

内蒙古二连盆地呼和勃尔和剖面中始新世 仓鼠类化石¹⁾

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摘要:描述了产自内蒙古二连盆地呼和勃尔和剖面伊尔丁曼哈组底部砂岩中的3种仓鼠类化石: 内蒙古祖仓鼠(新种)*Pappocricetodon neimongolensis* sp. nov., 中条祖仓鼠(相似种)*Pappocricetodon* cf. *P. zhongtiaensis* 和祖仓鼠(未定种)*Pappocricetodon* sp.。*P. neimongolensis*的特征是有P4或者DP4; M1前附尖细小, 前叶小, 原尖前棱通常至原小尖横向延伸, 再转向前颊侧与前附尖相连, 无原尖后棱, 原小尖与前尖通过前脊相连; M2原尖后棱较为发育; M3次尖不退化; m1下后尖比下原尖位置靠前; m2下原尖后棱完整, 连接下后尖或直达下后尖基部; m3不退化, 下外脊S型。新种形态与早期仓鼠类*Pappocricetodon antiquus*接近, 但又略显原始。同时, 在该层位还出现有M1前叶已经增大的*Pappocricetodon* sp. 和中脊发育的*Pappocricetodon* cf. *P. zhongtiaensis*, 表明当时仓鼠类已出现多样化, 其起源可能要早于中始新世的伊尔丁曼哈期。

关键词:内蒙古呼和勃尔和, 中始新世, 伊尔丁曼哈组, 仓鼠类

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MIDDLE EOCENE CRICETIDS (RODENTIA, MAMMALIA) FROM THE ERLIAN BASIN, NEI MONGOL, CHINA

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Abstract New cricetids (*Pappocricetodon neimongolensis* sp. nov., *Pappocricetodon* cf. *P. zhongtiaensis*, *Pappocricetodon* sp.) are reported from the basal strata of the Irдин Manha Formation in the Huheboerhe section in Nei Mongol, China. *P. neimongolensis* is characterized by the following features: presence of a P4 or DP4; anterocone small; anterior arm of protocone on M1 well-developed and connected to anterocone; distinct paraloph joining protoconule and paracone; protocone on M1 lacking posterior arm; posterior arm of protocone present on M2; hypocone of M3 prominent; protoconid generally positioned anterior to metaconid on m1; posterior arm of protoconid on m2 complete; m3 unreduced, with “S”-shaped ectolophid. *P. neimongolensis* is morphologically similar to the early cricetid *Pappocricetodon antiquus*. *Pappocricetodon* sp. has a prominent anterior lobe, and *Pappocricetodon* cf. *P. zhongtiaensis* has a distinct mesoloph. These fossils suggest that cricetids were already diversified in the Middle Eocene, and probably originated earlier than the Irдинmanhan.

Key words Huheboerhe, Nei Mongol; Middle Eocene; Irдин Manha Formation; Cricetidae

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1 Introduction

Most known Eocene cricetids are from East and Central Asia, especially China and Kazakhstan. The genus *Pappocricetodon* (Tong, 1992; Wang and Dawson, 1994) is considered to be the most primitive cricetid. *Palasiomys* and *Raricricetodon* (Tong, 1997) were described more recently, and have provided new insight into the earliest cricetids. The origin of Cricetidae and the relationships among the earliest species from Central and East Asia are still disputed, but most evidence suggests that cricetids originated in Asia rather than North America (Emry, 2007). Rodrigues et al. (2010) suggested that the earliest offshoot of the cricetid clade is the Asian genus *Palasiomys*, and that the genus *Pappocricetodon* displays a complete cricetid plan associated with both the loss P4 and the development of an anterocone on M1.

Twelve mammal-bearing horizons have been recognized in the Paleogene of the Huheboerhe area, and these horizons are labeled in ascending order as NM-1 to NM-4, AS-1 to AS-6, and IM-1 to IM-2 (Wang et al., 2010). This paper reports new cricetids from the IM-1 horizon of the Irdin Manha Formation in the Huheboerhe section of the Erlian Basin. The specimens were collected by screenwashing. A rich fossil assemblage, including rodents, lagomorphs, artiodactyls, perissodactyls, the primate *Tarkops mckennai* (Ni et al., 2010) and the gliran *Gomphos shevyreva* (Meng et al., 2009), has been recovered from the IM-1 horizon. The new specimens display some typical cricetid dental features, and cast new light on the origin of cricetids during the Middle Eocene.

The terminology used in the tooth descriptions follows Rodrigues et al. (2010) and Wang and Dawson (1994).

2 Systematic description

Rodentia Bowditch, 1821

Cricetidae Rochebrune, 1883

Pappocricetodon Tong, 1992

Pappocricetodon neimongolensis sp. nov.

Holotype A right M1 (IVPP V 16498.1) (Fig. 1A) (IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing.)

Referred specimens IVPP V 16498.2-3, left M1; V 16498.4-11, right M1; V 16498.12-15, left M2; V 16498.16, right M2; V 16498.17, left M3; V 16498.18, right M3; V 16498.19-20, left m1; V 16498.21-25, right m1; V 16498.26-32, left m2; V 16498.33-35, right m2; V 16498.36-41, left m3; V 16498.42-43, right m3.

Locality and horizon Huheboerhe, Erlian Basin, Nei Mongol (Inner Mongolia); IM-1 horizon of the Irdin Manha Formation; Middle Eocene.

Diagnosis Small cricetid; P4 or DP4 present, as indicated by a contact facet at the anterior end of some examples of M1; anterocone small; paraloph complete, connecting paracone to protoconule; protocone on M1 lacking posterior arm; anterior arm of protocone on M1 developed and contacting anterocone; posterior arm of protocone present on M2; hypocone on M3 prominent; protoconid generally positioned posterior to metaconid on m1; posterior arm of protoconid on m2 complete; m3 unreduced, with “S”-shaped ectolophid.

Etymology The specific name refers to Nei Mongol, the province-level autonomous region where the fossils were found.

Description M1 is trapezoidal in occlusal view, with the buccal wall slightly longer than the lingual one. The existence of a contact facet at the anterior surface of some examples sug-

gests the presence of a P4 or DP4. The anterior lobe of M1 is small, and bears a small anterocone that is more distinct than the parastyle. The anterior cingulum extends from the paracone to the anterior part of the protocone. The protocone is bulbous. Usually (7 of 11 case) the anterior arm of the protocone is long enough to reach the anterocone (Fig. 1A); in some cases (3/11) it extends close to the base of the anterocone (Fig. 1B, 1E). However, the anterior arm of the protocone is short in the remaining specimen, V 16498.5 (Fig. 1C). The posterior

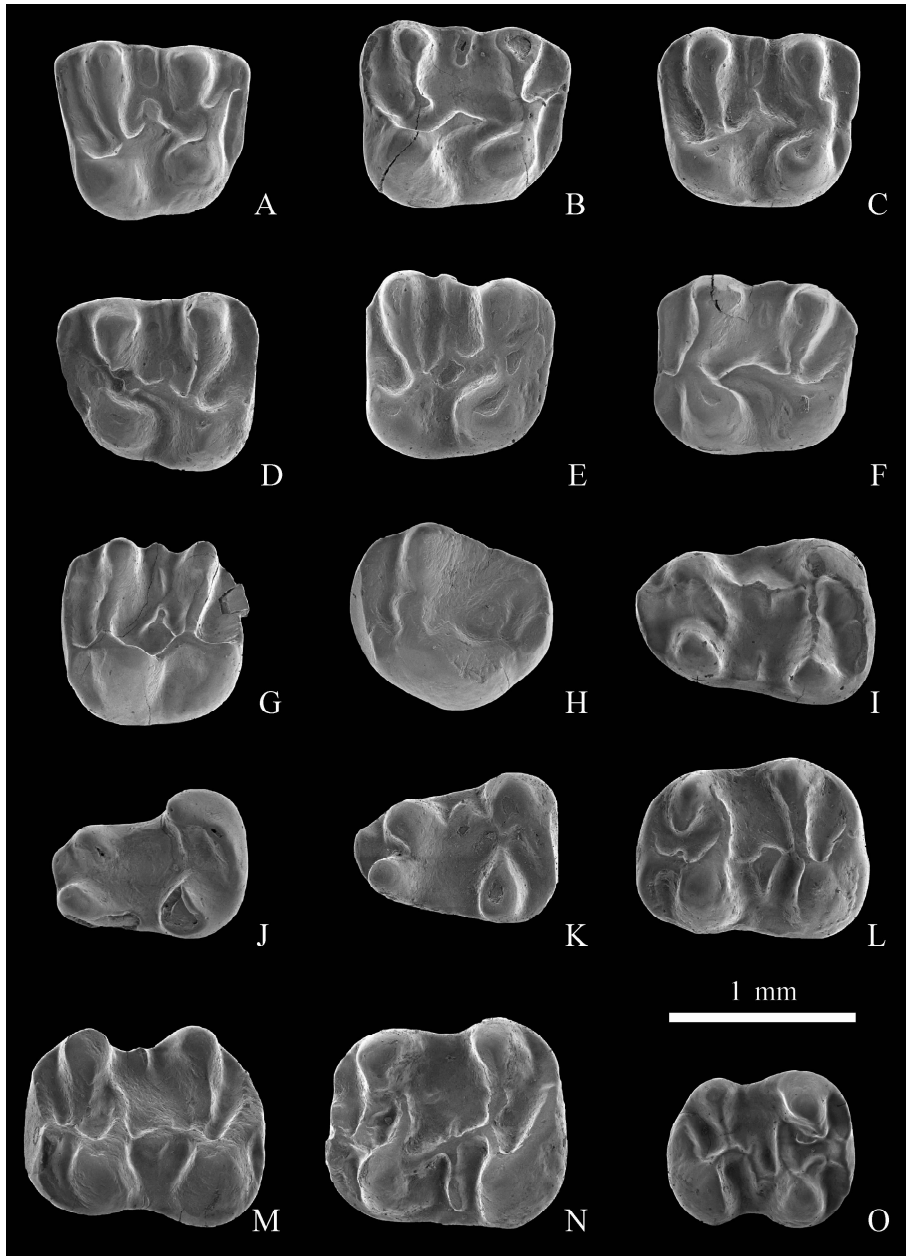


Fig. 1 Molars of *Pappocricetodon neimongolensis* sp. nov., in occlusal view
 A-C. right M1 (IVPP V 16498. 1, V 16498. 4-5); D. left M1 (V 16498. 2); E. right M1 (V 16498. 6); F-G. left M2 (V 16498. 12-13); H. left M3 (V 16498. 17); I-K. right m1 (V 16498. 21-23); L-N. left m2 (V 16498. 26-28); O. right m3 (V 16498. 42)

arm of the protocone is absent. The paracone and the metacone are similar in size. The paraloph is complete, and extends lingually to contact the anterior arm of the protocone (9/11). A distinct protoconule is present on the paraloph. The metaloph is complete and joins the mure. The hypocone is conical. The mure is long and extends anteriorly, meeting either the protocone (6/11) (Fig. 1A, 1E) or the protoconule (4/11) (Fig. 1D). The mesostyle is usually distinct. The mesoloph is moderately long (7/11) or missing (4/11).

The occlusal surface of M2 is rectangular, being slightly longer than wide. The anterior cingulum is prominent. A crest from the parastyle extends to the anterior arm of the protocone. The protoloph is transverse, and extends from the protocone to the paracone. The posterior arm of the protocone is variably developed. In most cases (3/5) it contacts the mure (Fig. 1G), but it is occasionally weakly developed and free (Fig. 1F). The mure is smaller than that of M1 and extends to the central basin (2/5) (Fig. 1G) or turns towards the lingual side of the protocone (3/5) (Fig. 1F). In other respects M2 is similar to M1.

The M3 has a rounded triangular outline in occlusal view, and is broader anteriorly than posteriorly (Fig. 1H). It is smaller than M1 and M2. The anterior cingulum, the protocone, the paracone and the protoloph are developed. The paracone is the largest cusp on M3. The hypocone is still distinct on a worn example of M3. The metaloph is weakly developed and shorter than the protoloph, and forms a small basin in combination with the posteroloph. The mesostyle and mesoloph are absent.

The m1 is trapezoidal in occlusal view, and is longer than wide. The m1 has a narrow trigonid. The protoconid and hypoconid are lower than the metaconid and entoconid, respectively. Either the protoconid and the metaconid are opposite one another (2/7) (Fig. 1I), or the former is posterior to the latter (5/7) (Fig. 1J, 1K). The anteroconid is distinct and isolated (2/7) (Fig. 1K), or has a weak connection with the protoconid (5/7) (Fig. 1I, 1J). The posterior arm of the protoconid is usually (5/7) complete and connected to the metaconid, but is sometimes (2/7) (Fig. 1J) short or weak. The hypolophid is complete and extends to the hypoconid (Fig. 1I) in most specimens (5/7) but is weak and has a free end in others (2/7). The posterolophid is complete. The mesostylid is small and isolated or missing. The mesoconid is larger than the mesostylid. The mesolophid is weak. The ectolophid is usually (5/7) complete and straight (5/7), and sometimes (2/7) slim and curved.

The m2 is rectangular in occlusal view and its four main cusps are subequal in size. The anteroconid is weakly developed. The anterior arm of the protoconid extends anterolingually to contact the anteroconid. The anterior arm of the metaconid usually (7/10) joins the anterior arm of the protoconid (Fig. 1M, 1N), but is sometimes (3/10) less developed (Fig. 1L). The posterior arm of the protoconid is prominent, and either meets the metaconid to close the trigonid basin (5/10) (Fig. 1L) or extends almost to the base of the metaconid (5/10) (Fig. 1M). The hypolophid connects to the prehypocristid (8/10) (Fig. 1M, 1N) or the hypoconid (2/10) (Fig. 1L). The hypoconulid is weak. The mesostylid is weak (6/10) or missing (4/10). The mesoconid is distinct. The ectolophid is complete and usually oblique, contacting both the prehypocristid and the hypolophid (6/10) (Fig. 1N). The mesolophid is weak or absent. A weak ectomesolophid is present in a few specimens (4/10) (Fig. 1N).

The trigonid of m3 is similar to that of m2. The anterior arm of the metaconid joins the anterior arm of the protoconid. The posterior arm of the protoconid is complete and extends to the base of the metaconid. The hypolophid is shorter than that of m2, and either contacts the prehypocristid (5/8) or is weakly developed (3/8). The mesoconid is weak. The mesostylid is absent (7/8) or weak (1/8). The mesolophid is short and weak. The ectolophid is "S"-shaped.

Measurement See Table 1.

Table 1 Measurements of teeth of *Pappocricetodon neimongolensis* sp. nov. (mm)

Tooth	n	Length		Width	
		Min-max	mean	Min-max	mean
M1	11	1 – 1.32 (buccal)	1.12	0.96 – 1.2	1.01
		0.8 – 1.16 (lingual)	0.93		
M2	5	1 – 1.28	1.12	0.96 – 1.2	1.05
M3	2	1.08 – 1.08	1.08	1 – 1	1
m1	7	1.04 – 1.28	1.19	0.8 – 0.96	0.87
m2	10	1 – 1.32	1.22	0.8 – 1.12	0.98
m3	8	0.96 – 1.08	1.03	0.76 – 0.96	0.84

Comparisons The new specimens from the IM-1 horizon of the Irдин Manha Formation of Huheboerhe section possess several primitive cricetid features, including molars bunodont and with low crowns, P4 present, anterocone on M1 small, paraloph complete, protolophule II absent, m1 smaller than m2, and anteroconid weakly developed. The species *Pappocricetodon neimongolensis* sp. nov. is erected for the specimens.

Early cricetids and dipodoids are difficult to distinguish from each other. The major putative difference traditionally used to tell these groups apart was the presence of P4 in dipodoids, but supposedly not in cricetids. However, recent studies have shown that the cricetids *Pappocricetodon antiquus* (Tong, 1992; Wang and Dawson, 1994) and *Palasiomys conulus* (Tong, 1997) have a small P4 or DP4.

Pap. neimongolensis has a P4 or DP4, but shows differences from the Middle Eocene dipodoids *Aksyiromys dalos* (Emry et al., 1998), *Elymys complexus* (Emry, 2007) and *Primitminthus yuenus* (Tong, 1997). The mures of *A. dalos*, *E. complexus*, and *P. yuenus* are short, whereas that of *Pap. neimongolensis* is long and extends to the labial protocone or even farther forward. The anterior arm of the protocone on M1 of *Pap. neimongolensis* contacts the anterocone. In *A. dalos* and *P. yuenus*, by contrast, the anterior arm of the protocone contacts the paracone. In *Pap. neimongolensis* the anterior arm of the metaconid seen in m2 and m3 of *A. dalos*, *E. complexus* and *P. yuenus* is absent. In these taxa the posterior arm of the protoconid of m1 is also more distinct than in *Pap. neimongolensis*. The hypolophid is developed only in *A. dalos* and *Pap. neimongolensis*.

Erlanomys combinatus (Li and Meng, 2010) from the Nuhetingboerhe section of the Erlian Basin is among the earliest myodonts. It is smaller than *Pap. neimongolensis*, and was recovered from stratigraphically lower beds. In *E. combinatus* the anterior arm of the protocone does not extend anterolingually, but contacts the paracone, and a distinct posterior arm of the protocone joins with the mure in the central basin of each upper molar. The mesoloph and mesostyle are also less well-developed in *E. combinatus* than in *Pap. neimongolensis*, and in the latter species the anterior and posterior arms of the protoconid and the anterior arm of the metaconid are all more distinct. However, the crests contacting the main cusps of *E. combinatus* are simple. The morphological character of the genus is stable, displaying the primitive condition. But some characters of *Pap. neimongolensis*, such as the lengths of the anterior arm of the protocone and of the mure, are variable.

Middle Eocene cricetids include *Palasiomys*, *Pappocricetodon* and *Raricricetodon*.

Palasiomys conulus was described by Tong (1997) on the basis of specimens from the Middle Eocene Hetaoyuan Formation of Xichuan, Henan Province. Based on specimens from the Yuanqu Basin of Shanxi, China, Huang (2004) named *Palasiomys yuanquensis*. Wang (2007) suggested that *Pal. yuanquensis* is a junior synonym of *Pap. antiquus*, based on the

fact that its tooth morphology is identical to that of the latter taxon.

Pappocricetodon is one of the oldest known cricetid genera, and includes four previously described species: *Pap. rencunensis* from Mianchi, Henan Province (Tong, 1992); *Pap. schaubi* from the Hedi Formation of Yuanqu, Shanxi Province (Zdansky, 1930; Tong, 1992, 1997; Dawson and Tong, 1998); *Pap. antiquus* (Wang and Dawson, 1994) from Liyang, Jiangsu and Urtyn Obo, Nei Mongol; and *Pap. kazakstanicus* from the Shizhaly fauna of East Kazakhstan (Emry et al., 1998).

Raricricetodon was established by Tong (1997) based on specimens from Henan, China. *Raricricetodon* includes three species: *R. zhongtiaensis*, *R. minor* and *R. trapezius*.

Parsimony analyses using cranial and dental characters were performed to assess phylogenetic affinities within early Myomorpha, including the whole array of Asian Eocene cricetids, by Rodrigues et al. (2010). Their study implied that the genus *Raricricetodon* is polyphyletic, and that some species currently assigned to the genus should be transferred to *Palasiomys* or *Pappocricetodon*. According to Rodrigues et al. (2010), *Pappocricetodon* includes *Pap. rencunensis*, *Pap. schaubi*, *Pap. antiquus*, *Pap. kazakstanicus* and *Pap. zhongtiaensis*, and *Palasiomys* contains *Pal. conulus*, *Pal. trapezius* and *Pal. minor*. The present study accepts the phylogeny of Rodrigues et al. (2010).

The new specimens from the Huheboerhe section are more similar to *Pappocricetodon* than to *Palasiomys*. They obviously possess several characters of *Pappocricetodon*, including: cuspidate anterocone and distinct protoconule on M1, anterior arm of protocone long and reaching anterocone; protolophule II absent on M1-M2; weak ectomesolophid on m2; hypoconulid nearly missing or present on posterolophid as a small conulid. They are distinguished from *Palasiomys* by the following characteristics: larger size; mure extending forward; better developed mesostyle, mesoloph and anterior cingulum; hypocone of M3 not reduced; limited contact between anteroconid and protoconid of m1; less developed hypoconulid.

These characteristics justify the attribution of the new specimens to *Pappocricetodon* as a new species. *Pap. neimongolensis* is smaller than *Pap. schaubi*, *Pap. kazakstanicus*, *Pap. rencunensis* and *Pap. zhongtiaensis*. It also differs from those species in having smaller anterocones and less well-developed mesolophids on M1 and M2. The mesolophids and ectomesolophids of m2 and m3 are prominent in *Pap. rencunensis* and *Pap. schaubi*. The anterior arm of the protocone contacts the paracone in *Pap. zhongtiaensis*. Within the genus *Pappocricetodon*, *Pap. neimongolensis* is similar to *Pap. antiquus*, but differs from this species in a number of features: less inflated molar cusps and smaller anterocone on M1; smaller ratio of length to width of M1 (L/W: 1.11 in *Pap. neimongolensis*, 1.25 in *Pap. antiquus*); shorter mure; better-developed posterior arm of protocone, which contacts the mure, on half of specimens of M2; more prominent hypocone on M3, but longitudinal crest between protoloph and metaloph absent; posterior arm of protoconid on m2 usually longer and connecting to metaconid, hypolophid joining prehypocristid.

***Pappocricetodon* cf. *P. zhongtiaensis* Tong, 1997**

1997 *Raricricetodon zhongtiaensis* Tong, p. 118, fig. 58, table 24

2010 *Pappocricetodon zhongtiaensis* Rodrigues et al., p. 265

Specimen A left M1 (L/W: 1.28/1) (IVPP V 16499) (Fig. 2A).

Locality and horizon Huheboerhe, Erlan Basin, Nei Mongol; IM-1 horizon of the Irдин Manha Formation; Middle Eocene.

Description and comparisons There is no contact facet on the anterior surface of M1. The anterior lobe is small and the anterocone is poorly developed. The anterior arm of the protocone joins the paracone, and a small paraconule is present on the complete protoloph. The posterior arm of the protocone is short and weak. The mure is short and contacts the posterior arm of the protocone in the central basin. The metaloph is complete and extends to the mure. The mesoloph is moderate in length, and the mesostyle is prominent. All these features are reminis-

cent of *Pappocricetodon zhongtiaensis* (Tong, 1997; Rodrigues et al. 2010). However, the specimen from Huheboerhe differs from *Pap. zhongtiaensis* in being smaller, and in having a less well-developed anterocone and mure. It is tentatively attributed to *Pappocricetodon* cf. *P. zhongtiaensis*, given that only a single tooth is known.

Pappocricetodon sp.

Specimen A right M1 (L/W: 1.32/1.08) (IVPP V 16500) (Fig. 2B).

Locality and horizon Huheboerhe, Erlian Basin, Nei Mongol; IM-1 horizon of the Irдин Manha Formation; Middle Eocene.

Description and comparisons

The anterior lobe is developed. The anterocone is single and cuspidate. A short anterior arm of the protocone extends to the anterior lobe, but does not connect with the anterocone. The posterior arm of the protocone is short. A complete protoloph connects with the protocone and the paracone. The protoconule is weak. A short mure joins with the posterior arm of the protocone and the metaloph. The mesostyle and mesoloph are absent.

The specimen bears a cuspidate anterocone morphologically similar to that of *Pappocricetodon*. However, it differs from the known species of the genus (*Pap. rencunensis*, *Pap. schaubi*, *Pap. antiquus*, *Pap. kazakstanicus*, *Pap. zhongtiaensis* and *Pap. neimongolensis*) in having a short anterior arm of the protocone that does not connect with the anterocone, a better-developed protoloph and posterior arm of protocone that joins the metaloph, and a short mure. The molars of *Pap. rencunensis*, *Pap. schaubi* and *Pap. kazakstanicus* are larger than the new specimen, which differs from molars of *Pap. rencunensis*, *Pap. schaubi*, *Pap. kazakstanicus* and *Pap. zhongtiaensis* in having no mesoloph. Here it is tentatively referred to *Pappocricetodon*, but it cannot presently be identified at the specific level.

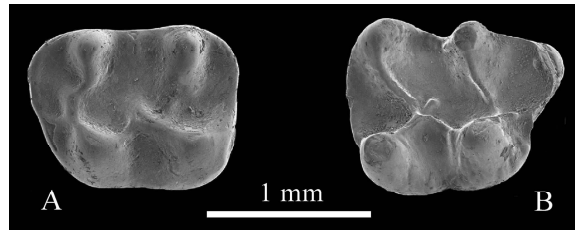


Fig. 2 Left M1 (IVPP V 16499) of *Pappocricetodon* cf. *P. zhongtiaensis* (A) and right M1 (IVPP V 16500) of *Pappocricetodon* sp. (B), in occlusal views

3 Discussion

Pappocricetodon neimongolensis sp. nov., *Pappocricetodon* cf. *P. zhongtiaensis* and *Pappocricetodon* sp. were found in the IM-1 horizon of the Irдин Manha Formation in the Huheboerhe section. *Pap. neimongolensis* is more primitive than other species of *Pappocricetodon* in having a smaller anterocone, a shorter mure and mesoloph, a more prominent hypocone on M3, and a longer posterior arm of the protoconid. A prominent anterior lobe is present on M1 in *Pappocricetodon* sp. The anterior lobe is larger and more distinct than its counterparts in previously known early Middle Eocene cricetids such as *Pal. conulus*, *Pal. trapezius*, *Pap. antiquus* and *Pap. neimongolensis*. An evolutionary trend towards enlargement of the anterior lobe on M1 was present in early cricetids in the Eocene and Oligocene (Tong, 1992, 1997; Wang, 2007). However, the short anterior arm of the protocone, short mure and weak mesoloph seen in *Pappocricetodon* sp. show that it is a primitive cricetid. The presence of three cricetid species in the IM-1 horizon of the Huheboerhe section suggests that cricetids had already begun to diversify at the time when these strata were deposited.

The presence of the primate *Tarkops mckennai* (Ni et al., 2010) and the gliran *Gomphos shevyreva* (Meng et al., 2009) in the same beds as *Pappocricetodon neimongolensis* suggests that the base of the Irдин Manha Formation is Middle Eocene. A recent paleomagnetic study

carried out in the Huheboerhe area also indicated that the Irdin Manha Formation is Middle Eocene in age (Sun et al., 2009).

Tong (1997) discussed the systematic position of *Palasiomys* from the Hetaoyuan Formation. He suggested that *Palasiomys* is very close to *Pappocricetodon* and *Raricricetodon* in dental pattern, and that *Palasiomys* could be recognized as ancestral to the later cricetids. Rodrigues et al. (2010) suggested that the cricetid group seemingly originated in Asia and that *Palasiomys* species, rather than *Pappocricetodon*, should be considered as basal cricetids. The new cricetids from the IM-1 horizon of the Huheboerhe section suggest that cricetids were already diversified in the Middle Eocene, and probably originated earlier than the Irdinmanhan.

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