An Early Miocene Microtoid Cricetid Rodent from the Junggar Basin of Xinjiang, China

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An Early Miocene microtoid cricetid rodent from the Junggar Basin of Xinjiang, China

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Microtoid cricetids are widely considered to be the ancestral form of arvicoline rodents, a successful rodent group including voles, lemmings and muskrats. The oldest previously known microtoid cricetid is *Microtocricetus molassicus* from the Late Miocene (MN9, ca. 10–11 Ma) of Europe. Here, we report a new microtoid cricetid, *Primoprismus fejfari* gen. et sp. nov., from the Junggar Basin of Xinjiang, northwestern China. The rodent assemblage found in association with this specimen indicates a late Early Miocene age, roughly estimated at 18–17 Ma, and thus more than 6 million years older than *M. molassicus*. While morphological comparisons suggest that the new taxon is most closely related to *M. molassicus*, it differs from the latter in a striking combination of primitive characters, including a lower crown, smaller size, a differentiated posterolophid and hypolophid, a faint anterolophid, the absence of an ectolophid, and the presence of a stylid on the labial border of the tooth. Arid conditions prevailing across the mid-latitude interior of Eurasia during the Early Miocene, enhanced by the combined effects of the Tibetan uplift and the gradual retreat of the Tethys Ocean, likely played a role in the appearance of grasslands, which in turn triggered the evolution of microtoid cricetids and, ultimately, the origin of arvicoline rodents.

Key words: Mammalia, Rodentia, Cricetidae, Arvicolinae, Miocene, Junggar, China, Central Asia.

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Introduction

Arvicolines, which include voles, lemmings, and muskrats, represent of one of the most successful groups of rodents, having colonized all continents except Antarctica and Australia (McKenna and Bell 1997; Musser and Carleton 2005; Fejfar 1999; Fejfar et al. 2011). The group is characterized by hypsodont and prismatic check teeth adapted to hard plant foods (Fejfar 1999; Fejfar et al. 2011). The earliest undoubted arvicoline rodents appeared in northern Eurasia during the Early Pliocene, before rapidly dispersing into North America and southern Asia (Chaline et al. 1999; Fejfar et al. 2011; Musser and Carleton 2005). It is widely accepted that arvicoline rodents are derived from cricetid ancestors (Kretzoi 1955; Zheng and Li 1990; Michaux et al. 2001), with some Late Miocene cricetids from Eurasia and North America showing arvicoline-style cheek teeth with various degrees of hypsodonty and prismatic morphology. The latter are also known as microtoid cricetids, and are believed to have preceded the appearance of true arvicoline rodents (Schaub 1934; Fejfar 1999; Fejfar et al. 2011). Here, we describe a new microtoid cricetid from the Early Miocene deposits of the Junggar Basin in Xinjiang, China. This new record is about 6 million years older that the earliest previously-known microtoid cricetid, *Microtocricetus molassicus* Fahlbusch and Mayr, 1975 from the Late Miocene (MN9) of Europe (Fejfar 1999), thus indicating a much deeper origin of microtoid rodents than previously assumed.

Geological and paleontological investigations in the Junggar Basin have been going on for more than 50 years. Since the 1980s, the Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences, Beijing (IVPP) has been excavating and screen-washing samples from this region every year in order to collect mammalian fossils. During the field season of 2006, a new fossiliferous locality (XJ200604) was discovered about 35 km northwest of Burqin Town (47°58.780’N 86°38.266’E; Fig. 1), northwest of other, previously known Early Miocene localities of the Junggar Ba-

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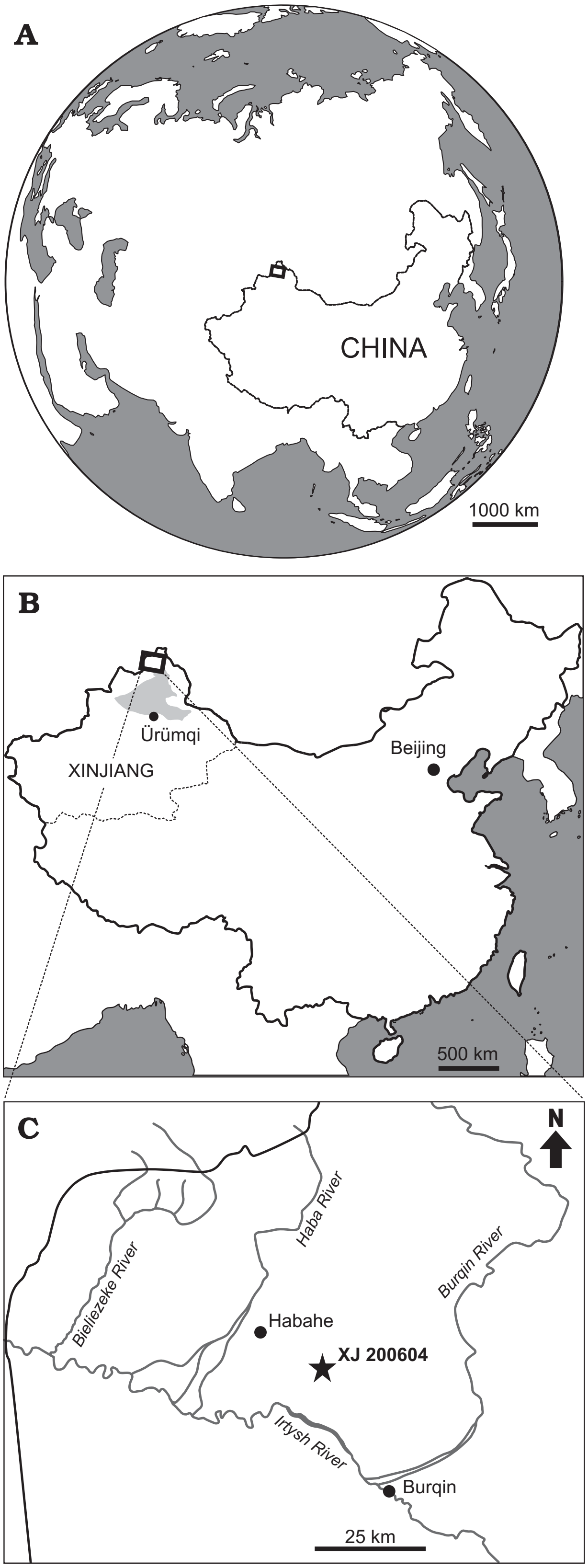

Fig. 1. Map showing the location of locality XJ200604 in the northwestern Junggar Basin (modified from Maridet et al. 2011b, c). **A**. Central position of Junggar Basin in Asia at the continental scale. **B**. Location of Burqin County within the northwestern Junggar Basin, with the latter shown in light gray. **C**. Location of XJ 200604 north of the Irtysh River.

sin (e.g., Wu 1988; Ye 1989; Ye et al. 1999; Bi 1999, 2000; Meng et al. 1999, 2006; Wu et al. 2000, 2003). The sediments exposed at this locality belong to an unnamed rock unit consisting of grayish- to blackish-yellow fluvial sandstone and sandy mudstone. Mammalian fossils were discovered in a lens of pebbly coarse sandstone in the basal layer of these fluvial sediments, which overlies the brightly-coloured Irtysh River Formation (Ye et al. 2005), and is separated from the latter by a disconformity. Owing to its central position within Asia (Fig. 1A), this locality plays a crucial role in the dispersion and diversification of mammalian faunas.

The rich and diverse small mammal fauna discovered at this locality includes isolated teeth belonging to Gliridae, Eomyidae, Cricetidae, Aplodontidae, Sciuridae, Mylagaulidae, Erinaecidae and Soricidae, and Lagomorpha. A preliminary study of the small mammals identified two lagomorphs, three glirids (*Miodyromys asiamediae* Maridet, Wu, Ye, Ni, and Meng, 2011c, *Microdyromys* aff. *orientalis* Wu, 1986, and one unidentified species of *Eliomys*), four eomyids (*Asianeomys* aff. *engesseri* Wu, 1986, *Asianeomys* sp., *Keramidomys* sp., and an unidentified eomyid), three cricetids (*Democricetodon* sp., *Cricetodon* sp., and the new microtoid cricetid reported here), and a new species of *Ansomys*. Eight of these taxa are also present or are represented by close relatives in the middle Shanwangian (about 17–18 Ma) Sihong, Gashunyin'adege, and Suosuoquan S-u faunas (Fig. 2). The association of *Democricetodon* and *Cricetodon* is so far only known from the Early Miocene and early Middle Miocene of China (Wu et al. 2009; Qiu 2010; Maridet et al. 2011b), with *Cricetodon* being replaced by more hypsodont forms such as *Gobicricetodon* and *Plesiodipus* from the late Middle Miocene onwards (e.g., Qiu 1996). The discovery of *Asianeomys* aff. *engesseri* and *Microdyromys* aff. *orientalis* confirms an Early Miocene age for the locality. However, while *Asianeomys engesseri* is known from the Suosuoquan Formation Zone II, dated to between 21.7 and 21.9 Ma based on paleomagnetostratigraphic data (Meng et al. 2006), *Microdyromys orientalis* is known from the late Early Miocene Shanwangian locality of Sihong, thus possibly suggesting a younger age for XJ200604. Paleomagnetostratigraphic and isotopic dating suggest that the Shanwang and Sihong localities are about the same age (Deng 2006), with basalts underlying the Shanwang Formation having been dated to 18.05 ± 0.55 Ma (Cheng and Peng 1985). *Keramidomys* sp. and the new species of *Ansomys* from XJ200604 also resemble specimens from Sihong (Qiu 1987) and Gashunyin'adege in Inner Mongolia (Qiu Zhuding, personal communication 2011), thus corroborating a middle Shanwangian age for XJ 200604 (Fig. 2).

Systematic paleontology

Order Rodentia Bowdich, 1821

Superfamily Muroidea Illiger, 1811

Family Cricetidae Fischer de Waldheim, 1817

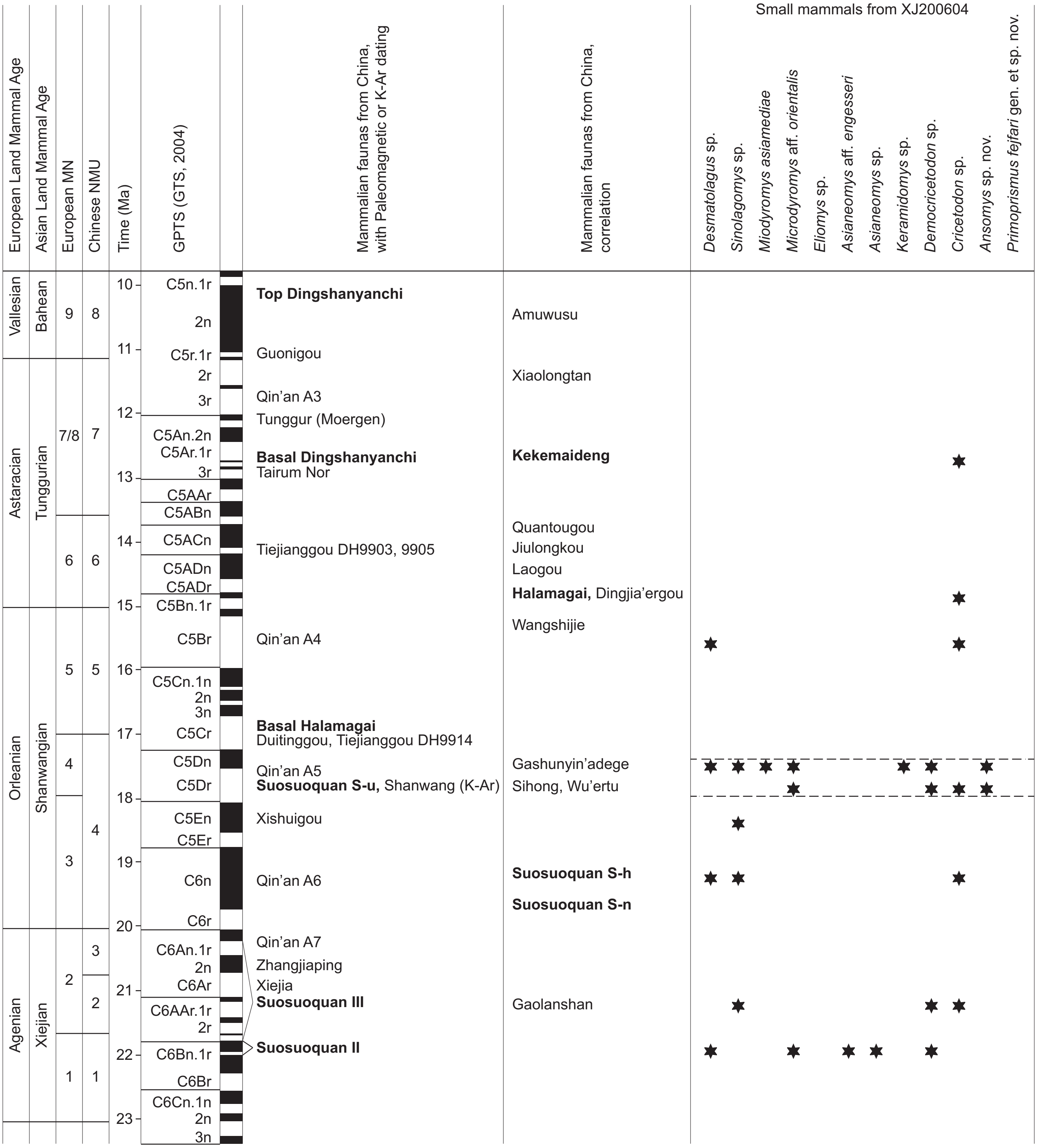

Fig. 2. Comparison of the small mammals from locality XJ200604 with their occurrences (or those of their close relatives) in other mammalian faunas from China. Chinese Early–Middle Miocene mammalian faunal succession with dating and correlation is based on Deng (2006), Meng et al. (2006), Qiu et al. (2006), and Sun et al. (2010). The dashed lines show the suggested correlation of XJ200604 and other middle Shanwangian faunas. Faunas in bold are from the Junggar Basin.

Genus *Primoprismus* nov.

Type species: *Primoprismus fejfari* sp. nov.; monotypic, see below.

Etymology: From the Latin *primo*, first, and *prismus*, prism; in reference to the early trend toward a prismatic morphology displayed by the specimen.

Diagnosis.—Small-sized cricetid rodent with incomplete lophodonty; low crown with prismatic pattern; metaconid and entoconid located anterior to protoconid and hypoconid, respectively; mesolophid and ectomesolophid developed into cuspids; lingual anterolophid absent, and labial one faintly developed.

Differs from *Microtocricetus* Fahlbusch and Mayr, 1975 in its smaller size, lower crown, smaller posterolophid differentiated from the hypoconid, the presence of a cingulum on the labial border, and a weakly developed labial anterolophid. Differs from *Rotundomys* Mein, 1966 in having a well-developed mesolophid and ectomesolophid. Differs from *Microtoscoptes* Schaub, 1934, *Goniodontomys* Wilson, 1937, *Paramicrotoscoptes* Martin, 1975, and *Pannonicola* Kretzoi, 1965 in its much lower crown and less advanced prismatic morphology. Differs from *Celadensia* Mein, Moissenet, and Adrover, 1983, *Anatolomys* Schaub, 1934, *Trilophomys* Deperet, 1892, *Bjornkurtenia* Kowalski, 1992, and *Baranomys* Kormos, 1933 in the absence of a mesodont tooth morphology. Differs from all other cricetids in its anteriorly shifted lingual cuspids and sub-lophodont morphology, and in having the mesolophid and ectomesolophid developed into cuspids. Differs from undoubted arvicolines in having roots, the absence of cementum in the re-entrants, and the lack of a true association of prismatic and hyposodont morphology.

Primoprismus fejfari sp. nov.

Fig. 3A–C.

Etymology: Named after Oldrich Fejfar, in honor of his work on "microtoid cricetids".

Holotype: IVPP V18128, one left lower m2, L = 1.25 mm, W = 0.92 mm.

Type locality: Locality XJ 200604, northwestern Junggar Basin, Xinjiang, China.

Type horizon: Early Miocene, about 17–18 Ma.

Diagnosis.—As for the genus.

Description.—The only available tooth has just two roots. The tooth crown is mesiodistally elongated and has a roughly rectangular outline in occlusal view, with the mesial and distal sides of the tooth bearing flat contact facets. Together, these features suggest the tooth to be an m2. The crown is low and marked by a flat occlusal surface. The cuspids are elongated and form an incomplete lophodont pattern. The prismatic morphology, though evident, is not fully developed. The metaconid and entoconid are located anterior to the protoconid and hypoconid, respectively. The lingual anterolophid is absent, while the labial anterolophid is short and weakly developed. The mesolophid and ectomesolophid are developed into elongated cuspids, with the mesolophid forming a transverse crest together with the protoconid, while the ectomesolophid forms an oblique crest with the entoconid. There ectolophid is absent. A stylid is present on the labial border at the extremity of the ectomesolophid, along with a faint cingulum closing the two labial posterior sinusids. Although both the hypolophid and the posterolophid are elongate and form a nearly transverse posterior crest, they remain clearly differentiated.

Remarks.—No other muroid rodent resembling *Primoprismus fejfari* has ever been reported from the Late Oligocene–Middle Miocene of Central Asia. Previously reported Early Miocene cricetids from the Junggar Basin, such as *Cricetodon* Lartet, 1851, *Eumyarion* Thaler, 1966, *Democricetodon* Fahlbusch, 1964 and *Megacricetodon* Fahlbusch, 1964 (Maridet et al. 2011a, b), all lack the combination of anteriorly shifted lingual cuspids and a semi-lophodont morphology. The monotypic genus *Microtocricetus* Fahlbusch and Mayr, 1975, including only *M. molassicus* Fahlbusch and Mayr, 1975, is known from the early Late Miocene of Germany, France, Austria, Hungary, and Poland (Falhbusch and Mayr 1975; Bachmayer and Wilson 1984, Kowalski 1993; Welcomme et al. 1991; Hír and Kókay 2010), as well as possibly the latest Middle Miocene of Germany (see discussion about the biostratigraphy of Hammerschmiede in Prieto et al. 2011). In addition, some unpublished material from the middle Late Mio-

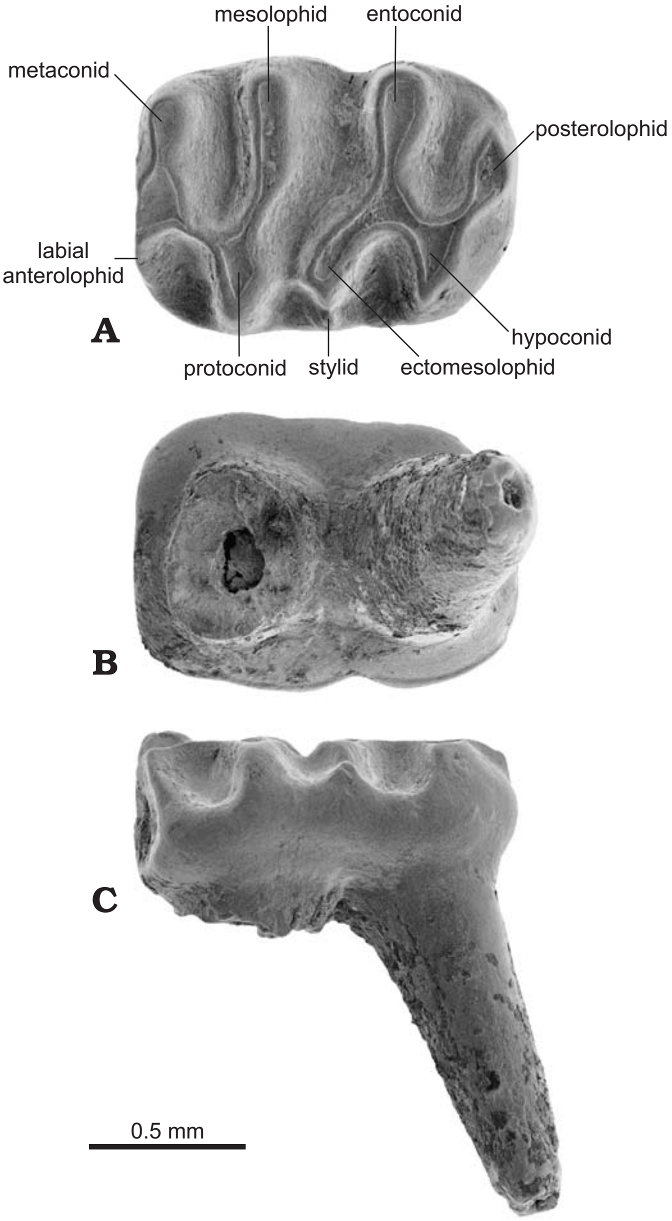

Fig. 3. Left lower m2 of cricetid rodent *Primoprismus fejfari* gen. et sp. nov. from Junggar Basin, China. IVPP V18128 in occlusal (**A**), ventral (**B**), and labial (**C**) views.

cene locality of Sala in Inner Mongolia likely also belongs to this taxon (Qiu and Li 2003). *Microtocricetus* and *P. fejfari* may be closely related, and share a flat occlusal surface, the development of the ectomesolophid and mesolophid into elongated cuspids, an incomplete prismatic morphology, and the presence of transverse crests formed by the protoconid-mesolophid and entoconid-ectomesolophid ("external transversal ridge" or "äußerer Quersporn" sensu Fejfar 1999), respectively.

Other Late Miocene microtoid cricetids, such as *Rotundomys* Mein, 1966, *Celadensia* Mein, Moissenet, and Adrover, 1983, and *Blancomys* van de Weerd, Adrover, Mein and Soria, 1977 lack the ectomesolophid. Finally, microtoscoptine cricetids, such as *Microtoscoptes* Schaub, 1934, *Goniodontomys* Wilson, 1937, *Paramicrotoscoptes* Martin, 1975, and *Pannonicola* Kretzoi, 1965, display much more advanced hyposodont and prismatic morphologies.

Discussion

Previous authors proposed some general morphological trends for microtoid cricetids and true arvicoline rodents (Fejfar 1999; Fejfar et al. 2011; Chaline et al. 1999). For Late Miocene "microtoid cricetids", these include an increase in the degree of hypsodonty; reinforcement of the lophodont and prismatic morphologies; the disappearance of cingula and the opening of sinuses/sinusids; and the transformation of anterolophs/anterolophids and posterolophs/posterolophids into transverse crests (Fejfar 1999). By contrast, later arvicoline evolution is characterized by the convergent development of cement in the re-entrant angles of the molars, the gradual disappearance of roots, and the appearance of an enamel tract (Chaline et al. 1999). With regard to these trends, our specimen displays a striking combination of primitive characters compared with Late Miocene microtoid cricetids, include its small size, the retention of roots, a low crown, a differentiated posterolophid and hypolophid, a faint labial anterolophid not developed into a crest, the absence of an ectolophid, and the presence of a stylid on the labial border, with a faint cingulum closing the two labial posterior sinusids. These primitive features suggest that *P. fejfari* is much more archaic than all previously described microtoid cricetids, including *Microtocricetus molassicus*.

Fejfar et al. (2011) concluded that the morphological peculiarities of *Microtocricetus* exclude any affinities with other microtoid cricetids, and suggested that *Microtocricetus* could be an isolated lineage which went extinct before the end of the Miocene. However, the resemblance of *Microtocricetus* and *Primoprismus* suggests that these two taxa may be related, with *Primoprismus* probably representing a relatively early stage. It should be noted that the labial synclines of *Primoprismus* are not exactly opposite to its lingual anticlines, a feature present in some Microtoscoptinae (such as *Microtoscoptes*, *Paramicrotoscoptes* and *Goniodontomys*), but absent in *Microtocricetus*. However, given its age and retention of many generalized features, it is possible that *Primoprismus fejfari* falls very close to the common ancestor of all Northern Hemisphere Late Miocene microtoid cricetids, including *Microtocricetus* and *Microtoscoptes* from Europe, and *Paramicrotoscoptes* and *Goniodontomys* from North America.

Several authors have suggested that the progressive development of hypsodonty and a prismatic tooth morphology among microtoid cricetids from the Late Miocene onwards gave rise to true arvicoline rodents, which ultimately replaced their ancestors (Gromov and Polyakov 1977; Kretzoi 1955; Fejfar 1999; Michaux et al. 2001; Fejfar et al. 2011). Recent molecular phylogenetic studies indicate that arvicolines, cricetines and sigmodontines form a monophyletic group (e.g., Dubois et al. 1999; Michaux and Catzeflis 2000; Michaux et al. 2001; Jansa and Weksler 2004), with the time of divergence of arvicolines and cricetines estimated to be either 15.5 ± 0.6 Ma or 18.8 ± 1.0 Ma, depending on the calibration point (Michaux et al. 2001). The present results may help to resolve this question, with the discovery of *P. fejfari* in the Early Miocene of China not only providing fossil evidence supporting the earlier estimate of Michaux et al. (2012), but also a new, solid calibration point for further molecular clock analyses.

Based on their occurrence in paludal or fluvial deposits, Fejfar et al. (2011) proposed that microtoid cricetids, such as *Microtocricetus*, *Microtoscoptes*, and *Goniodontomys*, inhabited a moist environment. However, the gradual development of the hypsodont and prismatic tooth morphology in microtoid cricetids and arvicolines is usually interpreted as an adaptation to graminivorous feeding (Chaline et al. 1999). In the Asian interior, arid to semi-arid regions probably existed by the latest Oligocene, with deposition of eolian sediments in the Junggar Basin first occurring around 24 Ma (Sun et al. 2010). During the Early Miocene, the combined effects of the Tibetan uplift and the gradual retreat of the Tethys Ocean enhanced the aridity across the mid-latitude interior of Eurasia (Guo et al. 2002, 2008; Sun et al. 2010). Changes in mammalian faunas indicate a progressive reduction of forest environments and the spreading of open landscapes in Central Asia during the Early Miocene (Maridet et al. 2011c). The evolution of high-crowned molars among perissodactyls and artiodactyls has been suggested as an adaptation to abrasive diets associated with the spreading of grasslands, particularly the expansion of C_3 grasslands during the Early Miocene (MacFadden 2000; Janis 2008; Eronen et al. 2010; Mihlbachler et al. 2011). The origin and gradual enhancement of a hypsodont and prismatic tooth morphology in microtoid rodents and their arvicoline descendants could thus be interpreted as a convergent response to the same environmental changes.

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