens of *Yuomys*. Through several years of field expeditions (2009-2017), a large number of rodent fossils were recovered at Ula Usu. This study focuses on the systematics of these new rodent materials, which complement the Sharamurunian mammalian fauna in the Erlian Basin and improve the successional sequence of rodent assemblages from the early Eocene to early Oligocene in the region.

2 Geological Setting

Ula Usu proper is the type locality for both the Shara Murun Formation and the Tukhum Formation. The upper part of the Shara Murun Formation consists of white and light gray sandstone, whereas the lower part comprises variegated sandy clay (Berkey and Morris, 1927; Chow and Rozhdestevensky, 1960; Bai et al., 2018). Below the Shara Murun Formation lies an interval of hard red clay (Granger, 1925), which Berkey and Morris (1927) named the Tukhum Formation. In recent field investigations, we remeasured the lithological strata in this area.

Eight distinct sedimentary layers are exposed at Ula Usu [Figure 1: see original paper]. The lowermost layer (layer 1, 0-13.50 m) is the Tukhum Formation, consisting of muddy dark red siltstone and silty mudstone that has yielded a few perissodactyl fossils. Layer 2 (13.50-28.50 m), from which the new rodent fossils reported here were recovered, is dominated by grayish green and dark red mudstone or silty mudstone. Layer 3 (28.50–45.00 m) comprises grayish green mudstone and has yielded abundant postcranial bones and cheek teeth from perissodactyls and artiodactyls. Layer 4 (45.00–49.00 m) consists of grayish white silty mudstone and fine sandstone in the upper part and has yielded many perissodactyl fossils. Layer 5 (49.00–55.15 m) is composed of white fine sandstone and siltstone interspersed with grayish green pebbled silty mudstone, which is rich in large calcareous nodules. Layer 6 (55.15–57.40 m) is dominated by light red mudstone with some Fe-Mn nodules. Layer 7 (57.40–59.27 m) is white gravelly coarse sandstone or fine sandstone. Layer 8 represents Quaternary cover.

All newly described specimens were collected from Layer 2 in the section, which corresponds to the lower part of the Shara Murun Formation at Ula Usu, where several field expeditions were carried out between 2009–2017 by a team from the IVPP [Figure 1: see original paper].

3 Material and Methods

Dental terminology generally follows Wang (1997a, 2019b) and Li and Meng (2015) for ctenodactyloids, Li (2018) and Wang et al. (2020) for cricetids and dipodids, Dashzeveg and Meng (1998) for ischyromyids, and Wang (2019a) for cylindrodontids. Tooth measurements were taken using a reticle with an accuracy of 0.01 mm mounted in a LEICA S9D microscope. Specimens were CT-scanned using a GE v|tome|x m 300&180 micro-computed tomography scanner (GE Measurement & Control Solutions, Wuntsdorf, Germany) housed at the Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese Academy of Sciences. Graphic processing was performed using VGstudio Max 2.1 software (Volume Graphics, genuine authorized). Analysis of rodent assemblages employed the minimum number of individuals (MNI), which refers to the fewest possible number of individuals in a skeletal assemblage. The MNI for each group was calculated from the total specimens by first separating elements (teeth or bones) into left and right, then counting each element and selecting the maximum count among them (Rose, 1981; Tong, 1997). All fossil specimens collected are housed at the IVPP and are available for examination by qualified researchers.

Abbreviations: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; AMNH, American Museum of Natural History, New York; PSS, Paleontology and Stratigraphy Section of the Geological Institute, Mongolian Academy of Sciences. The measurement value "–" represents a partially broken specimen with no measurement data.

4 Systematics

Order Rodentia Bowdich, 1821

Family Cylindrodontidae Miller & Gidley, 1918

Genus *Proardynomys* Dashzeveg & Meng, 1998 *Proardynomys ulausuensis* sp. nov.

Holotype: IVPP V28608, a right mandible with p4–m3.

Locality and horizon: Ula Usu, Erlian Basin, Nei Mongol; lower part of the Shara Murun Formation.

Diagnosis: Smallest species of the genus. Its lower cheek teeth have a narrow sinusid and short posterolophid. It differs from *P. borkhoii* in having a narrower sinusid and shorter posterolophid on the lower cheek teeth, as well as a straighter ectolophid and more developed lophids on m3. It differs from *Proardynomys* sp. in having a stronger posterolophid and a more buccally positioned ectolophid on the lower cheek teeth.

Etymology: The specific epithet is derived from the type locality Ula Usu.

Measurements: See .

Description: The right mandible (IVPP V28608) is broken. The horizontal ramus is straight and robust, with the highest point of the horizontal ramus measuring 0.95 cm at m2. The masseteric fossa extends anteriorly to between m1 and m2 [Figure 2: see original paper]. A small mental foramen is located below the trigonid of m1.

The lower cheek teeth are low-crowned and have four transverse lophs. On p4, the protoconid and metaconid are well developed, with the protoconid being larger and lower than the metaconid after wear. Metalophid I is absent and the trigonid basin opens forward. Metalophid II is low, connecting the protoconid and metaconid. Compared to the metaconid and entoconid, the hypoconid is larger and extends anterolabially clearly beyond the labial margin of the protoconid. The anterolabial elongation of the hypoconid gradually decreases from p4 to m3. The metastylid crest extends backwards from the metaconid along the lingual edge of the crown and is separated from the entoconid by only a narrow groove. The ectolophid extends from the posterolabial side of the protoconid to the anterolingual side of the hypoconid. There is no mesoconid on the ectolophid. The hypolophid is thin and connects the entoconid to the hypoconid. The posterosinusid between the hypolophid and posterolophid is narrow and opens lingually. The sinusid is deep, wide, and opens anterolabially [Figure 2: see original paper].

On m1, the talonid is wider than the trigonid, and the protoconid is lower than the metaconid. The straight metalophid I connects the protoconid and metaconid, forming the anterior edge of the tooth. Metalophid II extends anterolingually to the metaconid and encloses the trigonid posteriorly. After wear, the hypoconid is similar in size to the protoconid. The metastylid crest is well developed, and a well-developed mesostylid is present on the metastylid crest [Figure 2: see original paper]. The ectolophid is short but strong, and the mesoconid is absent on the ectolophid. The hypolophid is complete and straight, dividing the talonid basin into a broad mesosinusid and a narrow posterosinusid. The sinusid opens anterolabially and is narrower than that on p4. The ectostylid in the sinusid is well developed. The posterolophid is strong but the hypoconulid is less developed.

The morphology of m2 is similar to that of m1, but m2 is larger in size . The trigonid of m2 is slightly narrower than the talonid, whereas the width of the trigonid is slightly wider than that of the talonid on m1. The protoconid is higher than the metaconid. The deep sinusid is wider than that of m1. The ectostylid on m2 is less developed than that on m1.

The m3 is slightly longer than m1 and m2. The trigonid of m3 is relatively wider but longer than those of m1 and m2. The mesostylid and metastylid crest are distinct. There is no mesoconid, ectostylid, or mesolophid [Figure 2: see original paper].

Comparisons: The new material shares the following features with cylindrodontids: four transverse lophids, a well-developed mesostylid, absence of mesolophid on p4–m3, weak hypolophid close to the posterolophid on p4, complete ectolophid and hypolophid, and metalophid directed toward the buccal side of the metaconid on m1–3. It differs from *Cylindrodon* (Douglass, 1901) in having larger lower cheek teeth, p4 longer than m1, and a thin hypolophid on p4. *Pseudocylindrondon* (Burke, 1935) differs from the new material in having smaller size, two mental foramina, and a complete metalophid II on m3. The new specimen shares many features with *Ardynomys* (Burke, 1936), but also exhibits many more primitive characteristics. Compared with *Ardynomys* (Matthew and Granger, 1925; Wood, 1970), the cheek teeth of V28608 have a lower crown, the metaconid is higher than the entoconid, narrower and less developed lophids, a less expanded hypoconid, and a lower metastylid crest on molars. The new specimen from Ula Usu possesses several common features of *Proardynomys*, including a low crown, low and narrow entoconid, wide sinusid, and thin lophid.

Dashzeveg and Meng (1998) first named *Proardynomys* based on materials from the Middle Eocene Mergen locality of the Eastern Gobi, Mongolia. Until now, *Proardynomys* included *P. borkhoii* (Dashzeveg and Meng, 1998) and *Proardynomys* sp. from the "Middle Red" beds of the Erden Obo section, Siziwangqi, Nei Mongol (Li, 2021). The differences between the new specimen and *P. borkhoii* are as follows: on the lower cheek teeth of the new specimen, the posterolophid is shorter, the sinusid of p4–m3 is narrower, the ectostylid is more developed, and the new specimen is smaller than *P. borkhoii* . The m2 hypolophid of the new specimen is straighter, and the lophids of m3 are better developed than those in *P. borkhoii*.

The new specimen differs from *Proardynomys* sp. in the Erden Obo section in having smaller size , stronger and shorter posterolophid of m1–3, narrower sinusid, more curved hypolophid, and more lingually positioned ectolophid. Additionally, the occlusal outline of m2 in the new specimen is rhomboid, whereas that of *Proardynomys* sp. is trapezoidal.

Proardynomys ulausuensis sp. nov. is erected for the new specimen.

Superfamily Ctenodactyloidea Tullberg, 1899

Family Yuomyidae Li, 1975 Genus *Yuomys* Li, 1975

Yuomys cavioides Li, 1975

Specimens: IVPP V28604.1, right maxilla with P4–M2; V28604.2, left maxilla with P3–M3; V28604.3, left maxilla with M2; V28604.4, left maxilla with M1–2 and alveoli of P4–M1; V28604.5, left maxilla with broken P4 and M1–2; V28604.6, left mandible with m2–3; V28604.7, left mandible with m3; V28604.8, left mandible with m2; V28604.9, left M1; V28604.10–11, right M1s; V28604.12, left M2; V28604.13–15, right M2s; V28604.16–17, left m1s; V28604.18, right m1; V28604.19, left m2; V28604.20–22, right m2s.

Locality and horizon: Ula Usu, Erlian Basin, Nei Mongol; lower part of the Shara Murun Formation.

Measurements: See .

Description and comparisons: The tapered P3 has a single root, with a distinct main cusp on the buccal side [Figure 3: see original paper]. P4 is larger than M1 and has a hypocone significantly smaller than the protocone. The metaconule is as large as the metacone, located close to the metacone and free from contact with both the protocone and hypocone. The metaloph is approximately parallel to the protoloph and points to the posterior side of the protocone but does not connect to it. The P4 parastyle on the buccal terminal of the anteroloph extends anterolingual-posterolabially and is well developed but slightly smaller than the paracone. The hypocone of M1–2 is developed and nearly equal in size to the protocone. The M1–2 metaloph connecting the metacone and metaconule points obliquely to the protocone. Most M1s have a postparacrista (6/7) and a very short crest on the anterolingual side of the metaconule that extends toward the protocone but fails to connect (5/7). M2 often has a small mesostyle (6/9). The metaloph of M3 is more oblique and points anterolingually toward the protocone. The hypocone is also developed on M3 and separated from the protocone by a shallow cleavage.

Trigonids of m1–2 are higher than talonids [Figure 3: see original paper]. Metalophid I is complete, while metalophid II is short. The straight hypolophid is well developed, and the mesoconid is absent. The hypoconulid on the posterolingual side of the hypoconid is distinct. The m2 is larger than m1, the mesostylid of m2 is more developed than that of m1, and a conulid (4/6) on the hypolophid is often present on m2. The m3 has a distinct mesostylid and the posterosinusid is closed [Figure 3: see original paper].

The new Ula Usu specimens possess many characters of *Yuomys*, such as a well-developed hypocone similar in size to the protocone on M1–2, a distinct metaconule, the metaloph directed toward but not in contact with the protocone on upper molars, and a transverse hypolophid that extends to the ectolophid. *Yuomys* includes ten species: *Y. cavioides* (Li, 1975; Tong, 1997), *Y. eleganes* (Wang, 1978), *Y. minggangensis* (Wang and Zhou, 1982), *Y. weijingensis* (Ye, 1983), *Y. yunnanensis* (Huang and Zhang, 1990), *Y. huangzhuangensis* (Shi, 1989), *Y. huheboerhensis* (Li and Meng, 2015), *Y. altunensis* (Wang, 2017), *Y. magnus* (Li, 2017), and *Y. robustus* (Gong et al., 2021). The new materials are smaller than *Y. altunensis*, *Y. magnus*, and *Y. robustus*, but larger than *Y. huheboerhensis* [Figure 4: see original paper]. The new materials are similar to *Y. eleganes*, but the latter differs in that the protoconid and metaconid on the lower teeth are isolated and the conulid on the hypolophid is missing.

The size of the new materials falls within the range of variation of *Y. cavioides*, and most features are identical to those of *Y. cavioides* . Compared with the holotype of *Y. cavioides* (V4796.1–4), the hypoconid on m2 (V28604.6) is larger and the mesostyle on M2 (V28604.2) is weaker.

Family Gobiomyidae Wang, 2001 Genus *Gobiomys* Wang, 2001

Gobiomys neimongolensis (Meng et al., 1999)

Specimens: IVPP V28605.1, left M1; V28605.2, right M1; V28605.3, left M2; V28605.4-7, right M2s; V28605.8, left M3; V28605.9, right M3; V28605.10-11, left p4s; V28605.12-16, left m1s; V28605.17-18, right m1s; V28605.19-20, left m2s; V28605.21-22, right m2s; V28605.23-26, left m3s; V28605.27-33, right m3s.

Locality and horizon: Ula Usu, Erlian Basin, Nei Mongol; lower part of the Shara Murun Formation.

Measurements: See .

Description and comparisons: The new specimens from Ula Usu share many common characters with *Gobiomys*, including cheek teeth that increase in size distally, distinct but not swollen main cusps, P4 that is non-molariform with a weak or absent metaloph, well-developed metaconule of upper molars, lower molars with ectolophid located slightly labial to the middle longitudinal line and a narrow sinusid, and hypoconulid located at the middle of the posterior margin of m1-2. *Gobiomys* includes three known species: *G. neimongolensis*, *G. asiaticus*, and *G. exiguus* (Meng et al., 1999; Wang, 2001). The new specimens are larger than *G. asiaticus* and *G. exiguus*. The Ula Usu specimens differ from *G. asiaticus* in having a weaker anterolophid, thin hypolophid, and well-developed metalophid II on lower molars. They differ from *G. exiguus* in lacking an anteroconid on p4 and in having the anterolophid and metalophid II on lower molars. The Ula Usu specimens have M1 with a well-developed metaconule but lack a metaloph, have a short metaloph on M2 and M3, more developed metalophid II on m1-3, weak or absent hypolophid, and lack mesoconid on lower cheek teeth [Figure 5: see original paper]. All these features are identical to those of *G. neimongolensis*. Compared with *G. neimongolensis* described in Wang (2001) and Li (2017), the new specimens from Ula Usu are slightly smaller .

Gobiomys exiguus Wang, 2001

Specimens: IVPP V28606.1, right P4; V28606.2-7, right M1s; V28606.8-10, left M2s; V28606.11-17, left M3s; V28606.18-23, right M3s; V28606.24-25, left m1s; V28606.26-28, right m1s; V28606.29-33, right m2s; V28606.34-35, left m3s; V28606.36, right m3.

Locality and horizon: Ula Usu, Erlian Basin, Nei Mongol; lower part of the Shara Murun Formation.

Description and comparisons: The new specimens from Ula Usu possess the typical features of *Gobiomys exiguus* (Wang, 2001; Li, 2017) , including a weak entoloph and strong metaconule on M1-2 and the lack of anterolophid, hypolophid, and metalophid II on lower molars [Figure 6: see original paper]. In size, the new specimens are smaller than *G. neimongolensis* and *G. asiaticus*.

Morphologically, they differ from *G. neimongolensis* and *G. asiaticus* in having a stronger metaconule, less developed metaloph on M1–2 and anterolophid on m1–3, and in lacking a hypolophid and metalophid II on lower molars. Compared with *G. exiguus* reported by Wang (2001), the P4 of the new specimens lacks postparacrista, the hypocone of M3 is slightly weaker, and the ectolophid of m1–2 is better developed.

Gobiomys asiaticus Wang, 2001

Specimens: IVPP V28607.1, right P4; V28607.2–5, left M2s; V28607.6–8, right M2s.

Locality and horizon: Ula Usu, Erlian Basin, Nei Mongol; lower part of the Shara Murun Formation.

Description and comparisons: Compared to *G. neimongolensis* and *G. exiguus*, the new specimens show several differences including a smaller metaconule, well-developed metaloph, and weaker entoloph on the upper molars. Compared with the holotype and paratype of *G. asiaticus* (Wang, 2001), the new specimens from Ula Usu are slightly smaller and have a weaker posterior arm of the protocone on P4 and a weaker entoloph on M2 [Figure 7: see original paper].

Family Cricetidae Fischer von Waldheim, 1817

Genus *Pappocricetodon* Tong, 1992 *Pappocricetodon rencunensis* Tong, 1992

Specimens: IVPP V28610.1, a right mandible with m2–3; V28610.2–6, left M1s; V28610.7–9, right M1s; V28610.10–12, left M2s; V28610.13–18, right M2s; V28610.19, right M3; V28610.20–26, left m1s; V28610.27–36, right m1s; V28610.37–39, right m2s; V28610.40–42, left m3s.

Locality and horizon: Ula Usu, Erlian Basin, Nei Mongol; lower part of the Shara Murun Formation.

Description and comparisons: The new specimens from Ula Usu share many characters with *Pappocricetodon* (Tong, 1992), such as brachyodont cheek teeth, an obvious mesoloph on the upper cheek teeth, a bulbous protocone on M1–3, M1 with a small anterior lobe and low anterocone, a long anterolophule extending to the anterocone, a weak ectomesolophid on m1–3, m1 with a small anteroconid, and a metalophid II that connects to the middle part of the anterior arm of the protoconid on m2–3 [Figure 8: see original paper].

Pappocricetodon contains six species: *P. rencunensis*, *P. antiquus*, *P. neimongolensis*, *P. schaubi*, *P. siziwangqiensis*, and *P. kazakstanicus* (Wang et al., 2020). Compared with *P. antiquus* (Wang and Dawson, 1994) and *P. kazakstanicus* (Emry et al., 1998), the anterior lobe and anterocone on M1 of the new specimens are larger, and the ectomesolophid on the lower molars is present. The mesoloph on M1–2 of the new specimens is shorter than that of *P. kazakstanicus*. The new specimens are smaller than *P. kazakstanicus*, *P. antiquus*, and *P. schaubi* (Zdansky, 1930; Tong, 1997; Li, 2018). They differ from *P. schaubi* in having a smaller anterior lobe and lower anterocone on M1, as well as a smaller anteroconid and weaker mesoconid on m1. *Pappocricetodon siziwangqiensis* (Li et al., 2016) differs from the new specimens in having a protoloph connected to the posterior side of the paracone on M1 and lacking a contact facet on the anterior surface of M1 (absence of premolar).

The new specimens differ from *P. neimongolensis* (Li, 2012) in having larger anterocones and more developed mesolophs on M1 and M2, a narrower anterior groove and mesosinus on M3, a larger anteroconid on m1, a longer and more complete metalophid I, and a less developed mesolophid and ectomesolophid on m2. The new specimens from Ula Usu have a developed mesostyle and mesoloph on the upper molars, a small anterocone, low anterior lobe, developed anterolophule connecting to the anterocone on M1, less developed hypocone and metacone on M3, narrow trigonid, complete metalophid II on m1–3, and developed ectomesolophid on m1. All these features are identical to those of *P. rencunensis* (Tong, 1992, 1997). The size of the new specimens falls within the range of variation of *P. rencunensis* (Tong, 1992, 1997) .

Family Dipodidae Fischer von Waldheim, 1817

Genus *Allosminthus* Wang, 1985 *Allosminthus uniconjugatus* (Tong, 1997)

Synonymy: *Banyuesminthus uniconjugatus* Tong, 1997; *Allosminthus uniconjugatus* Wang, 2008.

Specimens: IVPP V28611.1–2, left M1s; V28611.3–6, right M1s; V28611.7–8, left M2s; V28611.9, left M3; V28611.10, right M3; V28611.11–13, left m1s; V28611.14–21, left m2s; V28611.22–31, right m2s; V28611.32–33, left m3s; V28611.34–35, right m3s.

Locality and horizon: Ula Usu, Erlian Basin, Nei Mongol; lower part of the Shara Murun Formation.

Description and comparisons: Wang (1985) named *Allosminthus* based on specimens from Qujing in Yunnan, which was later revised by Wang (2008), Daxner-Höck (2001), and Daxner-Höck et al. (2014). To date, *Allosminthus* includes six species: *A. ernos* (Wang, 1985), *A. majusculus* (Wang, 1985), *A. diconjugatus* (Tong, 1997), *A. uniconjugatus* (Tong, 1997), *A. minutus* (Daxner-Höck, 2001; Daxner-Höck et al., 2014), and *A. khandae* (Daxner-Höck, 2001).

The new specimens from Ula Usu are smaller than *A. majusculus*, *A. diconjugatus*, and *A. ernos*, but larger than *A. khandae* and *A. minutus*. They differ from *A. diconjugatus* in lacking protoloph II and the posterior arm of the protocone on M1, and in lacking a distinct mesolophid on m1 [Figure 9: see original paper].

Allosminthus majusculus differs from the new specimens in having a smaller anteroconid and stronger hypolophid on m1, a closed trigonid, and more developed ectomesolophid on m2. The specimens from Ula Usu differ from *A. khandae* and *A. minutus* in having a weaker entoloph on M2, a more complete metalophid II on m2-3, and in lacking metalophid I on m2-3 [Figure 9: see original paper]. Compared with *A. ernos* (Wang, 1985), the new specimens lack a complete entoloph on M1 and have a thin hypolophid and anterior arm of the hypoconid on m1.

The materials from Ula Usu share the following features with *A. uniconjugatus*: a strong anterior arm of the protocone that connects with the paracone on M1, no protoloph II and weak posterior arm of the protocone on M1, metaloph connecting the metacone and anterior arm of the hypocone on M2-3, and complete hypolophid on m1-2. Compared to the holotype of *A. uniconjugatus* (Tong, 1997) from the Rencun Member of the Hedi Formation of Henan Province , the metaloph on M1 from Ula Usu is shorter and connected to the anterior arm of the hypocone (4/6) or does not reach the hypocone (2/6), and the protoconid on m2 is smaller.

Genus *Primisminthus* Tong, 1997 *Primisminthus shanghenus* Tong, 1997

Specimens: IVPP V28612.1-3, left M1s; V28612.4-5, right M1s; V28612.6-11, left M2s; V28612.12-17, right M2s.

Locality and horizon: Ula Usu, Erlian Basin, Nei Mongol; lower part of the Shara Murun Formation.

Description and comparisons: The new specimens have a trapezoidal M1 and rectangular M2 in occlusal outline, no protoloph II and a lophate metacone on M1-2, a complete protoloph I (which connects the paracone and protocone), a long anterior arm of the hypocone connecting to the mesocone, and a short metaloph that extends to the anterior arm of the hypocone or connects to the mesocone on M1, and a more developed posterior arm of the protocone on M2 [Figure 10: see original paper]. All these features are identical to those of *Primisminthus shanghenus* (Tong, 1997). Compared to the type specimens of *P. shanghenus* from the Rencun Member of the Hedi Formation of Henan, the specimens reported here are slightly larger , the mesoloph of M1 is thinner, and the posterior arm of the protocone on M2 is better developed. The new specimens differ from those of *A. uniconjugatus* from the same horizon at Ula Usu in having tapered main cusps on the upper molars and a stronger posterior arm of the protocone on M2.

Family Ischyromyidae Alston, 1876

Genus *Hulgana* Dawson, 1968 *Hulgana* cf. *H. ertnia* Dawson, 1968

Specimens: IVPP V28609.1, right P4; V28609.2-5, left M1s; V28609.6-10, right M1s; V28609.11-12, left M2s; V28609.13, left M3; V28609.14, right dp4; V28609.15-17, left p4s; V28609.18-19, right p4s; V28609.20, right m1; V28609.21-22, right m2s; V28609.23, right m3.

Locality and horizon: Ula Usu, Erlian Basin, Nei Mongol; lower part of the Shara Murun Formation.

Description and comparisons: The upper cheek teeth have a simple crown structure with either a small hypocone or none at all and no conules or styles. On P4, the protocone, paracone, and metacone are prominent, while it lacks a hypocone. The complete protoloph and metaloph separately extend from the lingual side of the paracone and metacone, both making contact with the labial side of the protocone. The protoloph is slightly curved and the metaloph is straight. The anteroloph connects to the paracone and is lower and narrower than that of M1.

M1 is nearly square in occlusal view and larger than P4. M1 has distinct paracone, metacone, and protocone, but no independent hypocone. The metacone is slightly larger than the paracone. The straight protoloph and curved metaloph are separately connected to the labial side of the protocone. The centrocrista between the paracone and metacone is concave [Figure 11: see original paper]. The crown of M2 is narrower than that of M1. The metacone is slightly smaller than the paracone and the centrocrista is low. The anteroloph is longer and narrower than that of M1 [Figure 11: see original paper]. M3 is smaller than M1-2. The metacone is very low and small. The protoloph is straight and the metaloph is short [Figure 11: see original paper].

The p4 is slightly narrower anteriorly than posteriorly and smaller than the lower molars. The hypoconid extends anterolabially. On p4, metalophid I is absent, metalophid II is complete, the ectolophid is short, the hypolophid is absent, and the deep sinusid opens anterolabially. The posterolophid connects to the entoconid and sometimes multiple conules are present on the posterolophid (4/5) [Figure 11: see original paper].

V28609.14 is noticeably smaller than p4. Metalophid I is complete and the trigonid opens posteriorly. Compared with p4, the ectolophid of V28609.14 is stronger and the sinusid is shallower and wider. A distinct hypoconulid is present on the posterolophid [Figure 11: see original paper]. Based on these characteristics, it is tentatively identified as a dp4.

The m1 is rhomboidal in occlusal view. The prominent protoconid, metaconid, hypoconid, and entoconid are positioned on the edge of the crown of the lower molars and surround a large mesosinusid (talonid basin). The entoconid is weaker than the protoconid and metaconid. The trigonid is slightly wider than the talonid. Metalophid I is straight and metalophid II is short and does not connect to the metaconid on m1-3. The m2 is larger than m1. The posterior end of m3 is rounded [Figure 11: see original paper].

The new specimens from Ula Usu are similar to *Hulgana ertnia* from Jhama Obo, Nei Mongol (Dawson, 1968) in having well-developed anteroloph and posteroloph, no independent hypocone, no conules on P4–M3, main cusps on the edge of the crown of lower molars, wide mesosinusid, and no mesostylid or hypolophid on the lower teeth.

The new materials differ from *H. ertnia* in having smaller size , a longer and straighter protoloph and shorter, more curved metaloph on P4, multiple hypoconulids on the posterolophid of lower cheek teeth, and a shorter m3. We regard the new specimens as *Hulgana* cf. *H. ertnia.* The M3 and dp4 of *Hulgana* are reported herein for the first time.

5.1 The Sharamurunian Rodent Fauna in the Erlian Basin

The rodent materials from the middle Eocene Sharamurunian at Ula Usu in the Erlian Basin include the ctenodactyloids *Yuomys cavioides*, *Gobiomys neimongolensis*, *G. exiguus*, and *G. asiaticus*; the cricetid *Pappocricetodon rencunensis*; the ischyromyid *Hulgana* cf. *H. ertnia*; the cylindrodontid *Proardynomys ulausuensis*; and the dipodids *Allosminthus uniconjugatus* and *Primisminthus shanghenus.* These specimens are referred to nine species belonging to seven genera, four families, and one superfamily of Rodentia. These fossils represent the best-known Sharamurunian rodent assemblages with high species diversity in the Erlian Basin.

In the Erlian Basin, mammal taxa from the "Lower Red" beds of Erden Obo and Nomogen, Siziwangqi indicate that this horizon is correlative with the Sharamurunian (Fostowicz-Frelik et al., 2012, 2015; Li, 2018), and rodent fossils from the "Lower Red" beds of Erden Obo have been studied in detail (Li, 2017, 2018, 2021). Although the "Lower Red" beds of Erden Obo contain fewer rodent fossils and lower generic richness than Ula Usu, the rodents found there—such as the ctenodactyloids *Gobiomys* and *Yuomys* and the dipodids *Allosminthus* and *Primisminthus*—are also present in the Ula Usu rodent fauna. The rodent assemblages from both localities share similar characteristics.

Because the rodent assemblages from Ula Usu and the "Lower Red" beds of Erden Obo have similar characteristics and both localities are in the same basin, we selected rodent fossils from these two sites for comprehensive analysis of the Sharamurunian rodent fauna in the Erlian Basin. Approximately 248 rodent specimens collected from the Ula Usu locality and the "Lower Red" beds of Erden Obo in the Erlian Basin represent at least 67 individuals as counted by the minimum number of individuals (MNI) .

Based on the MNI, ctenodactyloids are the dominant elements (constituting 47.76% of the total) and include five species of two genera. The diversity and proportion of *Gobiomys* is higher than that of *Yuomys.* Dipodids include *Allosminthus uniconjugatus* and *Primisminthus shanghenus* and occupy 26.87%, making them the second most dominant group. The cricetid *Pappocricetodon rencunensis* and the ischyromyid *Hulgana* cf. *H. ertnia* occupy 14.93% and 7.46%, respectively. Cylindrodontids occupy less than 3% and have low diversity in the Sharamurunian rodent fauna of the Erlian Basin.

5.2 Comparison with the Irdinmanhan and Ulangochuian Rodent Faunas

Romer (1966) proposed several related Asian Paleogene Land Mammal Ages (APLMA) based on mammalian faunas from the Mongolian Plateau. Subsequently, the age and nomenclature of the APLMA were revised by different researchers, and these land mammal ages have frequently been used in discussions of intercontinental biostratigraphical correlation and mammalian dispersals (Li and Ting, 1983; Tong et al., 1995; Wang, 1997a, b; Wang et al., 2012, 2019).

The Bumbanian, Arshantan, Irdinmanhan, Sharamurunian, Ulangochuian, and Ergilian ages in the Eocene have been widely adopted as the Asian Paleogene Land Mammal Ages in the Geologic Time Scale (Luterbacher et al., 2004; Vandenberghe et al., 2012; Speijer et al., 2020). To better understand the characteristics of Sharamurunian rodents and the evolution and turnovers of rodent faunas in the Erlian Basin, we compared this rodent fauna in detail with the adjacent Irdinmanhan and Ulangochuian rodent faunas.

In the Erlian Basin, Irdinmanhan rodents were recorded from the lower part of the Irdin Manha Formation in the Nuhetingboerhe-Huheboerhe area (Wang et al., 2010; Li and Meng, 2015; Li, 2016) and the middle part of the "Basal White" beds of Erden Obo (Li, 2017, 2018, 2021; Li et al., 2017). The compositions of the Sharamurunian and Irdinmanhan rodent faunas are similar at the family level but differ in generic composition [Figure 12: see original paper]. Ctenodactyloids are dominant in both the Sharamurunian and Irdinmanhan rodent faunas, but the species richness of ctenodactyloids obviously declined and their proportion dropped from 65.76% to 47.76% from the Irdinmanhan to the Sharamurunian. The ctenodactyloids show distinct substitution: *Tamquammys*, *Simplicimys*, and *Yongshengomys* were abundant during the Irdinmanhan but did not survive into the Sharamurunian. Instead, *Gobiomys* became the dominant ctenodactyloid during the Sharamurunian. Although the genus *Yuomys* appears in both the Irdinmanhan and Sharamurunian rodent faunas, it is represented by different species. The cricetid *Pappocricetodon* was present in both the Irdinmanhan and Sharamurunian rodent faunas, but its proportion in the Irdinmanhan is slightly higher than that in the Sharamurunian. *Pappocricetodon neimongolensis* (Li, 2012; Li et al., 2017) from the Irdinmanhan fauna is more primitive than *P. rencunensis* (Tong, 1992, 1997) of the Sharamurunian fauna. Both the species richness and proportion of ischyromyids declined from the Irdinmanhan to the Sharamurunian rodent faunas. Dipodids and cylindrodontids were absent in the Irdinmanhan rodent fauna, but dipodids were present and became the second most dominant element (26.87%) in the Sharamurunian rodent fauna. The cylindrodontids *Proardynomys ulausuensis* and *Gobiocylindrodon* sp. were also present.

Numerous Ulangochuian rodents in the Erlian Basin were reported from the "Lower White" to the "Middle White" beds of the Erden Obo section (Li, 2018, 2020, 2021). The Ulangochuian rodent fauna consisted of ctenodactyloids, cricetids, dipodids, and cylindrodontids. Compared to the Sharamurunian rodents, the generic richness and abundance of cricetids and dipodids in the Ulangochuian rodents increased significantly. Cricetids (5 species of 3 genera) and dipodids (4 species of 2 genera) became the dominant elements in the Ulangochuian rodent fauna [Figure 12: see original paper]. Although the cricetid *Pappocricetodon* and the dipodid *Allosminthus* were present in both the Sharamurunian and Ulangochuian rodent faunas, they are represented by different species. From the Sharamurunian to Ulangochuian, the proportion of ctenodactyloids in the rodent faunas declined and generic richness decreased to two genera (*Gobiomys* and *Yuomys*). Additionally, ischyromyids were present in the Sharamurunian fauna but absent in the Ulangochuian fauna. The generic richness of Ulangochuian cylindrodontids is slightly higher than that in the Sharamurunian.

5.3 The Evolution and Turnovers of Rodent Faunas in the Erlian Basin

The Erlian Basin is an important Asian Paleogene fossil-producing area, and the Tertiary beds in the Erlian Basin were first explored by the Central Asiatic Expeditions (CAE) in the 1920s (Granger and Berkey, 1922; Berkey and Granger, 1923; Matthew and Granger, 1926). Since the CAE investigations, numerous fossils have been collected from the Erlian Basin, but rodents and other micromammals were rare. During the past two decades, the IVPP has led comprehensive investigations in the Erlian Basin that included lithostratigraphy, biostratigraphy, and paleomagnetic research. Thousands of teeth and numerous maxillary and jaw fragments of rodents have been collected and systematically reported (Wang, 2001, 2007; Wang et al., 2010; Li and Meng, 2015; Li, 2012, 2016, 2017, 2018, 2020, 2021; Li et al., 2016, 2017, 2019). These rodents are distributed in different layers and assemblages, providing important evidence for stratigraphic division as well as lithological and biostratigraphic correlations (Li, 2016, 2018). A partial rodent sequence in the Erden Obo section of the Erlian Basin has been established, and the rodent assemblages show a transformation (Li, 2018).

We counted the rodent fossils from the Erlian Basin and analyzed their species richness per family [FIGURES:13, 14] following the Asian Paleogene Land Mammal Ages framework (Speijer et al., 2020). In the Bumbanian age of the early Eocene, ctenodactyloids had relatively high diversity. From the Bumbanian to the Irdinmanhan, the species richness of ctenodactyloids continuously increased. Cricetids and dipodids first appeared in the Irdinmanhan and Sharamurunian ages, respectively. Since the Sharamurunian age, the species richness of ctenodactyloids was reduced, whereas that of cricetids and dipodids distinctly increased from the Ulangochuian. Based on species counts, it is evident that the rodent faunas of the Erlian Basin changed from ctenodactyloid-dominant assemblages during the Bumbanian to Sharamurunian ages to cricetid- and dipodid-dominant assemblages during the Ulangochuian and Ergilian [Figure 13: see original paper].

Furthermore, the early Oligocene strata in the Erlian Basin were discontinuous and rodent fossils from these strata were limited. Although the known early Oligocene rodent fossils reveal differences from those of Eocene assemblages, discussing this change across the Eocene-Oligocene boundary is beyond the scope of this study.

5.4 Comparison with the Shanghe-Zhaili Fauna in the Yuanqu Basin, Shanxi

In addition to the Erlian Basin of Nei Mongol, the Shanghe-Zhaili area in the Yuanqu Basin of Shanxi is another important Sharamurunian fossil-producing area in China. Rodent fossils from the Yuanqu Basin are also abundant and have been studied using MNI (Tong, 1997). The rodent faunas from the Erlian Basin and Yuanqu Basin are similar, sharing ctenodactyloids, cricetids, dipodids, and ischyromyids, even some of the same genera and species, such as the ctenodactyloid *Yuomys cavioides*, the cricetid *Pappocricetodon rencunensis*, and the dipodids *Allosminthus uniconjugatus* and *Primisminthus shanghenus* . However, differences also exist between the two rodent faunas. Rodent species richness from the Yuanqu Basin is slightly higher than that in the Erlian Basin. Ctenodactyloids are the dominant group in the Sharamurunian rodent fauna of the Erlian Basin, whereas cricetids and dipodids dominate in the Yuanqu Basin rodent fauna. The ctenodactyloid *Gobiomys* is abundant and *Yuomys* is rare in the Erlian Basin, but *Yuomys*, *Xueshimys*, *Anadianomys*, and *Zodiomys* are common ctenodactyloids in the Yuanqu Basin. Additionally, cylindrodontid rodents are present in the Erlian Basin but absent in the Yuanqu Basin. These differences may be related to the paleoclimate and paleoenvironment of the fossil localities. Based on the composition and characteristics of plant fossils and pollen assemblages, Jin et al. (2003) divided the Eocene flora in China into three paleobotanical geographic regions: a northern subtropical humid zone, a central subtropical arid zone, and a southern tropical humid zone. The Erlian Basin belongs to the northern subtropical humid zone, where vegetation types are mainly deciduous trees and shrubs interspersed with a few evergreens, and vegetation diversity is high. The Yuanqu Basin is located in the central subtropical arid zone, where vegetation is relatively scarce and includes symbiotic angiosperms, gymnosperms, warm temperate and subtropical ferns, and a few subtropical and tropical evergreens. The different Sharamurunian rodent assemblages from the Erlian and Yuanqu basins likely reflect these different regional environments.

6 Conclusion

The new rodent materials discovered from the middle Eocene lower part of the Shara Murun Formation at Ula Usu, Erlian Basin, Nei Mongol, China are identified as nine species belonging to seven genera, four families, and one superfamily of Rodentia. The new rodent assemblage shows high similarity with that of the "Lower Red" beds of Erden Obo, and together they represent the Sharamurunian rodent fauna in the Erlian Basin. Analysis using the minimum number of individuals and species richness shows that ctenodactyloids are the most abundant element, comprising five species. Dipodids represent 26.87% of the assemblage, with *Allosminthus* being the dominant genus, while cricetids and ischyromyids are also present. Finally, with just two species present, cylindrodontids make up the smallest proportion of the rodent fauna in the Erlian Basin.

The Sharamurunian rodent fauna from the Erlian Basin is similar to the contemporaneous assemblage from the Yuanqu Basin, but distinct differences exist between these rodent faunas. The different compositions and characteristics of the Sharamurunian rodent faunas in the Erlian and Yuanqu basins likely result from responses to regional environmental disparity.

The Paleogene rodent assemblages of the Erlian Basin show a noticeable evolution from the dominance of ctenodactyloids in the Early Eocene to early Middle Eocene (Bumbanian to Sharamurunian) to the dominance of cricetids and dipodids in the late Middle to Late Eocene (Ulangochuian and Ergilian).

Acknowledgements

We thank Wang Yuanqing, Meng Jin, Bai Bin, Xu Rancheng, Wang Xiaoyang, Zhou Wei, Wang Yongxing, Wang Yongfu, Li Shijie, and Li Qi of the field team for their hard work and dedication. Hou Yemao and Yin Pengfei assisted with CT scanning. We also thank the editors and reviewers for their constructive comments on our manuscript. This work was supported by the National Natural Science Foundation of China (Grant no. 42072023) and the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000, XDA20070203). The fieldwork was funded by the Special Fund for Fossil Excavation and Preparation, CAS.

References

Bai B, Wang Y Q, Li Q et al., 2018. Biostratigraphy and diversity of Paleogene perissodactyls from the Erlian Basin of Inner Mongolia, China. *Am Mus Novit*, 3914: 1-60.

Berkey C P, Granger W, 1923. Later sediments of the desert basins of central Mongolia. *Am Mus Novit*, 77: 1-16.

Berkey C P, Morris F K, 1927. Geology of Mongolia—a reconnaissance report based on the investigations of the years 1922-1923. In: *Natural History of Central Asia*, Vol II. New York: American Museum of Natural History. 1-475.

Burke J J, 1935. *Pseudocylindrodon*, a new rodent genus from the Pipestone Springs Oligocene of Montana. *Ann Carnegie Mus*, 25: 1-4.

Burke J J, 1936. *Ardynomys* and *Desmatolagus* in the North American Oligocene. *Ann Carnegie Mus*, 25: 135-154.

Chow M C, Rozhdestvensky A K, 1960. Exploration in Inner Mongolia—a preliminary account of the 1959 field work of the Sino-Soviet Paleontological Expedition (SSPE). *Vert PalAsiat*, 4: 1-10.

Dashzeveg D, Meng J, 1998. A new Eocene cylindrodont rodent (Mammalia, Rodentia) from the eastern Gobi of Mongolia. *Am Mus Novit*, 3253: 1-18.

Dawson M R, 1968. Oligocene rodents (Mammalia) from East Mesa, Inner Mongolia. *Am Mus Novit*, 2324: 1-12.

Daxner-Höck G, 2001. New Zapodids (Rodentia) from Oligocene-Miocene deposits in Mongolia. Part 1. *Senckenbergiana lethaea*, 81: 351-389.

Daxner-Höck G, Badamgarav D, Maridet O, 2014. Dipodidae (Rodentia, Mammalia) from the Oligocene and Early Miocene of Mongolia. *Ann Naturh Mus Wien*, Ser A, 116: 131-214.

Douglass E, 1901. Fossil Mammalia of the White River Beds of Montana. *Trans Am Philos Soc*, Philadelphia, 20: 237-.

Emry R J, Tyutkova L A, Lucas S G et al., 1998. Rodents of the Middle Eocene Shinzhaly Fauna of eastern Kazakhstan. *J Vert Paleont*, 18: 218-227.

Fostowicz-Frelik Ł, Li C K, Meng J et al., 2012. New *Gobiolagus* (Mammalia: Lagomorpha) from the Middle Eocene of Erden Obo (Nei Mongol, China). *Vert PalAsiat*, 50: 219-236.

Fostowicz-Frelik Ł, Li C K, Mao F Y et al., 2015. A large mimotonid from the Middle Eocene of China sheds light on the evolution of lagomorphs and their kin. *Sci Rep*, 9394: 1-9, doi: 10.1038/srep09394.

Gong H, Li Q, Ni X J, 2021. New species of *Yuomys* (Rodentia, Ctenodactyloidea) from the upper Eocene of eastern Ningxia, China. *J Vert Paleont*, doi:10.1080/02724634.2021.1938099.

Granger W, 1925. Records of fossils, Mongolia 1925. Third Central Asiatic Expeditions (Field Notes). New York: American Museum of Natural History. 1-76.

Granger W, Berkey C P, 1922. Discovery of Cretaceous and older Tertiary strata in Mongolia. *Am Mus Novit*, 42: 1-7.

Huang X S, Zhang J N, 1990. First record of Early Tertiary mammals from southern Yunnan. *Vert PalAsiat*, 28: 296-.

Jin J H, Liao W B, Wang B S et al., 2003. Global change in Cenozoic and evolution of flora in China. *Guihaia*, 23: 217-.

Li C K, 1975. *Yuomys*, a new ischyromyid rodent genus from the Upper Eocene of North China. *Vert PalAsiat*, 13: 58-.

Li C K, Ting S Y, 1983. The Paleogene mammals of China. *Bull Carnegie Mus Nat Hist*, 21: 1-93.

Li Q, 2012. Middle Eocene Cricetids (Rodentia, Mammalia) from the Erlian Basin, Nei Mongol, China. *Vert PalAsiat*, 50: .

Li Q, 2016. Eocene fossil rodent assemblages from the Erlian Basin (Inner Mongolia, China): Biochronological implications. *Palaeoworld*, 25: 95–103.

Li Q, 2017. Eocene ctenodactyloid rodent assemblages and diversification from Erden Obo, Nei Mongol, China. *Hist Biol*, 31: 813–823.

Li Q, 2018. Additional cricetid and dipodid rodent material from the Erden Obo section, Erlian Basin (Nei Mongol, China) and its biochronological implications. *Palaeoworld*, 27: 490–505.

Li Q, 2020. New late Eocene cylindrodontid rodents from the Erlian Basin (Nei Mongol, China). *Palaeobio Palaeoenv*, 100: .

Li Q, 2021. Additional tsaganomyid, cylindrodontid and ctenodactyloid rodent materials from the Erden Obo section, Erlian Basin (Nei Mongol, China). *Vert PalAsiat*, 59: 1–17.

Li Q, Meng J, 2015. New ctenodactyloid rodents from the Erlian Basin, Nei Mongol, China, and the phylogenetic relationships of Eocene Asian ctenodactyloids. *Am Mus Novit*, 3828: 1–58.

Li Q, Meng J, Wang Y Q, 2016. New cricetid rodents from strata near the Eocene–Oligocene boundary in Erden Obo Section (Nei Mongol, China). *PloS One*, 11: 1–17.

Li Q, Gong Y X, Wang Y Q, 2017. New dipodid rodents from the Late Eocene of Erden Obo (Nei Mongol, China). *Hist Biol*, 29: 692–703.

Li Q, Wang Y Q, Mao F Y et al., 2019. A new Eocene cylindrodontid rodent from the Erlian Basin (Nei Mongol, China) and its implications for phylogeny and biochronology. *J Vert Paleont*, 39: e1680990, doi: 10.1080/02724634.2019.1680990.

Luterbacher H P, Ali J R, Brinkhuis H et al., 2004. The Paleogene Period. In: Gradstein F M, Ogg J G, Smith A eds. *A Geological Time Scale 2004*. Cambridge: Cambridge University Press. 384–408.

Matthew W D, Granger W, 1925. New creodonts and rodents from the Ardyn Obo formation of Mongolia. *Ibid*, 197: .

Matthew W D, Granger W, 1926. Two new perissodactyls from the Arshanto Eocene of Mongolia. *Am Mus Novit*, 208: .

Meng J, Ye J, Huang X S, 1999. Eocene mammals from the Bayan Ulan of Nei Mongol (Inner Mongolia) and comments on related stratigraphy. *Vert PalAsiat*, 37: 165–174.

Romer A S, 1966. *Vertebrate Paleontology*. Chicago and London: University of Chicago Press. 1–467.

Rose K D, 1981. The Clarkforkian land-mammal age and mammalian faunal composition across the Paleocene-Eocene boundary. *Pap Palaeontol*, 26: 1–197.

Shi R L, 1989. Late Eocene mammalian fauna of Huangzhuang, Qufu, Shandong. *Vert PalAsiat*, 27: 87–102.

Speijer R P, Pälike H, Hollis C J et al., 2020. The Paleogene Period. In: Gradstein F M, Ogg J G, Schmitz M D et al. eds. *Geologic Time Scale 2020*. Oxford: Elsevier BV. 1087–1140.

Tong Y S, 1992. *Pappocricetodon*, a pre-Oligocene cricetid genus (Rodentia) from central China. *Vert PalAsiat*, 30: .

Tong Y S, 1997. Middle Eocene small mammals from Liguanqiao Basin of Henan Province and Yuanqu Basin of Shanxi Province, Central China. *Palaeon Sin*, New Ser C, 26: 1–256.

Tong Y S, Zheng S H, Qiu Z D, 1995. Cenozoic mammal ages of China. *Vert PalAsiat*, 33: 290–314.

Vandenberghe N, Hilgen F L, Speijer R P, 2012. The Paleogene Period. In: Gradstein F M, Ogg J G, Schmitz M D et al. eds. *The Geologic Time Scale 2012*. Oxford: Elsevier BV. 855–922.

Wang B Y, 1985. Zapodidae (Rodentia, Mammalia) from the Lower Oligocene of Qujing, Yunnan, China. *Mainzer geowiss Mitt*, 14: 354–367.

Wang B Y, 1997a. The Mid-Tertiary Ctenodactylidae (Rodentia, Mammalia) of eastern and central Asia. *Bull Am Mus Nat Hist*, 234: 1–88.

Wang B Y, 1997b. Chronological sequence and subdivision of Chinese Oligocene mammalian faunas. *J Stratigr*, 21: 183–.

Wang B Y, 2001. Eocene ctenodactyloids (Rodentia, Mammalia) from Nei Mongol, China. *Vert PalAsiat*, 39: 98–114.

Wang B Y, 2007. Late Eocene cricetids (Rodentia, Mammalia) from Nei Mongol, China. *Vert PalAsiat*, 45: 195–212.

Wang B Y, 2008. Additional rodent material from Houldjin Formation of Erenhot, Nei Mongol, China. *Vert PalAsiat*, 46: .

Wang B Y, 2017. Discovery of *Yuomys* from Altun Shan, Xinjiang, China. *Vert PalAsiat*, 5: 227–232.

Wang B Y, 2019a. "Cylindrodontidae" . In: Qiu Z X, Li C K eds. *Palaeovertebrata Sinica*, VIII, Basal Synapsids and Mammals, Fascicle 5, Glires II: Rodentia I. Beijing: Science Press. 449–478.

Wang B Y, 2019b. "Gobiomyidae" . In: Qiu Z X, Li C K eds. *Palaeovertebrata Sinica*, VIII, Basal Synapsids and Mammals, Fascicle 5, Glires II: Rodentia I. Beijing: Science Press. 436–440.

Wang B Y, Dawson M R, 1994. A primitive cricetid (Mammalia: Rodentia) from the Middle Eocene of Jiangsu Province, China. *Ann Carnegie Mus*, 63: 239-256.

Wang B Y, Zhou S Q, 1982. Late Eocene mammals from Pingchangguan Basin, Henan. *Vert PalAsiat*, 20: 203-215.

Wang B Y, Wu W Y, Qiu Z D, 2020. "Cricetidae" . In: Qiu Z X, Li C K, Zheng S H et al. eds. *Palaeovertebrata Sinica* VIII, Basal Synapsids and Mammals, Fascicle 5, Glires II: Rodentia II. Beijing: Science Press. 10-151.

Wang J W, 1978. Fossil Amynodontidae and Ischyromyidae of Tongbo, Henan. *Vert PalAsiat*, 16: 22-29.

Wang Y Q, Meng J, Ni X J et al., 2007. Major events of Paleogene mammal radiation in China. *Geol J*, 42: 415-430.

Wang Y Q, Meng J, Christopher K B et al., 2010. Early Paleogene stratigraphic sequences, mammalian evolution and its response to environmental changes in Erlian Basin, Inner Mongolia, China. *Sci China Earth Sci*, 53: 1918-.

Wang Y Q, Meng J, Jin X, 2012. Comments on Paleogene localities and stratigraphy in the Erlian Basin, Nei Mongol, China. *Vert PalAsiat*, 50: 181-203.

Wang Y Q, Li Q, Bai B et al., 2019. Paleogene integrative stratigraphy and timescale of China. *Sci China Earth Sci*, 62: .

Wood A E, 1970. The Early Oligocene rodent *Ardynomys* (Family Cylindrodontidae) from Mongolia and Montana. *Am Mus Novit*, 2418: 1-18.

Woodburne J M, 1987. Mammal ages, stages, and zones. In: Woodburne M O ed. *Cenozoic Mammals of North America: Geochronology and Biostratigraphy*. Berkeley: University of California Press. 18-23.

Ye J, 1983. Mammalian fauna from the Late Eocene of Ulan Shiren Area, Inner Mongolia. *Vert PalAsiat*, 21: 109-118.

Zdansky O, 1930. Die alttertiären Säugetiere Chinas nebst stratigraphischen Bemerkungen. *Palaeont Sin*, New Ser C, 6: .

Note: Figure translations are in progress. See original paper for figures.