

内蒙古大庙晚中新世仓鼠科一新种¹⁾

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摘要:晚中新世是古老仓鼠类型向现代属种演化的重要转折时期。描述了产自内蒙古四子王旗大庙村附近 DM02 地点新发现的仓鼠科化石一新种, 吴氏微仓鼠 *Nannocricetus wuae*。该种臼齿低冠, 齿尖呈尖锥形; m1 的下前边尖呈单尖, 具有向唇、舌两侧延伸的脊, 无下中脊或极微弱; m2 下前小脊很退化, 下中脊有或无; M1 前边尖窄, 轻度二分; M3 长大于宽。不同于被归入 Cricetodontinae 的 *Megacricetodon* 和 *Democricetodon*, 新种显示出牙齿结构的简化, 上臼齿无前尖刺、前中脊和内外侧的附尖, 下臼齿无下前小脊刺和内外侧的附尖, 上臼齿 3 个齿根, 下臼齿 2 个齿根。新种在牙齿形态上与陕西蓝田灞河组发现的原始微仓鼠 *Nannocricetus primitivus* 和内蒙古二登图的蒙古微仓鼠 *N. mongolicus* 最为接近, 前者的 m1 下前边尖完全单尖, 下前边尖与后面齿尖的连接完全缺失或极微弱, 上下臼齿的中脊(下中脊)在部分标本上存在。这 3 个种皆为中国北部的地方类群, 显示出明显的演化趋势: m1 下前边尖的二分, M2/m2 中脊(下中脊)的退化和前小脊(下前小脊)的发育。根据形态特征推测吴氏微仓鼠可能起源于众古仓鼠(*Democricetodon*), 并在中国渐进演化出原始微仓鼠和蒙古微仓鼠。依据吴氏微仓鼠的进化水平, 参照已有的化石记录, 并结合共生哺乳动物化石, 推测该地点的时代可能为晚中新世最早期。

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A NEW SPECIES OF LATE MIOCENE HAMSTER (CRICETIDAE, RODENTIA) FROM DAMIAO, NEI MONGOL

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Abstract The Late Miocene witnessed the transition of cricetids from ancient to modernized taxa. Here we describe a new cricetid species, *Nannocricetus wuae*, from DM02, near the Damiao Village, Siziwangqi, Nei Mongol. The new species is characterized by having low crowned molars with conical shaped cusps, single anteroconid on m1 with developed labial and/or lingual flanges, very weak to absent mesolophids on m1, variable mesolophid and very reduced anterolophulid on m2, narrow and slightly bifid anterocone on M1, and relatively long M3. Differing from the pattern of Cricetodontinae, *Nannocricetus wuae* shows great simplification of tooth structure. There is no paracone spur, anteromesoloph, or styles on upper molars, no spur of anterolophulid or stylids on lower molars. Root numbers are conservative, three for upper molars and two for lower molars. Morphologically, the new species shows close similarity to *Nannocricetus primitivus* and *N. mongolicus*. These three species constitute an

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endemic group confined to North China, and show progressive evolution in the splitting of the anteroconid on m1, reduction of the mesoloph(id), and development of anterolophule(id) on m2/M2 etc. Based on the evolutionary stage of the new species and associated fossils, we tentatively suggest an earliest Late Miocene age pending further confirmation by systematic study of other taxa and the paleomagnetic data.

Key words Damiao, Nei Mongol; Late Miocene; Cricetinae

1 Introduction

Hamsters (Cricetinae) are well known rodents inhabiting steppe and semi-arid habitats as well as agricultural land throughout the Palaearctic. Two species, the golden hamster *Mesocricetus auratus* and the Chinese hamster *Cricetulus griseus* are important laboratory animals for biological and medical research. The origin of Cricetinae is often associated with Democricetodontini, a widely distributed tribe in the Northern Hemisphere during the Early and Middle Miocene (Fahlbusch, 1969). Recent molecular study also suggested that the modern Cricetinae diversified during the Late Miocene (Neumann et al., 2006). However, with the paucity of early Late Miocene fossil records, the transition from the ancient to modern group remains unclear.

Recent exploration and study of Chinese Late Miocene sediments have improved our knowledge of the early evolutionary stage of Cricetinae. For example, the primitive *Nannocricetus* found from the basal Bahe Formation extended the history of modernized cricetids back to early Late Miocene (Zhang et al., 2008).

In the field excursion of 2006, we found some new Neogene mammal fossil localities near Damiao Village along the Shalamurun River, Siziwangqi, Nei Mongol. Extensive excavations and wet sieving during 2007 and 2008 seasons produced rich faunas of different ages, including a Middle Miocene pliopithecoid fauna (Zhang and Harrison, 2008). Just 3 meters above a Middle Miocene locality along the same gully, we found another fossil-rich locality, DM02, which yielded abundant micromammal fossils including some small cricetids. These cricetids showing very primitive cricetine characters, may shed light on the turnover from ancient Democricetodontini to modernized cricetines. In this paper we will describe in detail these fossils and try to discuss the taxonomy and phylogeny of Cricetinae.

Terminology of tooth morphology in this paper follows Mein & Freudenthal (1971) and Kálin (1999). Measurements are made under Zeiss V12 with an accuracy of 0.01 mm. The specimens described in this paper are housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing.

2 Systematic paleontology

Rodentia Bowdich, 1821

Cricetidae Fischer de Waldheim, 1817

Cricetinae Fischer de Waldheim, 1817

Nannocricetus Schaub, 1934

Nannocricetus wuae sp. nov.

(Fig. 1; Table 1)

Holotype One partial left lower jaw with m1–m2 (V 16894.1).

Materials included 4 left and 4 right m1 (V 16894.2–9), 3 left and 2 right m2 (V 16894.10–14); 1 broken left maxilla with M1–M2 (V 16894.15), 1 broken left M1 (V 16894.16) and 1 right M1 (V 16894.17), 2 left and 2 right M2 (V 16894.18–21), 1 left M3 (V 16894.22).

Type locality DM02, Damiao Village, Siziwangqi, Nei Mongol.

Etymology The species name is dedicated to Prof. Dr. Wu Wenyu for her great contribution to the study of fossil cricetids in China.

Diagnosis Molars are low crowned with conical shaped cusps. Anteroconid on m1 is single with developed labial and/or lingual flanges, mesolophid on m1 is absent or infrequently very weak. On m2 the mesolophid is variable, and its anterolophulid is very reduced. Anterocone of M1 is narrow, centrally located, and slightly bifid. Mesolophids on upper molars are very short or absent. M3 is longer than wide.

Measurements See Table 1.

Table 1 Tooth measurements of *Nannocricetus wuae* sp. nov. from DM02 (mm)

m1		m2		M1		M2		M3	
V 16894	L/W	V 16894	L/W	V 16894	L/W	V 16894	L/W	V 16894	L/W
.1	1.63/1.13	.1	1.3/1.13	.15	1.85/1.25	.15	1.25/1.13	.22	1.13/1.0
.2	1.63/1.08	.10	1.5/1.13	.17	1.88/1.2	.18	1.38/1.13		
.3	1.63/1.13	.11	1.58/1.28			.19	1.25/1.08		
.4	1.5/0.95	.12	1.32/1.13			.20	1.25/1.13		
.5	1.63/1.0	.13	1.38/1.0			.21	1.2/1.0		
.6	1.7/1.18	.14	1.3/1.08						
.7	1.5/0.98								
.8	1.5/1.0								
.9	1.63/1.08								

Description From the DM02 locality, we found only one partial lower jaw (V 16894.1), however, without the incisor and ascending ramus preserved. The diastema is very low and its dorsal surface is strongly curved. The mental foramen is located at the labial side of the diastema, positioned high and visible from the occlusal view. The masseteric ridge is strong, extending to the position under the protoconid of m1. The upper branch of masseteric ridge ascends to the alveolar level at the posterior edge of m2. The lower branch meets the upper one at an angle about 60 degree. The masseteric fossa is slightly concave. The longitudinal axis of molar row is at an angle of ~30 degree with the horizontal ramus. The incisor passes by the lingual side of m1, below the m2, and extends to the labial side of m3. From the labial side, m3 should be partly visible, though the ascending ramus is not well preserved. One partial maxilla (V 16894.15) with M1 and M2 shows the anterior zygomatic process starting from the labial side of the anterior root of M1. Molars are brachydont with conical shaped cusps.

The m1 is small sized with low and conical cusps. The tooth crown is long and narrow, tapering anteriorly. The anteroconid is single cusped, and relatively smaller than the four main cusps. There are developed labial and lingual flanges of the anteroconid on most of specimens, except one specimen having only a lingual flange. The anterolophulid is either absent (2/9) or very low and short (7/9). The anterolophulid when present is either connected with both protoconid and metaconid or with metaconid only. There is no spur on either side of the anterolophulid. The four main cusps are basically equally sized, alternately allocated with the labial cusps posteriorly positioned. There is no ectomesolophid on any specimens. The mesolophid is only recognizable on one specimen, and absent on all the others. The ectolophid, though very short, parallels the tooth longitudinal axis. The metalophulid and hypolophulid are slightly obliquely directed. The posterolophid is low.

The m2 is basically rectangular shaped with the lingual length shorter than the labial one. On the type specimen, the labial anterolophid is developed, while the lingual one is absent. There are short lingual anterolophids on 5 out of 6 specimens. The anterolophulid is very short, almost unrecognizable. No mesolophid is developed on two specimens including the type speci-

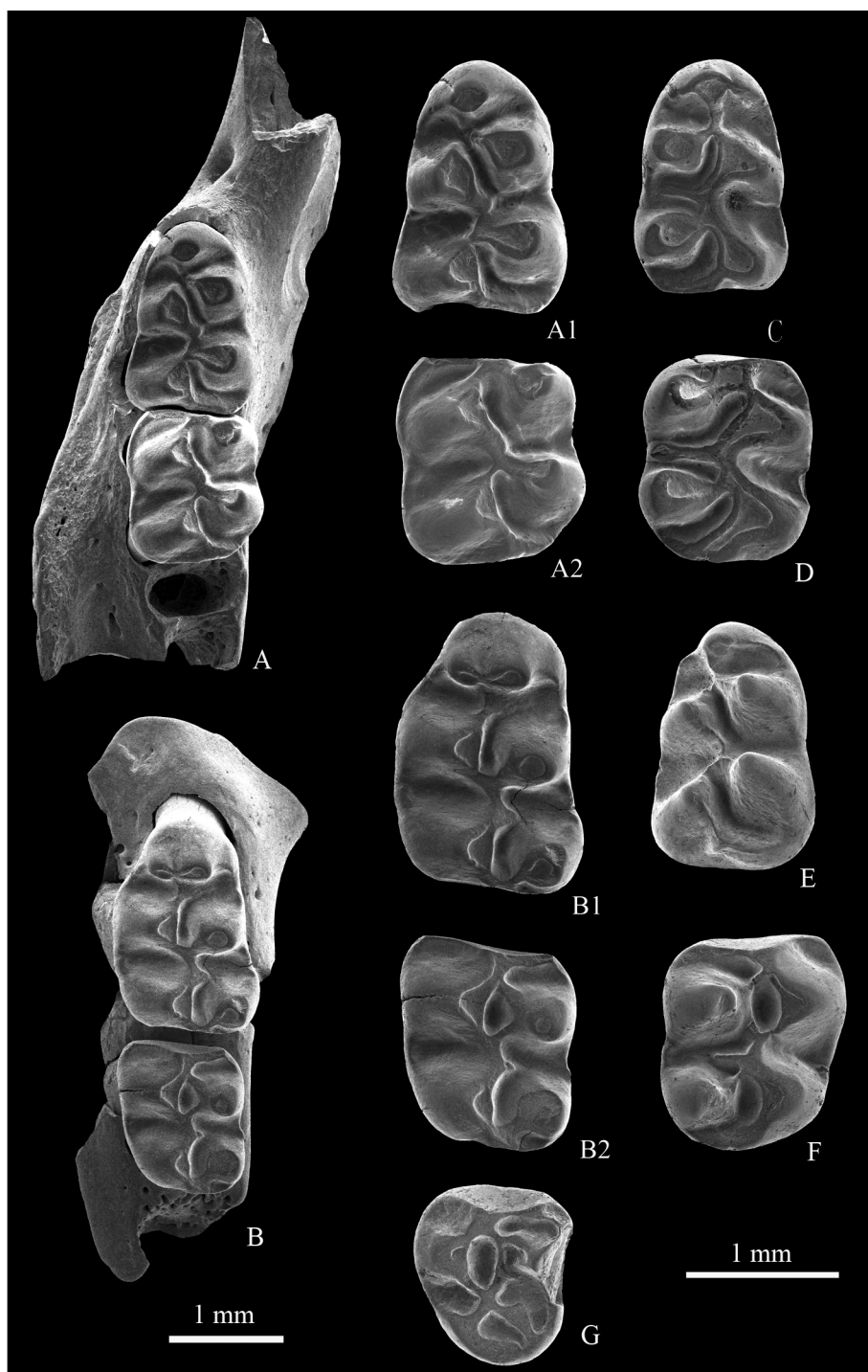


Fig. 1 Occlusal view of check teeth of *Nannocricetus wuae* sp. nov.
 A (A1–A2). partial left lower jaw with m1–m2, V 16894. 1 (holotype); B (B1–B2). partial left maxilla with M1–M2, V 16894. 15; C. right m1, V . 16894. 9; D. right m2, V 16894. 14; E. left m1, V 16894. 2; F. right M2, V 16894. 20; G. left M3, V 16894. 22

men. On 4 specimens, the mesolophid, though low and not strong, extends to the lingual side of the tooth. The posterolophid curves anteriorly, forming a short lingual ledge. Compared with the slightly labial location on m1, the hypoconid is more lingually positioned on m2.

The M1 has a convex lingual edge and a slightly concave labial edge. The anterocone is narrow and slightly bifid. Its lingual portion is generally lower and smaller than the labial one. The anterolophule is low and weak, connected with the lingual anterocone cusp. No anteromesoloph is visible. The protolophule I is absent on two specimens and present on one tooth. The mesoloph, weak and short, is only present on one specimen. The metalophule I is absent on 2 specimens and present on one, and metalophule II is always present, though not strong. The posteroloph is relatively weak. The four main cusps are paired. The protocone and hypocone are only slightly anterior to the paracone and metacone respectively. All specimens have three roots, a large and strong lingual root and two labial roots.

The M2 has roughly equal length labial and lingual anterolophs. The lingual one is lower. The anterolophule is short and perpendicular to them. The protolophule I and protolophule II are both present. The endoloph is longitudinally directed, in the same line with the anterolophule. Mesolophs are present on 2 specimens though very short and low, absent on the others. The metalophule I is developed on 3 specimens, and the metalophule II is also present on 3 specimens. All teeth have three roots.

The M3 has similarly developed labial and lingual anterolophs. The paracone is smaller, and sharply conical shaped. Both protolophule I and II are visible. The hypocone and metacone are diminished to a ridge, enclosing the talon together with the posteroloph. The endoloph is very short. The mesoloph is also just recognizable. There are three roots.

Comparison Fossil cricetids are mostly known by isolated teeth or fragmentary jaws. Therefore, the generic and specific determination is mainly based on tooth morphology. Mein and Freudenthal (1971) classified subfamilies and tribes of Cricetidae based on some cranial characters, such as the position of incisive foramen, inclination of mandible etc. However, the scheme of classification is often questioned for lacking sufficient materials (Bruijn and Saraç, 1991; Kålin, 1999; Van der Meulen et al., 2004). Till now, there is no consensus on the classification of Cricetidae (Fahlbusch, 1996).

Fossils described herein are very small or small sized according to the classification of Mein and Freudenthal (1971) by length of M1/m1 (see Table 1). The homogeneous tooth size and characters all show that the fossil cricetids found from DM02 should be considered one species.

Characters of the only lower jaw known, such as the inclination of ramus, position of mental foramen (visible from the occlusal view), are similar with those of Cricetodontinae rather than Cricetinae in which the mental foramen is lower positioned and not visible from occlusal view (Mein and Freudenthal, 1971). Further, the Damiao form is closer to Megacricetodontini by having a strong masseteric crest, and m3 partially visible in labial view. However, tooth characters of the Damiao form show obvious differences from those of Cricetodontinae. The Damiao form shows great simplification of tooth structure. There is no paracone spur, anteromesoloph, or styles on upper molars, no spur of anterolophulid and stylids on lower molars. Root numbers are three for upper molars and two for lower molars, the primitive state.

The tribe Megacricetodontini includes only one genus *Megacricetodon* according to Mein and Freudenthal (1971). Teeth from Damiao show some similarities with those of *Megacricetodon*, e. g. short and slender m1 with single anteroconid, M1 having bifid anterocone, three roots. Nevertheless, the Damiao form has no spur of the paracone on upper molars, the connection between the paracone and protocone is double and symmetric on M2, very short or absent mesolophs on upper molars, and very weak to absent mesolophid on m1. Hence, the Damiao form is different from genera attributed into Cricetodontinae including *Megacricetodon*.

Among genera grouped as Middle and Late Miocene brachydont cricetids by Fahlbusch

(1996), *Democricetodon* may be regarded as the ancestral stem of several younger lineages characterized by simplified tooth structures (Freudenthal et al., 1998). This genus is widely distributed in the Miocene of Eurasia from MN4 to MN10, especially well documented in Europe (Fahlbusch, 1964; Mein and Freudenthal, 1971) and has older records. During recent years, *Democricetodon* has also been found in China from several localities, including the well known Tunggur locality (Qiu, 1996), and other Middle Miocene localities, e. g. Junggar Basin, Xinjiang (Wu et al., 2009), Qin'an, Gansu (Guo et al., 2002). However, only two species were described in detail by Qiu (1996): *Democricetodon lindsayi* and *D. tongi*. The Damiao form shares characters with species of *Democricetodon*, including low crowned cheek teeth, short and simplified anteroconid on m1, three roots on upper molars, double and symmetric connections between paracone and protocone on M2 etc. In the Damiao material, mesoloph and mesolophids are much reduced or absent, and there are no spurs on the very short anterolophule(id), distinguishing it from all species of *Democricetodon*. The Damiao form is on the average larger than *D. tongi*, which shows more primitive characters including smaller size, lower tooth crown, simplified anterocone/anteroconid on M1/m1 etc (Qiu, 1996). The tooth size of the Damiao form falls in the range of *D. lindsayi* except for a shorter M2 on the average.

For the Late Miocene cricetines, *Neocricetodon* and *Kowalskia* are well documented. Neglecting taxonomic arguments concerning these two genera (Daxner-Höck et al., 1996; Freudenthal et al., 1998), the Damiao form can be easily distinguished from them by smaller size, less developed loph, and undeveloped mesoloph(id).

Two cricetines other than *Kowalskia* are also well documented from Chinese Late Miocene localities, *Nannocricetus* and *Sinocricetus* (Schaub, 1930, 1934; Wu, 1991; Zhang et al., 2008). *Sinocricetus zdanskyi* Schaub, 1930 was well defined by abundant materials from Ertemte and Harr Obo, Nei Mongol (Wu, 1991). Compared with the Damiao form, *Sinocricetus zdanskyi* from Nei Mongol shows elongated molars, and large and more sharply ridged occlusal surfaces. The M1 anterocone and m1 anteroconid of *S. zdanskyi* are all deeply and widely bifid posteriorly, metalophulid and hypolophulid on m1 are more developed and obliquely oriented, mesoloph(id)s are high and strong with variable length.

The morphologic characters of the Damiao form shared closely with species of *Nannocricetus* found from Nei Mongol and Lantian are small size, low crown molars, mesoloph on upper molars and mesolophids on lower molars undeveloped, less bifid anteroconid on m1 and mesosinusid on m2 extending lingually. Zhang et al. (2008) recently named *Nannocricetus primitivus*, and considered it ancestral to the type species of *Nannocricetus*, *N. mongolicus*. In measurements, the average size of the Damiao form falls in between those of *Nannocricetus primitivus* from Lantian and *N. mongolicus* from Ertemte. The relative sizes of molars are in good accordance with the latter two species (Fig. 2). Morphologically, the Damiao form shows closer similarity with *Nannocricetus primitivus* than *N. mongolicus*. The anteroconids of m1 on all specimens are single cusped, compared with the slightly bifid *N. primitivus* and more frequently bifid *N. mongolicus*. Posterior to the anteroconid, connections are either absent or very weak on the Damiao form in contrast to the better developed anterolophulid on the other two species. There exists the mesolophid on one m1 and more cases on m2 from the Damiao materials, which is absent on all specimens from Ertemte, and present on only one specimen from Lantian. Mesolophs on the upper molars show a similar tendency. There are more cases having mesolophs on the Damiao materials, though very short and low. As for the Lantian form, there are three roots on each upper molar, differing from the four roots on the Ertemte form. Hence, the Damiao form may represent the most primitive form of *Nannocricetus*, and is named *Nannocricetus wuae*, herein.

Comments on taxonomy and phylogeny of Cricetinae The monophyly of living hamsters is supported by morphological traits and reinforced by analyses of nuclear gene sequences

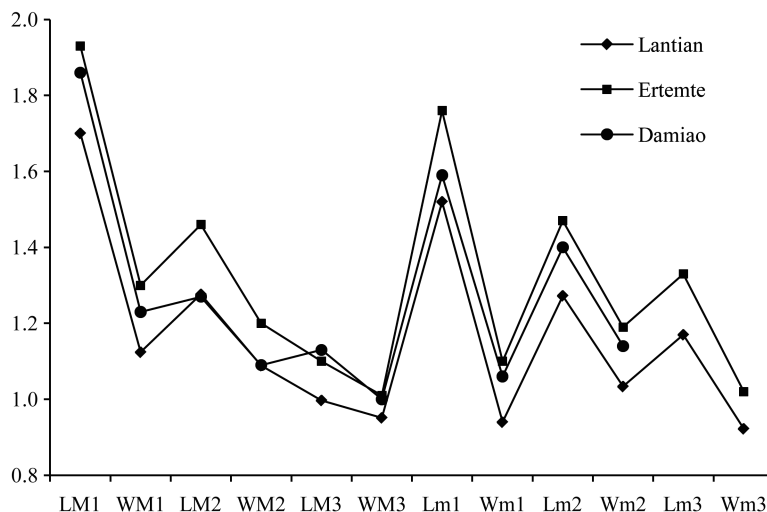


Fig. 2 Plotted diagram of tooth measurements of *Nannocricetus*
 Lantian: *Nannocricetus primitivus* from Loc. 12 (Zhang et al., 2008); Ertemte: *N. mongolicus*
 (Wu, 1991); Damiao: *N. wuae* sp. nov.; Y-axis: mm

(Wilson and Reeder, 2005; Michaux et al., 2001). However, taxonomy of fossil cricetids is still greatly controversial and systematic analysis is still pending (Fahlbusch, 1996). McKenna and Bell (1997) listed *Democricetodon* together with *Copemys* of North America under Copemyini of Subfamily Cricetodontinae. However, Mein and Freudenthal (1971) assigned *Democricetodon* as Subfamily Cricetinae, and was followed by Qiu (1996).

As we have described above, the genus *Nannocricetus* shows distinct modernized characters, and should be attributed to Cricetinae with no argument. Including the new taxon described herein, there are three species in the genus *Nannocricetus*. These three species constitute an endemic group confined to North China, and show anagenetic evolution of the bifid anteroconid on m1, reduced mesoloph(id), and development of anterolophule(id) on M2/ m2 etc. The morphologic similarities between the most primitive species *Nannocricetus wuae* and those of the *Democricetodon* suggest a possible ancestor-descendant relationship. Considering the high diversification and taxonomic uncertainty of *Democricetodon* species, it is premature to discuss which species should be ancestral to *Nannocricetus*, pending finding of better specimens and systematic study. Future study may reveal a clade derived from *Democricetodon* and endemically evolving in East Asia into *Nannocricetus* and later to other modern genera.

3 Biochronology

Paleomagnetic sampling of the Damiao section during the last two field seasons will be published soon. The localities producing *Nannocricetus primitivus* from the Bahe Formation, Lantian were dated from ~10.7 to ~8 Ma by recent paleomagnetic calibration (Zhang et al., 2008; Zhang et al., in press). The more primitive characters of the new species *N. wuae* suggest its age should not be later than this time interval. On the other hand, its relationship with *Democricetodon* suggests its later age than typical Middle Miocene localities, such as Tunggur, Nei Mongol.

Together with the cricetid described herein, we discovered many mammalian species.

Among them, we preliminarily recognized two deer (*Micromeryx* and *Euprox*), three lagomorphs (? *Desmatolagus*, *Ochotona* and *Alloptox*), two insectivores (*Mioechinus* and *Talpidae* indet.), and more than ten rodents (*Protolactaga*, *Lophocricetus*, *Eozapus*, *Gobicricetodon*, *Prosiphneus qiui*, Cricetidae gen et sp. nov., Gliridae, Eomyidae, Aplodontidae and Castoridae). Faunal composition is similar to the Tunggur fauna (Qiu, 1996). However there occurred some new elements such as *Lophocricetus*, *Prosiphneus* and *Ochotona* replacing *Heterosminthus*, *Plesiodipus* and *Bellatona*, respectively. *Heterosminthus* is confined to Early and Middle Miocene, while *Lophocricetus* is to Late Miocene and Early Pliocene (Qiu et al., 2008). *Prosiphneus*, widely accepted as a successor to *Plesiodipus*, is documented mainly from Late Miocene and later faunas. *Ochotona* was also confined to the Late Miocene and should be the direct descendant of Middle Miocene *Bellatona* (Dawson, 1961; Qiu, 1996). Compared with the faunas from the Bahe Formation, e. g. those from Loc. 12 and Loc. 19, this fauna shows obvious earlier age characters with more typical Middle Miocene elements, such as *Protolactaga*, *Gobicricetodon*, *Micromeryx*, ? *Desmatolagus*, and *Alloptox* etc. The age of the DM02 fauna is most probably between those of the Tunggur fauna and faunas from the lower part of the Bahe Formation. Considering the dominance of *Ochotona*, *Lophocricetus* and *Prosiphneus*, which have been recorded from typical Late Miocene localities, we suggest the age of the DM02 fauna to be the earliest Late Miocene, while we await confirmation from systematic studies of other groups and the paleomagnetic data.

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