

贝加尔湖区中中新世 Aya 洞穴地点 戈壁古仓鼠一新种

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摘要:报道了产自贝加尔湖区中中新世 Aya 洞穴的戈壁古仓鼠 (*Gobicricetodon*) 一新种 *G. filippovi* sp. nov.。该种以较小的个体和牙齿上的一些原始特征区别于该属其他种类。先前的研究认为 *Gobicricetodon* 与近古仓鼠 (*Plesiodipus*) 同属于戈壁古仓鼠亚科,然而,它们与欧亚大陆一些置于古仓鼠亚科 (*Cricetodontinae*) 内的属在牙齿形态上的高度相似性表明其亲缘关系。为了理清 *Gobicricetodon* 和 *Plesiodipus* 与 *Cricetodontinae* 之间的系统发育关系,也为了阐明这一类群属和属以上级别的分类,使用 Mesquite 2.72 软件作了分支系统学分析。结果获得了3个主要的分支类群, *Gobicricetodon*, *Plesiodipus*, *Mixocricetodon* 和 *Tsaganocricetus* 同属于其中的一个分支。令人惊奇的是,一些欧洲古仓鼠 (*Cricetodon*) 的种,包括其模式种 *C. sansaniensis* 也在这一分支内。此外,支序分析还显示上述类群可能起源于欧亚大陆西部的 *Cricetodon* 支系。分析的另一项结果指示, *Cricetodon* 属显然是一个多系类群,需要进一步划分为多个属。

关键词: 贝加尔湖, 中中新世, 哺乳动物, 古仓鼠亚科, 系统发育

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A NEW SPECIES OF *GOBICRICETODON* QIU, 1996 (MAMMALIA, RODENTIA, CRICETIDAE) FROM THE MIDDLE MIOCENE AYA CAVE, LAKE BAIKAL

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Abstract A new species of *Gobicricetodon* is described from the Middle Miocene of Aya Cave in the Lake Baikal area. It differs from the other species of this genus by its smaller size and some primitive characters of the dentition. In previous studies, *Gobicricetodon* together with *Plesiodipus* has been considered as belonging to a distinct Subfamily Gobicricetodontinae. However, great similarities of dentition suggest affinities with several other Eurasian genera grouped in the subfamily Cricetodontinae. To clear up phylogenetic relationships of *Gobicricetodon* and *Plesiodipus* with Cricetodontinae, and to enlighten generic and supra-generic systematics of this group, a cladistic analysis using Mesquite 2.72 was done. It reveals three main clades. One of them groups *Gobicricetodon* and *Plesiodipus* together with the genera *Mixocricetodon* and *Tsaganocricetus* and, surprisingly, with some European species of *Cricetodon*, including its type species *C. sansaniensis*. In addition, this analysis suggests an origin for the group from within a *Cricetodon*-stock of western Eurasia. Another result of this study is that the genus *Cricetodon* is

apparently polyphyletic and needs division into several genera.

Key words Lake Baikal; Middle Miocene; Cricetodontinae; Mammalia; phylogeny

1 Introduction

The aim of the present paper is to describe a new species of Cricetodontinae from the Middle Miocene locality of Aya Cave, which is situated along the southwestern shore of Lake Baikal (Russian Federation) (Fig. 1). The coordinates of the site are $N52^{\circ}47'37''$ and $E106^{\circ}37'25''$. This study has also led to new views on the origin and paleobiogeographic relationships of the eastern Asian representatives of this subfamily.

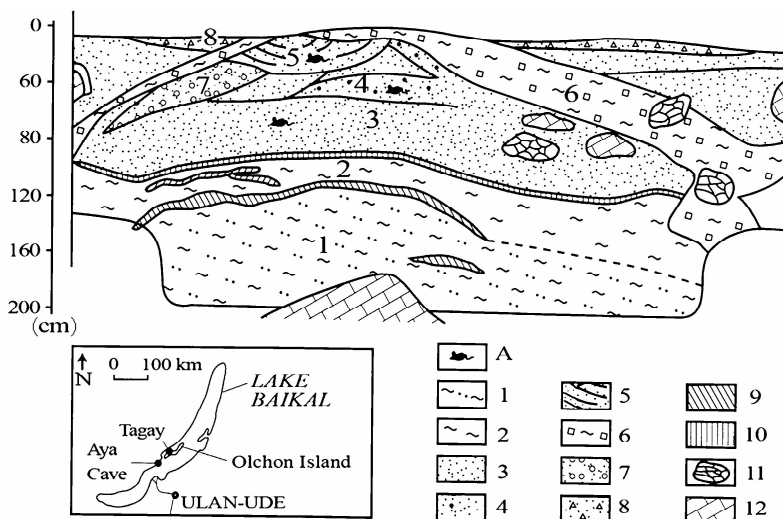


Fig. 1 The location map of the Miocene mammal localities (Aya Cave and Tagay) in the Baikal Lake area, and the stratigraphy of deposits in Aya Cave (after Erbajeva and Filippov, 1997, modified)

A. horizons with concentrations of Middle Miocene mammals; 1. white argillite; 2. white sandy clay; 3. sand; 4. sandy gravel; 5. sand; 6. dark-brown soil; 7. lens with coarse gravel; 8. sand with rock debris; 9. yellowish sandy clay; 10. brown laminated clay; 11. dropstone; 12. basement marble

In the Baikal area, Miocene mammal faunas are poorly documented. The two sites from which some mammalian taxa are described are Tagay on Olchon Island and Aya Cave (Logatchev et al., 1964, 1982; Erbajeva and Filippov, 1997). They were both considered Early Miocene. However, a recent investigation at the Tagay section (Daxner-Höck et al., in press) clearly shows that this locality includes a late Middle Miocene vertebrate fauna, tentatively correlated to the European mammalian zone MN7/8. Concerning the Aya Cave locality, as shown below, its age likely is older, i. e. MN6 or early Middle Miocene. These sites provide the most northern record of Middle Miocene mammals in East Asia.

Erbajeva and Filippov (1997) and Filippov et al. (2000) have already documented the location, stratigraphy, vertebrate record and biostratigraphy of Aya Cave. This cave is developed in Archean age graphitic marbles, and is at present 240 m above the Baikal Lake surface. It is filled by about two metres of detrital sediments (Fig. 1). Layers 3 to 5 yielded the mammalian remains that Erbajeva and Filippov (1997) identified as *Amphilagus* cf. *A. fontannesi*, *Plesiosminthus* aff. *P. myarion*, Dipodidae indet., and *Cricetodon* cf. *C. sansaniensis*. The dipodids were later referred by Lopatin (2001) to a new species *Heterosminthus erbajevae*. The

cricetid is described here as a new species of *Gobicricetodon*. The material under study was collected by A. G. Filippov in 1987 in layers 4 and 5 by washing and screening sediments. The specimens are numbered as AC4- or AC5- (Aya Cave layer 4 or 5) according to their origin. They are stored in the collections of the Muséum National d'Histoire Naturelle in Paris.

The nomenclature used for cricetid tooth terminology is after Mein and Freudenthal (1971b). All specimens are illustrated as being from the left side; right side specimens are reversed and their labels are underlined. The measurements (mm) are maximum lengths and widths of teeth.

2 Systematic paleontology

Order Rodentia Bowdich, 1821

Family Cricetidae Rochebrune, 1883

Subfamily Cricetodontinae Stehlin & Schaub, 1951

Genus *Gobicricetodon* Qiu, 1996

Gobicricetodon filippovi sp. nov.

(Figs. 2, 3)

1997 *Cricetodon* cf. *C. sansaniensis* Erbajeva & Alexeeva, p. 242

1997 *Cricetodon* cf. *C. sansaniensis* Erbajeva & Filippov, p. 255, fig. 5a,b

2000 *Gobicricetodon* sp. Filippov et al., p. 760 – 761

Holotype Left maxilla with M1-M3, AC4-1 (M1-M3 = 7.66; M1 = 3.24 × 1.95; M2 = 2.44 × 2.00; M3 = 2.10 × 1.98)

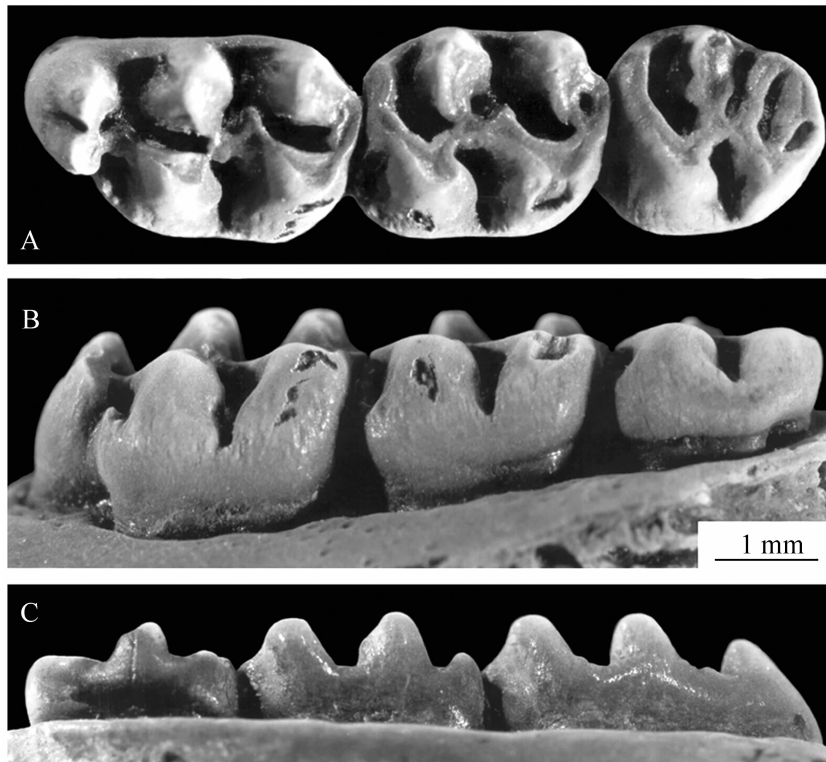


Fig. 2 *Gobicricetodon filippovi* n. sp., holotype, AC4-1, M1-M3 sin in occlusal (A), lingual (B) and labial (C) views

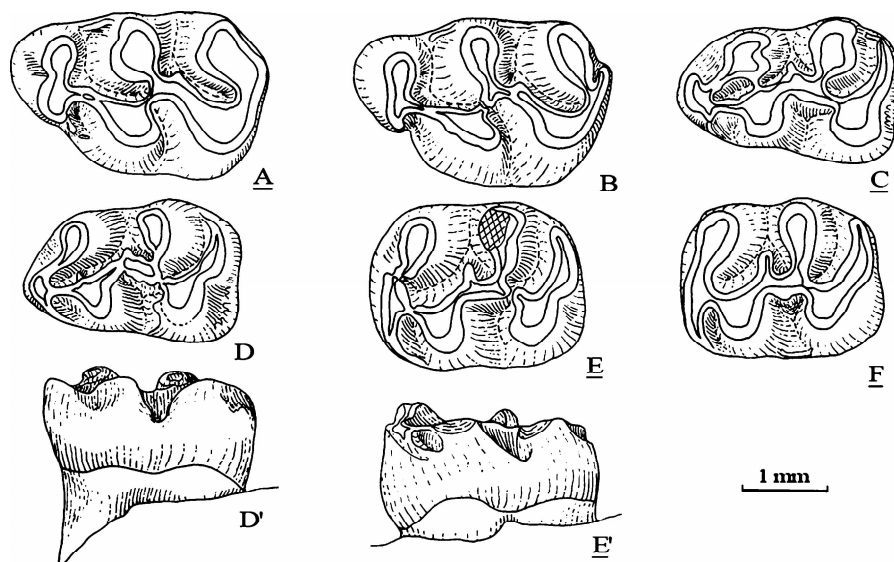


Fig. 3 *Gobicricetodon filippovi* n. sp.

A. M1 dex (reversed) AC5-2; B. M1 sin, AC5-1; C. m1 dex (reversed), AC4-2; D. m1 sin, AC5-4; E. m2 dex (reversed), AC5-6; F. m2 dex (reversed), AC5-7; D' and E' are labial views of m1 and m2, respectively

Other specimens 3 M1 (3.14×2.09 , 3.05×2.04 and $- \times 2.10$; AC5-1 to 3), 3 m1 (2.55×1.66 , 2.75×1.79 and 2.82×1.75 ; AC5-4 and 5, AC4-2), 2 m2 (2.40×1.94 and 2.54×2.00 ; AC5-6 and 7).

Type locality Aya Cave, eastern shore of Lake Baikal, Russian Federation.

Etymology Dedicated to Andrey G. Filippov, from the East Siberian Research Institute of Geology in Irkutsk, who collected the material under study.

Diagnosis Middle sized Cricetodontinae with upper and lower molars developing strong connections between paracone-hypocone and protoconid-entoconid, respectively. Upper molars without ectoloph, with a proverse (anteriorly directed) lingual sinus and three roots. M1 with a well divided anterocone and short mesoloph. Lower m1 with a simple anteroconid and two posterior ridges running separately to the protoconid and metaconid.

Differential diagnosis This species differs from all *Cricetodon* species in having a well formed "middle oblique crest" on both upper and lower molars, and three roots on M1 and M2. It differs from *Gobicricetodon flynni* (type species) by its smaller size, the less proverse sinus on the upper molars, a more divided anterocone on M1, the lack of ectoloph on M1 and M2, and double posterior connections from the m1 anteroconid. It differs from *G. robustus* in being smaller in size, and in having a wider anteroconid and a weaker hypoconid-entoconid connection.

Description M1 has a typical occlusal pattern in having three strong lophs formed by connections of anterocone-protocone, paracone-hypocone and metacone-posteroloph. Consequently, all sinuses are oblique, the lingual one anteriorly directed, and the labial ones posteriorly directed (from the margin of the tooth). The anterocone is divided in two distinct cusps with a marked anterior groove on two specimens while on two others the cusps are largely confluent, and the anterior groove is much less marked. In two specimens the protosinus is partly closed by a low cingulum issuing from the lingual anterocone. The anterocone width is about half of the maximum width of M1. The ectoloph is absent both on the labial anterocone and on the paracone. The posterior arm of the protocone is weak, and consequently the protocone-endoloph connection remains weaker than the other connections. On the contrary, the paracone and hypocone are strongly connected via an oblique crest. The mesoloph is very short; howev-

er, two specimens have a remnant of mesoloph in the mesosinus. The lingual sinus is open, while the anterosinus and mesosinus are closed by low ridges. There are three roots, of which the lingual one is large and transversely compressed.

Only one M2 is available. The lingual branch of the anteroloph is a weak and low crest, while the labial branch is strong, as high as the cusps and connected to the base of the paracone by a low ridge. The connection between the protocone and endoloph is weak as on the M1. The mesoloph is very short. The sinus is proverse. The metacone has two connections, one (the metalophule) with the posterior arm of the hypocone, and the other with the labial edge of the posteroloph. Consequently, the posterosinus is enclosed as an enamel island between the metalophule and posteroloph. The number of roots cannot be observed because the M2 and M3 are included in the maxillary bone. However, in lateral view, it seems that they are three rooted.

M3 lacks the lingual anteroloph, but a depression still exists on the anterolingual face of the tooth as the remnant of the protosinus. The labial anteroloph is a strong crest connected to the base of the paracone. Thus, the anterosinus is closed. The mesoloph forms a high ridge reaching the labial border; it is connected posteriorly to the metacone. The metacone has two other connections, one with the hypocone (by metalophule) and the other with the labial edge of the posteroloph. The sinus is less proverse than in the other molars.

The m1 has an almost triangular occlusal outline. The anteroconid is a single cusp, almost as high as the main cusps, and situated slightly labial to the longitudinal axis. It has a rather strong labial arm. Two crests issue from the tip of the anteroconid, the one (anterolophulid) connected to the protoconid, the other (anterior metalophulid) to the metaconid. These two crests are equal in thickness. The posterior metalophulid is absent (1) or very weak (2) and connected to the center of the protoconid. The mesolophid is short. The protoconid-entoconid connection forms the main oblique ridge of the occlusal pattern. The anterior arm of the hypoconid is weak. Consequently, the connection of the hypoconid with the longitudinal crest remains tenuous at any stage of attrition. The sinusid is wide and transverse. The posterolophid joins the base of the entoconid by a low crest. All three specimens have a weak cingulum along the distal face of the hypoconid. This molar has two roots.

The m2 is as long as the m1. The labial anterolophid is strong while the lingual one is lost. The mesolophid is a little more developed than on the m1. The hypolophid is transverse. The hypoconid is weakly connected to the longitudinal crest. The posterolophid ends free on the lingual border, and thus the posterosinusid is widely open. There are two strong roots.

Comparison The Aya Cave specimens are homogenous in size and tooth morphology, and can be attributed to one species. They were initially described as *Cricetodon* cf. *C. sansaniensis* by Erbajeva and Filippov (1997). Direct comparisons with the type material of *C. sansaniensis* from Sansan (France) showed that *C. sansaniensis* has molars similar in size, but differing in morphology from the Aya Cave cricetid by the following characters:

(1) On the M1 and M2 of *C. sansaniensis* the connection between the paracone and hypocone is not always straight and as strong as in *Gobicricetodon* where it forms an oblique crest; instead the upper molars have connections equally strong between the main cusps.

(2) In *C. sansaniensis* the protocone-endoloph connection is strong (weak in *Gobicricetodon*).

(3) In *C. sansaniensis* the posterosinus is lost or particularly reduced on M1 and M2 because the metalophule is connected with the labial edge of the posteroloph. In *Gobicricetodon* the metalophule is double, and the posterosinus persists as an enamel island.

(4) In *C. sansaniensis* the cusps of upper molars are squared; they are rounded in the Aya Cave molars.

(5) In *C. sansaniensis* the lower molar hypoconids are strongly connected to the median ridge.

(6) On the m1 of *C. sansaniensis*, the metalophulid connections are variable; metaconid

may be isolated, may have an anterior or a posterior or double connections. The three m1 from Aya Cave have only a strong anterior metalophid.

(7) In *C. sansaniensis* the posterolophid of m1 and m2 is cusp-shaped and the constriction between the hypoconid and posterolophid is well marked. Such a constriction is not observed in our specimens.

The dental features of the Aya Cave specimens, and in particular the strong connections of certain cusps to form oblique crests on both upper and lower molars, allow their attribution to the genus *Gobicricetodon* Qiu, 1996. *Gobicricetodon*, *Plesiodipus* and *Tsaganocricetus* are large sized cricetodontines found in the Asian Miocene. The best material representing the genera *Gobicricetodon* and *Plesiodipus* is for now from the Tunggur Formation in Nei Mongol. Indeed, Qiu (1996) described two new species, *Gobicricetodon flynni* and *G. robustus*, and he designated two lower molars as *Gobicricetodon* sp. The Aya Cave specimens are attributed to the genus *Gobicricetodon* mostly because of their morphological similarities with these species: similar size, M1 with three roots, upper and lower molars with oblique crests (in particular the middle crest of M1 and m1 due to the paracone-hypocone and protoconid-entoconid connections, respectively), weak mesolophs and mesolophids, m1 anteroconid with a single cusp connected to both protoconid and metaconid (Fig. 4).

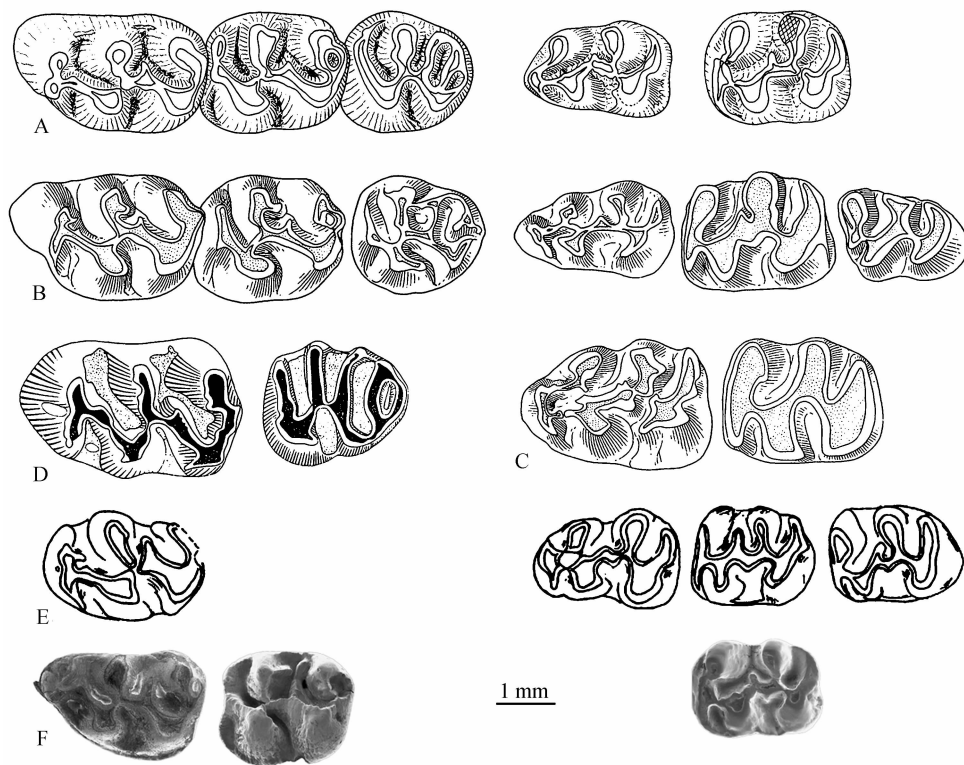


Fig. 4 Comparison of some species of *Gobicricetodon*, *Tsaganocricetus* and *Cricetodon* from East Asian Miocene localities

A. *Gobicricetodon filippovi* from Aya Cave; B. *G. flynni* from Moergen IV, Nei Mongol (after Qiu, 1996); C. *G. robustus* from Moergen V, Nei Mongol (after Qiu, 1996); D. *Tsaganocricetus irtyschensis* from Semipalatinskaya oblast, Kazakhstan (after Topachevsky and Skorik, 1988); E. *G. natalia* from Ashut, Kazakhstan (after Tyutkova, 2008); F. *Cricetodon volkeri* from the Dingshanyanchi Formation, North Junggar Basin, China (after Wu et al., 2009); all specimens are approximately to the same scale

Qiu (1996) accurately compared *Gobicricetodon* with the other genera grouped in the subfamily Cricetodontinae. Most of them are clearly different in having semi-hypsodont cheek teeth (*Byzantinia*, *Hispanomys*, *Ruscinomys*) or in having strong ectolophs on their upper molars (*Deperetomys*, *Byzantinia*, *Hispanomys*, *Ruscinomys*). Among the Cricetodontinae, some species of the genus *Cricetodon* share features with *Gobicricetodon*, such as: brachydont to mesodont crown height, globular cusps, weak protocone-endoloph connection on M1, short mesoloph and mesolophid on the first and second molars, ectolophs absent or spur-like on upper molars, m1 with simple anteroconid and its metaconid with simple or double metalophulid. However, the Early Miocene species of *Cricetodon* from Turkey and Greece, as well as *C. meini* and *C. aureus* from the Early-Middle Miocene of Europe (Mein and Freudenthal, 1971b; Klein Hofmeijer and de Bruijn, 1988; de Bruijn et al., 1993) are smaller than any *Gobicricetodon* species. *Gobicricetodon* is similar in size to some Middle Miocene representatives of *Cricetodon*, such as *C. hungaricus*, *C. sansaniensis* and *C. jotae* (Table 1). In morphology, *Gobicricetodon* differs from *Cricetodon* in having a three-rooted M1 and a strong “middle oblique crest” on upper and lower molars, as stated by Qiu (1996) (see below).

The type species of *Gobicricetodon*, *G. flynni*, differs from the Aya Cave specimens in having an M1 with a wide anterocone, ectolophs on the lingual anterocone and paracone, a much more proverse sinus, and in lacking the mesoloph. M2 and M3 of *G. flynni* also have a strong ectoloph on the paracone and a more proverse sinus, differing from the Aya Cave specimens. Concerning the m1, the main difference is lack of the anterolophulid in *G. flynni*. In *G. filippovi* n. sp., the anteroconid has two strong and distinct connections. In addition to these differences, the molars of *G. flynni* are a little larger than those of *G. filippovi* n. sp. (Table 1).

G. robustus is known only from two m1 and one m2 from the Moergen V locality in the Tunggur Formation. In size, these teeth are clearly larger than those of *G. flynni* or *G. filippovi* n. sp. Moreover, the *G. robustus* m1 has a wide anteroconid, a weak connection between the hypoconid and entoconid, and no posterior metalophulid.

A third species recently described as *Gobicricetodon natalia* Tyutkova, 2008 from late Middle Miocene (MN7/8) of Ashut, Kazakhstan, is known from four isolated molars. We believe that the molar described by Tyutkova (2008, fig. 2-4) as an m3 is in fact an m2. In size this species seems to be close to *G. flynni* and *G. filippovi*. It differs from the latter in its clearly more lophodont occlusal pattern. In addition, on its M1 the labial anterocone and paracone have posterior spurs, the anteroconid of the m1 is widened laterally, and the m2 has a strong mesolophid (Fig. 4). These characters are not seen in the Aya Cave specimens, and suggest that *G. natalia* is more derived than either of the others. Because of the differences from any known *Gobicricetodon*, the Aya Cave specimens are attributed to a new species.

The occurrence of the genus *Cricetodon* in Asia was mentioned in preliminary faunal lists from several localities, but without detailed description. Recently Wu et al. (2009) described the new species, *Cricetodon volkeri*, from the Dingshanyanchi Formation in the North Junggar Basin, Xinjiang, China. The locality is considered middle Tunggurian (Middle Miocene). The material is unfortunately poor and consists of three and half molars sharing several features with the specimens from Aya Cave: low crowned molars, M1 three rooted, anterocone of M1 slightly bilobed, ridge formation between paracone and hypocone, posterosinus of M2 enclosed as an enamel island. However, *C. volkeri* is smaller than *G. filippovi*, its M1 and M2 have strong mesolophs, and M1 has a short labial spur on the anterolophulid and a deep posterosinus (Fig. 4). Wu et al. (2009) revealed that Bi (2005) described in his PhD thesis a new species, *Cricetodon orientalis*, from the early Middle Miocene of the Halamagai Formation in the Junggar Basin. If unpublished, this new species name would be a nomen nudum.

A few other taxa from Asian localities have been included in the Cricetodontinae or Gobicricetodontinae. Among them *Plesiodipus* Young, 1927 is represented by two species (*P. leei* and

Table 1 Comparative measurements of upper and lower molars of some Cricetodontinae from Asia and Europe

Taxon	Locality	Age	Tooth	Length		N	Width		Reference
				Range	X		Range	X	
<i>Gobicricetodon filippovi</i>	Aya Cave	MN6	M1	3.05 ~ 3.24	3.14	3/4	1.95 ~ 2.10	2.05	This paper
<i>Gobicricetodon flynni</i>	Moergen IV	MN7/8	M1	—	3.50	1	—	2.25	Qiu 1996
<i>Gobicricetodon natalia</i>	Ashut	MN7/8	M1	—	>2.7	1	—	2.20	Tyutkova 2008
<i>Plesiodipus leei</i>	Moergen II	MN7/8	M1	2.65 ~ 3.10	2.84	22/25	1.75 ~ 2.00	1.87	Qiu 1996
<i>Plesiodipus progressus</i>	Moergen V	MN7/8	M1	—	2.80	1	—	1.65	Qiu 1996
<i>Tsaganocr. irtyschensis</i>	Kazakhstan	Vallesian	M1	—	3.75	1	—	2.39	Topachevsky & Skorik 1988
<i>Cricetodon meini</i>	Vx-Collonges	MN4/5	M1	2.58 ~ 3.13	2.90	105	1.82 ~ 2.11	1.96	Mein & Freudenthal 1971
<i>Cricetodon sansaniensis</i>	Sansan	MN6	M1	3.08 ~ 3.39	3.24	28	1.95 ~ 2.24	2.10	Baudelot 1972
<i>Gobicricetodon filippovi</i>	Aya Cave	MN6	M2	—	2.44	1	—	2.00	This paper
<i>Gobicricetodon flynni</i>	Moergen IV	MN7/8	M2	2.70 ~ 2.80	2.75	3/4	2.15 ~ 2.30	2.24	Qiu 1996
<i>Plesiodipus leei</i>	Moergen II	MN7/8	M2	2.05 ~ 2.40	2.22	26	1.60 ~ 1.80	1.73	Qiu 1996
<i>Plesiodipus progressus</i>	Moergen V	MN7/8	M2	2.15 ~ 2.25	2.20	2	1.45 ~ 1.50	1.48	Qiu 1996
<i>Cricetodon meini</i>	Vx-Collonges	MN4/5	M2	2.04 ~ 2.41	2.24	106	1.71 ~ 2.10	1.92	Mein & Freudenthal 1971
<i>Cricetodon sansaniensis</i>	Sansan	MN6	M2	2.24 ~ 2.51	2.38	20	1.91 ~ 2.12	2.02	Baudelot 1972
<i>Gobicricetodon filippovi</i>	Aya Cave	MN6	M3	—	2.10	1	—	1.98	This paper
<i>Gobicricetodon flynni</i>	Moergen IV	MN7/8	M3	—	2.60	1	—	2.30	Qiu 1996
<i>Tsaganocr. irtyschensis</i>	Kazakhstan	Vallesian	M3	—	1.95	1	—	1.67	Topachevsky & Skorik 1988
<i>Plesiodipus leei</i>	Moergen II	MN7/8	M3	1.50 ~ 1.80	1.63	9	1.35 ~ 1.55	1.47	Qiu 1996
<i>Cricetodon meini</i>	Vx-Collonges	MN4/5	M3	1.68 ~ 2.23	1.92	133	1.62 ~ 2.07	1.80	Mein & Freudenthal 1971
<i>Cricetodon sansaniensis</i>	Sansan	MN6	M3	1.80 ~ 2.07	1.94	18			Baudelot 1972
<i>Gobicricetodon filippovi</i>	Aya Cave	MN6	m1	2.55 ~ 2.82	2.71	3	1.66 ~ 1.79	1.73	This paper
<i>Gobicricetodon flynni</i>	Moergen IV	MN7/8	m1	—	2.85	1	—	1.85	Qiu 1996
<i>Gobicri. robustus</i>	Moergen V	MN7/8	m1	—	3.35	1/2	2.30 ~ 2.35	2.33	Qiu 1996
<i>Gobicricetodon natalia</i>	Ashut	MN7/8	m1	—	2.60	1	—	1.70	Tyutkova 2008
<i>Plesiodipus leei</i>	Moergen II	MN7/8	m1	2.10 ~ 2.35	2.23	22	1.25 ~ 1.70	1.47	Qiu 1996
<i>Plesiodipus progressus</i>	Moergen V	MN7/8	m1	—	2.60	1	—	1.50	Qiu 1996
<i>Cricetodon meini</i>	Vx-Collonges	MN4/5	m1	2.19 ~ 2.57	2.41	90	1.42 ~ 1.73	1.57	Mein & Freudenthal 1971
<i>Cricetodon sansaniensis</i>	Sansan	MN6	m1	2.62 ~ 2.88	2.75	24	1.71 ~ 1.89	1.80	Baudelot 1972
<i>Gobicricetodon filippovi</i>	Aya Cave	MN6	m2	2.40 ~ 2.54	2.47	2	1.94 ~ 2.00	1.97	This paper
<i>Gobicricetodon flynni</i>	Moergen IV	MN7/8	m2	—	2.55	1	—	2.20	Qiu 1996
<i>Gobicri. robustus</i>	Moergen V	MN7/8	m2	—	2.90	1	—	2.20	Qiu 1996
<i>Gobicricetodon natalia</i>	Ashut	MN7/8	m2	2.30 ~ 2.60	2.45	2	2.05 ~ 2.10	2.08	Tyutkova 2008
<i>Plesiodipus leei</i>	Moergen II	MN7/8	m2	2.10 ~ 2.30	2.20	23/24	1.60 ~ 1.90	1.70	Qiu 1996
<i>Plesiodipus progressus</i>	Moergen V	MN7/8	m2	2.25 ~ 2.50	2.40	3	1.55 ~ 1.65	1.60	Qiu 1996
<i>Cricetodon meini</i>	Vx-Collonges	MN4/5	m2	2.14 ~ 2.51	2.33	88	1.71 ~ 2.05	1.83	Mein & Freudenthal 1971
<i>Cricetodon sansaniensis</i>	Sansan	MN6	m2	2.42 ~ 2.68	2.55	25	1.92 ~ 2.10	2.01	Baudelot 1972
<i>Gobicricetodon flynni</i>	Moergen IV	MN7/8	m3	—	2.30	1	—	1.80	Qiu 1996
<i>Plesiodipus leei</i>	Moergen II	MN7/8	m3	1.95 ~ 2.30	2.05	18	1.40 ~ 1.80	1.55	Qiu 1996
<i>Plesiodipus progressus</i>	Moergen V	MN7/8	m3	—	2.60	1	—	1.65	Qiu 1996
<i>Cricetodon meini</i>	Vx-Collonges	MN4/5	m3	2.05 ~ 2.77	2.36	101	1.56 ~ 2.09	1.80	Mein & Freudenthal 1971
<i>Cricetodon sansaniensis</i>	Sansan	MN6	m3	2.42 ~ 2.57	2.50	16	1.74 ~ 2.00	1.87	Baudelot 1972

P. progressus) from the Middle Miocene of China, and a third poorly documented one from Tibet (? *P. tibetensis*). Qiu (1996) included this genus in his new subfamily Gobicricetodontinae. *Tsaganocricetus irtyschensis* Topachevsky & Skorik, 1988 from the Late Miocene of Semipalatinskaya, and *T. turgaiensis* Bendukidze, 1993 from the Middle Miocene of Kentiobek, both localities in western Kazakhstan, were attributed by their authors to Cricetodontinae. Indeed, the occlusal pattern of molars in *Plesiodipus* and *Tsaganocricetus* reproduces the main structures of the cricetodontine dentition. However, compared to *Gobicricetodon*, these genera have higher crowned teeth; the occlusal pattern is lophodont with strong and high crests, and thus they recall microtoid cricetids. Their attribution to the Cricetodontinae seems justified since they possess the main characters of the basic dental pattern seen in *Cricetodon*. According to Qiu (1996), *Plesiodipus* originated from a “*Cricetodon* stock”, and evolved towards the Asiatic endemic group Myospalacinae. The relationships of *Tsaganocricetus* remain unclear due to the poor documentation.

Another species to be compared with *Gobicricetodon* is *Aralocricetodon schokensis* Bendukidze, 1993 from the locality of Altyn Schokysu in western Kazakhstan. Bendukidze (1993) described one M1, but Lopatin (2004) and Bendukidze et al. (2009) referred to this species a rich material from the same locality. Its age is Early Miocene according to Lopatin (2004) but Late Oligocene according to Bendukidze et al. (2009). In some characters, this species is like *Gobicricetodon*: upper molars three rooted, weak protocone-paracone connection on M1 and M2, presence of a posterosinus on upper molars, strong connections between the anterocone-protcone and paracone-hypocone on the M1 and between protoconid-entoconid on the m1 and m2, anteroconid of the m1 with double connections to the metaconid and to the protoconid. However, this species differs from all species of *Gobicricetodon* in being much smaller (the holotype M1 measures 2.15×1.37 ; Bendukidze, 1993), the oblique ridges of the upper and lower molars are not yet fully formed, the posterosinus of upper molars is deep because of the metalophulid still directed to the posterior arm of the hypocone, and the lower molars have a strong mesolophid. Bendukidze et al. (2009) referred *Aralocricetodon schokensis* to the family of Tachyoryctoididae because of some similarities with *Tachyoryctoides*, but we believe that *Aralocricetodon* is better grouped with the Cricetodontinae.

The number of roots (three or four) in upper molars has been used as a diagnostic feature to distinguish species and sometimes genera. *Gobicricetodon*, *Aralocricetodon*, *Mixocricetodon* and some early representatives of the genus *Cricetodon* (*C. versteegi*, *C. kasapligili*, *C. tobieni* and *C. volkeri*) have upper molars with three roots, while the other representatives of Cricetodontinae have four roots. In fact, the presence of three roots in upper molars is a plesiomorphic feature that these genera share with many muroids of the Paleogene and early Neogene. The presence of four roots in upper molars is a derived state in Cricetodontinae, since the fourth root appears by the subdivision of a large lingual root. It is not excluded that this evolutionary process may have occurred independently in different lineages. As a primitive state, the presence of three roots on upper molars of *Mixocricetodon dehmi* Rummel, 1997 from the Middle Miocene of Petersburg in Germany as well as in *Gobicricetodon* and *Aralocricetodon* is not a diagnostic feature.

When describing the new genus *Gobicricetodon*, Qiu (1996) erected a new subfamily Gobicricetodontinae, including *Gobicricetodon* and *Plesiodipus* Young, 1927. He was followed in this by McKenna and Bell (1997). However, the dentition of *Gobicricetodon* displays many characters shared with the genera included in the subfamily Cricetodontinae, and in our opinion little distinguishes these two genera at the subfamily level. This opinion is also shared by Tyutkova (2008). Zazhigin (2003) suggested synonymy of *Gobicricetodon* with *Tsaganocricetus* Topachevsky & Skorik, 1988, another large cricetodontine from the Vallesian of Kazakhstan. However, this genus is too poorly documented (scarce material, descriptions and illustrations inappropriate for observation) to be helpful to solve the questions of synonymy of the genera or of these two subfamilies. In summary, our knowledge on this group of large hamsters in Asia is too poor to assess their synonymy without a detailed investigation of their evolutionary trends.

3 Systematics and phylogeny

Most large sized fossil hamsters of Eurasia and North Africa are grouped in the tribe Cricetodontini which includes, according to McKenna and Bell (1997), 13 genera: *Lartetomys*, *Fahlbuschia*, *Renzimys*, *Pseudofahlbuschia*, *Cricetodon*, *Deperetomys*, *Metamys*, *Byzantinia*, *Hispanomys*, *Zramys* and *Ruscinomys*. In addition, these authors retained the genera *Tsaganocricetus* and *Aralocricetodon* as Cricetodontinae incertae sedis, and *Gobicricetodon* and *Plesiodipus* apart in the subfamily Gobicricetodontinae. Qiu (1996) erected the subfamily Gobicricetodontinae based on the presence of a prominent “middle oblique crest” on both the upper and lower molars of *Gobicricetodon* and *Plesiodipus*. To a lesser extent, this character also occurs in some species of *Cricetodon* (e. g. *C. sansaniensis* and *C. soriae*) and in most species of *Byzantinia*, *Hispanomys* and *Ruscinomys*. Actually, the “middle oblique crest” of upper molars is formed by the strengthened crests between the paracone and hypocone, in particular when the posterior protolophule is directed posteriorly and the ridge is not interrupted by a funnel. In lower molars, the “middle oblique crest” exists when the protoconid and entoconid are firmly connected by strong crests, in particular when the hypolophulid is aligned with the protoconid. As noted above, this character is not restricted to the species included in Gobicricetodontinae; some other Eurasian cricetodontines have a tendency to develop a lophodont molar pattern. Consequently, the occurrence of a “middle oblique crest” cannot be used as a diagnostic feature for a high taxon like a new subfamily. The other characters used by Qiu (1996) as characteristic for Gobicricetodontinae (mesodont and bunolophodont cheek teeth, M1 three/four rooted, anterocone (id) and ectoloph weak, etc.) are commonly observed in several species of *Cricetodon* (see de Bruijn et al., 1993). Therefore, the synonymy of Gobicricetodontinae with the Cricetodontinae seems reasonable. To check this hypothesis, a phylogenetic analysis of the taxa included in Cricetodontinae and Gobicricetodontinae will be more instructive than a traditional systematic approach.

Another reason to analyze phylogenetic relationships between the main taxa included in the Cricetodontinae is that at least 20 species are referred to the genus *Cricetodon*. Their time range spans from the earliest Miocene to Late Miocene, and the pattern of the dentition differs greatly from one species to another. For instance, if we consider the species *C. kasapligili* from Early Miocene of Turkey with a simple dental pattern, and *C. sansaniensis* from the Middle Miocene of France (type species of the genus *Cricetodon*), it is obvious that the latter species has a much more complicated dental pattern than the first one. One can wonder if the content of this genus is homogenous. In addition, Qiu (1996) rightly noted that *Gobicricetodon* and *Plesiodipus* are probably derived from a *Cricetodon*-like ancestral stock, but without indicating which species of *Cricetodon*. In summary, Cricetodontinae has become so large and systematic groupings at the genus, tribe and subfamily levels so contradictory that the systematics of this group deserves a phylogenetic approach to enlighten the relationships of taxa.

Several authors have tentatively proposed some groupings of species and genera, or used traditional phylogenetic trees, although no one applied parsimony analysis (Mein and Freudenthal, 1971a; Aguilar, 1982; Agusti, 1982; de Bruijn et al., 1993; de Bruijn and Ünay, 1996; Qiu, 1996). To clear up species level relationships within the Cricetodontinae + Gobicricetodontinae, and to enlighten generic and supra-generic systematics of this group, a cladistic analysis using Mesquite version 2.72 (Maddison and Maddison, 2009) was conducted (Fig. 5). The selected outgroup taxon is *Democricetodon anatolicus* Theocharopoulos (2000), a species well documented in Early Miocene (MN1-2) localities in Turkey. It presents many plesiomorphic characters of early cricetids. Among the Cricetodontinae + Gobicricetodontinae, we selected 33 species reliably documented in Early to Late Miocene localities of Eurasia. These species and related information are given in Appendix 1.

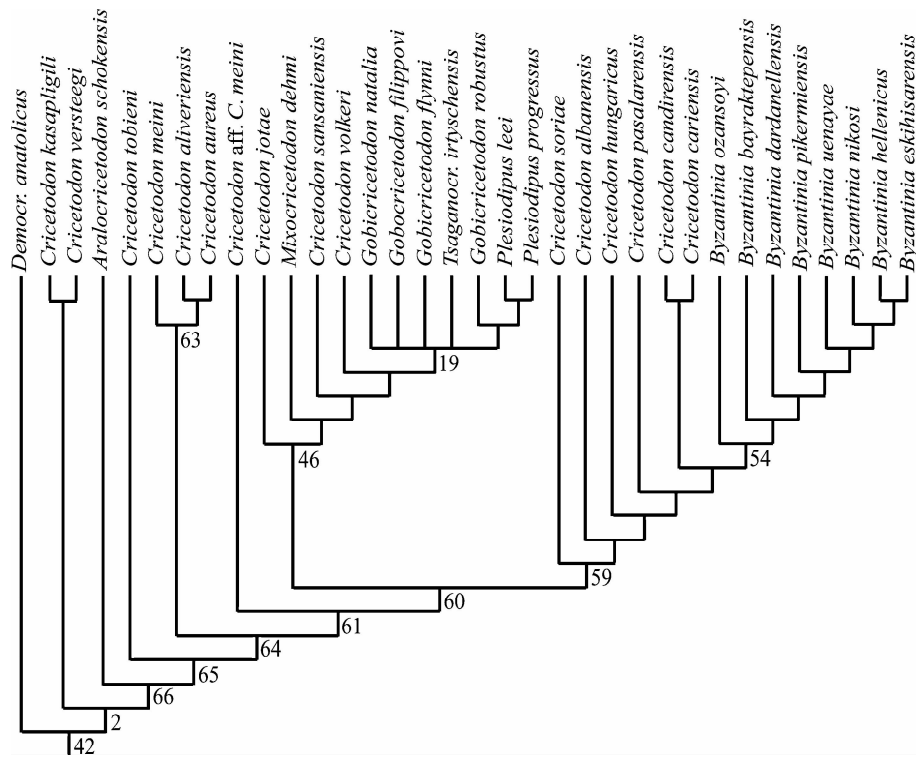


Fig. 5 Cladogram illustrating the relationships among the species referred to the genera *Cricetodon*, *Aralocricetodon*, *Mixocricetodon*, *Byzantinia*, *Tsaganocricetus*, *Gobicricetodon* and *Plesiodipus*
Tree length 277, consistency index 0.484 and retention index 0.621

As shown in Appendix 1, the samples analyzed for character states are almost all from their type localities. The species referred to the genera *Deperetomys*, *Fahlbuschia*, *Renzimys*, *Pseudofahlbuschia*, *Hispanomys* and *Ruscinomys* are not included in this analysis. *Deperetomys* has a peculiar dentition with many characters different from all other Cricetodontinae: slender cusps and long ridges connecting them, wide anteroconid on m1, sinuous ectolophs on upper molars, etc. (see de Bruijn et al., 1993). The genera *Fahlbuschia*, *Renzimys*, *Pseudofahlbuschia* and *Hispanomys* are restricted to the Iberian Peninsula, even though some records from a few Late Miocene localities of southern France have been referred to these genera. In other words, these genera are apparently endemic to southwestern Europe. The genus *Ruscinomys* includes derived species of Cricetodontinae having semi-hypsodont or hypsodont and lophodont molars. It is restricted to SW Europe during Late Miocene (Turolian) and Pliocene time, with a short incursion into North Africa across the Miocene-Pliocene transition. The phylogenetic relationships of western European genera and lineages have been debated by several authors (Mein and Freudenthal, 1971a,b; Agusti, 1982; Casanovas-Vilar, 2007). The prolific diversification of Cricetodontinae in SW Europe is beyond the scope of the present study.

Herein, we retained 33 species from Asia and Europe. They are not equally documented. The data for species from Turkey (*Cricetodon* and *Byzantinia*) and for all *Cricetodon* species from Europe are rich enough to analyse accurately character states of upper and lower molars and to take into account intraspecific variations. This is not the case for species from Asian localities, where most species are poorly documented; e. g. two molars for *Tsaganocricetus irtyschensis*, three for *Gobicricetodon robustus*, four for *G. natalia*, and four for *Cricetodon volkeri*. This im-

plies that the systematic resolutions of the present cladistic analysis suffer from the state of documentation, and they need to be improved with better knowledge of the Asiatic cricetodontines.

Forty-two phylogenetically informative characters of upper and lower molars were selected and their character states were identified using the main diagnostic features used in the descriptions of species (Appendix 2, 3); 23 of them are binary and 19 are multistate. Due to the lack of *a priori* information, the weight of all characters is identical (1). Because there is no rationale to order the multistate characters, all possible transformations of one state into another will cost one step. The relatively high number of terminal taxa and characters precluded the use of exact algorithms, so a heuristic search by stepwise addition ('closest' option) was performed. One most-parsimonious tree (Consensus tree) was generated, with the following characteristics: tree length = 277, CI = 0.484 and RI = 0.621.

The consensus tree differentiates three main clades in addition to unresolved branching of some *Cricetodon* and *Aralocricetodon* species:

Clade 1 (Node 63) includes some Early Miocene species from Europe, i. e. *Cricetodon aliveriensis*, *C. meini* and *C. aureus*. They are the earliest cricetodontines of Europe.

Clade 2 (Node 46) includes eleven species attributed to the genera *Cricetodon*, *Mixocrice-ton*, *Tsaganocricetus*, *Gobicricetodon* and *Plesiodipus*. According to this analysis, the Asiatic genera *Tsaganocricetus*, *Gobicricetodon* and *Plesiodipus* are derived from a *Cricetodon*-like ancestral stock as suggested by Qiu (1996). This analysis shows also that the type species of *Cricetodon*, *C. sansaniensis*, is grouped in the same clade together with *Gobicricetodon* and *Plesiodipus*. This suggests that the taxon *Gobicricetodontinae* is invalid at the subfamily level. In addition, the species *Mixocrice-ton dehmi*, from the Petersbuch fissure fillings (MN5/6) in Germany is intimately close to *Cricetodon jotae* and *C. sansaniensis*. This species was discriminated from the genus *Cricetodon*, mainly based on the presence of three roots and strong mesolophs on upper molars (Rummel, 1997). These characters, as discussed above, are plesiomorphic and shared with many Paleogene and early Neogene cricetids. As de Bruijn et al. (1993) rightly noted, the upper molars of *Cricetodon* may have three or four roots depending on the evolutionary step of the species. In addition, the mesolophs of upper molars in *M. dehmi* are not especially strong, contra Rummel (1997). *C. aliveriensis* from Early Miocene (MN4) of Greece has mesolophs as strong as or even stronger than in *M. dehmi* (Klein Hofmeijer and de Bruijn, 1988). Consequently, this species is better grouped within the genus *Cricetodon*.

Clade 3 (Node 59) includes 14 species referred to the genera *Cricetodon* and *Byzantinina*. It is interesting to note that two western and one central European species of *Cricetodon* (*C. soriae*, *C. albanensis* and *C. hungaricus*) as well as those from Turkey (*C. pasalarensis*, *C. candirensis* and *C. cariensis*) are included in this clade, together with the species of *Byzantinina*. The Turkish Middle Miocene *Cricetodon* species appear closely related to *Byzantinina*, although not uniquely grouped with this genus. We have to remember that these species were initially described as belonging to a different genus, *Turkomys* Tobien, 1978. Later on, Boon (1991) synonymized *Turkomys* with *Cricetodon*. Most later students (de Bruijn et al., 1993; de Bruijn and Ünay, 1996; Rummel, 1998) accepted this view without discussion. We believe that the attribution of these three species to the genus *Cricetodon*, as suggested by Boon (1991), should be reconsidered.

A special remark concerns the Early Miocene *Cricetodon* species from Turkey, i. e. *Cricetodon versteegi*, *C. tobieni* and *C. kasapligili*. The present parsimony analysis attributes to them a basal position in the tree but unresolved for their phylogenetic relationships. These species are "primitive" in having simple dental patterns seen in several species of the genera *Eucricetodon*, *Democricetodon* and *Spanocricetodon*. Our opinion is that these species cannot belong to the genus *Cricetodon*. All these observations show that the genus *Cricetodon*, as understood at present, is polyphyletic.

4 Conclusions

A new species of *Gobicricetodon* is described from the Middle Miocene deposits of Aya Cave on Olchon Island, Lake Baikal. The pattern of its molars is characterized by a strong trend to form oblique lophs, similar to the condition in species referred to the genera *Gobicricetodon*, *Tsaganocricetus* and *Plesiodipus*. The analysis of morphological resemblances between *Gobicricetodon* and *Cricetodon* brings us to the conclusion that the former genus, as well as other Asian genera (*Tsaganocricetus* and *Plesiodipus*), may be derived from an Early Miocene representative of *Cricetodon*. The best candidates for their ancestry are the Early Miocene species of *Cricetodon* from Turkey (*C. versteegi*, *C. kasapligili* and *C. tobieni*), where the Cricetodontinae seem to have flourished during the Miocene (de Bruijn et al., 1993) or *Aralocricetodon* from Late Oligocene or Early Miocene of Central Asia. In these species, the size is small and the dental pattern is still quite “primitive” (brachyodont cheek teeth, upper molars without ectoloph, mesolophs and mesolophids still quite strong, m1 metaconid often with a double metalophulid, etc.).

To clear up species level relationships within the Cricetodontinae, to test the monophyly of this subfamily and, in particular, to enlighten the phylogenetic relationships of the species referred to *Gobicricetodon*, a cladistic analysis was conducted. This analysis revealed three main clades, one of them grouping the genera included in the “Gobicricetodontinae” together with *Mixocricetodon*, *Tsaganocricetus*, and several species of *Cricetodon* (*C. jotae*, *C. sansaniensis*, *C. volkeri*). Gobicricetodontines are shown to form a derived taxon, but within Cricetodontinae, and not at the subfamily level. In conclusion, it can be suggested that *Gobicricetodon* is derived from a *Cricetodon*-stock and immigrated to East Asia some time during the Early-Middle Miocene.

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Appendix 1 The ingroup taxa retained for phylogenetic analysis

- Cricetodon hungaricus* (Kordos 1986); Hasznos, Hungary; MN6, de Bruijn et al. 1993.
- C. versteegi* de Bruijn et al. 1993; Kılçak 3a, Turkey; MN1.
- C. tobieni* de Bruijn et al. 1993; Horlak 1a, Turkey; MN4.
- C. kasapligili* de Bruijn et al. 1993; Keseköy, Turkey; MN3.
- C. aliveriensis* Klein Hofmeijer & de Bruijn 1988; Aliveri, Greece; MN4.
- C. pasalarensis* (Tobien 1978); Paşalar, Turkey; MN5, Ünay 1990.

- C. candirensis* (Tobien 1978); Çandır, Turkey; MN6, de Bruijn et al. 2003.
C. cariensis (Sen & Ünay 1979); Sarıçay, Turkey; MN7/8, Rummel 1998.
C. meini Freudenthal 1963; Vieux-Collonges, France; MN4/5, Mein and Freudenthal 1971a.
C. aff. C. meini Freudenthal 1963; Ebershausen, Germany; MN6, Boon 1991.
C. aureus Mein & Freudenthal 1971b; Vieux-Collonges, France; MN4/5.
C. sansaniensis Lartet 1851, type species of *Cricetodon*; Sansan, France; MN6, Baudelot 1972.
C. albanensis Mein & Freudenthal 1971a; La Grive M, France; MN7/8.
C. jotae Mein & Freudenthal 1971a; Manchones, Spain; MN6.
C. soriae Hernandez Fernandez et al. 2006; Somosaguas, Spain; MN5.
C. volkeri Wu et al. 2009; Dingshanyanchi Formation, North Junggar Basin, China; middle Tunggurian.
Mixocricetodon dehmi Rummel 1997; Petersbuch 31, Germany; MN5/6.
Aralocricetodon schokensis Bendukidze 1993; Altyn Schokysu, Kazakhstan; Late Oligocene or Early Miocene; Bendukidze et al. 2009.
Byzantinia nikosi de Bruijn 1976; Biodrak, Greece; MN10, de Bruijn 1976.
B. bayraktepenensis Ünay 1980; Bayraktepe 1, Turkey; MN7/8.
B. dardanellensis Ünay 1980; Bayraktepe 2, Turkey; MN10.
B. ozansoyi Ünay 1980; Bayraktepe 1, Turkey; MN7/8.
B. pikermiensis de Bruijn 1976; Pikermi (Chomateri), Greece; MN11-12.
B. hellenicus (Freudenthal 1970); Samos S3, Greece; MN12, de Bruijn 1976.
B. eskihissarensis (Tobien 1978); Yenieskihisar, Turkey; MN7/8, Rummel 1998.
B. unayae Rummel 1998; Karaözü, Turkey; MN10.
Gobicricetodon natalia Tyutkova 2008; Ashut, Kazakhstan; MN7/8.
G. filippovi n. sp.; Aya Cave, Russian Federation; MN6, this paper.
G. flynni Qiu 1996; Moergen IV, Nei Mongol; middle Tunggurian.
G. robustus Qiu 1996; Moergen V, Nei Mongol; late Tunggurian.
Tsaganocricetus irtyschensis Topachevsky & Skorik 1988; Semipalatinskaya oblast, Kazakhstan; Vallesian.
Plesiodipus leei Young 1927; Moergen II, Nei Mongol; MN7/8, Qiu 1996.
P. progressus Qiu 1996; Moergen V, Nei Mongol; MN7/8.

Appendix 2 Character matrix

1. Crown height of molars
0: brachydont; 1: semi-hypsodont
2. Crest between main cusps
0: thin; 1: thick
3. M1 occlusal outline
0: rather robust; 1: elongated
4. M1 anterocone
0: simple; 1: two cusps but undivided; 2: divided
5. M1 protosinus angle
0: smooth; 1: sharp angle
6. M1 anterostyle
0: present; 1: absent
7. M1 protostyle
0: present; 1: absent
8. M1 sinus
0: transverse; 1: anteriorly curved; 2: posteriorly directed
9. M1 sinus
0: wide; 1: narrow
10. M1 anterocone-protocone connection
0: rather central; 1: rather lingual
11. M1 protocone-endoloph connection
0: weak or absent; 1: strong
12. M1 mesoloph
0: reaches the labial border; 1: remains in the mesosinus; 2: absent or weak
13. M1 funnel
0: absent; 1: half formed; 2: complete
14. M1 anterior ectoloph

- 0: absent; 1: spur; 2: present; 3: ridge
15. M1 ectoloph between paracone and metacone
0: absent; 1: spur; 2: present; 3: ridge
16. M1 paracone-hypocone connection
0: not straight; 1: straight
17. M1 metalophule
0: rather transverse; 1: connected to the posterior arm of hypocone; 2: connected to the posteroloph
18. M1 posterosinus
0: deep; 1: reduced or absent; 2: enamel island
19. M1 number of roots
0: three; 1: four
20. M2 occlusal outline
0: squared; 1: elongated and posterior part reduced
21. M2 lingual anteroloph
0: strong; 1: reduced or absent
22. M2 ectoloph
0: absent; 1: spur, 2: present; 3: ridge
23. M2 funnel
0: absent; 1: half formed; 2: complete
24. M2 sinus
0: rather transverse; 1: curved anteriorly; 2: directed posteriorly
25. M2 mesoloph
0: strong; 1: reduced; 2: absent
26. M2 metalophule
0: rather transverse; 1: connected to the posterior arm of hypocone; 2: connected to the posteroloph
27. M2 posterosinus
0: deep and open; 1: reduced or absent; 2: enamel island
28. m1 anteroconid
0: wide laterally; 1: simple
29. m1 anteroconid
0: central; 1: labial
30. m1 labial anterolophid
0: present; 1: absent
31. m1 metalophulid
0: only posterior; 1: double; 2: only anterior
32. m1 mesolophid
0: strong; 1: reduced; 2: absent
33. m1 ectomesolophid
0: present; 1: absent
34. m1 sinusid
0: rather transverse; 1: strongly directed anteriorly
35. m1 hypolophulid
0: thin crest; 1: strong loph
36. m1 posterolophid
0: simple loph; 1: cusp-shaped
37. m2 lingual anterolophid
0: present; 1: low cingulum; 2: absent
38. m2 protosinusid
0: open; 1: enamel island
39. m2 protosinusid
0: deep; 1: reduced
40. m2 mesolophid
0: reaches the lingual border; 1: remains in the mesosinusid; 2: absent
41. m3 mesolophid
0: reaches the lingual border; 1: remains in the mesosinusid; 2: absent
42. m3 posterosinusid
0: open; 1: close

Appendix 3 Character matrix

Taxa/Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>Democriceto. anatolicus</i>	0	0	0	0	0	1	1	0	0	0&1	1	0	0	0	1	0	0	0	0	0	0	1
<i>Cricetodon hungaricus</i>	0	0	0	2	0	0	0	0	1	0	0	1	2	1	2	0	2	1	1	0	0	2
<i>Cricetodon versteegi</i>	0	0	0	2	1	1	1	0	0	1	1	1	2	1	1	0	1	0	0	0	0	1
<i>Cricetodon tobieni</i>	0	0	0	1	1	1	1	0	0	1	0	1	1	1	1	0	1	0	?	0	0	1
<i>Cricetodon kaspiigligli</i>	0	0	0	0&1	1	1	1	0	0	1	0	1	0	1	0	0	1&2	0&1	?	0	0	0&1
<i>Cricetodon altiensis</i>	0	0	0	2	1	1	1	0	0	0	0	1	1	0	0	0	1&2	1	1	0	0	0
<i>Cricetodon pascuarensis</i>	0	1	0	1&2	1	1	0&1	0	1	0	0	2	1&2	0	1&2	0	2	1	1	0	0	2
<i>Cricetodon candiensis</i>	1	1	0	2	0&1	1	1	0	0	1	1	2	2	2	2	0	2	1	1	0	0	1&2
<i>Cricetodon variensis</i>	0&1	1	0	2	0	1	1	0	0	0&1	1	1	2	1	1	0	2	1	1	0	0	2
<i>Cricetodon meini</i>	0	0&1	0	1	0	1	1	0	0	0	0	1	1	0	1	0	2	1	1	0	0	1
<i>Cricetodon aff. C. meini</i>	0	0	0	1	0	1	0	0	1	0	0	1	1	0&1	1	0	2	1	1	0	0&1	1
<i>Cricetodon aureus</i>	0	0	0	2	0	0&1	0&1	0	1	0	0	1	0&1	0	0	0	2	1	1	0	0	1
<i>Cricetodon sansaniensis</i>	0	1	0	1&2	0	0	0&1	0	0	1	0	1	0	1	0&1	1	2	1	1	0	0	1
<i>Cricetodon albanensis</i>	0	1	0	2	0	1	1	0	0	0	1	1	2	1	1	1	2	1	1	0	1	1
<i>Cricetodon jotae</i>	0	1	0	1	0	1	1	1	1	0	0	1	0	1	1	0	2	1	1	0	1	1
<i>Cricetodon soriae</i>	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
<i>Cricetodon volkeri</i>	0	1	0	1	0	0	1	1	0	0	0	0&1	0	?	0	1	1	0	0	0	0	1
<i>Mixocricetodon dehmi</i>	0	1	0	2	0	0	0	1	0	0	0	1	0	0	0	0	2	1	0	0	0	1
<i>Aralocricetodon</i>	1	1	0	0	0	1	1	1	1	1	0	2	1	1	1	0	1	0	0	0	1	1
<i>Byzantinia nikosi</i>	1	1	1	2	1	1	0	2	1	1	1	1	0	3	3	1	2	1	1	1	1	3
<i>B. bayraktépensis</i>	1	1	1	2	1	1	1	2	1	0	1	2	1	2	2	0	2	1	1	1	1	2
<i>B. dardanellensis</i>	1	1	1	2	1	1	1	2	1	0	1	2	0	2	2	1	2	1	1	1	1	2
<i>Byzantinia ozarsoyi</i>	1	1	1	2	1	1	1	2	1	0	1	1	2	2	2	0	2	1	1	1	1	3
<i>Byzantinia pikermiensis</i>	1	1	1	2	1	0	1	2	1	0	1	2	0	2	2	1	2	1	1	1	1	2
<i>Byzantinia hellenicus</i>	1	1	1	2	1	1	0	2	1	1	1	2	0	3	3	1	2	1	1	1	1	3
<i>B. eskisirensis</i>	1	1	1	2	1	1	1	2	1	0	0	2	1	3	3	0	2	1	1	1	0	3
<i>Byzantinia unayae</i>	1	1	0	2	1	1	0	0	1	1	0	2	0	2	2	0	2	1	1	1	1	2
<i>Gobicricetodon natalia</i>	1	1	1	1	0	1	1	1	1	0	0	2	0	1	0	1	2	?	1	?	?	?
<i>Gobicricetodon filippovi</i>	1	1	0	1	0	1	1	1	1	1	0	1	0	0	0	1	2	1	0	0	1	0
<i>Gobicricetodon flynni</i>	0&1	1	0	1	0	1	1	1	0	0	0	2	1	1	1	1	2	1	0	0	1	1
<i>Gobicricetodon robustus</i>	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Tsagonocri. trtyshensis</i>	1	1	0	2	0	1	1	1	0	0	0	2	0	0	0	1	2	1	?	?	?	?
<i>Plesioidipus leai</i>	1	1	0	0	0	1	1	0	1	0	0	2	0	0	0	1	2	1	1	0	1	0
<i>Plesioidipus progressus</i>	1	1	1	0	0	1	1	2	1	0	0	2	0	0	0	1	2	1	1	0	1	0

Taxa/Characters	continued																			
	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
<i>Democricetodon anatolicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1&2	1
<i>Cricetodon hungaricus</i>	2	1	1	2	1	1	0	0	1	0&1&2	1	1	0&1	0&1	1	1	0	1	1	0
<i>Cricetodon versteegi</i>	1	1	1	0	0	1	0	0	1	2	1	0	0&1	1	1	0	0	1	1	1
<i>Cricetodon tobiani</i>	0	0	0	2	1	1	0	0	0	1	0&1	0	0	0	1	0	0	1	1	1
<i>Cricetodon kasapligli</i>	0	1	1	1	0	0	0	0	0	2	0&1	0	0&1	0	?	?	?	?	1&2	1
<i>Cricetodon aliveriensis</i>	1	0	0	1&2	1	1	1	0	1	1	0	0	0&1	0	1&2	0	0	1	1	0&1
<i>Cricetodon pasdarensis</i>	1&2	1	1	2	1	1	0	1	1	2	1	1	1	0&1	1	1	0	1	1&2	0
<i>Cricetodon candirensis</i>	1&2	0	1	2	1	1	0	1	0	2	1	1	1	1	1	0	1	1	1	0
<i>Cricetodon cariensis</i>	2	0	1	2	1	1	1	1	0	2	1	1	1	1	1	0	1	1	?	?
<i>Cricetodon meini</i>	1	1	1	2	1	1	0	0	1	1&2	0	0	0&1	0	1	0&1	0	1	1	0&1
<i>Cricetodon aff. C. meini</i>	1	1	1	2	1	1	0	0	1	1&2	0	0	1	0	1&2	0	1	1	1	0
<i>Cricetodon aureus</i>	1	1	1	2	1	0	0	0	0	1	0	1	0	0&1	1&2	0	0	1	0	0
<i>Cricetodon sansaniensis</i>	0	1	1	2	1	1	0	0&1	1	1	1	0	1	1	2	0	0	1	1	0
<i>Cricetodon albanensis</i>	1	1	0&1	2	1	1	1	0	2	1	1	1	1	1	2	0&1	0	1	1	0
<i>Cricetodon jotae</i>	0	1	1	2	1	1	0	0	1	1	1	0	1	0	2	0	1	1	?	?
<i>Cricetodon soriae</i>	1	1&2	1&2	2	1	1	0	0	0	1	1	0	1	0	2	1	0	1	1	0
<i>Cricetodon volkeri</i>	0	1	0	1	2	?	?	?	?	?	?	?	?	?	?	1	0	1	?	?
<i>Mixocricetodon dehmi</i>	0	1	1	2	1	0	0	0	1	0	1	0	1	0	2	0	0	1	0	1
<i>Aralocricetodon</i>	0&1	1	1	0&1	0	1	1	1	1	1	0&1	0	1	0	0	0	0	0&1	0	1
<i>Byzantinina bayraktipensis</i>	0	2	2	2	1	1	1	0	2	1&2	1	1	1	1	1	0	1	1	1	0&1
<i>Byzantinina dardanelensis</i>	0	2	2	2	1	1	0	0	1&2	1	1	1	1	1	1	0	1	1	1	0
<i>Byzantinina ozansoyi</i>	0	2	2	2	1	1	0	1	2	1	1	1	1	1	?	?	?	?	?	?
<i>Byzantinina pikermiensis</i>	2	1	1	2	1	1	1	1	2	1	1	1	1	1	2	0	1	1	1	0&1
<i>Byzantinina hellenicus</i>	0	2	2	2	1	1	0	0&1	2	1	1	1	1	1	2	0	1	1	1	1
<i>Byzantinina nikosi</i>	0	2	2	2	1	1	0	0	2	1	1	1	1	1	2	0	1	1	1	0
<i>Byzantinina eschihisarenensis</i>	1	2	2	2	1	1	1	0	1&2	1	1	1	1	1	2	0	1	1	1	1
<i>Byzantinina unayae</i>	0	2	2	2	1	1	1	1	2	1	1	1	1	1	2	0	1	1	1	0
<i>Gobiericetodon natalia</i>	?	?	?	?	?	?	1	0	2	1&2	1	0	1	1	2	0	0	0&1	1	0
<i>Gobiericetodon filippovi</i>	0	1	1	2	2	1	0	0	2	1	1	0	1	0	2	0	0	1	?	?
<i>Gobiericetodon flynni</i>	1	1	1	2	2	1	0	0	2	1	1	0	1	1	0	0	0	1	2	0
<i>Gobiericetodon robustus</i>	?	?	?	?	?	?	0	0	2	2	1	0	1	?	2	0	0	2	?	?
<i>Tsagonoceri. irtyshensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Plestiodipus leei</i>	0	1	2	2	1	1	0	0	2	2	1	0	1	1	2	0	1	2	2	0
<i>Plestiodipus progressus</i>	0	0&1	2	2	1	1	1	1	2	2	1	0	1	0	2	0	1	2	2	1