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## Early Miocene cricetids (Rodentia) from the Junggar basin (Xinjiang, China) and their biochronological implications

*Les cricetidés (Rodentia) miocènes inférieurs du bassin du Junggar (Xinjiang, Chine) et leurs implications biochronologiques*

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### Abstract

Among the 14 small mammal species from the early Miocene locality of the northern area of the Junggar basin (northern Xinjiang, China), four species are cricetids (Rodentia): unnamed species of *Cricetodon* and *Eumyarion*, and two new species, *Karydomys debriujni* nov. sp. and *Megacricetodon beijiangensis* nov. sp. Some aspects of the morphology of *Cricetodon* sp. are shared by *Eucricetodon* from the late Oligocene, suggesting that these specimens could be of intermediate form between *Eucricetodon* and *Cricetodon*. One tooth of *Eumyarion* sp. was found, making its determination uncertain, but its morphology is clearly differentiated from the one of *Cricetodon* sp. The species *K. debriujni* nov. sp. is established based on its primitive features compared to the species known in Europe and Anatolia, and its specific association of characters compared to *Karydomys dzerzhinskii*. *M. beijiangensis* nov. sp. shows many plesiomorphic features compared to the species already described in the middle Miocene of China. Based on both the whole assemblage of rodents and the species of cricetids, the biochronologic position and the age of the locality are discussed. The locality appears to be biochronologically very close to the fauna from the Chul'adyr Formation in Aktau Mountains, but we propose an age slightly older than the one proposed for this fauna, probably equivalent to the MN3 biozone in Europe.

**Keywords:** Biochronology; Cricetidae; Early Miocene; Rodentia; Central Asia

### Résumé

Parmi les 14 espèces de mammifères provenant d'une localité miocène inférieure de la région nord du bassin du Junggar (Nord du Xinjiang, Chine), quatre espèces de cricetidés ont été trouvées : deux espèces indéterminées des genres *Cricetodon* et *Eumyarion*, et deux nouvelles espèces, *Karydomys debriujni* nov. sp. et *Megacricetodon beijiangensis* nov. sp. Certains aspects de la morphologie de *Cricetodon* sp. sont communs avec les formes de *Eucricetodon* de l'Oligocène supérieur, suggérant que les spécimens décrits pourraient constituer une forme intermédiaire entre *Eucricetodon* et *Cricetodon*. Une seule dent de *Eumyarion* sp. a été trouvée, rendant sa détermination incertaine ; toutefois sa morphologie se différencie clairement de celle de *Cricetodon* sp. L'espèce *K. debriujni* nov. sp. est établie en raison de ses caractéristiques primitives en comparaison des espèces connues en Europe et en Anatolie, et en raison d'une association spécifique de caractères qui la différencie de *Karydomys dzerzhinskii*. *M. beijiangensis* nov. sp. montre de nombreux caractères plésiomorphes en comparaison des espèces déjà connues dans le Miocène moyen de Chine. La position biochronologique et l'âge de la localité sont discutés sur la base de l'association de rongeurs et des espèces de cricetidés. La localité semble être biochronologiquement très proche de la faune provenant de la Formation Chul'adyr dans les montagnes Aktau, mais nous proposons un âge légèrement plus vieux que celui proposé pour cette faune, probablement contemporain de la biozone MN3 en Europe.

**Mots clés :** Biochronologie ; Cricetidae ; Miocène inférieur ; Rodentia ; Asie Centrale

## 1. Introduction

The geology of the Xinjiang province has been extensively studied over the last 50 years, because of its largely exposed continental Mesozoic and Cenozoic sediments. Since the 1980s many survey expeditions have been organized by the Institute of Vertebrate Paleontology and Paleoanthropology to investigate the Cenozoic deposits of northern Xinjiang and their fossil record, focusing especially on the northern part of the Junggar basin. From a geographical point of view, this area is indeed of considerable interest for understanding the dispersion and diversification of faunas during the Cenozoic due to its central position in Asia (Fig. 1(A)). The material studied here comes from one locality, XJ 200114, discovered in 2001 in the northern part of the Junggar basin (Fig. 1(B)), Fuhai County, Xingjiang Uygur Autonomous Region of China ( $46^{\circ} 18' 21.48'' \text{N} - 88^{\circ} 0' 59.58'' \text{E}$ ). This new locality is located about 30 km south of the Ulungur River (Fig. 1(C)), where numerous other Cenozoic localities have been previously discovered (e.g., Wu, 1988; Ye, 1989; Ye et al., 1999; Bi, 1999, 2000; Meng et al., 1999, 2006; Wu et al., 2000, 2003). The sediments have been recognized as belonging to the Suosuoquan Formation, probably the middle or upper part of the formation. Because this locality is distant from the more complete Tiersihabahe section (Meng et al., 2006), there is no certainty about its precise correlation with the Suosuoquan Formation in the Tiersihabahe section. However, the fossils from the locality do provide us a biostratigraphic correlation with those biozones in the Tiersihabahe section.

Altogether about 3.5 tons of screenwashed matrix provided 14 species of mammals: Soricidae gen. and sp. indet. (Insectivora); Galericiini nov. gen. and sp. (Insectivora, Erinaceidae); unnamed species of *Sinologomys* Bohlin, 1937 (Lagomorpha, Ochotonidae); *Protalactaga shevyrevae* Zazhigin and Lopatin, 2000; new unnamed species of *Litodonomys* Loomis, 1914; *Heterosmintus mongoliensis* Zazhigin and Lopatin, 2000; new unnamed species of *Heterosminthus* Schaub, 1930 (Rodentia, Dipodidae); unnamed species of *Atlantoxerus* Forsyth Major, 1893 (Rodentia; Sciuridae); *Cricetodon* sp.; *Eumyarion* sp.; *Karydomys debruijni* nov. sp.; *Megacricetodon beijiangensis* nov. sp. (Rodentia, Cricetidae); *Aksharomys mallos* Shevyreva, 1994 (Rodentia, Ctenodactylidae); Mustelidae indet. (Carnivora, one damaged M2). The present study focuses on the specimens belonging to the family Cricetidae.

## 2. Material and methods

All specimens are deposited in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology of Beijing, and all specimens are catalogued with the numbers: V16897.1–4 for *Cricetodon* sp.; V16898.1 for *Eumyarion* sp.; V16899.1–33 for *K. debruijni* nov. sp., and V16900.1–37 for *M. beijiangensis* nov. sp. Observation and measurement of the specimens were done with a binocular microscope Olympus SZX7 allowing precision to 0.01 mm; detailed measurements available on request. In the following, there are discrepancies in

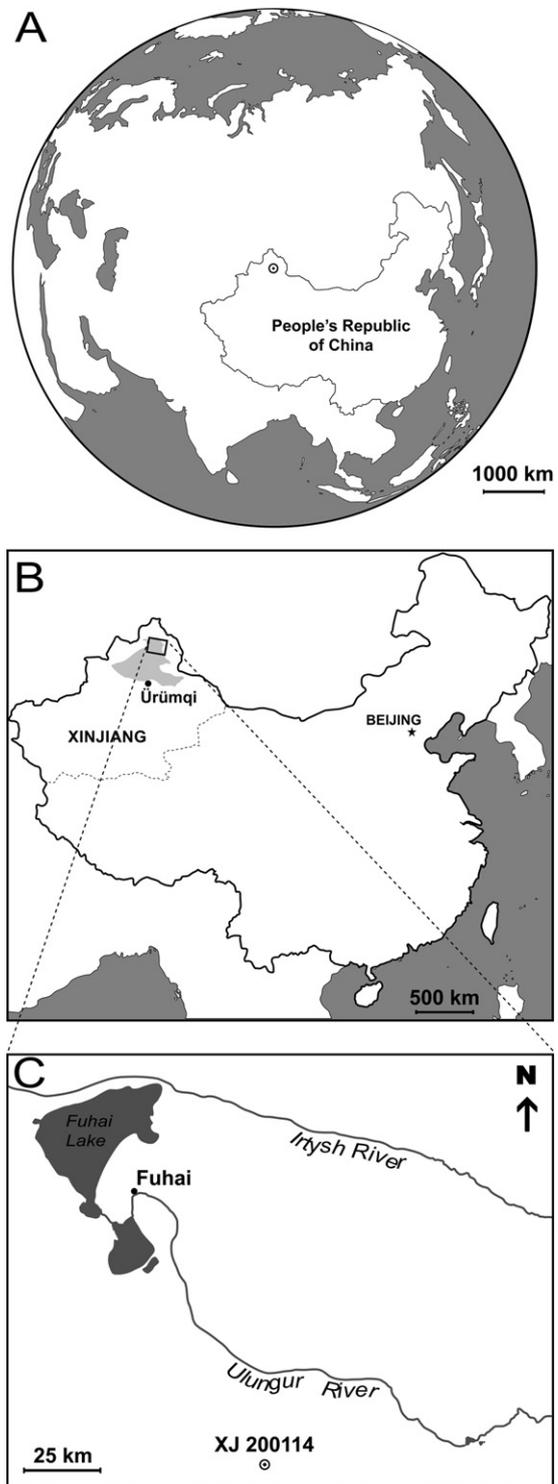


Fig. 1. Sketch map of the working area showing: A. Its central position in Asia at the continental scale. B. The location of the Fuhai County in the northern part of the Junggar Basin (in light grey). C. The location of the locality XJ 200114 south of the Ulungur River.

numbers of teeth for which features may be counted or measurements made. This difference is due to the fact that some teeth described cannot be measured or are partially broken, or some teeth that have been measured are too worn or badly preserved on their occlusal surface to be completely described.

The terminology used to describe the molars is taken from Maridet et al. (2009) as initially defined by Freudenthal (1988).

### 3. Systematic paleontology

Class MAMMALIA Linnaeus, 1758

Order RODENTIA Bowdich, 1821

Family CRICETIDAE Fischer de Waldheim, 1817

Subfamily CRICETODONTINAE Stehlin and Schaub, 1951

Genus *Cricetodon* Lartet, 1851

*Cricetodon* sp.

Fig. 2(A–D)

**Measurements:** Large sized cricetid. M1: -  $\times$  1.67 mm; M2: -  $\times$  1.47 mm; m3: 1.92  $\times$  1.40, 1.95  $\times$  1.53 mm.

**Description:** Maxilla: a part of the zygomatic arch is preserved; the zygomatic plate is broad but slightly inclined about 31°. The posterior end of the incisive foramen is close and anterior to M1; the palatine bone is lost but the palatine/maxillary suture can be observed at the level of the mesosinus of M2.

Upper dentition: the only M1 is on the maxillary fragment and is partially broken anteriorly and posteriorly. The observable morphological characters are: the cusps are massive and the mesosinus between the paracone and the metacone is quite narrow. The protolophule joins the protocone on its posterior area, but the entoloph is interrupted between the protoloph and the mesoloph. The labial cingulum is strong and connected to the base of the paracone, but does not reach the metacone. The mesoloph is thick, of medium length. The anterolophule is very thick and joins the anterocone lingually. The lingual anteroloph is lower and thinner than the labial one;

both are short. The enamel surface of the anterocone is partially broken, but well-preserved dentine of the anterocone underneath shows that it is high and likely not divided. The three roots of the tooth are included in the maxilla; the lingual root is composed of two distinct pulp cavities separated by a groove.

The only M2 is broken. The cusps are massive as for M1. The protolophule is single and anteriorly connected (protolophule I). Both anterolophs are long, the labial one reaching the paracone. Both the labial and lingual cingula are strong; the mesoloph is long and merges with the labial cingulum.

Lower dentition: two m3 display a similar general morphology: the lingual anterolophid is short but well developed, the metalophid directs obliquely and is connected directly to the lingual anterolophid, and the hypoconid is slightly elongated and slightly oblique. Weak cingula are present at the extremity of the mesosinusid and sinusid, the entoconid is well developed, and the large and rounded posterosinusid is delimited by a long posterolophid. However, a main difference can be observed between the two teeth in the central area. One of the teeth shows morphology as usually observed for *cricetodon*: the ectolophid starts from the protoconid posterior arm to join the base of the hypolophulid. In the second tooth, the ectolophid is much more labially located, starting from the posterolabial part of the protoconid and joining directly the base of the hypolophulid, and the protoconid posterior arm extends freely in the mesosinusid. This second morphological type is usually observed in *Eucricetodon*.

**Remarks:** altogether four teeth have been found that display massive cusps with thick enamel; the teeth are low-crowned but show a slightly more developed height compared to other cricetids of the locality. The M1 has three roots with the lingual one composed of two differentiated pulp cavities. Based on

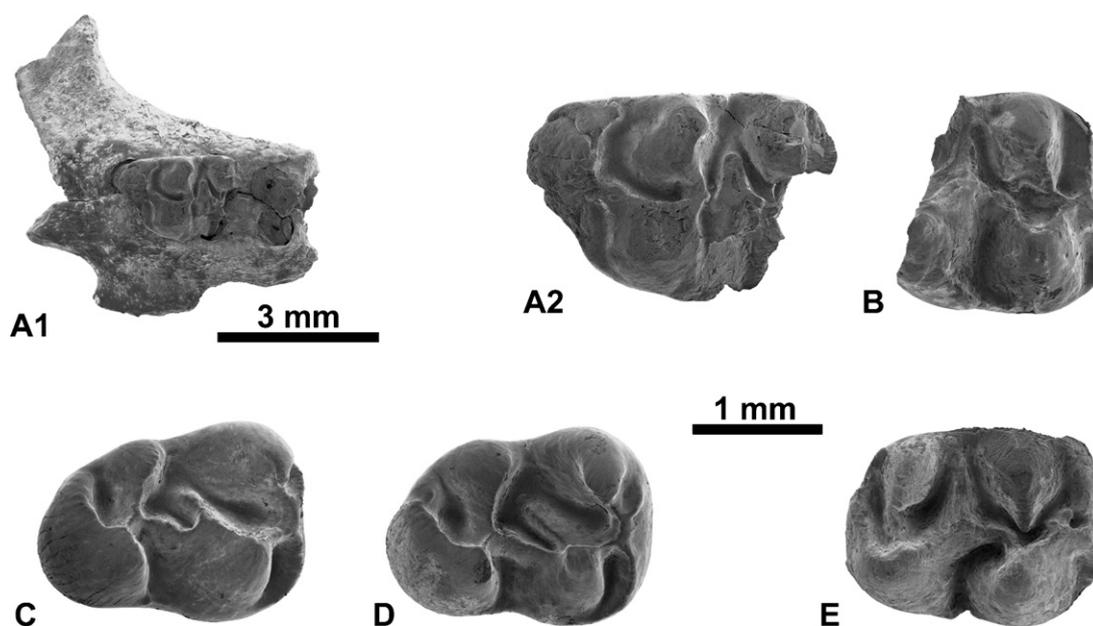


Fig. 2. Cheek teeth of *Cricetodon* sp. A. Left M1, V16897.1, tooth in place in the fragment of maxilla (A1) and tooth alone (A2). B. Right M2, V16897.2. C. Right m3, V16897.4. D. Right m3, V16897.3. E. *Eumyarion* sp., right M2, V16898.1. Scale bar = 3 mm for A1, 1 mm for A2–E.

these observations, this material can be attributed to the genus *Cricetodon*. Indeed, this material presents a clear difference with *Gobicricetodon* Qiu, 1996, from the middle Miocene of Tunggur in Inner Mongolia (Qiu, 1996): *Gobicricetodon* is meso-hypsodont and larger, it presents a characteristic 'middle oblique crest', the mesoloph(id)s are usually weakly developed on both lower and upper teeth, and the posterior spur of the paracone is frequent.

*Cricetodon* is actually rarely recorded in the Neogene of China, but has been recognized in Xiacaowan from the late early Miocene of Jiangsu (Qiu, 2010) and the middle Miocene of Xinjiang (Bi, 2005). Our material shows some similarities with both *C. wanhei* Qiu, 2010, from Xiacaowan and *C. orientalis* Bi, 2005, from Xinjiang, such as: the absence of ectoloph in M1, the anterolophule connected to the lingual part of the anterocone in M1, and the mesoloph developed, medium to long, in M1 and M2. The two types of morphologies of m3 can also be observed in the material from Xiacaowan. However, some clear differences can also be observed: *C. wanhei* from Xiacaowan is larger and more hypsodont and has four roots on the M1; the metalophule is transverse or posteriorly connected in M2 whereas it is connected in the anterior area of hypocone in our material; the entoconid is more developed in the m3 of *C. wanhei*. The species *C. orientalis* also differs from our material: the zygomatic plate is more inclined, the teeth are larger and more hypsodont, the M1 has four roots and the posterosinus is strongly reduced, the mesoloph of M2 is of medium length, and the protolophule is posteriorly connected.

In Europe, the type species *Cricetodon meini* Freudenthal, 1963, from Vieux-Collonges in France (Mein and Freudenthal, 1971a), also recognized in Greece (de Bruijn et al., 1993; Vasileiadou and Koufos, 2005), Austria and Germany (Rummel, 2000; Daxner-Höck, 2003), displays almost the same differences. Our material mainly differs by its lower crown, its smaller size, the incompletely divided lingual root in M1, the undivided anterocone in M1, the anterior connection of the protolophule in M2, and the more developed entoconid in m3. Different species, older in age, have also been described in the early Miocene of Anatolia (de Bruijn et al., 1993). *Cricetodon verteegi* de Bruijn et al., 1993, from Kilçak 3A and *C. aff. verteegi*, from Kilçak 3B show more similar characters to our material from Xinjiang: the protolophule is either anteriorly connected or absent, and in m3 the hypoconid has an oblique shape. However, some clear differences can also be noticed: both *C. verteegi* and *C. aff. verteegi* are slightly smaller and more low-crowned compared to our specimens; their M1 show a larger and divided anterocone and the posterior spur of the paracone is also more developed; *C. aff. verteegi* has two protolophules in M2. *Cricetodon kasapligili* de Bruijn et al., 1993, from Keseköy and *Cricetodon tobieni* de Bruijn et al., 1993, from Horlak are similar to our specimens in size and height of the crown but differ by a posterior connection of the protolophule in M2. *Cricetodon aliveriensis* Klein, Hofmeijer and de Bruijn, 1988, from Greece (recognized in the localities of Aliveri and Karydia; Doukas, 2003) and *C. tobieni* present a well-developed ectomesolophid in m3 that is not observed in our specimens.

As stated by Rummel (1999), the increasing size, hypsodonty and number of roots, and the development of the ectoloph and mesoloph in the upper molars are considered as apomorphic characters in the evolution of cricetodontines. Consequently, if one assumes that these evolutionary trends are also true in Asia, our material displays an association of characters that can be considered as plesiomorphic when compared to *C. meini*, *C. wanhei*, and *C. orientalis* and apomorphic when compared to *C. verteegi* and *C. aff. verteegi*. The evolutionary stage of our material seems more similar to that of *C. kasapligili*, *C. tobieni*, and *C. aliveriensis*. However, the morphologies of M2 and m3 in our material call for a closer relationship to *C. verteegi* and *C. aff. verteegi*. It is also noteworthy that some of the characters described in our material, such as: the hypoconid oblique-elongated in M3; the anterior connection of the protolophule in M2; and the m3 with a protoconid posterior arm independent from the ectolophid, recall morphological characters known for the genus *Eucricetodon* Thaler, 1966. The lingual root composed of two differentiated pulp cavities separated by a groove in M1 also suggests a transition between a single lingual root (as in *Eucricetodon*) and two lingual roots (as in the other species of *Cricetodon*). The inclination of the zygomatic plate is closer to *Eucricetodon asiaticus* (Matthew and Granger, 1923), or *Eucricetodon atavus* Misonne, 1957 (see Lindsay, 1977), than the late early Miocene and middle Miocene *Cricetodon* (see Mein and Freudenthal, 1971b; Bi, 2005). Qiu (1996) also described in the genus *Gobicricetodon* Qiu, 1996, a mixture of characters that can be observed in the Neogene genus *Cricetodon*, but also in the Oligocene-early Miocene genus *Eucricetodon*. This observation led him to consider the hypothesis that *Gobicricetodon* and *Cricetodon* might be derived from *Eucricetodon*. With regard to this hypothesis, our specimens from the early Miocene of Xinjiang could be interpreted as intermediate in form between *Eucricetodon* and the later *Cricetodon*. However, no conclusion can be given yet and more specimens are needed in order to solve the problem of the phylogenetic origin of *Cricetodon*. Whatever their origin, the new specimens from Xinjiang undoubtedly constitute a new species of the genus *Cricetodon*, but the scarcity of the material (especially without m1 and m2) does not allow diagnosing a new species until more material is found.

Subfamily EUMYARIONINAE Ünay, 1989

Genus *Eumyarion* Thaler, 1966

*Eumyarion* sp.

Fig. 2(E)

**Measurement:** M2: 1.90 × 1.54 mm.

**Description:** only one M2 was found; the roots are lost but the tooth displays a more slender and elongated shape of cusps compared to *Cricetodon*. The lingual and labial anterolophs are both well developed, but do not reach respectively the protocone and the paracone. The lingual anteroloph is lower than the labial one. In the middle of the anterolophule, a spur may be observed, making a short loop toward the labial anteroloph. This loop delimits a small narrow cavity at the base of the anterolophs. The paracone is isolated, the protolophule

being interrupted. The shape and the position of the protolophule suggest that it would be connected directly on the protocone or in its anterior area. The protocone is oblique, strongly extending posterolingually, and leading to a sinus curved forward.

The mesoloph is long and almost reaching the labial border. No cingulum closes the mesosinus and the sinus, but a small spur starts from the lingual extremity of the hypocone. In the posterior part of the tooth, the metalophule bends forward joining the metacone to the anterior area of the hypocone. The long posteroloph, well separated from the metacone, forms a large posterosinus.

**Remarks:** the size, the very oblique shape of the protocone, and the anteriorly connected metalophule are similar to the M2 of *Eumyarion tremulus* Lopatin, 1996, figured by Lopatin (2004: p. 279, fig. 35a); however, the single tooth does not allow a determination at the specific level. The *Cricetodon* sp. previously described and *Eumyarion* sp. are of similar size, but the latter differs mainly by the slenderness of the cusps and the shape of the protocone. Indeed, all the species of *Eumyarion* known from Europe exhibit this oblique shape of the protocone and curved sinus on the upper teeth as opposed to *Cricetodon*. The cusps of the teeth of *Cricetodon* usually show more massive morphology as is the case here for *Cricetodon* sp.

Subfamily CRICETINAE Stehlin and Schaub, 1951

Genus *Karydomys* Theodoropoulos, 2000

*Karydomys debruijni* nov. sp.

Figs. 3–5

**Etymology:** named after Hans de Bruijn in homage to his work on Cenozoic cricetids of Eurasia.

**Holotype:** V16899.11, left M2 (Figs. 3(C) and 4(C)).

**Hypodigm:** V16899.1, left M2; V16899.2, right M1 (Fig. 3(A)); V16899.3, right M1 (Fig. 3(B)); V16899.4, broken right M1; V16899.5, broken right M1; V16899.6, left M1; V16899.7, broken left M1; V16899.8, broken right M2 (Fig. 4(E)); V16899.9, broken right M2 (Fig. 4(D)); V16899.10, right M2 (Fig. 4(F)); V16899.12, left M2 (Fig. 4(A)); V16899.13, left M2 (Figs. 3(D), 4(B)); V16899.14, broken right M3; V16899.15, left m1; V16899.16, right m1 (Fig. 3(E)); V16899.17, right m1 (Fig. 3(F)); V16899.18, right m1 (Fig. 5); V16899.19, right m1; V16899.20, left m2 (Fig. 3(G)); V16899.21, right m2; V16899.22, right m2; V16899.23, right m3; V16899.24, broken left m3; V16899.25, right m3; V16899.26, right m3; V16899.29, broken and heavily corroded right M1; V16899.30, broken and heavily corroded right M2; V16899.31, left m3 (Fig. 3(H)); V16899.32, heavily corroded left M1; V16899.33, broken right M1.

**Type locality:** locality XJ 200114, middle-upper part of the Suosuoquan Formation, early Miocene. Junggar basin, Fuhai County, Xingjiang Uygur Autonomous Region of China.

**Disposition of material:** all specimens are housed in the collection of the Institute of Vertebrate Paleontology and Paleoanthropology (Chinese Academy of Sciences) in Beijing.

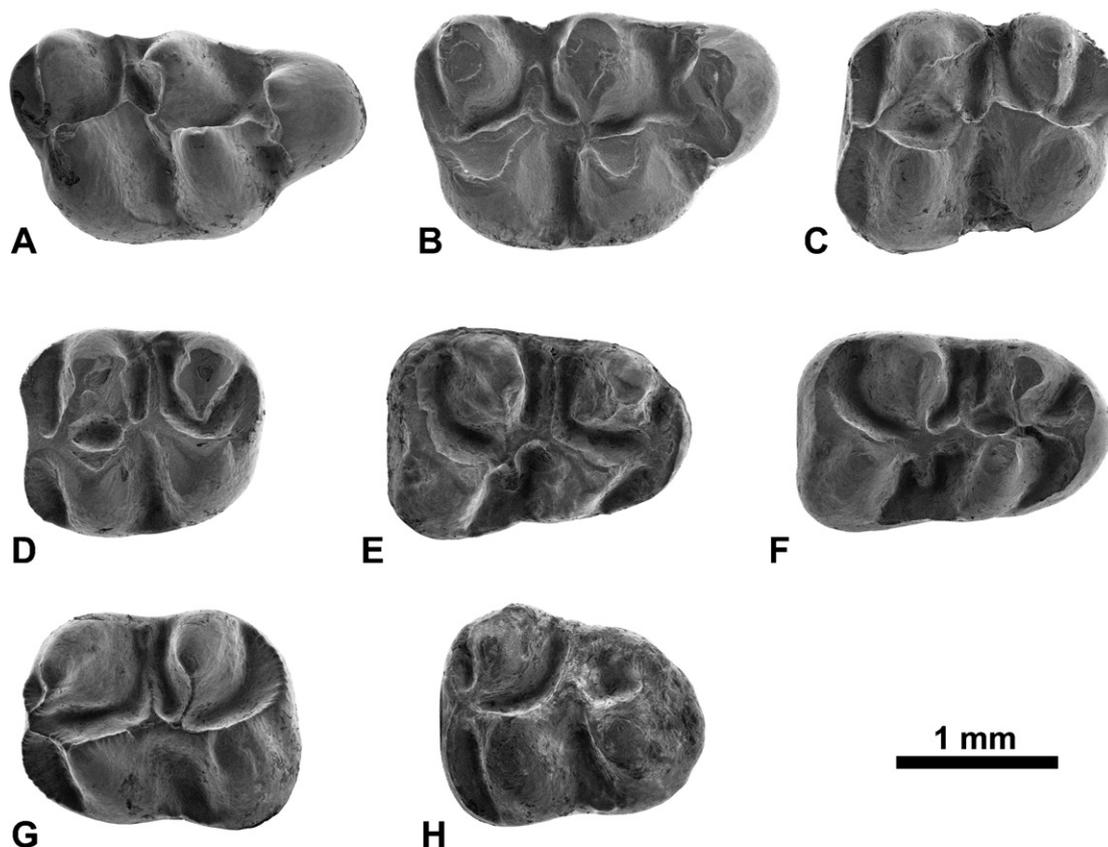


Fig. 3. Cheek teeth of *Karydomys debruijni* nov. sp. A. Right M1, V16899.2. B. Right M1, V16899.3. C. Holotype, left M2, V16899.11. D. Left M2, V16899.13. E. Right m1, V16899.16. F. Right m1, V16899.17. G. Left m2, V16899.20. H. Left m3, V16899.31.

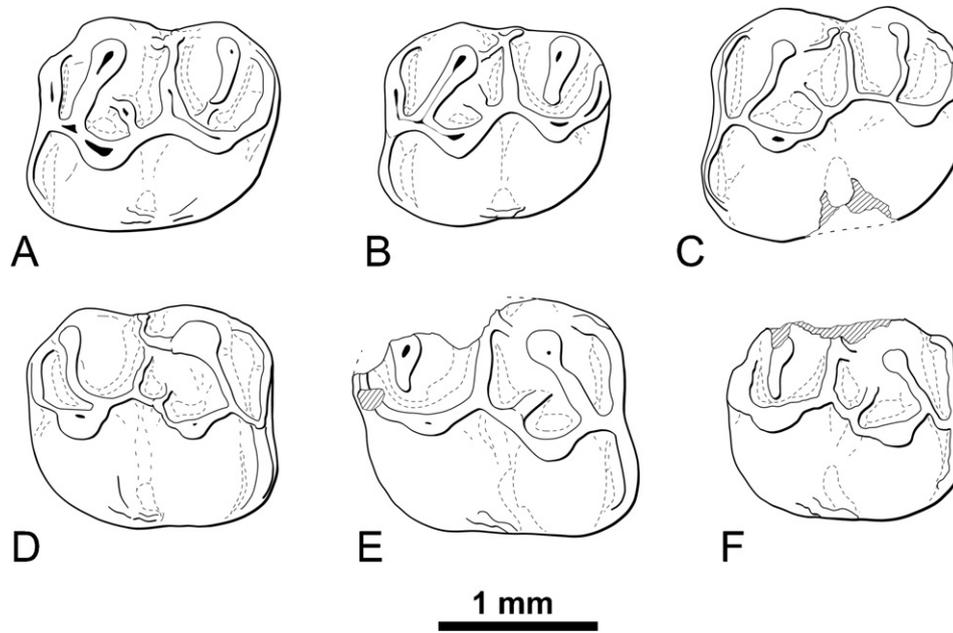


Fig. 4. Sketch drawings of M2 of *Karydomys debruijni* nov. sp. A. left M2, V16899.12. B. left M2, V16899.13. C. Holotype, left M2, V16899.11. D. Right M2, V16899.9. E. Right M2, V16899.8. F. Right M2, V16899.10.

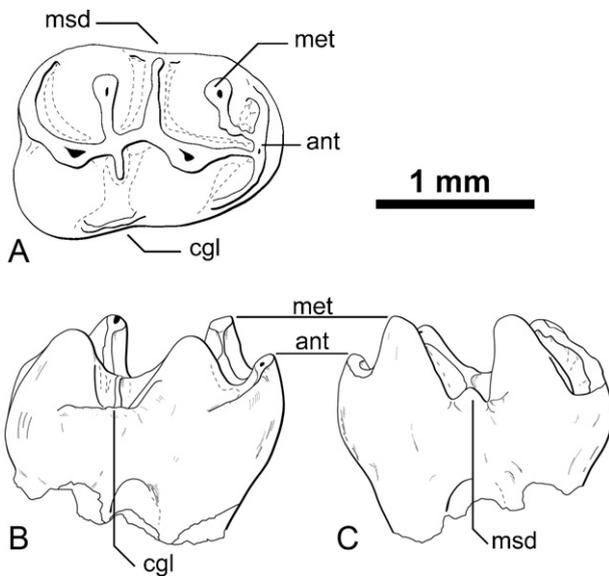


Fig. 5. Sketch drawing of the right m1 of *Karydomys debruijni* nov. sp., V16899.18. A. Occlusal view. B. Labial view. C. Lingual view. ant: anteroconid; cgl: labial cingulum; met: metaconid; msd: mesostylid.

**Measurements:** medium-sized (Table 1). Among the specimens attributed to this species, some teeth seem to be slightly larger (eg., Figs. 3(B, C), 4(C, E)), as shown by the high coefficient of variation on width for M2 and m2. However, these teeth present no significant difference in their morphology, and the size variation of M2 and m2 is similar to that of *Karydomys dzerzhinskii* (Kordikova and de Bruijn, 2001). Consequently, we assume in this study that all the specimens belong to the same species.

**Diagnosis:** a species of *Karydomys* rarely with labial spur on anterolophule and anterior protolophule (protolophule I) in M1; anterocone usually undivided with more developed labial part, or divided; paracone spur usually well developed in M2 but less frequent in M1; mesoloph long in M1 and M2; in m1, about half of specimens with a metalophid directly connected to anteroconid; ectomesolophid usually present and short in M1, but rare and weakly developed in m2; mesolophid long and reaching lingual border in almost all lower molars; in m3 metalophid directly connected to anterolophids, mesolophid absent, and entoconid merged into the posterolophid.

Table 1  
*Karydomys debruijni* nov. sp.: tooth measurements (in mm).

	Length						Width					
	<i>n</i>	Min	Max	Mean	$\sigma$	CV	<i>n</i>	Min	Max	Mean	$\sigma$	CV
M1	4	2.00	2.15	2.07	0.062	2.982	5	1.33	1.46	1.40	0.049	3.481
M2	6	1.46	1.74	1.56	0.101	6.426	7	1.26	1.53	1.40	0.112	8.056
M3	1	-	-	1.05	-	-	1	-	-	1.09	-	-
m1	5	1.61	1.84	1.75	0.085	4.843	4	1.19	1.28	1.22	0.039	3.184
m2	4	1.53	1.65	1.59	0.058	3.643	4	1.07	1.42	1.24	0.150	12.02
m3	2	1.40	1.54	1.47	-	-	2	1.16	1.31	1.24	-	-

*n*: sample size; Min: minimal length or width; Max: maximal length or width; Mean: mean length or width;  $\sigma$ : standard deviation; CV: coefficient of variation [=  $\sigma$ /Mean  $\times$  100].

**Differential diagnosis:** *K. dzerzhinskii* Kordikova and de Bruijn, 2001, is the only other species of *Karydomys* known from Asia. *K. debruijni* differs from *K. dzerzhinskii* by its smaller size; moreover the length of M1 indicates a more elongated shape of the teeth of *K. dzerzhinskii*. The morphology also shows noticeable differences: in M1, *K. debruijni* rarely has a labial spur on the anterolophule and the anterior protolophule (protolophule I) is usually absent, whereas it may be weak or strong in *K. dzerzhinskii*; in M2, the metalophule is either anteriorly connected or sometimes absent, whereas it may be transverse, or even posteriorly connected in *K. dzerzhinskii*; in M3, the mesoloph is weak and the metacone does not form a clear cusp in *K. debruijni*, whereas the mesoloph is long and the metacone more developed in *K. dzerzhinskii*. In m1, the metalophid can be directly connected to the anteroconid, as opposed to *K. dzerzhinskii* with metalophid usually connected to the anterolophulid. The ectomesolophid is also less developed in *K. debruijni*. The m2 displays no clearly formed ectomesolophid, whereas it is long in *K. dzerzhinskii*.

*K. debruijni* differs from all the other species of *Karydomys* from Europe and Anatolia by its smaller size and less inflated cusps. It also displays a wider anterocone in M1. In M2, the anterior protolophule (protolophule I) is stronger, whereas the posterior protolophule is stronger in other species; the metalophule is either anteriorly connected or interrupted, whereas it is always posteriorly connected with a reduced posterosinus in other species.

**Description:** Upper dentition: the anterocone of the M1 is usually single-cusped, but can show a trend to division with the labial part more developed (3/6); one tooth presents a clear division of the anterocone. The lingual anteroloph is usually short and strongly curved; it ends in the lingual anterosinus and does not reach the protocone. On the contrary, the labial anteroloph is always well developed and large; it continues to the paracone and forms a labial cingulum closing the anterosinus, sometimes with a bulge leading to the formation of a style at the border. There is usually one single protolophule connected to the posterior part of the protocone (protolophule II), but a second anterior (protolophule I) connected to the anterolophule may be present (2/6). The protocone is linked to the anterocone by a thin and sharply bent anterolophule; a weakly developed labial spur can be observed in one tooth. A posterior spur starting from the base of the paracone may be present (4/6), sometimes curved toward the labial side. The mesoloph is always well developed, sometimes long. When the mesoloph is long it merges with the paracone posterior spur. The labial cingulum, which closes the mesosinus, is usually weak, whereas the lingual one is more developed. The metalophule is always single and posteriorly connected, delimiting a short posterosinus. When preserved, three roots are present.

The M2 displays an asymmetrical shape with a larger anterior width. One noticeable aspect of the morphology is that the hypocone is more labially located than the protocone. Both the labial and lingual anterolophs are well developed, the lingual one being lower and thinner than the labial one. The protolophule is

strongly oblique, connected to the anterolophule in front of the protocone. All the teeth have a second and weaker posterior protolophule (protolophule II). The paracone posterior spur is also present in all teeth, and is usually curved toward the labial border. The mesoloph is long; it may reach the labial border independently from the paracone spur (1/6), but usually merges with it (5/6) and forms a small mesostyle. The lingual cingulum is usually well developed and forms a crest starting from the lingual base of the hypocone and closing the sinus. In most cases, the metacone is disconnected (4/6) and curved forward. When the metalophule is developed, it shows a forward bend and joins the entoloph anteriorly. The posteroloph is long and strongly curved, delimiting a large posterosinus. All teeth have three roots; however, the specimen V16899.12 shows a lingual root composed of two pulp cavities separated by a deep groove.

The single M3 displays a very rounded shape with a posterior area weakly developed. The hypocone and metacone are indeed not developed, reduced to simple styles. The labial anteroloph is long and well developed, whereas the lingual one is short and thinner. Two protolophules are present, the posterior one joining the 'hypocone-style'. A very weak mesoloph is present. The cingulum is strong, forming a mesostyle. Three roots are present.

Lower dentition: in m1, the anteroconid is undivided and transversely elongated. The anterolophulid usually joins the protoconid to the anteroconid, but can be interrupted (1/5). The metaconid has an anterior connection (metalophulid I), usually joining directly the anteroconid (3/5), but may also merge with the anterolophulid (1/5). The metaconid may also present a second posterior connection (metalophulid II), joining the posterior area of the protoconid, or the mesolophid. One tooth has a metaconid with only a posterior connection. The mesolophid is always long and reaches the lingual border, where it forms a mesostylid. The labial cingulum is also always well developed. A short ectomesolophid may be present (4/5). The position of the entoconid is very forward compared to the hypoconid. The hypolophulid is also connected very forward, sometime close to the mesolophid (2/5). The posterolophid is wide and may show a bulge in its labial part (3/5). In lateral view, the anteroconid is always lower than the four other main cusps, but higher than the mesostylid and the cingulum (Fig. 5). Two roots may be observed when preserved.

In m2, the labial anterolophid is well developed, but lower than the lingual one. The lingual anterolophid shows a noticeable variability; it may be long and reach the lingual extremity of the metaconid (2/4), or shorter forming a loop. The metalophulid is connected either to the anterior arm of the protoconid (2/4) or to the lingual anterolophid (2/4). The mesolophid is long and can reach the lingual border (2/4); in all cases a strong mesostylid closes the mesosinusid. The ectomesolophid also presents noticeable variability: absent (2/4), weakly developed (1/4), or well developed and long (1/4). The labial cingulum is usually well developed, but no clear ectostylid can be seen. As observed in m1, the position of the entoconid is forward compared to the hypoconid; the posterolophid is wide and may have a bulge in its labial part (2/4). All specimens have two roots.

Two m3 present a very similar and simple morphology. The teeth are sub-triangular in shape, with a reduced and rounded posterior area. Both lingual and labial anterolophids are equally well developed, but the labial one is lower. The metalophulid is connected anteriorly at the junction of the anterolophids. The mesolophids are absent. The hypolophulid is well developed, slightly oblique, but the entoconid is totally reduced, so it cannot be distinguished from the hypolophulid. One tooth shows a small ectostylid on the labial cingulum. The hypoconid is reduced in size compared to the protoconid. The posterolophid is long and rounded delimiting a large circular posterosinusid. Two roots can be observed on the well-preserved specimens.

**Remarks:** the comparison of *K. dzerzhinskii* from the early Miocene of Kazakhstan with our specimens shows strong morphological affinities, such as the posterior connection of the protolophule and metalophule in M1, the metalophule that can be anteriorly connected in M2, and also both the labial and lingual anterolophids well developed and mesoloph long in M2. In lower molars, the metalophid is oriented forward in m1; the metalophid is also oriented forward in M2 and connected to the lingual anterolophid in m2 and m3. The entoconid is not developed in m3. Some differences, however, may be noticed, justifying here the creation of a new species (see differential diagnosis). Theocharopoulos (2000) noticed that the main characteristic of *Karydomys* is to display an association of derived and primitive characters were compared to other contemporaneous cricetids. Among the derived characters he pointed out: the double protolophule with the posterior one stronger in M2, posteriorly directed metalophule in M2, and reduced M3/m3. With regard to these characters, *K. debruijni* nov. sp. and *K. dzerzhinskii* do not fit the current diagnosis of

*Karydomys*, the anterior protolophule being the stronger one and the metalophule being anteriorly connected or absent in M2. Mörs and Kalthoff (2004) also detailed the generic diagnostic characters of *Karydomys*, including the general inflated cusp morphology and thickness of enamel, the reduced posterosinus in M2, the anteroconid lower than other cusps in lateral view, and a characteristic structure of the enamel on lower incisors. Both the lower anteroconid and the thickness of the enamel can be observed in our specimen (even if the enamel seems not thick as in the European specimens). But our specimens show no clear inflated cusp morphology and the posterosinus in M2 is well developed due to the anterior position of the metalophule. As no mandible was found in the Junggar basin, no lower incisor can be surely attributed to this species; therefore, it was not possible to test if the enamel structure fits that described by Mörs and Kalthoff (2004). However, the differences observed, especially on the M2 (Fig. 4), compared to the European and Anatolian species do not justify the creation of a new genus and rather reflect more primitive evolutionary states for the genus *Karydomys* in Central Asia. Further discoveries in Asia and more comparisons with European forms will probably make necessary future revision of the diagnosis of this genus. Kordikova and de Bruijn (2001) already stated that *K. dzerzhinskii* from Kazakhstan displays a general morphology close to the type species *Karydomys symeonidisi* Theocharopoulos, 2000, but also with characters noticeably “less derived” than *K. symeonidisi*. The recent review of the genus and the description of new species from the middle Miocene of northern Germany by Mörs and Kalthoff (2004) allow confirmation of these morphological evolutionary trends on the upper cheek teeth: increasing size, disappearance of the labial spur on the anterolophule in M1,

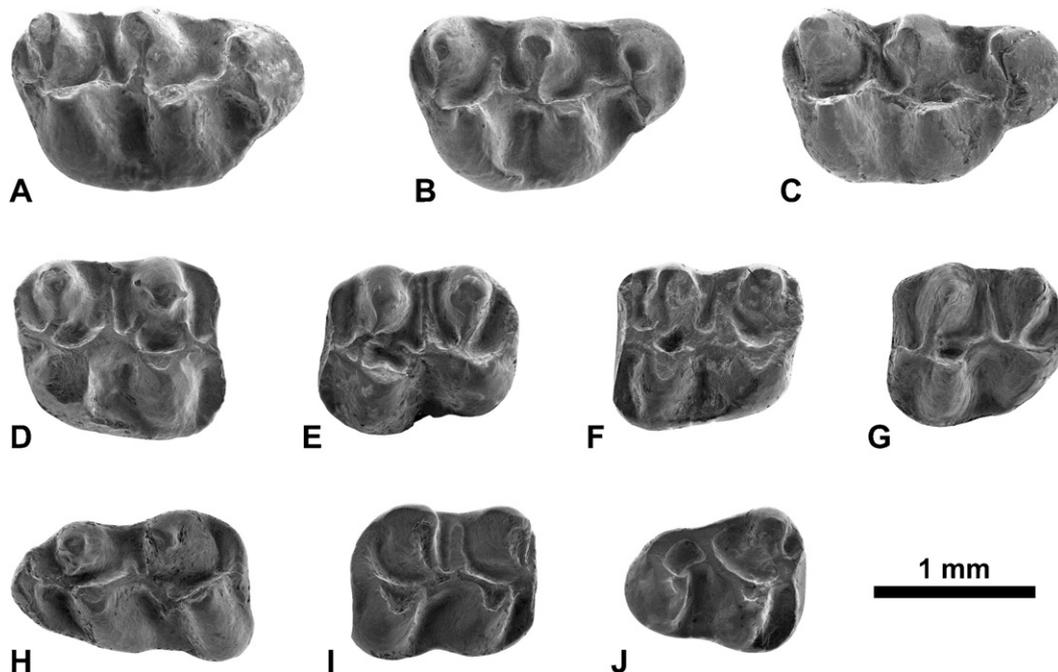


Fig. 6. Cheek teeth of *Megacricetodon beijiangensis* nov. sp. A. Holotype, right M1, V16900.4. B. Right M1, V16900.5. C. Right M1, V16900.6. D. Right M2, V16900.13. E. Left M2, V16900.19. F. Left M2, V16900.18. G. Left M2, V16900.17. H. Left m1, V16900.22. I. Right m2, V16900.25. J. Right m3, V16900.29.

presence of a protolophule I in M1, posterior connection of the metalophule in M2, and reduction of the metacone in M3 can be considered as apomorphies in the evolutionary history of the genus. Concerning the lower teeth, the morphology seems more conservative, the disappearance of the ectomesolophid in m1 and m2 through time being the most obvious trend. With respect to these trends, as in *K. dzerzhinskii*, our specimens from Xinjiang definitely display a plesiomorphic association of characters when compared to the European and Anatolian species. However, this association of characters differs from those of *K. Dzerzhinskii*, suggesting that they represent different lineages. Consequently, it is not possible to further interpret which one appears to be the more derived species.

Genus *Megacricetodon* Fahlbush, 1964  
*Megacricetodon beijiangensis* nov. sp.

Figs. 6 and 7

**Etymology:** Bei, meaning ‘North’ in Chinese, and Jiang, referring to Xinjiang province (literally North Xinjiang).

**Holotype:** right M1, V16900.4 (Figs. 6(A), 7(B)).

**Hypodigm:** V16900.1, right M2; V16900.2, left M2 (Fig. 7(U)); V16900.3, left M1 with a fragment of maxilla (Fig. 7(A)); V16900.5, right M1 (Figs. 6(B), 7(C)); V16900.6, right M1 (Figs. 6(C), 7(D)); V16900.7, right M1 (Fig. 7(E)); V16900.8, right M1 (Fig. 7(F)); V16900.9, right M1 (Fig. 7(H)); V16900.10, right M1 with a fragment of maxilla

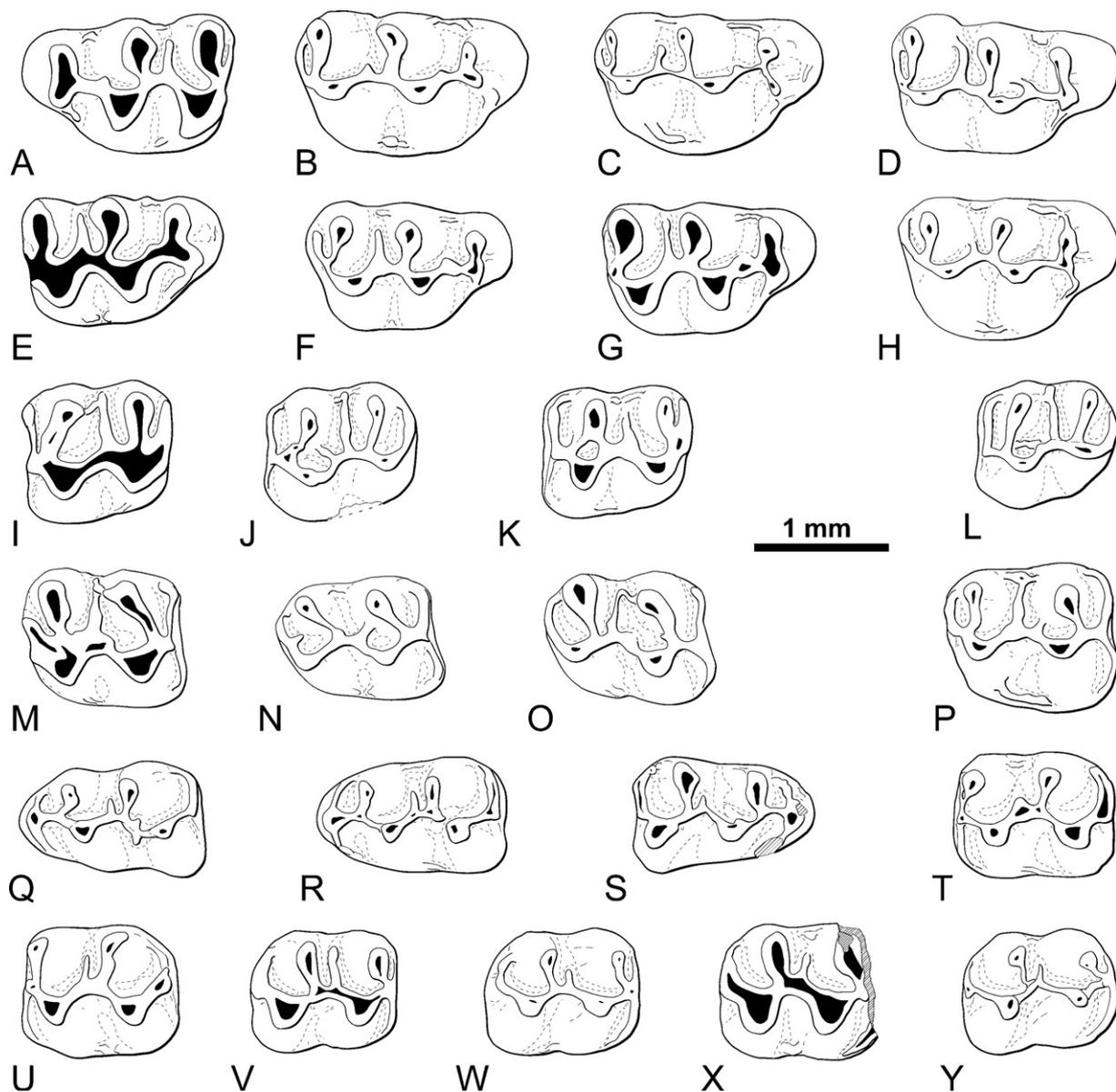


Fig. 7. Sketch drawings of *Megacricetodon beijiangensis* nov. sp. cheek teeth, illustrating its morphological variability. A. Left M1, V16900.3. B. Holotype, right M1, V16900.4. C. Right M1, V16900.5. D. Right M1, V16900.6. E. Right M1, V16900.7. F. Right M1, V16900.8. G. Right M1, V16900.10. H. Right M1, V16900.9. I. Left M2, V16900.16. J. Left M2, V16900.19. K. Left M2, V16900.18. L. Left M2, V16900.17. M. Right M2, V16900.14. N. Right M2, V16900.20. O. Right M2, V16900.21. P. Right M2, V16900.13. Q. Left m1, V16900.22. R. Left m1, V16900.36. S. Right m1, V16900.23. T. Left m2, V16900.28. U. Left m2, V16900.2. V. Right m2, V16900.25. W. Right m2, V16900.27. X. Right m2, V16900.26. Y. Right m2, V16900.37.

Table 2  
*Megacricetodon beijiangensis* nov. sp.; tooth measurements (in mm).

	Length						Width					
	<i>n</i>	Min	Max	Mean	$\sigma$	CV	<i>n</i>	Min	Max	Mean	$\sigma$	CV
M1	8	1.47	1.74	1.61	0.091	5.681	8	1.00	1.14	1.06	0.054	5.053
M2	10	1.07	1.24	1.17	0.060	5.151	10	0.93	1.10	1.00	0.050	4.979
M3	1	-	-	0.74	-	-	1	-	-	0.84	-	-
m1	3	1.35	1.40	1.37	0.031	2.237	3	0.86	0.89	0.88	0.018	1.996
m2	7	1.09	1.23	1.16	0.051	4.385	8	0.91	1.09	1.00	0.069	6.934

*n*: sample size; Min: minimal length or width; Max: maximal length or width; Mean: mean length or width;  $\sigma$ : standard deviation; CV: coefficient of variation [=  $\sigma$ /Mean  $\times$  100].

(Fig. 7(G)); V16900.11, heavily corroded right M1; V16900.12, broken left M1; V16900.13, left M2 (Figs. 6(D), 7(P)); V16900.14, left M2 (Fig. 7(M)); V16900.15, heavily corroded right M2 and M3 on a fragment of maxilla; V16900.16, right M2 (Fig. 7(I)); V16900.17, right M2 (Figs. 6(G), 7(L)); V16900.18, right M2 (Figs. 6(F), 7(K)); V16900.19, right M2 (Figs. 6(E), 7(J)); V16900.20, left M2 (Fig. 7(N)); V16900.21, left M2 (Fig. 7(O)); V16900.22, left m1 (Figs. 6(H), 7(Q)); V16900.23, right m1 (Fig. 7(S)); V16900.24, right m2 with a fragment of mandible; V16900.25, right m2 (Figs. 6(I), 7(V)); V16900.26, right m2 (Fig. 7(X)); V16900.27, right m2 (Fig. 7(W)); V16900.28, left m2 (Fig. 7(T)); V16900.29, right m3 (Fig. 6(J)); V16900.30, left m3; V16900.31, broken right M1; V16900.32, left M2; V16900.33, left M2; V16900.34, broken and heavily corroded right M2; V16900.35, right M3; V16900.36, left m1 (Fig. 7(R)); V16900.37, right m2 (Fig. 7(Y)).

**Type locality:** locality XJ 200114, middle-upper part of the Suosuoquan Formation, early Miocene. Junggar basin, Fuhai County, Xingjiang Uygur Autonomous Region of China.

**Disposition of material:** all specimens are housed in the collection of the Institute of Vertebrate Paleontology and Paleoanthropology (Chinese Academy of Sciences) in Beijing.

**Measurements:** small-sized cricetid (Table 2).

**Diagnosis:** medium-sized *Megacricetodon*; anterocone often divided; mesoloph in M1 long, but paracone spur rare and labial spur on anterolophule weakly developed; M2 often with double protolophule, with anterior one more developed, metalophule usually single and anteriorly connected, and mesoloph somewhat longer than in M1; M3 short and rounded, metacone indistinct; in m1, anteroconid undivided, anterolophulid straight and extended along the tooth axis, mesolophid short, ectomesolophid short or absent; m2 with short lingual anterolophid and no ectomesolophid.

**Differential diagnosis:** differs from *Megacricetodon dzhungaricus* (Kordikova and de Bruijn, 2001), in being slightly smaller. In M1, the anterocone is always divided, a cingulum anterior to the anterocone is sometimes present, and the labial spur on the anterolophule is weakly developed; in m1 the anterolophulid is never connected to the labial side of the anteroconid and the mesolophid is always short.

Differs from *Megacricetodon yei* Bi et al., 2008, in slightly greater size, less divided anterocone, weakly developed labial spur on the anterolophule, and rare posterior spur on paracone

in M1. In M2, a single posterior metalophule is rare and the mesoloph is longer. In m1, the anterolophulid is not connected to the labial side of the anteroconid, the mesolophid is short, and the ectomesolophid is frequently present. Mesolophids are also shorter in m1 and m2 compared to *M. yei*. The same morphological characteristics also allow the differentiation from *Megacricetodon sinensis* Qiu et al., 1981, and *Megacricetodon pusillus* Qiu, 1996.

Differs from the species from Pakistan *Megacricetodon aguilar* Lindsay, 1988, *Megacricetodon sivalensis* Lindsay, 1988, *Megacricetodon daamsi* Lindsay, 1988, and *Megacricetodon mythikos* Lindsay, 1988, in having less elongated M1, well-developed posterior protolophule in M2, and much shorter anterolophulid in m1. *M. beijiangensis* also differs from *M. aguilar* in having a smaller and less divided anterocone and generally less inflated cusps; from *M. sivalensis* in not having transverse lophids in M2; and from *M. mythikos* in having a smaller size, no oblique ectolophid in m1, and much smaller and less divided anterocone in M1.

Differs from the other known *Megacricetodon* species by a specific association of characters: the anterocone is often clearly divided in M1, the protolophule in M2 is often double with the anterior one being more developed, mesoloph in M1 and especially M2 is long and often merges with the posterior paracone spur, and the anteroconid in m1 is undivided.

**Description: Upper dentition:** in M1, the anterocone always tends to divide, but its lingual and labial parts are still connected. The anterolophule most of the time is connected to the lingual part of the anterocone (7/8). The labial spur on the anterolophule is either weak (limited to a triangular-shaped bulge; 6/8) or absent (2/8). One tooth presents a crest starting labially from the anterolophule and reaching the paracone that may be interpreted as a second anterior protoloph. However, the labial spur on the anterolophule is never well developed; consequently, when weakly developed it is difficult to interpret if this character is a real spur or an incomplete second anterior connection to the paracone. Two teeth present an anterior cingulum on the anterocone (Fig. 7(C, E)). The lingual anteroloph is always well developed, but usually not long enough to close the lingual anterosinus. The labial anteroloph is less developed and thinner and can close the labial anterosinus (5/8). The paracone is more posteriorly located compared to the protocone. The posterior protolophule (protolophule II) usually has a straight transverse shape. The mesoloph shows significant

variability (Fig. 7(A–H)): it may be short (2/8), long (4/8), or reach the labial border (2/8). One of the long mesolophs bends posteriorly and merges with the metacone. Two teeth show a weakly developed mesostyle closing the mesosinus. On the lingual side, the sinus may be closed by a strong cingulum connected to the hypocone (2/8), partially closed (2/8), or open (4/8). The metalophule is posteriorly connected, delimiting a small and narrow posterosinus. All the teeth have three roots.

In M2, the labial anteroloph is always well developed, but the lingual one is comparatively less developed and lower, and also shows much more variability (Fig. 7(I–P)). Two protolophules are often present (7/10); the posterior protolophule (protolophule II) is less developed and shows more variability (Fig. 7(I–P)): it may be complete (6/10), incomplete (1/10), or absent (3/10). The mesoloph is usually long and reaches the labial border (7/10), but it may also be half that long (1/10), short (1/10), or even absent (1/10). The cingulum that closes the mesosinus is usually weakly developed, but a clear mesostyle can be observed when the mesoloph merges with the cingulum. A posterior paracone spur may be present (6/10); when present this spur always merges labially with the mesoloph. Lingually, the sinus is usually open (6/10), it may be partially closed by a small cingulum (3/10), or more rarely closed by a well-developed cingulum. The metalophule also shows noticeable variability (Fig. 7(I–P)): it may be single and anteriorly connected (5/10), simply transverse (2/10), single posteriorly connected (2/10), or double with the posterior one incomplete (1/10). The posterosinus is small but comparatively more developed than in M1. All the teeth have three roots.

Only one M3 was found and is badly worn. The labial anteroloph is long but does not close the anterosinus. The mesoloph is absent. The metalophule is present but the metacone is not developed. This tooth has three roots.

**Lower dentition:** three m1 are present; they display an elongated shape and have a small, undivided wedge-shaped anteroconid (Fig. 7(Q–S)). The anterolophulid is long, delimiting two large anterosinusids. The anterolophids are both long, the lingual one reaching the metaconid and closing the anterosinusid. The metaconid is more anteriorly located

than the protoconid, and the metalophulid is anteriorly directed and connecting to the anterolophulid. The mesolophid is well developed but short. The entoconid is more anteriorly located than the hypoconid. The hypolophulid is connected anteriorly, close to the mesolophid, but less anteriorly directed than the metalophulid. Only one tooth has an ectomesolophid and a little lingual spur located exactly opposite to the ectomesolophid, pointing into the posterosinusid (Fig. 7(Q)). The sinusid is slightly oblique. One tooth has an incomplete crest between the hypoconid and the hypolophulid (Fig. 7(R)). The posterolophid is long and reaches the entoconid lingually, delimiting a large posterosinusid. The teeth have two roots.

In m2, both the labial and lingual anterolophids are well developed, but the lingual one is shorter, even absent in one tooth. The metalophulid joins the lingual anterolophid, delimiting a very small anterosinusid. The hypolophulid is also very anteriorly connected, close to the mesolophid. The mesolophid may be from short to long, but never reaches the lingual border. The ectomesolophid is absent. Both the labial and lingual cingula are generally absent or weakly developed. The posterolophid is long and wide and may have a bulge on its labial part associated with a fold of enamel on the posterolabial border, suggesting the formation of a labial posterosinus (3/7). When preserved, two roots are present.

**Remarks:** *M. beijiagensis* nov. sp. displays a general morphology close to the other species of *Megacricetodon* in China. Indeed, it shares with *M. yei*, *M. sinensis*, and *M. pusillus* the following characters: brachyodont molars with a tendency to division of the anterocone (more or less marked) with the labial part of the anterocone larger than the lingual part; the anteroconid in m1 is undivided and wedge-shaped, the shape is quite elongated, and the mesolophid is short in m1; the metalophid and entolophid are anteriorly connected in m2; and the anterior protolophule (protolophule I) is always more developed than the posterior one in M2. Unfortunately, no m3 was found for *M. beijiagensis* nov. sp. This character association seems typical of the Chinese *Megacricetodon*, as noticed by Qiu (1996) and Bi et al. (2008). The list of the species sharing this association of characters (Table 3) includes now *M. cf. sinensis* from

Table 3

List of localities where *Megacricetodon* species have been found in the early and middle Miocene of northeastern Asia.

Locality	Biozone	Region/Province	Country	Reference
<i>Megacricetodon dzhungaricus</i> Kordikova and de Bruijn, 2001 Chul'adyr Fm	MN4	Aktau Mountains	Kazakhstan	Kordikova and de Bruijn, 2001
<i>Megacricetodon yei</i> Bi et al., 2008 Halamaigai Fm	MN6	Xinjiang, Junggar Basin	China	Bi et al., 2008
<i>Megacricetodon sinensis</i> Qiu et al., 1981 Moergen + Tamuqin	MN7 + 8	Inner Mongolia, Gobi Basin	China	Qiu et al., 2006
Danshuilu	MN7 + 8	Qinghai, Xining Basin	China	Qiu et al., 1981
Quantougou	MN7+8	Gansu, Lanzhou Basin	China	Qiu, 2001
<i>Megacricetodon cf. sinensis</i> Qiu et al., 1981 Loh Fm - level. D1/2	MN5	Central Valley of Lakes	Mongolia	Daxner-Hock and Badamgarav, 2007
Qijiagoukou	MN7+8	Qinghai, Xining Basin	China	Qiu et al., 1981
<i>Megacricetodon pusillus</i> Qiu, 1996 Moergen + Tamuqin	MN7+8	Inner Mongolia, Gobi Basin	China	Qiu et al., 2006

The name of the locality, its biochronologic unit (sensu Mein, 1999), location, and bibliographic references are given for each species.

Mongolia (Daxner-Höck and Badamgarav, 2007) and *M. dzhungaricus* from Kazakhstan (Kordikova and de Bruijn, 2001). Consequently, this type of morphology appears to be characteristic of northern and central Asia, and suggests close phylogenetic relationships of those species, and also confirms that the species *M. dzhungaricus* initially defined under the genus *Aktaumys* Kordikova and de Bruijn, 2001, actually belongs to *Megacricetodon* as demonstrated by Bi et al. (2008).

Considering the age differences of the localities as proposed by various authors, we can address the question of the apparent evolutionary trends for those cricetids in Central Asia from the early Miocene to the late middle Miocene. The specimens of *M. beijiangensis* nov. sp. from the new Xinjiang locality (the age of which will be discussed below) have been compared to the four other species known in Central Asia: *M. dzhungaricus* from the early Miocene of the Chul'adyr Formation in Kazakhstan; *M. yei* from the early middle Miocene of the Halamagai Formation in Xinjiang; and *M. sinensis* and *M. pusillus* from the late middle Miocene of Moergen and Tamuqin in Inner Mongolia.

The proportion of morphological characters that significantly vary among the previously mentioned species is

summarized in Table 4. Even though the relative age of our locality with that from the Chul'adyr Formation in Kazakhstan is uncertain, some characters seem to present a likely continuous evolution from the early to the middle Miocene such as: decreasing size, increasing division of the anterocone, shortening of the mesolophs in M1 and M2, double protolophule and double metalophule evolving toward a single anterior one in M2, disappearance of the ectomesolophid in m1, and development of the lingual anterolophid in m2. But for the other characters, no clear evolution can be noticed, suggesting that those species may actually belong to different lineages. Bi et al. (2008) suggested that *M. dzhungaricus* and *M. yei* could constitute a distinct lineage from the other species, *M. sinensis* and *M. pusillus*. With respect to this hypothesis, the new species from the early Miocene of Xinjiang bring new insight on the potential phylogenetic relationships between those *Megacricetodon*. The frequency of morphological characters as shown in Table 4 has been turned into a presence-absence matrix of characters in order to process a parsimony analysis. All characters absent ('NO') in Table 4 have been coded '0', or '1' when present (whatever the frequency); the character 1.2 has been deleted because it was present in all species.

Table 4  
Proportions of the morphological characters that present significant differences between five species of *Megacricetodon*: *M. dzhungaricus* from the early Miocene of the Chul'adyr Formation in Kazakhstan (Kordikova and de Bruijn, 2001); *M. yei* from the early middle Miocene of the Halamagai Formation in Xinjiang (Bi et al., 2008); *M. sinensis* and *M. pusillus* from the late middle Miocene of Tunggur in Inner Mongolia (Qiu, 1996), and *M. beijiangensis* nov. sp. from the early Miocene of the Junggar Basin.

	<i>M. dzhungaricus</i>	<i>M. beijiangensis</i>	<i>M. yei</i>	<i>M. sinensis</i>	<i>M. pusillus</i>	<i>E. aff. E. caducus</i>
M1 – sample size	13	8	8	50	2	
1.1 Anterior crest to the anterocone	NO	FR	AL	FR	AL	1
1.2 Complete division of anterocone	FR	FR	VF	VF	AL	-
1.3 Long labial spur on anterolophule	FR	NO	FR	NO	NO	0
1.4 Posterior spur on paracone	NO	IN	AL	FR	FR	1
1.5 Mesoloph merges with the border	AL	FR	FR	RA	NO	1
1.6 Entomesoloph	NO	NO	IN	RA	NO	0
M2 – sample size	26	10	7	36	1	
2.1 Double protolophule	AL	FR	FR	IN	NO	0
2.2 Single anterior or single transverse protolophule	NO	FR	FR	VF	AL	1
2.3 Complete double metalophule	FR	IN	NO	NO	NO	0
2.4 Single anterior or single transverse metalophule	NO	FR	FR	AL	AL	1
2.5 Single posterior metalophule	RA	IN	FR	NO	NO	0
2.6 Posterior spur on paracone	?	FR	FR	FR	NO	1
2.7 Long mesoloph	AL	VF	FR	FR	NO	0
M3 – sample size	7	1	8	11	0	
3.1 Metacone developed in cusp	NO	NO	AL	FR	-	1
m1 – sample size	16	3	14	51	4	
4.1 Anterolophulid connected to the labial side of the anteroconid	FR	NO	AL	FR	NO	0
4.2 Anterolophid labial with bulge	NO	NO	FR	FR	FR	0
4.3 Long mesolophid	FR	NO	IN	IN	NO	0
4.4 Fusion of the mesolophid the entoconid	NO	NO	NO	IN	NO	0
4.5 Absent mesolophid	NO	NO	FR	FR	NO	1
4.6 Ectomesolophid	VF	FR	RA	RA	NO	1
m2 – sample size	29	4	17	52	1	
5.1 Long lingual anterolophid	NO	NO	RA	FR	AL	1
5.2 Ectomesolophid	FR	NO	NO	NO	NO	1

On the left column a code is given for each morphological character, and the number of teeth counted is provided at the top of each column. NO: none [0%]; RA: rare [< 10%]; IN: infrequent [10% – < 25%]; FR: frequent [25–75%]; VF: very frequent [> 75%]; AL: always [100%]. The last column gives the binary data of the phylogenetic analysis outgroup.

The origin of *Megacricetodon* in Central Asia is unknown so far, and *Eucricetodon* aff. *E. caducus*, which is the only cricetid found in the late Oligocene of the same basin (Maridet et al., 2009) has been selected as a potential outgroup. The parsimony analysis was processed with the software PAST (Hammer et al., 2001), using an exhaustive algorithm with characters reversible and unordered (Fitch optimization criterium). The processing provided two 28 step-long most parsimonious trees. The Fig. 8 illustrates the consensus tree based on these two most parsimonious trees, with high consistency indices (CI) and quite good retention indices (RI). The genus *Megacricetodon* remains monophyletic, but the test provides inconsistent results considering the relative age of the species in the fossil record, all giving *M. pusillus*, *M. sinensis*, and *M. yei* as the species sharing the most plesiomorphic association of characters, which would imply the co-existence of three undiscovered lineages of *Megacricetodon* in the early Miocene of Central Asia. The extensive samplings, made in the early Miocene of Central Mongolia, Xinjiang, and Inner Mongolia (e.g., Meng et al., 2006; Qiu et al., 2006; Daxner-Höck and Badamgarav, 2007; Bi et al., 2009) indicate that this hypothesis is unlikely. Besides the branch linking the outgroup to the rest of the tree is supported by no unambiguous morphological change, indicating that all the characters that change at that point change back at some point later in the tree, which mean that the characteristics of this outgroup are part of a mosaic of evolutionary changes and may be the cause of unusual results in the phylogeny. The implication of these observations is that a local evolution of *Megacricetodon* starting from the late Oligocene *Eucricetodon* aff. *E. caducus* appears unlikely, and that *Megacricetodon* is likely to be an immigrant genus.

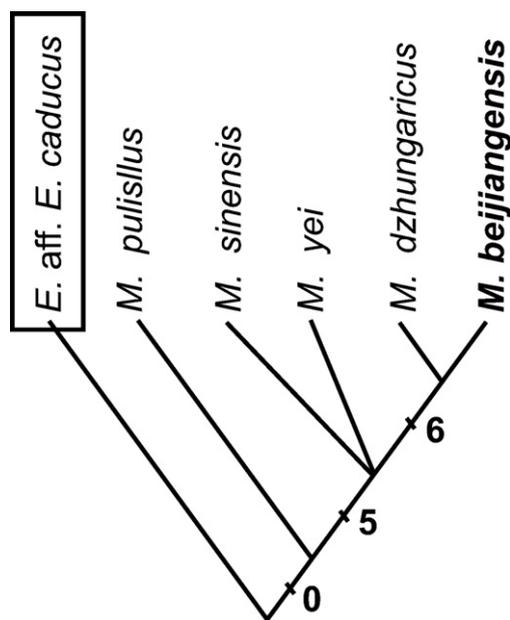


Fig. 8. Tentative parsimony analyses for *Megacricetodon* from the early Miocene of northern Central Asia (CI = 0.75; RI = 0.63). The outgroup, *Eucricetodon* aff. *E. caducus*, is framed in a box, the species *M. beijiagensis* nov. sp. described in this study is in bold characters, and the number of unambiguous morphological changes supporting the branches between nodes is given.

Therefore the question of the phylogenetic relationship of *Megacricetodon* species in Central Asia remains unsolved and the potential ancestor of the genus remains to be found in another region of Asia.

#### 4. Biochronology

##### 4.1. Rodent assemblage, age, and correlations

Altogether ten species of rodents have been recognized that undoubtedly indicate an early Miocene age for the XJ 200114 locality. The fauna includes the four species of cricetids described above: *Cricetodon* sp., *Eumyarion* sp., *K. debruijni* nov. sp., and *M. beijiagensis* nov. sp. The presence of *Megacricetodon* indicates that the locality is most likely Shanwangian rather than Xiejian in age (Meng et al., 2006; Qiu et al., 2006). However, the comparison of *Cricetodon* with Xiacaowan points to some clear differences indicating that the XJ 200114 fauna could be noticeably older than the Xiacaowan fauna. In addition, the associated species *Sinolagomys* sp. shows similarities with *Sinolagomys ulugurensis* Tong, 1989, which is very abundant in S-III zone in the lower part of the Suosuoquan Formation (Tong, 1989; Meng et al., 2006), supporting the idea that the studied locality is older than the typical Shanwangian fauna. Based on absolute dating and correlations proposed by Deng (2006), the Shanwang and Xiacaowan localities are about the same age. The Shanwang Formation overlies the basalt dated as  $18.05 \pm 0.55$  Ma (Cheng and Peng, 1985), and therefore the Shanwang fauna within this formation must be younger than 18.05 Ma. *Cricetodon*, *Eumyarion*, *Karydomys*, and *Megacricetodon* from XJ 200114 represent the first occurrences of these taxa in Xinjiang. Their absence in assemblages S-II and S-III of the Suosuoquan Formation in the Tiersihabahe section (Meng et al., 2006) indicates that XJ 200114 is younger than those assemblages. In addition, *Atlantoxerus* sp. is present in both S-III and XJ 200114, but shows a more derived morphology in XJ 200114, which also confirms this younger age. Meng et al. (2006) gave an age calibration of the Suosuoquan mammal assemblage zones using magnetostratigraphy, with the time span of the third zone (S-III zone) being estimated from 21.7 to 21.1 Ma. Considering that the XJ 200114 fauna is biostratigraphically older than Xiacaowan and younger than S-III in the Tiersihabahe section, its age may be roughly constrained between 21 and 18 Ma. *H. mongoliensis* in XJ 200114 is also known from two levels D1/1 and D1/2, roughly between 20 and 16 Ma (Daxner-Höck and Badamgarav, 2007), of the early Miocene Loh Formation in the Valley of Lakes, Mongolia, and is consistent with the age estimation of XJ 200114. On the polarity time-scale (Gradstein et al., 2004), the age range of XJ 200114 extends from the beginning of the chron C6A (Aquitanian) to the end of C5E (Burdigalian). Given the correlation that the chron C6A falls in MN2 whereas C5E falls in the upper part of MN3 in the European record (Sen, 1997; Steininger, 1999), then the XJ 200114 fauna can be either correlated to MN2 or MN3, or probably spans across MN2 and MN3.

Based on the presence of *Megacricetodon*, we may further consider that the XJ 200114 fauna represents an early period of the Shangwangian, an age of late early Miocene. Other associated species from other regions, such as *A. mallos* from the Akzhar Formation and *P. shevyreva* from the Akzhar and Zhaisan Formations in the Zaisan basin (eastern Kazakhstan), are dated as late early Miocene (Zazhigin and Lopatin, 2000), which supports our interpretation. Therefore, it is likely that the XJ 200114 fauna is more probably contemporaneous with the European MN3. This interpretation bears a significant implication for the Neogene biochronology in China in that *Cricetodon* and *Megacricetodon* appear earlier in China than previously admitted, and that their appearances are definitely not synchronous across their geographic range in Eurasia. It also indicates that the beginning of the Shangwangian Age defined, among other genera, by the first appearance of *Megacricetodon* (Qiu et al., 1999; Qiu and Li, 2003), is not isochronous with the beginning of the European MN4, as already stated by Qiu et al. (1999) and later by Deng (2006). As discussed below, the fauna from the Chul'adyr Formation in the Aktau Mountains (Kordikova and de Bruijn, 2001), which presents a strong similarity with XJ 200114, might roughly have the same age.

#### 4.2. Biochronologic significance of the *Cricetids*

*Cricetodon* is poorly known in the Neogene of China. Indeed, the late early Miocene locality of Xiacaowan in Jiangsu Province (Qiu, 2010) is one of a few localities that yield *Cricetodon* specimens. These specimens have been described as *C. wanhei* (Qiu, 2010). The comparison of the specimens from the XJ 200114 fauna, Junggar Basin, with those of Xiacaowan reveals that the former are clearly larger and more hypsodont, with a divided anterocone and a more developed posterior part of m3. If we assume that the evolutionary trends known in European *Cricetodon* are also true in Asia (the evolutionary trend of this genus in Asia has not yet been studied), then the previously cited characters should be derived characters, therefore suggesting an age noticeably younger for Xiacaowan. Based on sciurids (Qiu and Liu, 1986), tragulids, and cricetids (*Megacricetodon* and *Democricetodon* Fahlbush, 1964), Li et al. (1983) proposed that Xiacaowan could be correlated to the biochronological unit MN4 as initially defined by Mein (1975) in Europe. Concerning *Cricetodon*, the oldest record known in Eurasia so far is in the early Miocene of Anatolia (de Bruijn et al., 1993). Specimens from the XJ 200114 locality show noticeable differences in morphology when compared to those from Anatolia, though the size, height of the crown, and development of the entoconid in m3 are somewhat similar to *C. kasapligili* from Keseköy (MN3; de Bruijn et al., 1993), *C. tobieni* from Horlak (MN4; de Bruijn et al., 1993), and *C. Aliveriensis* from Greece (MN4; Doukas, 2003). All these observations are compatible with the age estimate previously proposed for XJ 200114.

The species *K. debruijni* nov. sp. and *K. dzerzhinskii* show many primitive characters when compared to European and Anatolian species. The similarities between *K. debruijni* nov.

sp. and *K. dzerzhinskii* suggest a similar age for XJ 200114 and the Chul'adyr Formation in the Aktau Mountains of Kazakhstan (Kordikova and de Bruijn, 2001). *M. beijiangensis* nov. sp. and *M. dzhungaricus* both display primitive characters compared to the other *Megacricetodon* known in the middle Miocene of China, which confirms the early Miocene assessment for our locality. As opposed to the observations made on the size of *Karydomys*, *M. dzhungaricus* from the Chul'adyr Formation of Kazakhstan has a more plesiomorphic combination of characters than *M. beijiangensis* nov. sp., which may indicate a slightly older age for the Kazakhstan locality. However, considering the possibility that these species may belong to different lineages and also considering the fact that the first appearance of *Megacricetodon* in Asia is still uncertain, it is hard to tell which of *M. beijiangensis* nov. sp. or *M. dzhungaricus* is more primitive, and therefore hard to say which locality is older.

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