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A NEW CRICETID RODENT FROM THE EARLY OLIGOCENE OF YUNNAN, CHINA, AND ITS EVOLUTIONARY IMPLICATIONS FOR EARLY EURASIAN CRICETIDS

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ABSTRACT—Here we report a new early Oligocene cricetid, *Paracricetops virgatoincisus*, gen. et sp. nov., discovered from the Caijiachong locality in Yunnan Province, China. This new cricetid shows a peculiar combination of characters, such as massive and transversely positioned cusps, crenulated cheek tooth enamel, and a deep fossette enclosed between protocone and paracone. These characters are also present in *Cricetops*, a cricetid rodent of which the phylogenetic relationship with other cricetids remains debatable. Our phylogenetic analysis based on a data matrix including 37 taxa and 67 morphological characters reveals that *Paracricetops* and *Cricetops* are sister groups. *Paracricetops*, *Cricetops*, *Deperetomys*, *Meteamys*, *Selenomys*, *Melissiodon*, *Mirrabella*, *Enginia*, *Muhsinia*, and *Aralocricetodon* constitute a monophyletic group. This result suggests that these genera should all be grouped in the subfamily Cricetopinae. Our phylogenetic analysis also casts new lights on the origin and early radiation of the family Cricetidae. The subfamily Pappocricetodontinae is a polyphyletic group. *Pappocricetodon* and *Raricricetodon*, two basal cricetid genera, are also polyphyletic. A thorough systematic revision of these basal cricetids is needed. Chronological distribution of Eucricetodontinae, Paracricetodontinae, Pseudocricetodontinae, and Cricetopinae indicates that the establishment of these cricetid clades should be in the late Eocene at least. We therefore deduced that the first diversification and dispersal of the family Cricetidae across Eurasia must have occurred well before the Eocene-Oligocene transition.

INTRODUCTION

The cricetids, including extant hamsters, constitute one of the most diverse families of rodents. In Europe and North America, cricetids appeared at the beginning of the Oligocene. Since then they underwent very rapid diversification, especially in western Europe, where about 40 species of cricetids are known in the Oligocene alone. The first appearance of cricetids in eastern Asia is much earlier. *Pappocricetodon antiquus* Wang and Dawson, 1994, from the middle Eocene Shanghuang fissure-filling in Jiangsu Province of China and *Palasiomys conulus* Tong, 1997, from the middle Eocene Irindinmanhan Hetaoyuan Formation in Henan Province of China are so far the oldest known representatives of the family Cricetidae. In the past two decades, many new cricetids have been discovered from Eocene and Oligocene Asian continental deposits. At least 12 genera (*Edirnella* Ünay, 1989; *Trakymys* Ünay, 1989; *Meteamys* de Bruijn, Ünay, van den Hoek Ostende, and Sarac, 1992; *Muhsinia* de Bruijn, Ünay, van den Hoek Ostende, and Sarac, 1992; *Aralocricetodon* Bendukidze, 1993; *Pappocricetodon* Tong, 1992; *Raricricetodon* Tong, 1997; *Palasiomys* Tong, 1997; *Ulaancricetodon* Daxner-Höck, 2000; *Witenia* de Bruijn, Ünay, G. Sarac, and Yilmaz, 2003; *Oxynocricetodon* Wang, 2007; *Eocricetodon* Wang, 2007) were added to the family Cricetidae. These discoveries have provided intriguing evidence for understanding the origin and early radiation of this family.

Here we report a new cricetid rodent discovered at the Caijiachong mammalian fossil locality in Yunnan Province, China. The Caijiachong locality lies in the north part of the Yuezhou Basin, and is about 20 km southeast of Qujing City. The Paleogene deposits near Caijiachong village consist of two rock units, the Caijiachong Formation and the Gelanghe Formation. The

Caijiachong Formation is a set of sediments consisting of gray and light grayish-green fluvial sandstone or sandy mudstone containing grayish-white marly concretions, and a grayish-white marlite bed. Underlying the Caijiachong Formation, is the Gelanghe Formation red bed, which contains reddish mudstone, sandy mudstone, and fine silts, and is usually structureless. Fossil collecting and study at the Caijiachong locality have a long history. Young (1932) first reported mammalian fossils from the Caijiachong locality. Bien (1940) reported the results of the first field survey, carried out in 1937 in this region. Since the 1960s, Zhou Mingzhen and other researchers from the IVPP continued to visit and collect at the Caijiachong locality. To date, more than 30 taxa have been collected from this locality (Xu, 1961; Wang and Zhang, 1983). Most of them are from three layers in or below the marlite bed of the Caijiachong Formation. These fossils constitute the Caijiachong mammalian fauna. The age of the Caijiachong Fauna is Ergilian (Naduan + Ulangochuan) of the Asian Land Mammalian Age, which has been correlated with the North American Chadronian or European MP19 (Wang, 1985, 1992, 1997; Emry et al., 1998). Very few fossils have been collected from the Gelanghe Formation (Wang and Zhang, 1983), and these poorly preserved fossil fragments from there were insufficient to indicate a precise mammalian age. However, an unpublished sivaladapid upper M3 from the Gelanghe Formation probably indicates a Sharamuronian age. In 2008, we discovered a new fossiliferous layer above the marlite bed in the Caijiachong Formation. About 10 taxa, including the new cricetid rodent reported here, have been collected. The entire fauna from this new fossiliferous bed has not been fully documented, but a few taxa clearly indicate a younger age than the Caijiachong fauna. For instance, the *Eucricetodon* specimen from the new layer is very similar to the early Oligocene *Eucricetodon caducus* Shevyreva, 1967, from Burqin of China and Hsanda Gol of Mongolia. These specimens from the new layer are more derived

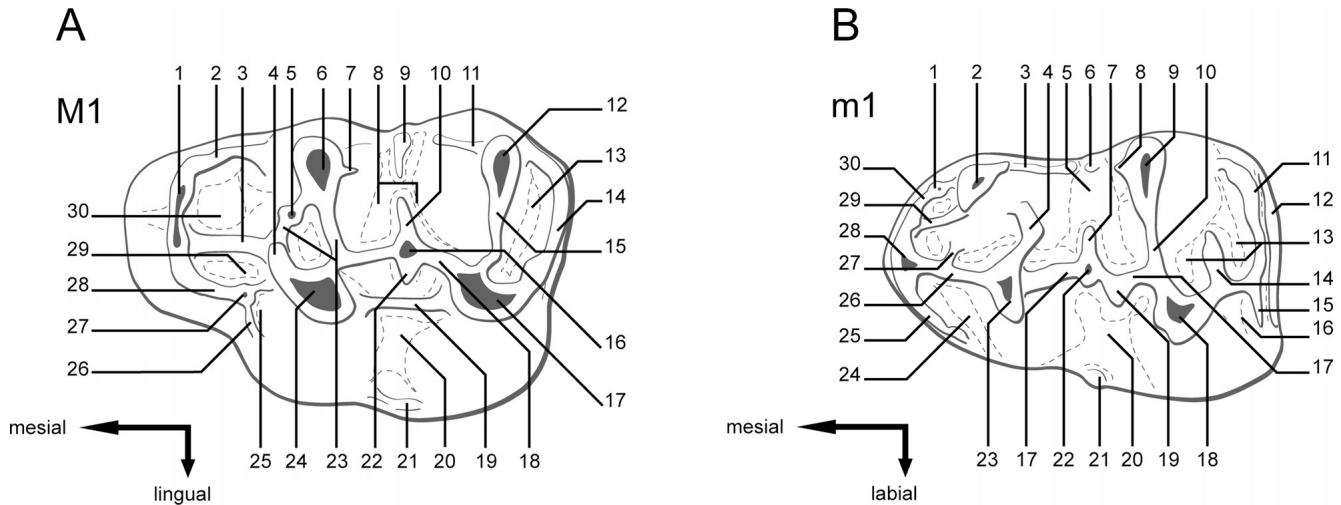


FIGURE 1. Terminology used for the cricetid molars, modified from Freudenthal and Daams (1988), Huguency (1999), and Maridet et al. (2009). (A) M1: 1, anterocone; 2, labial anteroloph; 3, anterolophule; 4, protocone spur; 5, protoconule; 6, paracone; 7, paracone spur; 8, mesosinus; 9, mesostyle; 10, mesoloph; 11, metacone ridge; 12, metacone; 13, posterosinus; 14, posteroloph; 15, metalophule; 16, mesocone; 17, hypocone; 18, entoloph; 19, protocone distal arm; 20, sinus; 21, lingual cingulum; 22, entomesoloph; 23, mesial and distal protolophules; 24, protocone; 25, protocone platform; 26, protostyle spur; 27, protostyle; 28, lingual anteroloph; 29, protosinus; 30, anterosinus. (B) m1: 1, metastylid; 2, metaconid; 3, metaconid ridge; 4, protoconid hind arm; 5, mesosinusid; 6, mesostylid; 7, mesolophid; 8, entoconid spur; 9, entoconid; 10, hypolophulid; 11, posterolophid; 12, additional distal cingulid; 13, posterosinusid; 14, hypoconid hind arm; 15, labial posterolophulid; 16, labial posterosinusid; 17, ectolophid; 18, hypoconid; 19, ectomesolophid; 20, sinusid; 21, ectostylid; 22, mesoconid; 23, protoconid; 24, protosinusid; 25, labial anterolophid; 26, anterolophulid; 27, metalophulid; 28, anteroconid; 29, metaconid spur; 30, lingual anterolophid.

than the *Eucricetodon* and *Eocricetodon* species from the late Eocene Caijiachong fauna by their larger size, broader anterocone in M1, and better-developed anteroconid in m1. Another taxon that could indicate an Oligocene age is a new amynodontid (*Perissodactyla*), which is about 20% larger than the late Eocene *Gigantamynodon giganteus* Xu, 1961, of the Caijiachong fauna. Hence, we believe that the fauna associated with the new cricetid reported here represents an early Oligocene mammalian assemblage.

The morphological terminology used for description and phylogenetic analysis (Fig. 1) is tentative synthetic terminology for all Paleogene cricetids, modified from Freudenthal and Daams (1988), Wang and Dawson (1994), Huguency (1999), and Maridet et al. (2009). The tooth orientation terminology follows that of Smith and Dodson (2003).

Institutional Abbreviation—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences, Beijing, China.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821

Family CRICETIDAE Fischer von Waldheim, 1817

Subfamily CRICETOPINAE Matthew and Granger, 1923

PARACRICETOPS, gen. nov.

Type Species—*Paracricetops virgatoincisus*, sp. nov.

Included Species—The type species only.

Occurrence—Early Oligocene Hsandaogolian, Yunnan Province, China.

Etymology—From the prefix ‘Para’ meaning ‘at the side of’ or ‘resembling’ and the genus *Cricetops*, to which this new genus is closely related (see Phylogenetic Analysis).

Diagnosis—Large cricetid rodent has massive cusps, cuspids, crenulated enamel. Upper and lower teeth emphasize on transverse wear. Protocone and paracone, hypocone and metacone,

protoconid and metaconid, and hypoconid and entoconid are about equally developed and positioned in transverse cusp pairs. Mandible is slender, with shallow, long, weakly curved diastema. Mental foramen is in middle of mandible diastema. Mandibular ascending ramus starting point is lateral to m3 distal part.

M1 has one complete anterolophule, one well-developed protostyle, double connection to paracone, one small entomesoloph, one long mesoloph, and one well-developed anterocone. Entomesoloph is slightly mesial relative to mesoloph. Well-developed lingual and labial anterolophs form complete loop with anterocone and enclose mesial lobe. M1 and M2 mesolophs reach labial border and merge with cingulum, paracone spur, and metacone ridge. Similar to *Cricetops* Matthew and Granger, 1923, protocone spur, mesial and distal protolophules, protocone, and paracone enclose one deep rhombic fossette. m1 has small, simple or slightly bilobed anteroconid. Anteroconid connects metaconid (metaconid spur), not protoconid (no anterolophulid). m1 ectolophid is strongly oblique and extends from hypoconid mesial part to protoconid hind arm. Large, elongated mesoconid is developed on ectolophid. m1 hypolophulid directly connects mesoconid. m2 hypolophulid connects mesoconid or hypoconid mesial part. Lower molars have ectomesolophids. m3 is slightly shorter than m1. M1 and M2 have three roots. Lower molars have two roots.

Differential Diagnosis—*Paracricetops* differs from *Cricetops* in exhibiting a shallower and less curved mandibular diastema. The lower incisor of *Paracricetops* bears complex ornamentation (two longitudinal parallel-raised ridges and faint enamel crenulations) on its rostrally facing surface, whereas the incisor of *Cricetops* has no or very weak ornamentation. M1 of *Paracricetops* has a narrower and less divided anterocone, and lacks a distal connection between the metacone and posteroloph. The mesoloph and entoloph of M1–2 in *Paracricetops* are much stronger than those in *Cricetops*. M3 of *Paracricetops* lacks the metacone. m1 of *Paracricetops* differs from that of *Cricetops*

by bearing a less developed anteroconid, and a more oblique ectolophid.

Paracricetops is different from *Deperetomys* Mein and Freudenthal, 1971, *Meteamys*, and *Enginia* by its smaller size, less divided anterocone, presence of fossette between protocone and paracone in both M1 and M2, orientation of the metalophule, and much stronger mesoloph and mesolophid.

Paracricetops differs from *Paracricetodon* Schaub, 1925, in having lower crown and crenulated enamel on the cheek teeth. Similar to *Cricetops*, but different from *Paracricetodon* and *Trakymys*, the M1 and M2 of *Paracricetops* have two protolophules, which enclose a fossette between the protocone and paracone, and a complete entoloph, which joins the protocone and hypocone. m1 of *Paracricetops* differs from that of *Paracricetodon* in having a well-developed anteroconid, a shorter hypoconid hind arm, and an oblique ectolophid.

Paracricetops differs from *Melissiodon* Schaub, 1920, and *Selenomys* Matthew and Granger, 1923, in having a shallow and weakly curved diastema of the mandible, three roots on M1, and very different molar morphology. All species of *Melissiodon* are characterized by possessing molars with long and high crests and ridges but with much reduced cusps. *Selenomys* molars are characterized by a selenodont-type and semi-hypsodont morphology.

Paracricetops differs from the Eocene cricetids *Palasiomys*, *Raricricetodon*, and *Pappocricetodon* by the following combination of characters: much larger size, absence of upper P4, crenulated enamel of the cheek teeth, stronger crests, presence of a large divided anterocone in M1, and presence of a well-developed anteroconid and an oblique ectolophid in m1.

Paracricetops differs from other Paleogene genera such as *Pseudocricetodon* Thaler, 1969, *Eucricetodon* Thaler, 1966, *Atavocricetodon* Freudenthal, 1996, *Aralocricetodon*, *Muhsinia*, *Ulaancricetodon*, *Heterocricetodon* Schaub, 1925, *Witenia*, *Edirnella*, *Eocricetodon*, and *Oxynocricetodon* by the following combination of characters: m3 almost as long as the m1, longitudinal axis of the lower tooth row strongly inclined in occlusal view relative to the longitudinal axis of the lower jaw, crenulated enamel, well-developed metacone and metaconid ridges of the cheek teeth, and an oblique ectolophid in m1.

PARACRICETOPS VIRGATOINCISUS, sp. nov.
(Figs. 2–4)

Holotype—IVPP V17821.1: a broken right mandible preserving incisor, m1, and m3 (Figs. 2 and 3). Measurements (length × width): m1, 2.12 × 1.53 mm; m3, 2.00 × 1.63 mm.

Hypodigm—IVPP V17821.2, a fragment of left mandible preserving m1 and m2 (Fig. 4F); m1, 2.07 × 1.51 mm; m2, 2.07 × 1.75 mm. IVPP V17821.3, a right m2 mesiolabially broken (Fig. 4G); 2.12 × 1.66 mm. IVPP V17821.4, a broken right m2 (Fig. 4H); width: 1.90 mm. IVPP V17821.5, a fragment of left maxilla preserving M1 (Fig. 4A, B); M1, 2.94 × 1.94 mm. IVPP V17821.6, a left M1 (Fig. 4C); 2.77 × 1.78 mm. IVPP V17821.7, a left M2 (Fig. 4D); 2.07 × 1.78 mm. IVPP V17821.8, a left M3 (Fig. 4E); 1.82 × 1.90 mm.

Etymology—From ‘virgatus’, meaning ‘striped’ and ‘incisus’ meaning ‘incisor.’

Diagnosis—As for the genus.

Type Locality—Caijiachong, Qujing, Yunnan Province, China.

Description

Maxilla—A maxillary fragment preserves a small part of the zygomatic arch (Fig. 4A, B). The zygomatic plate is broken. It is impossible to estimate its size and orientation. The caudal end of the incisive foramen is slightly rostral to M1. The palatine bone is broken, but a part of the palatine/maxillary suture can be observed at the level of the hypocone of M1.

Upper Dentition—M1 has a long, wide mesial lobe. One specimen shows a well-divided anterocone, but the other specimen has a faintly divided anterocone (Fig. 4B, C). Both lingual and labial anterolophes are strong, enclosing the mesial lobe from both sides. The lingual anteroloph bears a protostyle, which is linked to the protocone by a small spur. A long anterolophule links the mesial area of the protocone to the anterocone. In one M1 (Fig. 4B), the anterolophule is formed by the distal spur of anterocone and a labially bended protocone spur. In the other M1 (Fig. 4C), the anterolophule is straight and long. It directly connects the anterocone and protocone. Therefore, the distal spur of anterocone and the protocone spur cannot be distinguished. Both the mesial and distal protolophules (also known as protolophules I and II)

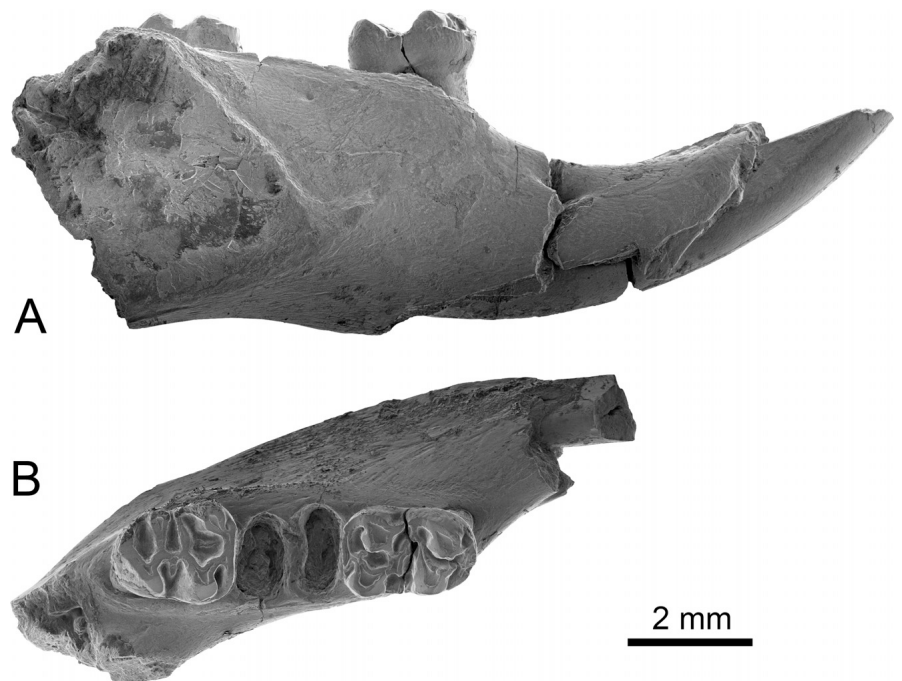


FIGURE 2. Holotype of *Paracricetops virgatoincisus*, gen. et sp. nov. (IVPP V17821.1), a broken right mandible preserving m1 and m3. **A**, labial view; **B**, occlusal view.

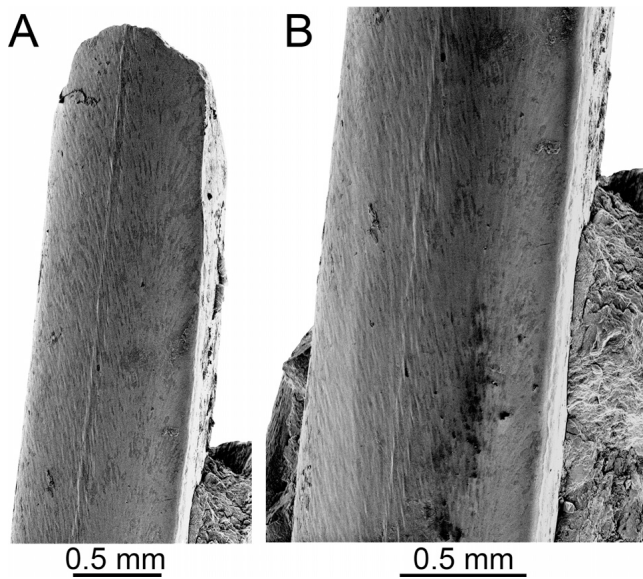


FIGURE 3. Ornamentation on the rostrally facing surface of the lower incisor of *Paracricetops virgatoincisus*, gen. et sp. nov. (IVPP V17821.1). **A**, tip of the incisor with longitudinal ridges and faint oblique enamel crenulation; **B**, detail of the oblique enamel crenulation.

are present. They enclose a deep fossette between the protocone and paracone. A spur begins on the mesial side of the paracone. It joins the anterolophule in one specimen and the labial anteroloph in the other specimen. Both the paracone spur and the metacone ridge join the labial extremity of the mesoloph on the labial tooth border. A mesostyle is present at this intersection. A small cingulum starts from the extremity of the mesoloph, forms a loop toward the paracone, and delimits a small pit. The same feature is also observed in *Paracricetodon*. A mesocone is present on both M1s. A weak entomesoloph is developed from the mesial part of the mesocone. The sinus (also known as hypoflexus) is closed by a thick cingulum. The metalophule is slightly curved and connects the middle part of hypocone. The M1s are three-rooted.

M2 is slightly rounded. Both lingual and labial anterolophs are long and thick (Fig. 4D). They join together and form a straight crista along the mesial tooth border. A similarly thick anterolophule links the anterolophs with the protocone. As in M1, both mesial and distal protolophules are present, and the paracone distal spur and the metacone ridge join the mesoloph on the labial border where the cingulum also forms a small pit. The protocone is distally extended, leaving the sinus in a mesially curved shape. The sinus is closed lingually by a ridge starting from the hypocone. This ridge is merged with the lingual cingulum. The metalophule is also curved, but different from that of M1, it connects to the mesial part of hypocone. M2 is three-rooted.

The presence of a deep fossette enclosed by crests between protocone and paracone in both M1 and M2 is a feature shared only by *Paracricetops* and *Cricetops*. This feature is not present in other Paleogene cricetid rodents. Although the anterocone of *Paracricetops* is much less developed than that of *Cricetops*, the bulky protocone-paracone, hypocone-metacone pairs in upper molars and protoconid-metaconid, hypoconid-entoconid pairs in lower molars are very similar to the cusp-arranging pattern in *Cricetops*.

M3 is roughly in a triangle shape from the occlusal view (Fig. 4E). As in the M2, the lingual and labial anterolophs are long and thick, and form a straight crista along the mesial tooth border. The protocone and paracone are mesiodistally compressed. The mesial protolophule and the protocone spur join to-

gether, and connect the anteroloph via the short anterolophule. The distal protolophule is absent, but a strong protocone hind arm is present. The paracone bears a strong paracone spur on its distolabial side. The entoloph is long. It extends mesiolabially towards the mesial protolophule, but does not join the latter. The mesoloph is relatively weak and runs distolabially. The hypocone is very weak and crista-like. It is confluent with the entoloph mesially, and with the posteroloph distally. The metacone is absent, but a long metalophule is present. M3 has three roots.

Mandible—The mandible (Fig. 2) is slender, with a shallow, long, weakly curved diastema. The coronoid process is not preserved, but its base shows an origin lateral to the distal part of m3. The masseter crests are ‘V’-shaped; both the dorsal and the ventral crests are strong. The dorsal masseter crest joins the ventral one at a point below the middle of m2. The ventral masseter crest extends even further, to a point below the distal edge of m1. The position of the mental foramen is so high that it is visible in the occlusal view. Mesiodistally, the mental foramen is near the middle of the diastema. The tip of the incisor is under the level of the molar crowns.

Lower Dentition—Ornamentation can be observed on the rostrally facing surface of the lower incisor (Fig. 3). It is present as two longitudinal parallel-raised ridges: one follows the mesial border of the rostrally facing surface, the other is located in the middle of the rostrally facing surface. The latter ridge is relatively weak and disappears soon towards the alveolar border. In addition to the raised ridges, faint enamel crenulations are also present on the rostrally facing surface of the incisor. Unlike some species of *Eucricetodon* (Maridet et al., 2009), no ornamentation is present on the distal surface of the incisor in *Paracricetops*.

The mesial part of m1 is slightly narrower than the distal part (Figs. 2B, 4F). The anteroconid lobe of m1 is short, rounded, and undivided. A mesial spur starts from the protoconid and extends toward the anteroconid, but it ends before reaching the anteroconid, therefore no complete anterolophulid is present. The metalophulid (also known as metalophulid I) connects directly to the anteroconid. The protoconid hind arm (also known as metalophulid II) is present. One of the most striking features of the m1 is its very oblique ectolophid. It begins labially from the hypoconid and joins the long protoconid hind arm lingually. There is also a small mesial spur developed from the ectolophid, connecting to the distal side of the protoconid. The mesoconid is well developed and elongated. The hypolophulid is short. It is oriented mesially, and connects directly to the mesoconid. Both the metaconid ridge and the entoconid spur join the protoconid hind arm on the lingual border. A cingulum begins from the lingual end of the protoconid hind arm and joins the entoconid, delimiting a small pit on the lingual border. On the labial side, a faint cingulum is also present that closes the sinusid (widely called hypoflexid). The hypoconid hind arm is short and forms a mesially oriented hook. The labial part of the posterolophid is well developed. It extends behind the hypoconid and delimits a short labial posterosinusid. The lingual part of the posterolophid forms a continuous ridge on the distolingual border, and extends to the top of the entoconid. m1 has two roots.

The length of m2 is similar to that of m1, but the width is greater (Fig. 4F, G, H). Mesially, the metalophulid is connected to the lingual anterolophid, whereas the anterolophulid starts from the protoconid and connects to the labial anterolophid. In two specimens, the protoconid hind arm is long and joins the metaconid ridge on the lingual border. In one specimen, however, the protoconid hind arm is much shorter and does not connect the metaconid. Both the mesolophid and the ectomesolophid are moderately developed, and there is a mesoconid positioned between these two crests. The hypolophulid connects either to the mesoconid or to the ectolophid between the mesoconid and the hypoconid. The mesosinusid is always open lingually, whereas

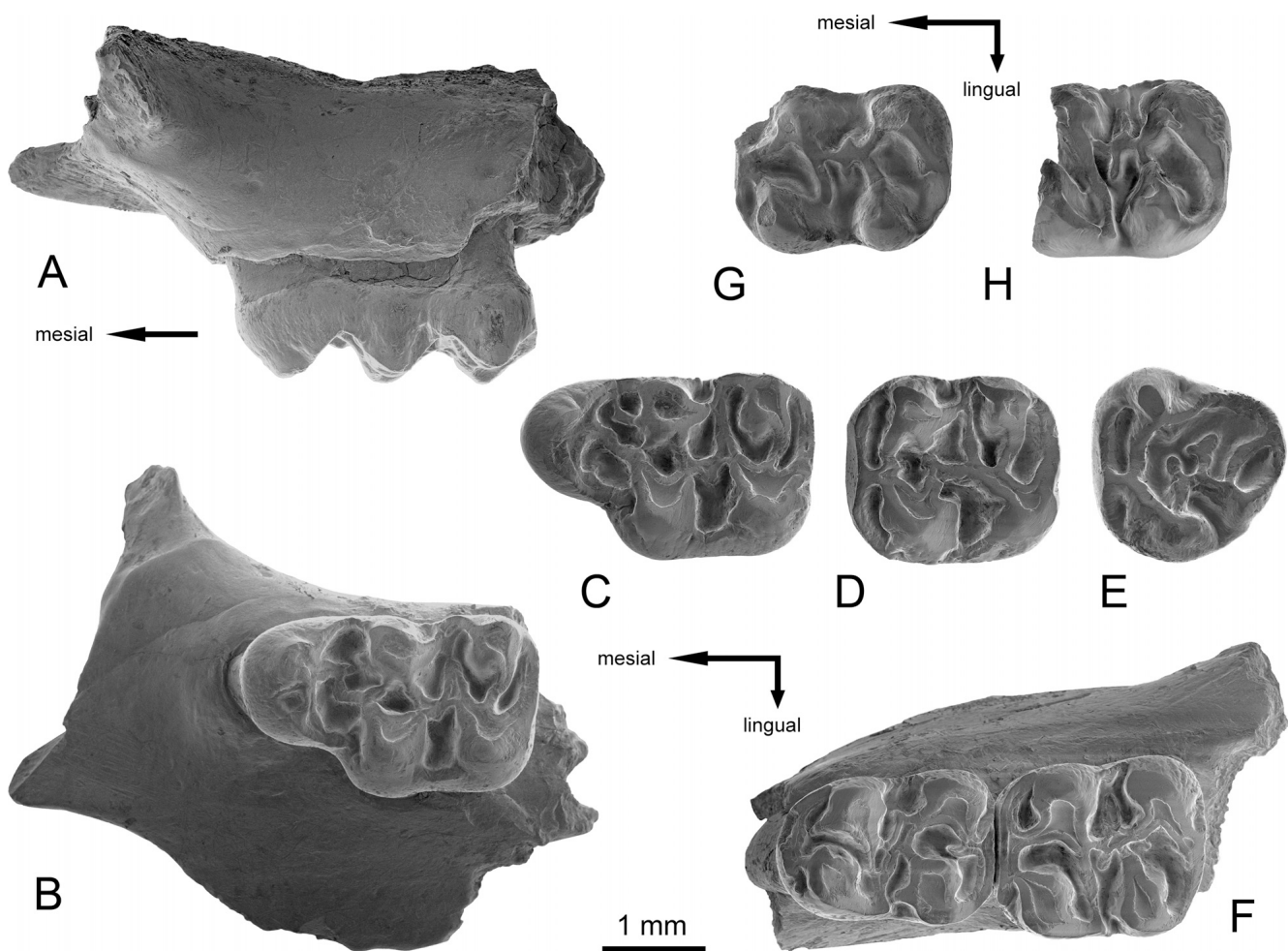


FIGURE 4. Dentition of *Paracricetops virgatoincisus*, gen. et sp. nov. **A–B**, V17821.5, left maxilla fragment with M1 (**A**, labial view; **B**, occlusal view); **C**, V17821.6, left M1; **D**, V17821.7, left M2; **E**, V17821.8, left M3; **F**, V17821.2, left mandible fragment with m1 and m2, reversed; **G**, V17821.3, right m2; **H**, V17821.4, right m2 fragment.

labially the sinusid is sometimes closed by a cingulid, or by an ectostylid. The posterosinusid is noticeably large. In two specimens, a very weakly developed hypoconid hind arm is present. Different from the m1, the labial posterolophid of m2 is either faint or totally absent. The hypoconulid is variably developed at the base of the posterolophid. m2 is two-rooted.

Only one m3 is available for description, preserved on the type specimen. As in m2, the metalophulid connects directly to the lingual anterolophid. The protoconid hind arm reaches the lingual border where it merges with the metaconid ridge. A low and weakly developed crest joins the metalophulid with the protoconid hind arm. Both the mesosinusid and the sinusid are open. The ectomesolophid is well developed. The hypolophulid is almost transverse and connects to the ectolophid. The hypoconid is reduced and is more elongated compared with the protoconid. It tends to form a continuous crest with the posterolophid. M3 has two roots.

PHYLOGENETIC ANALYSIS

The Eurasian Paleogene and early Neogene cricetid rodents are very diverse. The phylogenetic relationships among these cricetids remain unsolved. Rodrigues et al. (2010) carried out a

phylogenetic analysis based on a data matrix including 65 cranial and dental characters and 22 myomorphous taxa. Their analysis is a good attempt to resolve the phylogenetic relationship between dipodoid and basal cricetid rodents. Here, in order to decipher the phylogenetic position of *Paracricetops virgatoincisus*, gen. et sp. nov., we performed a phylogenetic analysis focusing on the early Eurasian cricetids, particularly the taxa showing morphological similarities to *P. virgatoincisus*. Our analysis is based on a newly developed morphological data matrix including 67 characters, two Eocene dipodids, and 35 Eocene, Oligocene, and early Miocene Eurasian cricetid rodents (see Supplementary Data). It is generally accepted that muroid and dipodoid rodents have very close phylogenetic relationships (Flynn et al., 1985; Wang and Dawson, 1994; Marivaux et al., 2004; Emry, 2007; Flynn, 2009; Gomes Rodrigues et al., 2010). We therefore selected two dipodids, *Primismithus yuenus* Tong, 1997, and *Banyuesminthus unconjugatus* Tong, 1997, as an outgroup in our analysis. They were used to root the optimal trees generated by our analysis. Thirty-five ingroup cricetids belonging to 27 genera cover most of the Paleogene cricetids at a genus level. Five early Miocene cricetids, *Muhsinia steffensi* de Bruijn, Unay, van der Hoek Ostende, and Sarac, 1992, *Enginia gertcheki*, *Deperetomys intermedius* de Bruijn, Unay, Sarac, and Klein Hofmeijer, 1987, *Mirrabella tuberosa* (de Bruijn, Unay, Sarac, and Klein Hofmeijer, 1987) (de

Bruijn et al., 2007, suggested *Mirrabella* as the new name for the genus *Mirabella* de Bruijn et al., 1987, which was preoccupied by *Mirabella* Emeljanov, 1982, and *Meteamys alpine* de Bruijn, Ünay, van der Hoek Ostende, and Sarac, 1992, are also included in our analysis, because these taxa share many similarities with *P. virgatoincisus* and could have close phylogenetic relationships between them. Among the 67 characters, seven are cranial and 60 are dental characters. Most of the scorings are based on direct observation on the specimens or casts. A few taxa are scored based on literature. The data matrix has a very low proportion of missing data: only 10.9% of the total cells contain question marks. The intraspecific variation was taken into account and coded as multistates. Twelve characters were set as ordered. All characters have equal weight. Characters scored as having multiple states are interpreted as polymorphisms. TNT (Tree analysis using New Technology) phylogenetic analysis program (Goloboff et al., 2008) was used to search for the most parsimonious trees. The Driven Search method was selected, with the best score hit set as 100 times, and for each hit the initial search set as 1000 replications. Bremer supports were calculated from the optimal and suboptimal trees during branch swapping. The absolute difference for suboptimality degree was set as five steps, and the relative fit difference (Goloboff and Farris, 2001) was set as 0.95. Tree description and character mapping were performed in PAUP* version 4.0b10 (Swofford, 2003). Two most parsimonious trees were found. Each tree is 230 steps long, with a consistency index of 0.3609 and a retention index of 0.6260.

Our phylogenetic analysis (Fig. 5) suggests that *Paracricetops* and *Cricetops* are a sister group. *Paracricetops*, *Cricetops*, *Deperetomys*, and *Meteamys* consist of a monophyletic clade. We named this monophyletic clade the *Cricetops* clade. *Selenomys* is the sister of *Melissiodon*, and the two constitute the sister of *Mirrabella*. The monophyletic clade including *Selenomys*, *Melissiodon*, and *Mirrabella* is called the *Melissiodon* clade. The *Cricetops* clade and *Melissiodon* clade are sister groups. *Enginia*, *Muhsinia*, and *Aralocricetodon* form another monophyletic group, which we named the *Enginia* clade. *Cricetops* clade, *Melissiodon* clade, and *Enginia* clade constitute a larger monophyletic group. *Pseudocricetodon*, *Ulaancricetodon*, *Heterocricetodon*, *Adelomyarion* Huguene, 1969, *Kerosinia*, *Oxynocricetodon*, *Edirnella*, and surprisingly *Raricricetodon zhongtiaensis* constitute a monophyletic group. This group is the sister of the *Cricetops-Selenomys-Enginia* clade. The Asian middle and late Eocene cricetid show a complicated phylogenetic relationship. *Pappocricetodon ren-cunensis*, *P. antiquus*, *P. schaubi*, *Raricricetodon ? minor*, and *Palasiomys conulus* form a paraphyletic group.

When character changes were traced along the strict consensus tree assuming accelerated transformations (ACCTRAN), three synapomorphies were found supporting the *Cricetops* clade. They are the presence of one longitudinal ridge on the mesial side of the rostrally facing surface of the lower incisor, the paired cusps of the cheek teeth being arranged in transverse ridges and standing in high relief, and the presence of cheek tooth enamel crenulation. The *Cricetops-Melissiodon* clade shares a combination of nine synapomorphic characters: the presence of long incisive foramen, M1 possessing metacone ridge, M2 possessing metacone ridge, M2 sinus mesiolabial expansion being absent, variable presence of hypoconid hind arm in m1, m1 hypolophulid connecting the mesoconid or the base of mesolophid, m1 possessing X-shaped cristid intersection, presence of m2 hypoconid hind arm, and m2 hypolophulid connecting the mesoconid or the base of the mesolophid. The synapomorphic features supporting the *Cricetops-Melissiodon-Enginia* clade include the presence of one longitudinal ridge in the middle part of the rostrally facing surface of the lower incisor, hystricomorphic zygomatic plate, the ventral masseter crest extending to m2, the orientation of the longitudinal axis of the tooth row relative to the longitudinal axis of the dental bone in occlusal view being strongly inclined, pres-

ence of divided anterocone in M1, and the metalophulid connecting the lingual anterolophid or the anterior tooth border in m1.

DISCUSSION

Paracricetops virgatoincisus, gen. et sp. nov., shows a striking morphology shared with some peculiar Oligocene and early Miocene cricetid rodents, such as *Cricetops*, *Deperetomys*, and *Meteamys*. The phylogenetic analysis including *Paracricetops* and other early cricetids not only asserts the systematic position of this new cricetid, but also illuminates the phylogenetic relationships among other cricetids.

Our phylogenetic analysis suggests that *Paracricetops* has close phylogenetic relationships with *Cricetops*, *Deperetomys*, *Meteamys*, *Selenomys*, *Melissiodon*, *Mirrabella*, *Enginia*, *Muhsinia*, and *Aralocricetodon* (Fig. 5). The origin of these cricetids and the phylogenetic relationships with other rodents still remained to be resolved (Simpson, 1945; Stehlin and Schaub, 1951; Schaub, 1958; Mein and Freudenthal, 1971; Ünay, 1989; Wang and Dawson, 1994; McKenna and Bell, 1997; Lopatin, 2004; Bendukidze et al., 2009). *Cricetops* is usually the dominant element of the early Oligocene faunas in northern Asia, occurring widely in early Oligocene deposits in Mongolia, Kazakhstan, and many localities in China (Russell and Zhai, 1987). It has a cricetid dental morphology but hystricomorphous zygoma (Lindsay, 1977; Wahlert, 1984; Carrasco and Wahlert, 1999). When they described *Cricetops* as new genus, Matthew and Granger (1923) put it in a new family, Cricetopidae, because they did not feel justified in assigning this genus to any then-recognized family. In the same paper, Matthew and Granger (1923:5) associated *Selenomys* with *Cricetops*, which had "some suggestion of approach in pattern." Later Simpson (1945) changed Cricetopidae into a tribe, Cricetopini, and placed it under the cricetid subfamily Cricetinae. In this tribe, he included *Cricetops*, *Selenomys*, and *Kanisamys* Wood, 1937. Mellett (1966, 1968) put *Selenomys* in the Aplodontidae family. Kowalski (1974) tentatively agreed with this assignment. Wang (1987) argued, however, that *Selenomys* does not show similarities to aplodontids but does share many dental and cranial characters with other cricetids and should be kept in the Cricetidae. McKenna and Bell (1997) did not follow Wang's suggestion, considering *Selenomys* to be a genus of Muridae incertae sedis. As far as *Kanisamys* is concerned, it is now generally accepted as a rhizomyine rodent (McKenna and Bell, 1997; Flynn, 2009).

Wahlert (1984) suggested that *Cricetops* is an extinct kin of the living maned rat *Lophiomys* and should be put in Lophiomyinae. But soon this suggestion was rejected by Aguilar and Thaler (1987), who discovered that *Protolophiomys* Aguilar and Thaler, 1987, from the late Miocene of Spain had a *Lophiomys*-like skull but lacked the bulky and transversely arranged cusp pattern. The dental similarities shared by *Cricetops* and *Lophiomys* must be a result of convergent adaptation.

The microstructure of the incisor enamel shows many similarities between *Cricetops*, *Melissiodon*, and *Selenomys* (Kalthoff, 2000, 2006; Koenigswald and Kalthoff, 2007). Instead of suggesting any phylogenetic correlation, however, Koenigswald and Kalthoff (2007) believed that the same incisor Schmelzmuster type shared by *Cricetops*, *Melissiodon*, and *Selenomys* is a primitive feature.

It is widely believed that *Melissiodon* belongs to a peculiar clade of its own (Mein and Freudenthal, 1971; McKenna and Bell, 1997). Ünay (1989) suggested that *Edirnella* from the Oligocene of Turkey is morphologically between *Paracricetodon* and *Melissiodon* and could be the ancestor of *Melissiodon*. She therefore assigned *Edirnella* and *Melissiodon* in the subfamily Melissiodontinae. De Bruijn et al. (2003) supported the assignment of *Melissiodon* and *Edirnella* in Melissiodontinae.

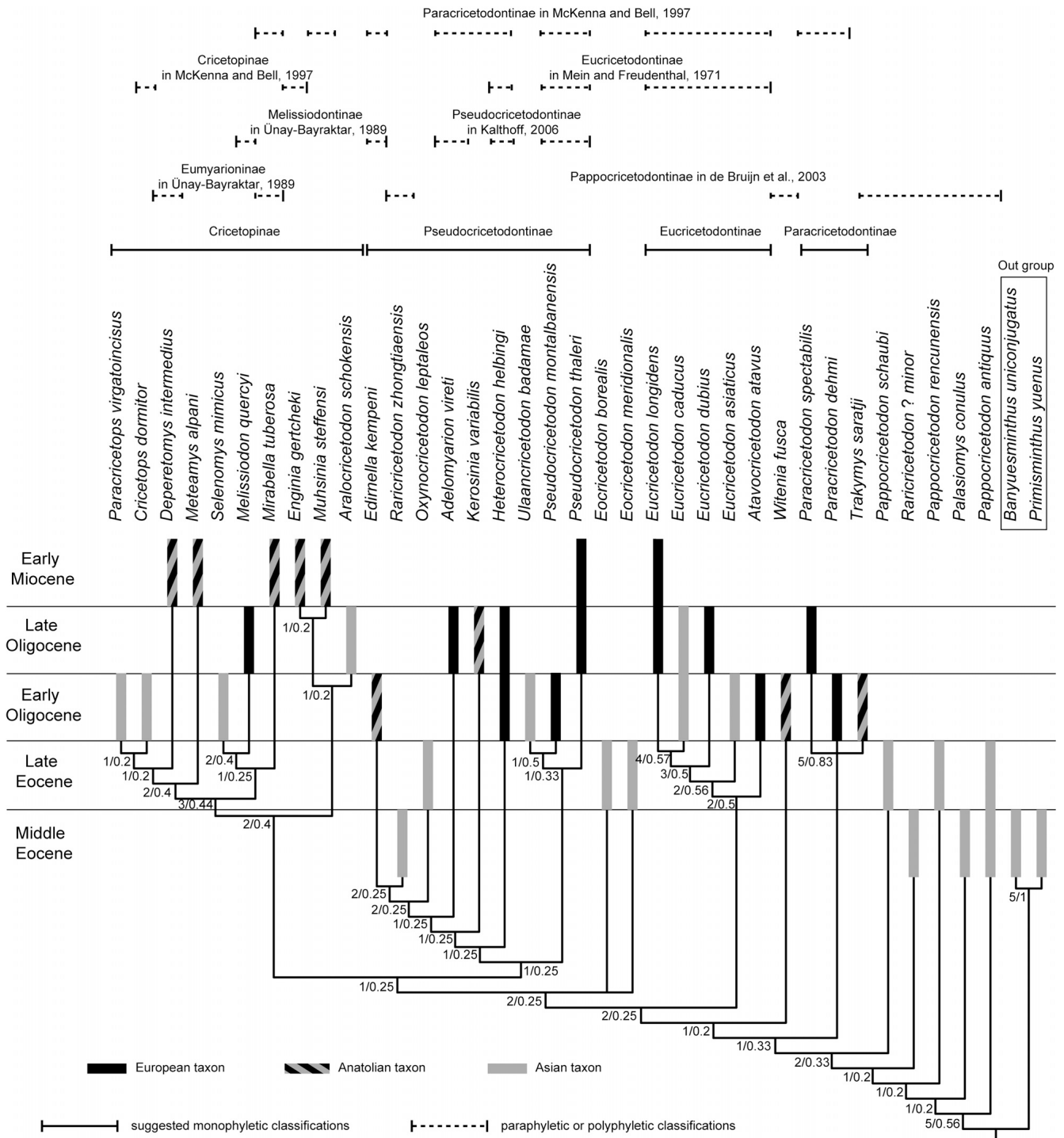


FIGURE 5. Phylogeny and distribution of early cricetid rodents. Strict consensus of two most parsimonious trees. Each tree is 230 steps long, with a consistency index of 0.3609 and a retention index of 0.6260. Branch lengths do not indicate the number of character changes, and have no temporal meaning. Numbers at the internal nodes indicate the absolute and relative Bremer supports calculated from 2501 optimal and suboptimal trees during branch swapping in TNT (Goloboff et al., 2008). The absolute difference for suboptimality degree was set as 5 steps, and the relative fit difference was set as 0.95.

Freudenthal et al. (1992), however, suggested that *Edirnella* probably had a closer relationship with *Paracricetodon*. McKenna and Bell (1997) followed this suggestion and assigned *Edirnella* in subfamily Paracricetodontinae, leaving *Melissiodon* as the only genus in Melissiodontinae.

De Bruijn and von Koenigswald (1994) established *Enginia* genus based on some isolated teeth and maxilla fragment from the eastern Mediterranean area. They noticed the overall similarity shared by *Cricetops* and *Enginia*, particularly its bulky cusps with peculiar crenulated enamel. They therefore proposed

ascribing *Enginia* and *Cricetops* to the same subfamily, Cricetopinae (they spelled Cricetopsinae). This systematic assignment is followed by McKenna and Bell (1997).

Deperetomys is a peculiar cricetid rodent. It first appeared in the earliest Miocene in Anatolia, and arrived in Europe in the middle Miocene (de Bruijn et al., 1993). Different from *Paracricetops* and *Cricetops*, the tooth cusps of *Deperetomys* are more slender, but the tooth cusp and ridge arrangement of *Deperetomys* are very similar to those of *Paracricetops* and *Cricetops*. Originally *Deperetomys* was raised as a subgenus of *Cricetodon* and assigned in the subfamily Cricetodontinae (Mein and Freudenthal, 1971). Ünay (1989) suggested that *Eumyarion*, *Deperetomys*, and *Mirrabella* represent a specialized branch of cricetid rodents and grouped them in the subfamily Eumyarioninae. She also pointed out that *Cricetops* shared many similarities with her Eumyarioninae, suggesting close relationship between them. This hypothesis links the Asian *Cricetops* with the Anatolian and European cricetids for the first time. However, the idea was largely ignored by later researchers.

Meteamys is another peculiar cricetid rodent. It is the dominant element of the late Oligocene rodent assemblage in Anatolia. At the beginning of the Miocene, *Meteamys*, together with *Muhsinia*, was gradually replaced by other cricetids (Wessels, 2009). De Bruijn et al. (1993) partly agreed with Ünay (1989), and suggested that *Cricetodon*, *Deperetomys*, *Eumyarion*, and *Meteamys* must be derived from the same stock, but *Mirrabella* should have its root in Paracricetodontinae. They also pointed out that the subfamily name Cricetodontinae Schaub, 1925 (cited as Stehlin and Schaub, 1951), has priority over Eumyarioninae Ünay, 1989.

Aralocricetodon occurs in the late Oligocene Aral Formation of Kazakhstan (Bendukidze, 1993; Lopatin, 2004; Bendukidze et al., 2009), and possibly also in the Biozone C/C' of the Hsanda Gol region of Mongolia (Höck et al., 1999; Bendukidze et al., 2009). McKenna and Bell (1997) and Lopatin (2004) assigned *Aralocricetodon* to Cricetodontinae, but Bendukidze et al. (2009) considered it to be a member of the Tachyoryctoidinae Bohlin, 1937.

Little attention has been paid to *Muhsinia*. But its systematic position is also uncertain. De Bruijn et al. (1992) tentatively assigned *Muhsinia* to Pseudocricetodontidae Engesser, 1987, whereas McKenna and Bell (1997) placed the genus in the tribe Eucricetodontini under the subfamily Paracricetodontinae.

Based on our phylogenetic analysis (Fig. 5), we suggest assigning *Paracricetops*, *Cricetops*, *Deperetomys*, *Meteamys*, *Selenomys*, *Melissiodon*, *Mirrabella*, *Enginia*, *Muhsinia*, and *Aralocricetodon* to the cricetid subfamily Cricetopinae. Because Melissiodontinae Schaub, 1925, was published two years later than Cricetopinae Matthew and Granger, 1923, Melissiodontinae therefore becomes the junior synonym of Cricetopinae. As discussed above, these genera consist of three monophyletic subgroups: the *Cricetops* clade, *Melissiodon* clade, and *Enginia* clade (Fig. 5). To reflect this phylogenetic relationship, three tribes should be defined within the subfamily Cricetopinae. They are Cricetopini Matthew and Granger, 1923, Melissiodontini Schaub, 1925, and Engini, trib. nov.

The Cricetopinae clade is paraphyletically related to a large group containing the taxa mostly assigned in the subfamily Eucricetodontinae by Mein and Freudenthal (1971), Paracricetodontinae by McKenna and Bell (1997), or Pseudocricetodontinae by Kalthoff (2006) (Fig. 5). Our phylogenetic analysis indicates that *Paracricetodon* and *Trakymys* form a monophyletic group, *Ulaancricetodon* and *Pseudocricetodon* form another monophyletic group, and *Atavocricetodon* is the sister of *Eucricetodon*. This result therefore supports the assignments of these taxa to Paracricetodontinae, Pseudocricetodontinae, and Eucricetodontinae, respectively. *Adelomyarion*, *Kerosinia*, and *Heterocricetodon* were suggested to be closely related to *Pseudocricetodon* (Ünay, 1989; McKenna and Bell, 1997;

Kalthoff, 2006). Our analysis shows that these three genera plus *Edirnella*, *Raricricetodon zhongtiaensis*, and *Oxynocricetodon* form a monophyletic group, with *Pseudocricetodon* and *Ulaancricetodon* being its sister. Such a result suggests that all these taxa, namely, *Edirnella*, *R. zhongtiaensis*, *Oxynocricetodon*, *Adelomyarion*, *Kerosinia*, *Heterocricetodon*, *Ulaancricetodon*, and *Pseudocricetodon*, could all be assigned in the subfamily Pseudocricetodontinae.

Pappocricetodon, *Palasiomys*, and *Raricricetodon* are among the most basal myodont rodents, and they are probably ancestral to all other cricetids. Tong (1997) proposed a new subfamily Pappocricetodontinae to include *Pappocricetodon*, *Palasiomys*, and a new subfamily Raricricetodontinae to include *Raricricetodon*. The phylogenetic relationships among these taxa and other more derived cricetids remain debatable (Tong, 1997; Dawson and Tong, 1998; Emry, 2007; Wang, 2007). In our analysis, these three genera are paraphyletically related to each other, and the so-called Pappocricetodontinae is a polyphyletic group (Fig. 5). Three *Pappocricetodon* species included in our analysis do not belong to a monophyletic group. One *Raricricetodon* species, *R. zhongtiaensis*, joins the subfamily Pseudocricetodontinae. The phylogenetic relationship among *Pappocricetodon*, *Raricricetodon*, and *Palasiomys* revealed by our analysis is different from that of Gomes Rodrigues et al. (2010). However, both analyses strongly suggest that a thorough revision of these genera is definitely needed. Discovery of more specimens of these basal cricetids will also help to resolve their systematic position.

The Eocene-Oligocene transition is marked by global climate change (Wolfe, 1971; Legendre, 1986; Elderfield, 2000; Zachos et al., 2001; Dupont-Nivet et al., 2007). Abrupt global cooling, continental aridification, and expansion of open habitats have been suggested as the main drivers of the diversification of rodents. The large change in the distribution and diversity of cricetids seems coincident with the Eocene-Oligocene transition. Our phylogenetic analysis, however, suggested that the divergence of major cricetid clades actually occurred in the Eocene (Fig. 5). The primary diversification and distribution of cricetids across Eurasia may also have occurred well before the Eocene-Oligocene transition. The dispersal of Asian cricetid rodents into Europe is now known earlier than the date traditionally believed. Some cricetids such as *Eucricetodon* and *Pseudocricetodon* have migrated to eastern Europe (Baciu and Hartenberger, 2001) in late Eocene. These late Eocene Asian migrants may have served as a stock for European faunal reorganization during the 'Grande Coupure' and the later rapid diversification of Oligocene European cricetids.

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