第49卷　第4期
2011年10月

古 脊 椎 动 物 学 报
VERTEBRATA PALASIATICA

pp.393－405
figs.1－3

新疆准噶尔盆地早中新世的最早众古仓鼠及其与稀古仓鼠的对比[1)]

Olivier MARIDET[1]　吴文裕[1]　叶　捷[1]
毕顺东[2]　倪喜军[1]　孟　津[1,3]
（1 中国科学院古脊椎动物与古人类研究所，脊椎动物进化系统学重点实验室　北京　100044）
（2 美国宾夕法尼亚州印第安纳大学生物系　印第安纳　PA 15705）
（3 美国自然历史博物馆　纽约　10024）

摘要：记述了新疆准噶尔盆地早中新世地层中发现的众古仓鼠类化石。材料采集于索索泉组的两个地点，古地磁年龄介于21.9～21.16 Ma之间。这是迄今为止中亚和东亚地区众古仓鼠的最早记录。材料可以归入两个种：苏氏众古仓鼠（新种）*Democricetodon sui* sp. nov. 和众古仓鼠未定种 *Democricetodon*? sp.，该未定种材料很少，不足以准确分类。与早中新世其他仓鼠的比较及对稀古仓鼠 *Spanocricetodon* 模式种的重新观察表明，苏氏众古仓鼠是中亚地区谢家期的指示性化石，李传夔（1977）所定义的稀古仓鼠为一个有效属，与 *Democricetodon* 和 *Primus* 属有明显区别；以前归入稀古仓鼠的某些种类应归入其他属。苏氏众古仓鼠与同一地区晚渐新世的 *Eucricetodon* aff. *E. caducus* 形态明显不同，表明它可能不是起源于该地区的古近纪仓鼠，而是迁移至中亚的外来种。

关键词：准噶尔盆地，早中新世，谢家期，索索泉组，啮齿类，仓鼠科

中图法分类号：Q915. 873　**文献标识码**：A　**文章编号**：1000－3118(2011)04－0393－13

EARLIEST OCCURRENCE OF *DEMOCRICETODON* IN CHINA, IN THE EARLY MIOCENE OF THE JUNGGAR BASIN (XINJIANG), AND COMPARISON WITH THE GENUS *SPANOCRICETODON*

Olivier MARIDET[1]　WU Wen-Yu[1]　YE Jie[1]　BI Shun-Dong[2]　NI Xi-Jun[1]　MENG Jin[1,3]
(1 *Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences* Beijing 100044, China olivier.maridet@ivpp.ac.cn)
(2 *Department of Biology, Indiana University of Pennsylvania* Indiana PA 15705, USA)
(3 *Division of Paleontology, American Museum of Natural History* New York NY 10024, USA)

Abstract　New *Democricetodon* fossils from the Early Miocene of the Junggar Basin (northern Xinjiang, China) are described. The specimens come from two localities within the Suosuoquan Formation, which have been dated by magnetostratigraphy to between 21.9 and 21.16 Ma (Aquitanian). This record of *Democricetodon* is the oldest so far known in Central and Eastern Asia. Two species are recognized: *De-*

1）国家自然科学基金（批准号：40872032，41050110135）和中国科学院外籍青年科学家计划（编号：2009*Y2BZ*3）资助。

收稿日期：2010－12－07

mocricetodon sui sp. nov. and *Democricetodon*? sp. The second species is based on few specimens, insufficient for secure taxonomic identification. Comparisons with other Early Miocene cricetids and re-examination of the type species of *Spanocricetodon* confirm that *D. sui* is characteristic of the Xiejian age in Central Asia. Our comparisons also confirm that the genus *Spanocricetodon* sensu lato Li (1977) is valid and clearly differs from *Democricetodon* and *Primus*, and show that some species that have previously been assigned to *Spanocricetodon* actually belong to other genera. The clear differences between *D. sui* and *Eucricetodon* aff. *E. caducus* from the Late Oligocene of the same region indicate that *D. sui* is unlikely to have originated from the Paleogene cricetids in the region, but probably represents a species that immigrated to Central Asia.

Key words Junggar Basin, China; Xiejian age, Early Miocene; Suosuoquan Formation; Rodentia, Cricetidae

1 Introduction

1.1 Geological and temporal framework

The term "Suosuoquan Formation" was first used by Pei et al. (1963), and later cited by others (Peng, 1975; Tong et al., 1989, 1990; Wu et al., 1998; Ye et al., 2000, 2001a,b; Ye et al., 2003). This formation is predominantly composed of aeolian sediments, intercalated with occasional layers of fluvial sandstone (Sun et al., 2010). In the northern Junggar Basin, the Suosuoquan Fm. overlies the Tieersihabahe Formation. As demonstrated by Meng et al. (2006), the base of the Suosuoquan Fm. coincides with the end of the Oligocene. At most localities the top of the formation is eroded and the Halamagai Fm. disconformably overlies the Suosuoquan Fm.

Some of the cricetid specimens studied here come from the XJ 99005 section (46°39.415'N, 88°20.623'E), correlated to the Suosuoquan Assemblage Zone II-III (Meng et al., 2006). Others come from the locality XJ 200205 within the Tieersihabahe section (46°39.906'N, 88°28.436'E), correlated to the Suosuoquan Assemblage Zone III (Meng et al., 2006). Both assemblages have been recognized by Meng et al. (2006) as characteristic of the Xiejian age. The estimated age of both zones ranges from 21.9 to 21.16 Ma based on magnetostratigraphic correlations, dates that fall within the Aquitanian Stage/Age based on the calibrated time scale of Gradstein et al. (2004) and can be correlated to the European biozone MN2 according to the biochronological unit calibration of Sen (1997) and Steininger (1999).

1.2 Materials and methods

All specimens are deposited in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology, CAS. They are catalogued under the numbers IVPP V 17683.1-14 and V 17684.1-4 (Table 1).

The specimens were observed and measured under a binocular Olympus SZX7 microscope, allowing measurements to be taken to a precision of 0.01 millimeters. The terminology used to describe molars is taken from Maridet et al. (2009), which was in turn modified from Freudenthal (1988). The classification used follows the one proposed by Mein and Freudenthal (1971).

Table 1　List of the specimens described in this study, including their origin, identification, and measurements

Section	Location in section (m)	Species	Specimen	Length (mm)	Width (mm)	Specimen number	Year of sampling	Comments
XJ 99005	1.5 ~ 2.0	*D. sui*	Left M1		0.89	V 17683.1	2002	Anterior part lost
	2.5 ~ 3.0	*D.* ? sp.	Left M1	1.59	1.09	V 17684.1	2002	
	4.0 ~ 4.5, 5.1, 6.7	*D. sui*	Left M1	1.51	1.02	V 17683.6	2000	
		D. sui	Left M1	1.44	0.98	V 17683.4	2002	
		D. sui	Left M2	1.17	1.03	V 17683.2	1999	
		D. sui	Left m1	1.31	0.91	V 17683.3	1999	
		D. sui	Left m1	1.30	0.86	V 17683.7	2000	
		D. sui	Right m1	1.28	0.81	V 17683.8	2000	
		D. sui	Right m2	1.07	0.88	V 17683.5	2002	
		D. ? sp.	Right m2	1.21	1.02	V 17684.2	2002	
	7.5	*D. sui*	Left M1	1.49	1.00	V 17683.9	2002	
		D. sui	Left m1	1.20	0.80	V 17683.10	2002	Holotype
		D. sui	Left m1	1.22	0.82	V 17683.11	2002	
		D. sui	Right m2	1.15	0.89	V 17683.12	2002	
	10.5	*D. sui*	Right M1			V 17683.13	2002	Half posterior part lost
	16.5	*D.* ? sp.	Left m1	1.43	0.88	V 17684.3	2002	
	19.5	*D.* sui	Left m1			V 17683.14	2002	Strongly worn
Tieersihabahe	68	*D.* ? sp.	Right maxilla			V 17684.4	2002	Fragment, tooth row preserved
			M1	1.57	1.03			
			M2	1.24	1.09			
			M3	0.86	0.93			

2　Systematic paleontology

Rodentia Bowdich, 1821

Cricetidae Fischer de Waldheim, 1817

Cricetinae Stehlin & Schaub, 1951

***Democricetodon* Fahlbusch, 1964**

***Democricetodon sui* sp. nov.**

(Fig. 1A-F and 2A-G)

1999? *Democricetodon* sp. Höck et al., p. 119, fig. 21/4
2003 *Democricetodon* sp. Ye et al., p. 579, fig. 21.5-d, e
2006 *Democricetodon* sp. Meng et al., p. 213, 229

Holotype　Left m1, IVPP V 17683.10 (Fig. 2A).

Hypodigm　V 17683.1-14, see Table 1.

Type locality　XJ 99005 from the Junggar Basin (Xinjiang, China), Suosuoquan Assemblage Zone II and III. The holotype was collected at 7.5 m in the section (see Meng et al., 2006).

Etymology　Species name after Mr. Jianfeng Su, who helped us greatly in collecting fossils during our Xinjiang fieldwork.

Diagnosis Small cricetine with low-crowned teeth and gracile cusps. The anterocone and anteroconid of the first molar are undivided. In M1, the protolophule is usually single but an incomplete anterior one can also be present, whereas the anterior protolophule is the better developed of the two in M2. The mesoloph is located posteriorly in the mesosinus, closer to the metacone, and the metalophule is slightly oblique and anteriorly connected in M1 and M2. In contrast, the mesolophid of each lower molar is anteriorly located in the mesosinusid, and in m1 the anterior part of the mesosinusid is often higher than the posterior part. In lower molars, the metaconid and entoconid are anteriorly located relative to the protoconid and hypoconid, respectively. The metalophulid and the hypolophulid are almost transverse; the metalophulid joins the middle of the anterolophulid and the hypolophulid joins the ectolophid between the apex of the curve and the hypoconid. A small but clearly developed mesoconid is often present at this junction of the hypolophulid and the ectolophid. The ectomesolophid, starting from the mesoconid, can be either present or absent.

Differential diagnosis Among Chinese species, *D. sui* differs from *D. lindsayi* Qiu, 1996 in being smaller and having an undivided anterocone, from *D. tongi* Qiu, 1996 in lacking a posteriorly connected metalophule in M1, and from *D. suensis* Qiu, 2010 in being smaller and lacking a posteriorly connected metalophule in M1. It differs from the small European species *D. gracilis* Fahlbush, 1964 and *D. franconicus* Fahlbush, 1966 mainly in having an anteriorly connected metalophule in M1, from *D. anatolicus* Theocharopoulos, 2000 in being slightly larger and in seldom having a posterior paracone spur in M1 and M2, in having a poorly developed anterior protolophule in M1, and a small mesoconid in m1, and from *D. doukasi* Theocharopoulos, 2000 in being slightly smaller, in lacking a well developed anterior protolophule, and in lacking variability in the anterior connection of the metalophule in M1.

D. sui also differs from all known species of *Karydomys* Theocharopoulos, 2000 in being much smaller and having gracile cusps, and from all known species of *Megacricetodon* Fahlbush, 1964 in having a less anteroposteriorly elongated shape, an undivided anterocone and anteroconid, and a slightly curved ectolophid in m1 that gives the sinusoid a rounded shape (whereas the shape of the ectolophid is more angular in *Megacricetodon*).

D. sui differs from *Primus microps* de Bruijn et al., 1981 in being larger and in having variably long mesolophids and a connection between the posterior protolophule and entoloph of M1 (whereas the posterior protolophule is connected to the protocone in *P. microps*). It contrasts with *Spanocricetodon kanii* de Bruijn et al., 1981 in being smaller, in having variably long mesolophids in the lower molars, and in that hypoconid of m2 lacks a posterior arm.

The differences that separate *D. sui* from *Spanocricetodon ningensis* Li, 1977 and the other species of *Spanocricetodon* Li, 1977 are discussed below.

Size of teeth The size of each specimen is given in Table 1, and measurements for the population are summarized in Table 2. The specimens were from different levels of the XJ 99005 section (see Table 1). So far the sample is too small to allow testing for significant changes in size along the XJ 99005 section.

Table 2 Measurements of *Democricetodon sui* sp. nov. from XJ 99005 (mm)

Tooth	Length			Width		
	N	Range	Mean	N	Range	Mean
M1	3	1.44 ~ 1.50	1.48	4	0.89 ~ 1.02	0.97
M2	1		1.24	1		1.09
m1	5	1.20 ~ 1.31	1.26	5	0.80 ~ 0.91	0.84
m2	2	1.07 ~ 1.15	1.11	2	0.88 ~ 0.89	0.88

Upper dentition The anterocone of the M1 is large and undivided, and often more developed labially than lingually. The anterolophule usually joins the lingual part of the anterocone. The lingual and labial anterolophs are both long, but the latter one is usually thinner. The paracone is distant from the anterocone, forming a large labial anterosinus. The protolophule always joins the posterior area of the protocone, and is either transverse or slightly oblique. The anterior protolophule is present in some specimens (2/5), but it is always incomplete or weakly developed compared to the posterior one. One tooth has a small posterior spur starting from the paracone and oriented toward the labial border (Fig. 1E). The entoloph is slightly curved, and gives the lingual sinus a rounded shape. The mesoloph can be short or long enough to join the labial border; it is always posteriorly located in the mesosinus, close to the metacone. Both anterior cingula are well developed, and one tooth shows a small style on the

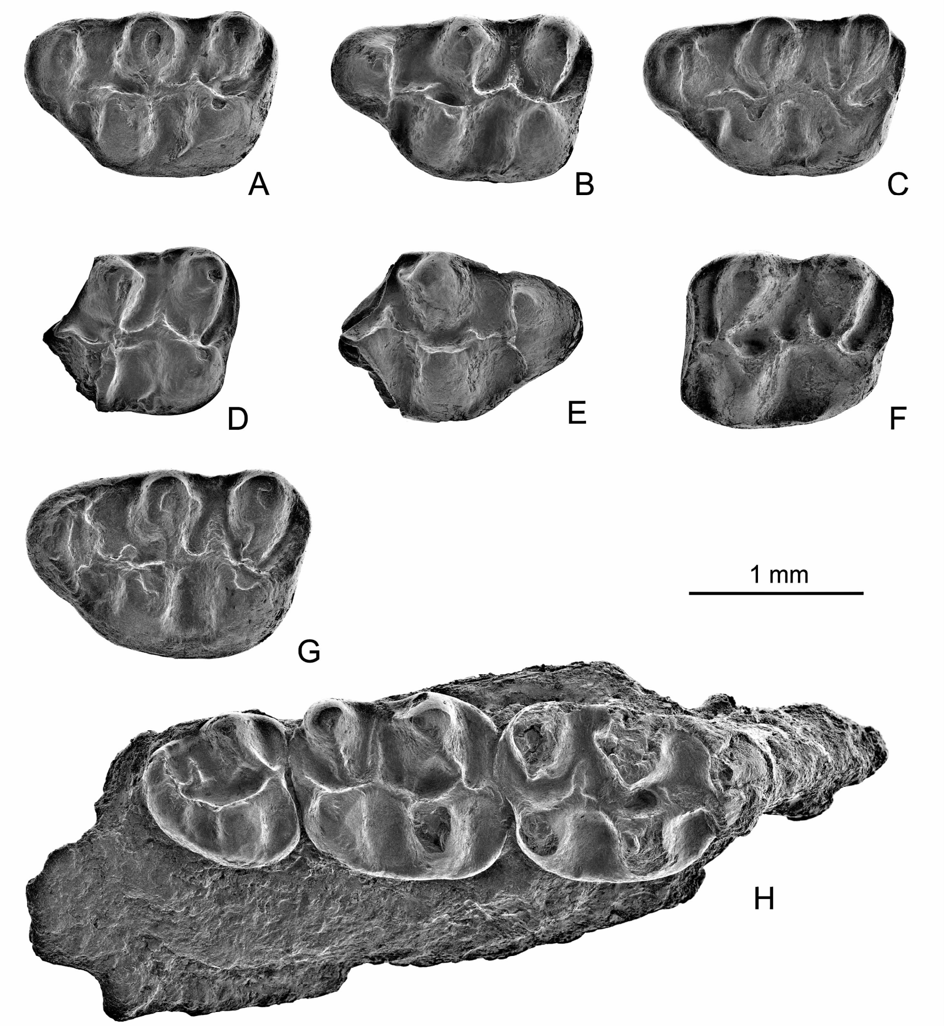

Fig. 1　Upper cheek teeth of *Democricetodon sui* sp. nov. from XJ 99005 locality (A-F), *Democricetodon*? sp. from XJ 99005 locality (G), and *Democricetodon*? sp. from XJ 200205 locality (H)

A. left M1 (V 17683.4); B. left M1 (V 17683.9); C. left M1 (V 17683.6); D. left M1 (V 17683.1); E. right M1 (V 17683.13); F. left M2 (V 17683.2); G. left M1 (V 17684.1); H. fragmentary maxilla with M1-M3 (V 17684.4) labial one. The metalophule is anteriorly oriented, connected either to the hypocone or anteriorly to the hypocone. Each M1 has three roots.

The M2 is slightly longer than wide, the anterior part being slightly wider than the posterior part. Both anterolophs are equally long, and curved to delimit large anterosinuses. Two protolophules are present, the anterior one being more developed than the posterior one. The mesoloph is short, and as in the M1 it is posteriorly located in the mesosinus. The metalophule is anteriorly connected. Each M2 has three roots.

Lower dentition The m1 has an elongated shape, with its posterior part slightly wider than its anterior part. The anteroconid is small and simple. In lateral view it is lower than the four other main cusps. The labial and lingual anterolophids are equally long. The metaconid is clearly anteriorly located compared to the protoconid; the metalophulid is transverse and joins the middle of the anterolophulid. The distance between the anterior cusps and the posterior ones is long, resulting in a large sinusid and mesosinusid. The ectolophid is long and thin, and is curved toward the mesosinusid in the middle of the tooth. There is at most one mesolophid, and this structure may be long (2/6), weak (1/6) or absent (3/6). When present, it starts from the ectolophid between the apex of its curve and the protoconid, and is consequently closer to the metaconid than the entoconid. It is noteworthy that in all available examples of the m1, the anterior part of the mesosinusid, located between the protoconid and the metaconid, forms a "plateau" higher than the rest of the mesosinusid. In this area, one tooth shows a bulge of enamel, starting from the protoconid and reaching the posterior side of the metaconid, which could be interpreted as a vestigial protoconid hind arm (Fig. 2A). The entoconid is anteriorly located compared to the hypoconid. The ectolophid is slightly curved, and gives the labial sinusid a rounded shape. The hypolophulid is either transverse or slightly anteriorly arched; it joins the ectolophid between the apex of its curve and the hypoconid. Several m1s (4/6) have a small mesoconid located at this junction point of the hypolophulid and the ectolophid. One tooth also has a short ectomesolophid arising from this mesoconid. The lingual posterolophid is always long and distant from the entoconid, delimiting a large posterosinusid. The labial posterolophid is absent except for one tooth, this tooth possesses a bulge borne by the lingual posterolophid that gives rise to a short but well-formed labial posterolophid.

The m2 has a sub-rectangular shape, and is equally wide anteriorly and posteriorly. The labial anterolophulid is longer than the lingual one, delimiting a large labial anterosinus. As in the m1, the metaconid and entoconid are anteriorly located with respect to the protoconid and hypoconid respectively; the metalophulid and the hypolophulid are transverse, respectively joining the anterolophulid and the ectolophid. The mesolophid is short but well developed. The lingual posterolophid is long, delimiting a large posterosinusid, and as in m1 it bears a bulge at its labial extremity. The m2s have two roots.

Discussion The association of the following features confirms that the specimens described in this paper are attributable to the genus *Democricetodon*: the gracile cusps, the well developed but undivided anterocone on M1, the slightly curved entoloph and ectolophid, the rounded aspect of the sinus and sinusid, the presence of mesolophids, the undivided anteroconid and the generally small size.

Höck et al. (1999: 119, fig. 21/4) figured an M1 of *Democricetodon* sp. from the beginning of the Miocene of Central Mongolia. This tooth resembles the M1 of *D. sui* in size, and also in having a large and undivided anterocone, a posterior protolophule and an anterior metalophule. Consequently, the specimen could belong to *D. sui*, but a more detailed comparison including more specimens from Central Mongolia will be necessary to confirm this tentative conclusion.

Democricetodon sui shares with *D. anatolicus* Theocharopoulos, 2000 and *D. doukasi* Theocharopoulos, 2000 (Early Miocene of Greece and Turkey: MN1-3) the following association of characters: an undivided anterocone, a strong posterior protolophule of the M1, a double protolophule of the M2 with the anterior one more developed, and an anteriorly connected metalophule on both M1 and M2. It is noteworthy that the species *Spanocricetodon kanii* de Bruijn et al., 1981 also displays a similar association of characters (see comparison with the genus *Spanocricetodon* bellow). *D. gracilis* Fahlsbusch, 1964 and *D. franconicus* Fahlbusch, 1966 (late Early Miocene of Europe: MN4) also share some common features with *D. sui*, such as a weakly-developed or absent anterior protolophule in M1, a well-developed anterior protolophule and an anteriorly connected metalophule in M2. These taxa also resemble *D. sui* in that the mesolophid of m1 is often weakly developed or absent.

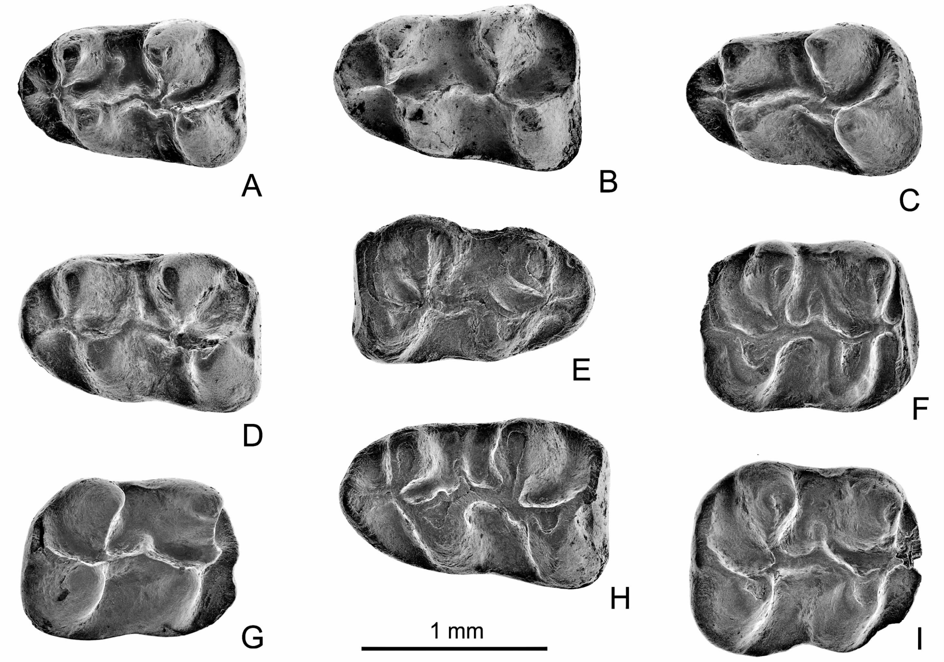

Fig. 2　Lower cheek teeth of *Democricetodon sui* sp. nov. (A-G) and *Democricetodon*? sp. (H-I) from XJ 99005 locality

A. left m1 (type specimen: V 17683.10); B. left m1 (V 17683.3); C. left m1 (V 17683.11); D. left m1 (V 17683.7); E. right m1 (V 17683.8); F. right m2 (V 17683.5); G. right m2 (V 17683.12); H. left m1 (V 17684.3); I. right m2 (V 17684.2)

The similarity of *D. sui* to the two Anatolian and Greek species *D. anatolicus* and *D. doukasi* suggests that the three species are quite closely related, which would imply a rapid dispersion and diversification of the genus in Eurasia around the Oligocene-Miocene boundary.

Only one species of cricetid, *Eucricetodon* aff. *E. caducus*, is known from the Late Oligocene of the Junggar Basin (Maridet et al., 2009). In the regional fossil record, this species does not survive beyond the Oligocene-Miocene boundary, and *Democricetodon sui* is the first cricetid to replace it in the Early Miocene. This raises the question of whether or not *D. sui* could have evolved from *Eucricetodon* aff. *E. caducus*. The size of the teeth and the development of the crests usually show a lot of variability and evolve at independent rates in the evolutionary history of cricetid rodents. One main difference in the lower teeth between *D. sui* and *Eucricetodon* aff. *E. caducus* is the location of the mesoconid, which is usually a character showing little variability. The m1 mesoconid of *E.* aff. *E. caducus* is located in the middle of the ectolophid, where the mesolophid and the ectomesolophid start (as is also the case in other Paleogene cricetids). In *D. sui*, in contrast, the mesoconid is located at the junction of the hypolophulid and the ectolophid, which is also the starting point of the ectomesolophid, but posterior to the apex of the ectolophid's curve and to the mesolophid (as can be observed in some Late Oligocene and Early Miocene dipodids such as *Heterosminthus* and *Litodonomys*). This one observation is not enough to infer the origin of *Democricetodon*, but highlights the fact that the relationship between Paleogene and early Neogene cricetids is not clear. However, the idea that the first Neogene small cricetids (such as *Democricetodon*, *Primus* and *Spanocricetodon*) could have evolved from another family of myomorph rodents, for instance dipodids, has to be proposed as a new alternative hypothesis. Such a hypothesis carries one major implication, namely that all the Paleogene rodents currently considered to be cricetids would really constitute a totally different clade from that containing Neogene cricetids and their extant relatives. In other words, the so-called "Paleogene cricetids" would not be actual cricetids at all. Regarding this implication, it is noteworthy that the possibility that the traditional Family Cricetidae (comprising all extant, Neogene and Paleogene species) might constitute a paraphyletic group has already been proposed by Flynn (2009) in his tentative phylogeny of muroid rodents, in which the "Paleogene cricetids" (including *Cricetops*, *Pseudocricetodon*, *Eumys* and *Eucricetodon*) are clearly more primitive and very distant from Neogene cricetids (especially the cricetines *Democricetodon* and *Megacricetodon*). Future discoveries in the Late Oligocene-Early Miocene of Asia will definitely be crucial in testing competing hypotheses about the origin of modern cricetids.

Democricetodon? sp.

(Fig. 1G-H and 2H-I)

Specimens IVPP V 17684. 1-4, see Table 1.

Locality Specimens are sampled at 4. 0 ~ 4. 5 m and 16. 5 m in the section XJ 99005 and XJ 200205, 68 m in the Tieersihabahe section, from the Junggar Basin Suosuoquan Assemblage Zone II and III (see Meng et al., 2006).

Size of teeth Slightly larger than in *D. sui*, see Table 1.

Upper dentition The M1 is morphologically very similar to that of *D. sui*. However the cusps present a more massive aspect and the anterior lobe is wider. One tooth has an incomplete, posteriorly oriented metalophule.

The M2 also has massive cusps. The posterior spur of the paracone of M2 joins the labial cingulum, and the mesoloph also reaches this cingulum to form a style.

The M3 is short and rounded due to reduction of the posterior part of the tooth: the hypocone is clearly smaller than the protocone and is elongated, almost forming a lingual posteroloph. The metacone is indistinguishable from the labial posteroloph. As for the M2, both anterolophs are long and curved. The tooth has only one oblique protolophule, which is connected very anteriorly to the base of the anterolophs. The mesosinus is large and appears to lack an axioloph, mesoloph or metalophule, but a short spur that extends from the hypocone and curves toward the labial border might in fact represent an incomplete metalophule.

Lower dentition The lower teeth also show more massive cusps, compared to those of *D. sui*.

The m1 is more elongated, with a long mesolophid merging with the lingual cingulum. In addition to the mesolophid, a weakly developed spur that may represent a vestigial protoconid hind arm extends from the protoconid (Fig. 2H). In other respects the m1 is morphologically similar to that of *D. sui*.

The m2 has a long lingual posterolophid that delimits a large posterosinusid, and bears at its labial extremity a bulge from which extends a weakly developed labial posterolophid.

Discussion The *D.* ? sp. specimens described in this paper are quite similar in morphology to specimens of *D. sui*, indicating that they are closely related to *D. sui* and may share a common ancestor with this taxon. In this study they are distinguished from *D. sui* mainly on the basis of the massive aspect of the cusps, the wider anterocone of the M1 and the elongated shape of the m1. They are also somewhat larger. The massive aspect of the cusps, the wide anterocone of the M1, the double protolophule of the M2 (the anterior one being stronger), the anteriorly connected metalophule in M2 and the reduced M3 are points of resemblance to *Karydomys dzerzhinskii* Kordikova & de Bruijn, 2001 and *K. debruijni* Maridet et al., in press. Pending the discovery of more material, however, we provisionally identify these specimens as belonging to *Democricetodon* because of their relatively small size. However we do not exclude the hypothesis that *Karydomys* from the late Early Miocene of Central Asia (Kordikova and de Bruijn, 2001; Maridet et al., in press) could be closely related.

However, thesmall number of available specimens and our limited knowledge of the variation in both species preclude a rigorous test of whether a significant difference in size exists. More material will be necessary in the future to confirm the taxonomic identity of these specimens.

3 Comparison with *Spanocricetodon* Li, 1977

D. sui and *Spanocricetodon ningensis* are both Early Miocene Chinese species and are relatively similar in size, justifying a detailed comparison between the two. Accordingly, we have re-examined the type specimen of the genus *Spanocricetodon* Li, 1977 (IVPP V 4342; Fig. 3)

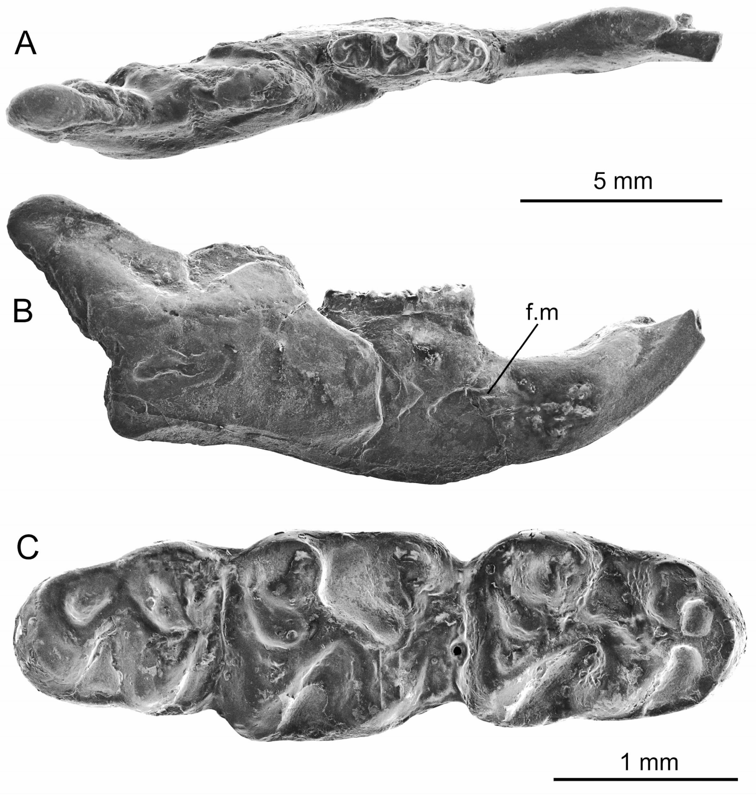

Fig. 3 Type specimen of *Spanocricetodon ningensis* Li, 1977: right mandible with complete m1-m3 (V 4342)
A. occlusal view; B. labial view; C. tooth row in occlusal view; f. m. mental foramen

from the Lower Dongxuanguan deposits of Fangshan. Our new measurements of the teeth are: m1 = 1.49 mm × 1.07 mm; m2 = 1.24 mm × 1.12 mm; m3 = 1.09 mm × 0.93 mm. The mandible shows many cracks and has been protected with a layer of glue that makes details of tooth morphology difficult to observe. However, our observations confirm the diagnostic characters identified by Li (1977) for *Spanocricetodon ningensis*: absence of mesolophids; strongly curved ectolophids and oblique sinusids; no protoconid hind arm or ectomesolophid; very anteriorly connected hypolophulid reaching middle of ectolophid in m2, whereas metalophulid is transverse; and short m3 with centrally located hypolophulid. In addition, as also observed in *Spanocricetodon janvieri* Mein & Ginsburg, 1997, the cuspids of the lower molars are located closer to the borders of the tooth than in other cricetids (i. e. the metaconid and entoconid are more lingually located, and the protoconid is more labially located). The morphology of the mandible generally conforms to the description given by Li (1977), although the area of the mental foramen is broken. Its opening might be slightly more anterior than Li (1977) indicated, below the front of the anteroconid.

D. sui clearly differs from *S. ningensis* in having a longer anterolophulid and larger anterosinusids in m1, and in that m2 of *D. sui* has non-oblique sinusids, longitudinal ectolophulids and long mesolophids. Based on the new measurements of the type specimen of *S. ningensis*, the m1 is less elongated in this taxon than in the *Democricetodon* material described above (ratio L/W = 1.39 for *Spanocricetodon ningensis*; between 1.43 and 1.59 for *Democricetodon sui*; 1.61 for *Democricetodon*? sp.).

As stated by de Bruijn et al. (1981) the mesolophid is usually a rather variable structure among cricetid rodents, and consequently might not be a reliable diagnostic feature for a genus. On the one hand, this observation led de Bruijn et al. (1981) to question the validity of the genus *Spanocricetodon*, but on the other hand the same authors considered the absence of mesolophids to be a reliable diagnostic feature for the genus *Primus* de Bruijn et al., 1981 and the species *Spanocricetodon lii* de Bruijn et al., 1981. From our point of view, the fact that the variability of this character is unknown in the type species of *Spanocricetodon* compels us to accept it as a diagnostic feature until more material is found, keeping in mind that total absence of mesolophids in the lower tooth row is rare among cricetids. Moreover, the other morphological characteristics previously listed also confirm that *Spanocricetodon* is a valid genus. However, we believe that confusion has arisen because not all species that have been assigned to *Spanocricetodon* over the years actually belong to this genus.

The morphological features of the species *S. lii* de Bruijn et al., 1981, including lack of mesolophids, shortness of m3 and presence of a very anteriorly connected hypolophulid in m2, do fit the diagnosis of the genus *Spanocricetodon*. Similarly, the lower molar of *S. janvieri* Mein & Ginsburg, 1997 is comparable to the type specimen of *Spanocricetodon* in lacking mesolophid and in that the cusps lie close to the borders of the tooth.

In contrast, *Spanocricetodon sinuosus* Theocharopoulos, 2000 is characterized by a clearly developed protoconid hind arm and mesolophid, the presence of an ectomesolophid, a nearly transverse orientation of the hypolophulid of m2, and a relatively elongated m3. This species must belong to a genus other than *Spanocricetodon*, or may require a new genus of its own. *S. kanii* also clearly differs from the type species of *Spanocricetodon* in having mesolophids on m2 and m3, a more elongated m1 and m3 (mean L/W length ratio = 1.48 for m1), a short hypoconid hind arm and a transverse hypolophulid on m2. As previously discussed, the similarities among *D. sui*, *S. kanii*, *D. anatolicus* and *D. doukasi* suggest that the species *S. kanii* should probably be reassigned to the genus *Democricetodon*. It is noteworthy that the emended diagnosis of *Spanocricetodon* proposed by de Bruijn et al. (1981) is partially based on *S. kanii* and might therefore be too broad. For instance the cingulum on the anterior face of the anterocone (observed in *S. kanii* but not *S. lii*) is presented as a diagnostic character in the emended diagnosis, but has been in fact observed in *Democricetodon affinis* (Schaub, 1925) and *Democricetodon gaillardi* (Schaub, 1925), as noted by Maridet (2003) and Maridet and Sen (in press).

In the future, a revision of the genus *Spanocricetodon* will certainly be necessary in order to understand the emergence and diversification of Neogene cricetids. Within Asia, the genus *Spanocricetodon* sensu Li, 1977 has so far been recognized in the Early Miocene of Jiangsu Province (Fangshan: *Spanocricetodon ningensis* Li et al., 1977), in Thailand (Li Mae Long: *Spanocricetodon janvieri* Mein & Ginsburg, 1997), and in Pakistan (Murree Formation: *Spanocricetodon lii* de Bruijn et al., 1981). Consequently, the genus *Spanocricetodon* seems to be restricted to southern and south-eastern parts of Asia.

4 Conclusions

Two species of *Democricetodon* have been identified in the Early Miocene of the Junggar Basin, and represent the oldest examples of *Democricetodon* known from central and eastern Asia. *D. anatolicus* from Turkey is older if the biochronological age estimate proposed by Theocharopoulos (2000) is correct. The discovery of *Democricetodon* in the Early Miocene of Central Asia, nonetheless, challenges the hypothesis of Theocharopoulos (2000) that *Democricetodon* originated in Anatolia.

By morphology and size, *D. sui* is typical of the Xiejian age as defined by Meng et al. (2006) in the Junggar Basin. A specimen of *Democricetodon* sp. figured by Höck et al. (1999: 119, fig. 21/4), also from the beginning of the Miocene (Biozone "D" from Central Mongolia; Daxner-Höck and Badamgarav, 2007), shows a similar morphology and similar size. If it is later confirmed that this specimen belongs to the same species, the known distribution of *D. sui* will then be broad enough to allow biochronological correlations with the Xiejian age in Central Asia. This would support the choice of *D. sui* as a defining taxon for the lower boundary of the Xiejian age (Meng et al., in prep.).

The second species is represented by few specimens, and is only differentiated from *D. sui* by its slightly larger size and more massive morphology. It is at the moment not possible to definitely state whether these specimens really belong to a second species, which might have evolved from a common ancestor with *D. sui*, or whether the range of variation in size and morphology present in *D. sui* has been underestimated and should include these specimens.

The morphological similarities noticed between *D. sui* and the earliest *Democricetodon* species of Europe and Anatolia imply that this genus spread quickly across Eurasia soon after its appearance. The abundant samples collected in the Late Oligocene of the Junggar Basin (Ye et al., 2003; Maridet et al., 2009) indicate that the presence of *Democricetodon* in this region before the Miocene is unlikely. The morphology of *D. sui* is different in many respects from that of *Eucricetodon* aff. *E. caducus* from the Late Oligocene of the same basin. In particular, the location of the mesoconid in the first lower molar of *D. sui* differs from that seen in *E.* aff. *E. caducus* and all Paleogene cricetids. This difference indicates that *D. sui* is likely an immigrant species in Central Asia, and also emphasizes the fact that the relationship of Paleogene cricetids to *Democricetodon* (and to the other early Neogene cricetines *Primus*, *Spanocricetodon* and *Megacricetodon*) remains unclear. At present, all Paleogene and Neogene cricetids are usually considered to belong to a single clade of myomorph rodents. As regards this assumption, the differences observed between *D. sui* and the Paleogene cricetids, in addition to observations from another recent study (Flynn, 2009), call for an alternative hypothesis concerning the origin of at least some Neogene cricetids.

Acknowledgements We want to thank Zhang W. D. for taking the SEM pictures of the material and Li P. for her help with bibliographic research. We also thank L. J. Flynn, who contributed to this work through instructive discussions and comments on the manuscript, as well as two anonymous reviewers. C. Sullivan kindly helped to improve the English text. This work is supported by the Chinese National Natural Science Foundation (40872032). The first author's research is supported by the Chinese National Natural Science Foundation (41050110135) and a Research Fellowship for International Young Researchers from the Chinese Academy of Sciences (2009Y2BZ3).

References

Daxner-Höck G, Badamgarav D, 2007. Geological and stratigraphic setting. In: Daxner-Höck ed. Oligocene-Miocene Vertebrates from the Valley of Lakes (Central Mongolia): Morphology, Phylogenetic and Stratigraphic Implciations. Ann Naturhist Mus Wien, **108A**: 1–24

De Bruijn H, Hussain S T, Leinders J J M, 1981. Fossil rodents from the Murree Formation near Banda Daud Shah, Kohat, Pakistan. Proc K Ned Akad Wet, **84**(1): 71–99

Fahlbusch V, 1964. Die *Cricetodon* (Mamm.) der Oberen süßwasser-molasse Bayerns. Abh Bayer Akad Wiss Math-Natur Kl, **118**: 1–152

Fahlbusch V, 1966. Cricetidae (Rodentia, Mammalia) aus der mittelmiozänen Spaltenfüllung Erkertshofen bei Eichstätt. Mitt Bayer Staatssamml Paläont hist Geol, **6**: 109–131

Flynn L J, 2009. Chapter 4. The antiquity of *Rhizomys* and independent acquisition of fossorial traits in subterranean muroids. In: Voss R S, Carleton M D eds. Systematic Mammalogy Contributions in Honor of Guy G. Musser. Bull Am Mus Nat Hist, **331**: 128 – 156

Freudenthal M, 1988. Cricetidae (Rodentia) from the type-Aragonian; the genera *Democricetodon*, *Fahlbuschia*, *Pseudofahlbuschia* nov. gen. and *Renzimys*. Scr Geol, Spec Issue, **1**: 133–252

Gradstein F M, Ogg J G, SmithA G et al., 2004. A new geologic time scale, with special reference to Precambrian and Neogene. Episodes, **27**: 83–100

Höck V, Daxner-Höck G, Schmid H P et al., 1999. Oligocene-Miocene sediments, fossils and basalts from the Valley of Lakes (Central Mongolia)—an integrated study. Mitt Österr Geol Ges, **90**: 83–125

Kordikova E G, de Bruijn H, 2001. Early Miocene rodents from the Aktau mountains (South-Eastern Kazakhstan). Senckenbergiana lethaea, **81**(2): 391–405

Li C K(李传夔), 1977. *Spanocricetodon*, a new Miocene cricetodontine rodent from Fangshan, Nanjing. Vert PalAsiat(古脊椎动物学报), **15**(1): 67–75(in Chinese with English abstract)

Maridet O, 2003. Révision du genre *Democricetodon* (Mammalia, Rodentia, Cricetinae) et dynamique des faunes de rongeurs du Néogène d'Europe occidentale: évolution, paléobiodiversité et paleobiogéographie. Ph. D. dissert. Villeurbanne: University Claude Bernard Lyon 1. 1–252

Maridet O, Sen S (in press). Les Cricetidae du gisement de Sansan. Mem Mus Natl Hist Nat Paris

Maridet O, Wu W Y, Ye J et al.,2009. *Eucricetodon* (Rodentia, Mammalia) from the Late Oligocene of the Junggar Basin, northern Xinjiang, China. Am Mus Novit, (3665): 1–21

Maridet O, Wu W Y, Ye J et al. (in press). Early Miocene cricetids from the Junggar Basin (Xinjiang, China) and their biochronological and paleoenvironmental implications. Geobios

Mein P, Freudenthal M, 1971. Une nouvelle classification des Cricetidae (Mammalia, Rodentia) du Tertiaire de l'Europe. Scr Geol, **2**: 1–37

Mein P, Ginsburg L, 1997. Les mammifères du gisement miocène inférieur de Li Mae Long, Thaïlande: systématique, biostratigraphie et paléoenvironnement. Geodiversitas,**19**(4): 783–844

Meng J(孟津), Ye J(叶捷), Wu W Y(吴文裕) et al., 2006. A recommended boundary stratotype section for Xiejian stage from northern Junggar Basin: implications to related bio-chronostratigraphy and environmental changes. Vert PalAsiat(古脊椎动物学报), **44**(3): 205–236(in Chinese with English summary)

Pei W Z(裴文中), Zhou M Z(周明镇), Zheng J J(郑家坚), 1963. Chinese Cenozoic. Beijing: Science Press. 1-33(in Chinese)

Peng S L(彭希龄), 1975. Cenozoic vertebrate localities and horizons of Dzungaria Basin, Sinkiang. Vert PalAsiat(古脊椎动物学报), **13**(3): 185-189(in Chinese)

Qiu Z D(邱铸鼎), 1996. Middle Miocene Micromammalian Fauna from Tunggur, Nei Mongol. Beijing: Science Press. 1-216(in Chinese with English summary)

Qiu Z D(邱铸鼎), 2010. Cricetid rodents from the Early Miocene of Xiacaowan Formation, Sihong, Jiangsu. Vert PalAsiat (古脊椎动物学报), **48**(1): 27-47

Schaub S, 1925. Die hamsterartigen Nagetiere des Tertiärs. Abh Schweiz Palaeont Gesell, **45**: 1-100

Sen S, 1997. Magnetostratigraphic calibration of the European Neogene mammal chronology. Palaeogeogr, Palaeoclimatol, Palaeoecol, **133**: 181-204

Steininger F F, 1999. The continental European Miocene. Chronostratigraphy, geochronology and biochronology of the Miocene European Land Mammal Mega-Zones (ELMMZ) and the Miocene Mammal-Zones (MN-Zones). In: Rössner G E, Heissig K eds. The Miocene Land Mammals of Europe. München: Verlag Dr F Pfeil. 9-24

Sun J M, Ye J, Wu W Y et al., 2010. Late Oligocene-Miocene mid-latitude aridification and wind patterns in Asian interior. Geology, **38**: 515-518

Theocharopoulos C D, 2000. Late Oligocene-Middle Miocene *Democricetodon*, *Spanocricetodon* and *Karydomys* n. gen. from the eastern Mediterranean area. Gaia, **8**: 1-103

Tong Y S(童永生), 1989. A new species of *Sinolagomys* (Lagomorpha, Ochotonidae) from Xinjiang. Vert PalAsiat(古脊椎动物学报), **27**(2): 103-116(in Chinese with English summary)

Tong Y S(童永生), Qi T(齐陶), Ye J(叶捷) et al., 1990. Tertiary stratigraphy of the north of Junggar Basin, Xinjiang. Vert PalAsiat(古脊椎动物学报), **28**(1): 59-70(in Chinese with English summary)

Wu W Y(吴文裕), Ye J(叶捷), Meng J(孟津) et al., 1998. Progress of the study of Tertiary biostratigraphy in North Junggar Basin. Vert PalAsiat(古脊椎动物学报), **36**(1): 24-31(in Chinese with English summary)

Ye J, Meng J, Wu W Y, 2003. Oligocene/Miocene beds and faunas from Tieersihabahe in the northern Junggar Basin of Xinjiang. Bull Am Mus Nat Hist, **279**: 568-585

Ye J(叶捷), Wu W Y(吴文裕), Meng J(孟津) et al., 2000. New results in the study of Tertiary biostratigraphy in the Ulungur River Region of Xinjiang, China. Vert PalAsiat(古脊椎动物学报), **38**(3): 192-202 (in Chinese with English summary)

Ye J(叶捷), Wu W Y(吴文裕), Meng J(孟津), 2001a. Tertiary stratigraphy in the Ulungur River Area of the northern Junggar Basin of Xinjiang. J Stratigr(地层学杂志), **25**(3): 193-200(in Chinese with English abstract)

Ye J(叶捷), Wu W Y(吴文裕), Meng J(孟津), 2001b. The age of Tertiary strata and mammal faunas in Ulungur River Area of Xinjiang. J Stratigr(地层学杂志), **25**(4): 283-287(in Chinese with English abstract)