

陕西蓝田晚中新世灞河组的仓鼠化石¹⁾

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摘要:陕西蓝田是我国晚中新世地层发育最完整的地区之一。新近纪哺乳动物分期中的灞河期即根据该地区灞河组发现的化石而命名。1997至2001年度的中芬合作在灞河组发现大量的新层位与化石标本。连续的地层剖面与大量的化石资料为进一步认识晚中新世哺乳动物的演化历史提供了很好的基础。

灞河组发现的仓鼠可以归入两个属:微仓鼠 *Nannocricetus* 和科氏仓鼠 *Kowalskia*。微仓鼠的分布时限较长,从灞河组的底部到中上部层位,古地磁研究指示其年代为 10.2~8 Ma。根据形态特征与测量数据,发现的微仓鼠标本被归入同一种 *Nannocricetus primitivus*。其主要特征有:个体很小;m1的下前边尖在中度或重度磨蚀的标本上呈单尖,metalophulid I存在,但metalophulid II缺如;M1前边尖与原尖单连接;M3很退化。与 *Nannocricetus mongolicus* 相比,m1的下前边尖更少分开,且在唇侧有向后延伸的弱脊,下前小脊很弱或缺失,m2的舌侧前边尖较发育,M1前边尖与原尖单连接,M3次尖较发育且缺失后尖。推测 *Nannocricetus primitivus* 是 *N. mongolicus* 的直接祖先类型,向后者转换的时间大约发生在 7~8 Ma。

根据新的化石材料重新修订了微仓鼠的属征:个体很小的仓鼠;上白齿的中脊与下白齿的下中脊完全缺失或极不发育;m1下前边尖呈单尖或较少分开;m2的下次尖靠舌侧,使得m2的后部较窄,m2中原谷向前延伸不太远;M3很退化。

科氏仓鼠的标本很少,仅发现在剖面的上部,其时代稍早于 8 Ma,与云南禄丰的年代大致相当,是目前中国发现的最早纪录之一。推测科氏仓鼠在 8 Ma 前从欧洲迁移至中国。

关键词:陕西蓝田,晚中新世,灞河组,仓鼠

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LATE MIOCENE CRICETIDS FROM THE BAHE FORMATION, LANTIAN, SHAANXI PROVINCE

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Abstract Fossil cricetids found from the Bahe Formation, Lantian are assigned to *Nannocricetus primitivus* sp. nov. and *Kowalskia* indet. respectively by their dental characters and measurements. The new species *Nannocricetus primitivus* is characterized by its smaller size and having single cusped anteroconid of m1 on moderate and heavily worn teeth, presence of metalophulid I, absence of metalophulid II,

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no mesoloph on upper molars, absent or very weak mesolophid on lower molars, and very reduced M3. Magnetostratigraphic results of the Bahe Formation indicate that the localities produced *Nannocricetus primitivus* range from the early Late Miocene to the middle Late Miocene (~10.2–8 Ma). The primitiveness of the new species and its earlier geologic records suggest that it might be the direct ancestor of *Nannocricetus mongolicus*. The turnover from *Nannocricetus primitivus* to *N. mongolicus* should occur at about 7–8 Ma. There found only one m2 of *Kowalskia*. The fossil level of *Kowalskia* indet. is in the upper part of the main section, dated to slightly earlier than 8 Ma. Except the material from Lufeng (MN11), the Lantian material is one of the earliest immigrants from the western Eurasia.

Key words Lantian, Shaanxi; Late Miocene; Bahe Formation; Cricetidae

1 Introduction

The Lantian area is well known by the discovery of *Homo erectus* sites, well developed Late Miocene sequences, and rich mammalian fossils. Bahean, one of the Chinese Late Neogene Mammalian ages, was named based on fossil mammals from the Bahe Formation in this area (Li et al., 1984). Extensive exploration and multidisciplinary research were carried out in this area by our multinational group during the period 1997–2001, and produced extra new localities and rich fossils (Zhang et al., 2002; Kaakinen and Lunkka, 2003; Kaakinen, 2005). Systematic studies on the fossils from the Bahe Formation greatly improved our understanding of the evolutionary history of mammals during the Late Miocene (Zhang et al., 2002; Qiu et al., 2003), especially for small mammals (Qiu et al., 2004a,b, 2008; Li and Zheng, 2005). Here we report the fossil cricetids discovered from the Bahe Formation. Fossils were collected by screen washing. Detailed stratigraphic horizons of the fossil localities mentioned herein can be referred to Kaakinen and Lunkka (2003) and Kaakinen (2005).

Cricetids are a large group of rodents with high diversity and wide geographic distribution. The cricetid-murid question has persisted as the dominant theme, or uncertainty, involving the higher level classification of murid rodents over the past century (Wilson and Reeder, 2005). We follow the taxonomy of Wilson and Reeder (2005) herein, listing Cricetidae as an independent family. The subfamilial and tribal level taxonomy within this group is also ongoing argued (Fahlbusch, 1996) and beyond the scope of this paper. We simply follow McKenna and Bell (1997), attribute the two genera described in this paper in the subfamily Cricetinae. Terminology of tooth descriptions follows Mein and Freudenthal (1971) and Wu (1991). Measurements are made under Zeiss Microscope V8.

2 Systematic paleontology

Rodentia Bowdich, 1821

Cricetidae Fisher de Waldheim, 1817

Cricetinae Fischer de Waldheim, 1817

Nannocricetus Schaub, 1934

Type species *Nannocricetus mongolicus* (Schaub, 1934).

Diagnosis (Revised) Size very small. Mesolophids on lower molars and mesolophids on uppers are either absent or very weak. The m1 has a less bifid anteroconid. Hypoconid on m2 is lingually allocated, shaping the posterior part narrower than the anterior part. The mesosinusid on m2 does not extend forward too far. M3 very reduced.

Species included *Nannocricetus mongolicus*, *Nannocricetus primitivus* sp. nov.

Geological and geographic distribution Late Miocene to Pliocene, North China.

***Nannocricetus primitivus* sp. nov.**

(Fig. 1A–M; Table 1–2)

Cricetidae gen et sp. nov. Qiu et al., 2003

Holotype 1 left broken maxilla with M1–M2 (V 15700).**Type locality** Loc. 12, Lantian, Shaanxi Province, China.**Geological age and horizon** Lower and middle part of the Bahe Formation, early Late Miocene.**Materials included** Loc. 12: 1 right fragmentary mandible with m1–m2 (V 15701.1), 10 left 4 right complete and 3 broken M1s (V 15701.2–18), 9 left 6 right complete and 1 fragmentary M2s (V 15701.19–34), 6 left and 2 right M3s (V 15701.35–42), 2 left 4 right m1s (V 15701.43–48), 8 left 8 right and 1 well worn left m2s (V 15701.49–65), 6 left 5 right and 1 broken m3s (V 15701.66–77); Loc. 19: 1 left 2 right M1s (V 15702.1–3), 1 right M2 (V 15702.4), 1 right M3 (V 15702.5), 1 left m1 (V 15702.6), 1 left 3 right broken m1s (V 15702.7–10), 2 right m2s (V 15702.11–12); Loc. 38: 1 left m2 (V 15703); Loc. 30: 1 left and 1 right m2s (V 15704.1–2); MS4: 1 left m2 (V 15705); Loc. 6: 1 right M1 (V 15706.1), 1 right M3 (V 15706.2), 1 right m2 (V 15706.3), 1 right m3 (V 15706.4); MS21: 1 right m3 (V 15707).**Etymology** The species name refers to its primitiveness in the genus *Nannocricetus*.**Diagnosis** Very small size. Anteroconid of m1 is single cusped on the moderate and heavily worn teeth. Metalophulid I present, while the metalophulid II absent. No mesoloph on upper molars. Mesolophid on lower molars either absent or very weak. M3 very reduced.**Measurements** See Table 1, 2.**Description** From Loc. 12 of the Bahe Formation, we found one fragmentary mandible with two heavily worn teeth m1–2 (V 15701.1). The longitudinal axis of tooth row makes an angle of $\sim 45^\circ$ with the horizontal ramus. The diastema part is very low, at the level of the masseteric process. The mental foramen is near the anterior root of m1. A maxillary fragment is too broken to give any detailed morphologic characters, however with well preserved M1–M2 (Fig. 1A, V 15700). Besides these specimens, others are all isolated teeth. There are totally 76 isolated teeth found from Loc. 12. Tooth measurements (Table 1; Fig. 2) show that the sizes are very homogeneous. Lengths decrease greatly from the first to the third molar, especially for upper molars. The m1 is slightly narrower than m2. Of all the molars, M3 is the most variable tooth in size.

m1; very small sized. The tooth crown is long and narrow, anteriorly tapering. The anteroconid is bifid from behind on unworn teeth, and single-cusped on moderate and heavily worn teeth. The labial side of anteroconid extends posteriorly as a flange. The anterolophulid is either very low in young individuals or absent with wear in aged ones. On one specimen (V 15701.46), the anterolophulid connects to the labial anteroconid and on the other it connects with both cusplets of anteroconid (V 15701.45). The metalophulid I presents in all cases, connecting with the protolophulid, while metalophulid II is lacking. There is no mesolophid. The hypolophulid connects the entoconid and ectolophid at a low level. The ectolophid locates in the middle line of the tooth crown and anteroposteriorly oriented. The posterolophid almost extends to the lingual side. There are 2 roots.

m2; the tooth is rectangular shaped in occlusal view. The general tooth morphology is very similar to m1 except for lacking the anteroconid part and slightly wider (Fig. 2). The labial anterolophid is well developed, and the lingual anterolophid is very short and disappears in heavily worn teeth. Compared with that on m1, the hypoconid is slightly lingually allocated, shaping the posterior part narrower than the anterior part. There is only one specimen having a very low but recognizable mesolophid.

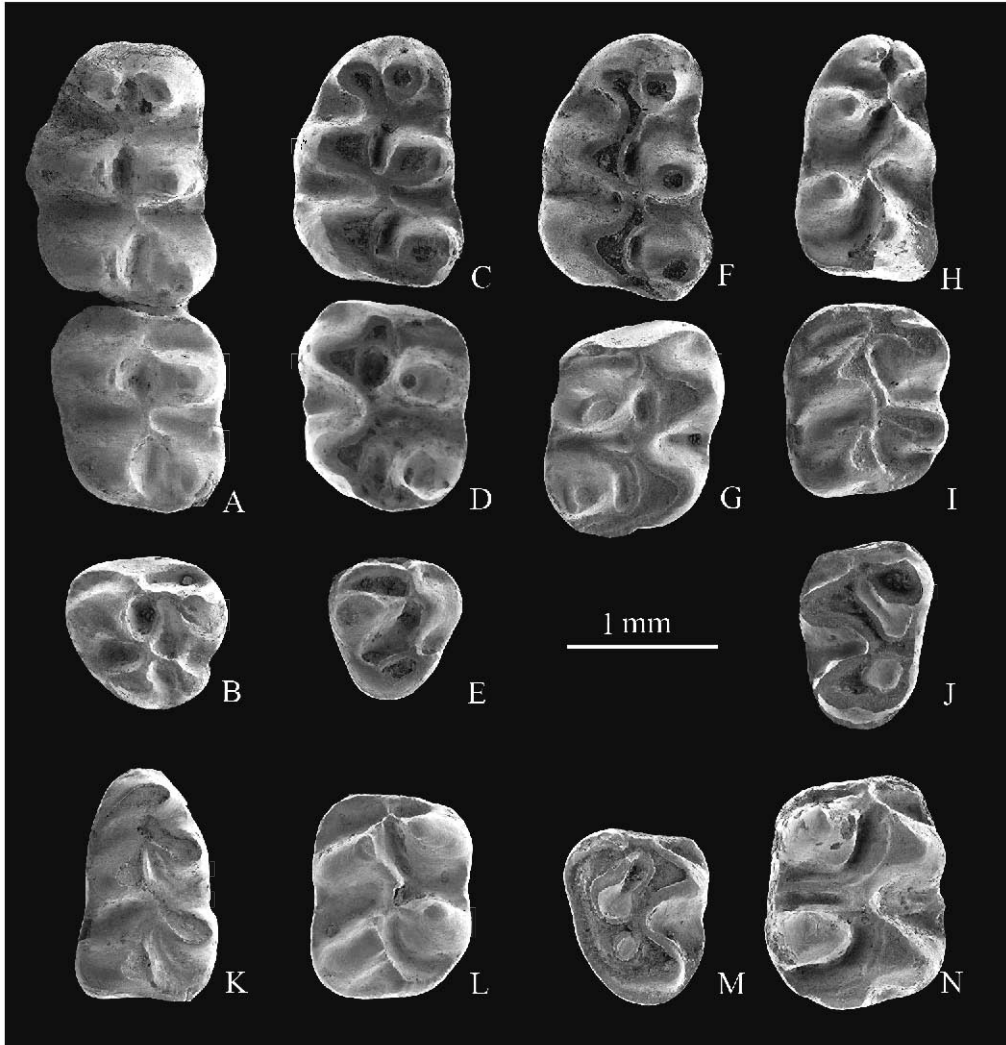


Fig. 1 Occlusal view of molars of *Nannocricetus primitivus* sp. nov. (A–M) and *Kowalskia* indet. (N) A. left M1–M2 (V 15700), B. left M3 (V 15701.39), C. left M1 (V 15701.2), D. left M2 (V 15701.26), E. right M3 (V 15701.35), F. left M1 (V 15701.4), G. right M2 (V 15701.24), H. right m1 (V 15701.45), I. left m2 (V 15701.52), J. left m3 (V 15701.66), K. left m1 (V 15701.44), L. left m2 (V 15701.51), M. right m3 (V 15701.72); N. right m2 (V 15708)

m3; the labial anterolophid is developed, and the lingual one is more developed than that on m2 (6/11). Entoconid is strongly reduced to a narrow ridge, connected with the posterolophid to enclose the posterosinusid. No mesolophid.

M1; the outline of the tooth is slender with a convex lingual side and slightly concave labial side. Gradual constriction anterior to the protocone makes the anterocone narrower. The anterocone is bifid. The labial cusp is large and conical shaped, isolated to other cusps, and the lingual one is smaller and elongated, connected with protocone in a very low level by the undeveloped anterolophule or the forearm of protocone. The protocone and hypocone are “V” shaped and slightly labially inclined, while the paracone and metacone are conical and upright. The protolophule I is absent in all available teeth except one aged individual, and the protolophule

II is always present, though very weak and low leveled. There is no mesocone and mesoloph in all cases. The entoloph is also in a very low level, connecting the anterior arm of hypocone and the protolophule II. Metalophule is absent in young individuals, and visible in aged ones. The posteroloph extends labially to the central line of metacone. There are three roots, one below the anterocone, one below the protocone and hypocone, and one below the metacone.

M2: the occlusal outline of the tooth is subrectangular with the anterior border slightly angled the longitudinal axis, and the posterior part narrower. The labial and lingual anteroloph is about equal size, intersected by the short but prominent anterolophule. Both protolophule I and II exist, though the protolophule II is less developed. The metalophule I is present, though not developed, however, no metalophule II exists. There is no mesocone and mesoloph in all cases. There are 3 roots, one on the lingual side, and the other two on the labial side.

M3: it is very reduced in size. The outline is about triangular shaped. The hypocone is reduced and labially located, and the metacone is reduced to an almost unrecognized ridge, connecting with the posteroloph. The metalophule I is, however, well developed. There are 3 roots.

Specimens from Loc. 19 show the comparable sizes with those found from Loc. 12 (Table 2), and tooth morphology also shows no difference.

Table 1 Tooth measurements of *Nannocricetus primitivus* from Loc. 12 (mm)

		Loc. 12														Mean	Max	Min		
M1	L	1.7	1.7	1.8	1.76	1.78	1.7	1.7	1.64	1.7	1.7	1.4	1.7	1.72	1.76	1.74	1.70	1.8	1.4	
	W	1.1	1.2	1.1	1.24	1.12	1.2	1.1	1.2	1.0	1.16	1.0	1.1	1.04	1.2	1.1	1.12	1.24	1.0	
M2	L	1.2	1.3	1.36	1.36	1.24	1.26	1.34	1.3	1.3	1.4	1.2	1.26	1.2	1.24	1.26	1.28	1.4	1.2	
	W	0.9	1.1	1.1	1.1	1.14	1.06	1.14	1.1	1.12	1.14	1.1	1.04	1.14	1.1	1.1	1.04	1.09	1.14	0.9
M3	L	0.9	0.74	1.0	1.04	1.1	1.2	1.0									1.00	1.2	0.74	
	W	0.9	0.7	0.94	1.06	1.0	1.1	0.96									0.95	1.1	0.7	
m1	L	1.44	1.5	1.62	1.52	1.52											1.52	1.62	1.44	
	W	0.96	0.9	1.0	0.9	0.94											0.94	1.0	0.9	
m2	L	1.3	1.24	1.3	1.2	1.24	1.26	1.36	1.3	1.26	1.3	1.3	1.2	1.3	1.2	1.3	1.3	1.27	1.36	1.2
	W	1.06	1.0	1.0	1.08	1.0	1.0	1.14	1.08	1.02	1.06	1.0	1.0	1.0	1.04	1.06	1.03	1.14	0.86	
m3	L	1.26	1.2	1.2	1.2	1.1	1.1	1.3	1.0									1.17	1.30	1.00
	W	0.9	0.96	0.96	0.96	0.9	0.9	0.9	0.9									0.92	0.96	0.90

Table 2 Measurements of isolated teeth referred to *Nannocricetus primitivus* (mm)

		Loc. 19		Loc. 38	Loc. 6	Loc. 30	MS21	MS4
M1	L	1.7	1.74	1.8		1.6		
	W	1.1	1.12	1.22		1.06		
M2	L	1.28						
	W	1.1						
M3	L	0.9				1.0		
	W	0.76				1.0		
m1	L	1.56						
	W	0.9						
m2	L	1.26		1.2		1.26	1.2	1.2
	W	0.86		0.96		1.04	1.0	0.96
m3	L				1.16		1.14	
	W				0.8		0.82	

Comparison Having same tooth morphology and comparable measurements, the above described specimens from Loc. 12 and Loc. 19 can readily be assigned into one species.

Though with only fragmentary jaws and isolated teeth found, the Lantian form shows evidently modernized simplification of tooth morphology comparing those from the Early and Middle Miocene cricetids, such as *Eumyarion*, *Democricetodon*, and *Megacricetodon*. There are no spurs and mesoloph(id) developed on molars.

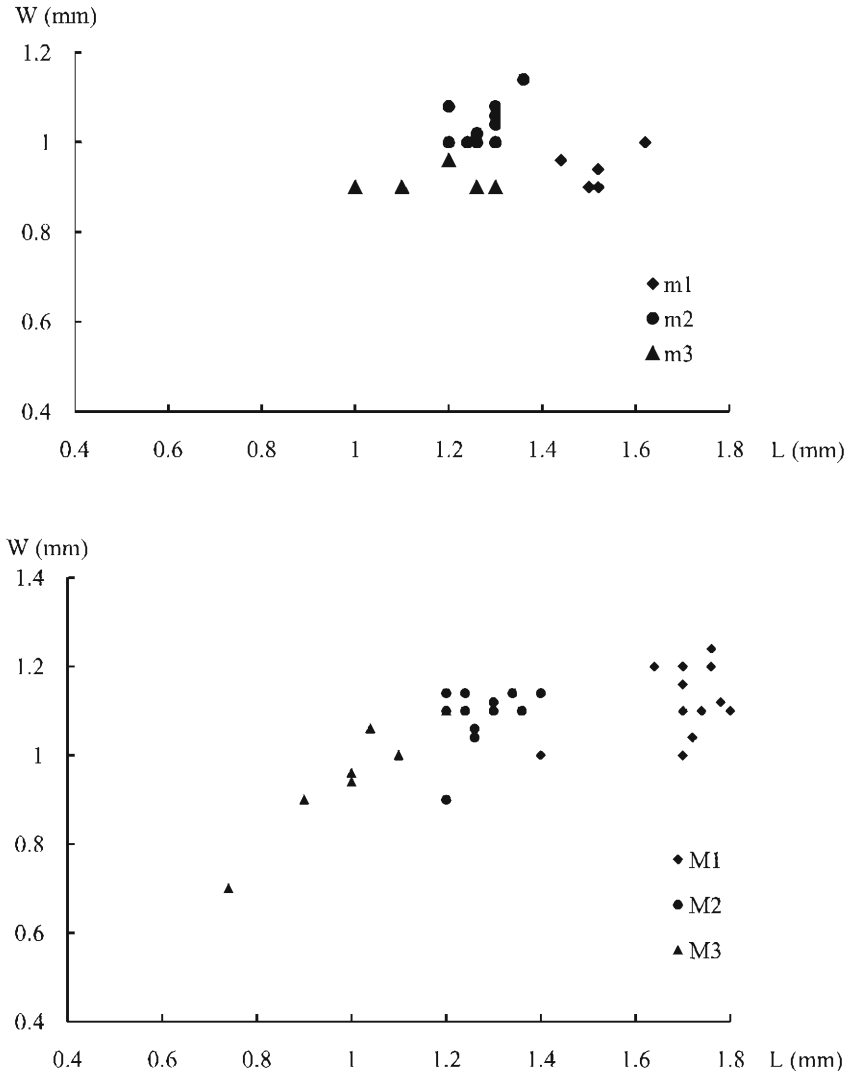


Fig. 2 Diagram showing the tooth size variation of *Nannoericetus primitivus* from Loc. 12, Bahe Formation

From the Late Neogene of Eurasia, the widely distributed *Neocricetodon* and *Kowalskia* are well documented. The taxonomy of these two genera is still in debate (Daxner-Höck et al., 1996; Freudenthal et al., 1998). According to Freudenthal et al. (1998), *Neocricetodon* is characterized by small to medium size, dominantly labial anterolophulid of m1, well developed labial spur on the anterolophule of M1, maintaining of the mesoloph(id)s, and not very reduced third molars. Daxner-Höck et al. (1996) excluded from *Kowalskia* all species with distinctly divided anterocones(id)s, strongly reduced or missing mesoloph(id)s, and well deve-

loped funnels between opposed inner and outer main cusps. Neglecting the argue of the taxonomy of these two genera, the Lantian form can easily be distinguished from them by having strongly reduced or absent mesoloph(id)s, no labial spur on the anterolophule of M1, and reduced third molars.

Except for *Kowalskia*, two cricetine rodent genera are also well documented from the Chinese Late Miocene localities, e. g. *Nannocricetus* and *Sinocricetus* (Schaub, 1930, 1934; Wu, 1991). *Sinocricetus zdanskyi* Schaub, 1930 was well defined by abundant materials from Ertemte and Harr Obo, Nei Mongol (Wu, 1991). Comparing with the Lantian form, *Sinocricetus zdanskyi* from Nei Mongol show elongated molars, large and more ridge-like occlusal surface. The M1 anterocone and m1 anteroconid are all deeply and widely bifid posteriorly, differing from the Lantian form which has slightly bifid anteroconids on unworn m1s; metalophulid and hypolophulid on m1 are more developed and obliquely oriented than those of Lantian form; mesoloph(id)s are high and strong with variable length differing from the absence on the Lantian form. The tooth morphology and size of the Lantian form is mostly comparable with those of *Nannocricetus mongolicus* from Ertemte (Wu, 1991). They share simplified tooth morphology, such as the narrow and less bifid anteroconid on m1, no mesoloph(id)s on molars developed. However, the Lantian form differs from *Nannocricetus mongolicus* by some primitive characters, e. g. the anteroconid of m1 less frequently bifid and its labial anteroconid extending posteriorly as a flange, the anterolophulid either low or absent, the m2 having more developed lingual anterolophid than those on *Nannocricetus mongolicus*, and the m3 having less prominent and isolated entoconid, the M1 showing single connection of lingual anterocone with the protocone comparing with the double connection on those of *Nannocricetus mongolicus*, and the M3 having more pronounced hypocone and lacking metacone. Therefore, it is highly possible that the Lantian specimens represent an ancestral form of *Nannocricetus mongolicus*, named herein as a new species *Nannocricetus primitivus*.

There also discovered some specimens from other localities, e. g. MS4, Loc. 6, Loc. 30, Loc. 38, MS21. The m2 from MS4 is just slightly narrower than those from Loc. 12, but comparable with those from Loc. 19. One M1 from Loc. 6 shows the same morphology with *Nannocricetus primitivus* except for having a very weak and low protolophule I. One of the two m2s from Loc. 30 has a low but distinct mesolophid. Considering of the few specimens and minor morphologic differences, these specimens are tentatively referred to *Nannocricetus primitivus*.

Discussion Besides the materials from Ertemte and Harr Obo, there was no *Nannocricetus* reported with certainty elsewhere as Wu stated in 1991. After 1991, more materials were discovered from Nei Mongol and Lingtai, Gansu Province. Qiu et al. (1999, 2006) reported that some materials referred to *Nannocricetus* sp. from Baogedawula, Nei Mongol. By faunal comparison, the Baogedawula fauna was thought to be of Middle Baodean age, equivalent to MN12. Materials from the Lingtai sections were listed as *Nannocricetus mongolicus* by Zheng and Zhang (2001). According to the biostratigraphic and magnetostratigraphic correlation, the horizons produced *Nannocricetus mongolicus* cover the latest Miocene and Early Pliocene. However, no detailed description published till now. Qiu and Storch (2000) described some material from Bilike, Nei Mongol. The morphology of Bilike form is only slightly more derived than those from Ertemte and Harr Obo. Other material of *Nannocricetus mongolicus* from Gaotege was also reported by Li (2006) in his doctoral thesis. The age of this fauna is thought to be equivalent to MN15. Hence, fossil records of *Nannocricetus mongolicus* range from the latest Late Miocene to Middle Pliocene. *Nannocricetus primitivus* from Lantian was found from the lower and middle part of the Bahe Formation. Magnetostratigraphic results of the Bahe Formation (Kaakinen, 2005) indicate that the localities produced *Nannocricetus primitivus* range from the early Late Miocene to the middle Late Miocene (~10.2–8 Ma). The primitiveness of the new species fit the geologic records of *Nannocricetus mongolicus* which is later than 8 Ma. The turnover from

the primitive *Nannocricetus primitivus* to *Nannocricetus mongolicus* should occur at about 7~8 Ma.

***Kowalskia* Fahlbusch, 1969**

***Kowalskia* indet.**

(Fig. 1N)

Material One right m2 (V 15708) (L/W: 1.48 mm/1.1 mm), MS24.

Description The occlusal outline is rectangular shaped. Both the labial and lingual anterolophids are developed. The mesolophid is low but distinct, extending to the lingual border of the tooth. There is a small ectostylid, and a weak ectomesolophid. The ectolophid is strong, and longitudinal oriented. The posterolophid is well developed.

Comparison The tooth size exceeds those of *Nannocricetus primitivus* from the lower part of the Bahe Formation, comparable with those of *N. mongolicus* from Ertemte, Nei Mongol. By the developed mesolophid and small but distinct ectomesolophid, the present specimen can be excluded from *Nannocricetus*. The strong and longitudinal oriented ectolophid also distinguishes it from those of *Sinocricetus*. The tooth morphology resembles those of *Kowalskia* defined by Daxner-Höck et al. (1996). The size is larger than *Kowalskia neimengensis*, but smaller than *K. similis* from Ertemte and Harr Obo (Wu, 1991), comparable with *K. hanae* from Lufeng (Qiu, 1995), but narrower. However, with the only isolated m2, it is almost impossible to infer it to any species with certainty. By the measurements, the Lantian form is longer but narrower than those of *K. gansunica* from Tianzhu, Gansu (Zheng and Li, 1982).

Discussion Similar with *Nannocricetus*, *Kowalskia* is also recorded from the Late Miocene and Pliocene. Kälin (1999) mentioned some new unpublished material from Switzerland (Nebelgerweg), Austria (Götzensdorf) and Hungary (Rudabanya) which suggests *Kowalskia* is a derivation from a hitherto unnamed small *Democricetodon* species. The transition from a *Democricetodon* species to *Kowalskia* would therefore have taken place in Europe during the middle Vallesian. The fossil level of *Kowalskia* indet. is in the upper part of the main section, dated to slightly earlier than 8 Ma. Except the material from Lufeng (MN11), the Lantian material is one of the earliest immigrants from the western Eurasia.

3 Biostratigraphy

Both Loc. 12 and Loc. 19 are located at the lower part of the Bahe Formation (Kaakinen, 2005), produced rich small mammals, which constitute a fauna including *Nannocricetus primitivus*, *Progonomys sinensis* (Qiu et al., 2004a), *Myocricetodon lantianensis*, *Myocricetodon liui*, *Abudhabia baheensis* (Qiu et al., 2004b), *Protolactaga lantianensis*, *Salpingotus primitivus*, *Cardiocranius pussilus* (Li and Zheng, 2005), *Lophocricetus xianensis*, *Lophocricetus* sp., *Eutamias lishanensis*, *Sciurotamias pussilus* (Qiu et al., 2008), *Ochotona* cf. *O. lagreli* (Qiu et al., 2003). According to the stratigraphic correlation and magnetostratigraphic data (Kaakinen, 2005), this fauna is dated to 9.9~9.95 Ma, then can be correlated to MN9 (Steininger, 1999).

From the middle part of the Bahe Formation, Loc. 6 and Loc. 30 are among the richest localities. These localities are in the comparable level with those of 1950's and 1960's (Zhang et al., 1978), typical localities for the Bahe fauna (Li et al., 1984). Small mammals are less abundant. Cricetids from this level are referred to *Nannocricetus primitivus* with slightly differences. Murids were described as Muridae gen. et sp. indet. (Qiu et al., 2004b), similar to *Progonomys sinensis*, but with more derived characters. Gerbillids are referred to *Myocricetodon liui* and *Abudhabia baheensis*. *Protolactaga lantianensis* is also recorded from this level (Li and Zheng, 2005). *Eutamias lishanensis* persisted to this level (Qiu et al., 2008). The small

mammal assemblage from this level is very similar to the earlier fauna from the lower part of the Bahe Formation in composition, with some slightly advanced forms. Magnetostratigraphic results show that this fauna can be dated to 8.0 ~ 8.2 Ma. Considering of the difficulties of comparison with the European mammalian faunas by sharing less common elements, this fauna can only be correlated to MN11 by age (Steininger, 1999). Hence, the representative fauna of Bahean stage in the concept of Li et al. (1984) can thereafter be correlated to the early Turolian rather than Vallesian. The Vallesian equivalent fauna, however, should be from the lower part of the Bahe Formation.

4 Conclusions

1) Two genera and species of cricetids were discovered from the Bahe Formation, e. g. *Nannocricetus primitivus* and *Kowalskia* indet.

2) *Nannocricetus primitivus* was found from the lower and middle part of the Bahe Formation, dated to ~10.2–8 Ma. It might be the direct ancestor of *Nannocricetus mongolicus*. The turnover from *Nannocricetus primitivus* to *N. mongolicus* should occur at about 7 ~ 8 Ma.

3) Material of *Kowalskia* is rare from the Bahe Formation, only found from one locality, dated to ~8 Ma.

4) *Kowalskia* probably originated in Europe, and migrated to China before 8 Ma.

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