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Qaidamomys fortelii, a new Late Miocene murid from Qaidam Basin, north Qinghai-Xizang Plateau, China

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A new fossil murid from Eboliang III Anticline in western Qaidam Basin, northern Qinghai-Xizang Tibetan, China, is described. *Qaidamomys fortelii* gen. & sp. nov. from Eboliang III Anticline is characterized by its large size, high crown and robust cusps in molars. It possesses a mixture of characters from the *Apodemus* and *Occitanomys* groups, which suggests an early divergence from the murid stem lineages. Based on the associated mammalian assemblages, ostracod biostratigraphy, and magnetostratigraphy, the occurrence of the new genus is roughly restricted to the early Late Miocene (early Bahean Chinese Land Mammal Stage/Age), in the 9.4 to 11 Ma interval. The high crown and robust cusps of the new species indicate its adaptation to the tough and coarse food. It also hints that in the early Late Miocene, the western Qaidam Basin was already rather arid.

Introduction

At present at least 30 genera and more than 50 species of murids are distinguishable in the Late Miocene to Pleistocene of China. However, most of them are restricted to the areas outside of the Qinghai-Xizang Plateau. Beyond the north slope of the Himalaya Mountains, and in the hinterland of the Qinghai-Xizang Plateau, fossil murids were sparsely reported. The only species so far described is *Huerzelerimys exiguus* from the early Late Miocene Shengou Fauna in eastern Qaidam Basin, northeastern Qinghai-Xizang Plateau (Qiu & Li 2008). Additional species have been collected from the Pliocene of vari-

ous basins in the high plateau, but they are yet to be described. These include *Apodemus* sp. from Zanda Basin in southwestern Tibet, *Chardinomys* from Kunlun Pass Basin in Kunlun Mountain, and *Chardinomys* and *Micromys* from the Huaitoutala Fauna in eastern Qaidam Basin (Wang *et al.* 2007, Wang *et al.* 2013a, Wang *et al.* 2013b).

Since the late 1990s, the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) have organized systematic reconnaissance expeditions to Qaidam Basin. Around a dozen Neogene vertebrate faunas have been found (Wang *et al.* 2007). During the 2008 field season, our exploration in the axis of the Eboliang III Anticline, western Qaidam Basin, an

area previous known for producing fossil fishes only, yielded several dentitions of a new murid species. This paper formally describes this new genus and species.

Geologic setting

IVPP CD08108 locality (38°06′17.8″N, 93°20′20.4″E, 3001 m a.s.l.), where the murid materials were collected, is located at the axis of the Eboliang III Anticline (Figs. 1A–B and 2B) in western Qaidam Basin. The Eboliang III Anticline is near the late Miocene depositional center of the basin, and a thick sequence of the Upper Youshashan and Shizigou formations is exposed due to erosion of the domed anticline. Fine-grained lacustrine siltstones are predominant with occasional coarse sands and lignite, as is also consistent with occurrences of fossil fishes. Alternating dark grey, rusty brown and light buff colored sediments clearly delineate fine bedding planes, and various amounts of gypsum are present, increasing toward the top of the section. Fossil woods, freshwater snails, and insect burrows are also frequently seen.

Material, methods and terminology

The murid fossils were collected by the first author from two sites about 20 m apart in the same stratigraphic layer. In the field, only tips of the incisors and parts of molars were exposed. The matrix containing fossils were packed into two separate jackets. After laboratory preparation, the jacket from the eastern site produced remains belonging to the same individual, including a fragmentary maxillary with associated jaws (Fig. 3A–B). The jacket from the western site produced a pair of incomplete lower jaws (Fig. 3C). All the materials are housed in the IVPP in Beijing.

Photographs were taken with SEM (NEC S-3700N). Dental terminologies for Murinae from Storch (1987: fig. 1) and Freudenthal and Martín-Suárez (1999: fig. 39.2) are generally adopted. However, their usage is not consistent, especially for the lower molars. Here we mainly follow the terminology of Freudenthal and Martín-Suárez (1999). Moreover, our definition of

“stephanodonty” follows the original concept of Schaub (1938), which was defined as the t4, t5, t6, t9, and t8 forming a continuous garland, and in the most complete form of stephanodonty, t4 and t8 are connected too.

Taxonomy

Qaidamomys Li & Wang *gen. nov.*

Order Rodentia Bowdich, 1821

Family Muridae Illiger, 1811

Subfamily Murinae Illiger, 1811

TYPE SPECIES: *Qaidamomys fortelii* *sp. nov.*

ETYMOLOGY: Named after the Qaidam Basin, where the type locality is located.

SPECIES INCLUDED: Type species only.

DIAGNOSIS: Large-sized murid; molars high-crowned and robustly-cusped; stephanodonty (*sensu* Schaub 1938) complete on M1, but incomplete (t6 not connected to t9) on M2; on M1–2, ridge-like t7 distinctly developed, t12 strong, and t1 always connected with t5 through a strong ridge; posterior spur of t3 developed on M1; t9 distinctly developed on M3; labial accessory cusps of lower molars strongly developed; antero-central cusp on m1 strong, and either single or double; no longitudinal crest on lower molars present; no enamel funnel on m1; posterior tubercle wide and robust on m1–2.

DISTRIBUTION: So far known from the type locality only, the early Late Miocene (early Bahean Chinese Land Mammal Stage/Age (LMS/A), equivalent to European Vallesian age, MN9 + 10) of Qaidam Basin, northern Qinghai-Xizang Plateau, Qinghai Province, China.

REMARKS: *Qaidamomys* *gen. nov.* represents a large-sized fossil murid found in northern Qinghai-Xizang Plateau, China. Its size is slightly larger than that of *Allorattus engesseri* Qiu & Storch, 2000. Its diagnostic characters are so distinct that there is no doubt that it is very different from other large-sized Neogene taxa such as *Pelomys* Peters, 1925, *Anthracomys* Schaub, 1938, *Arvicanthis* Bate, 1942, *Valerymys* Michaux, 1969, *Saidomys* James & Slaughter, 1974, *Parapelomys* Jacobs, 1978, *Yunomys* Qiu & Storch, 1990, and *Allorattus* Qiu &

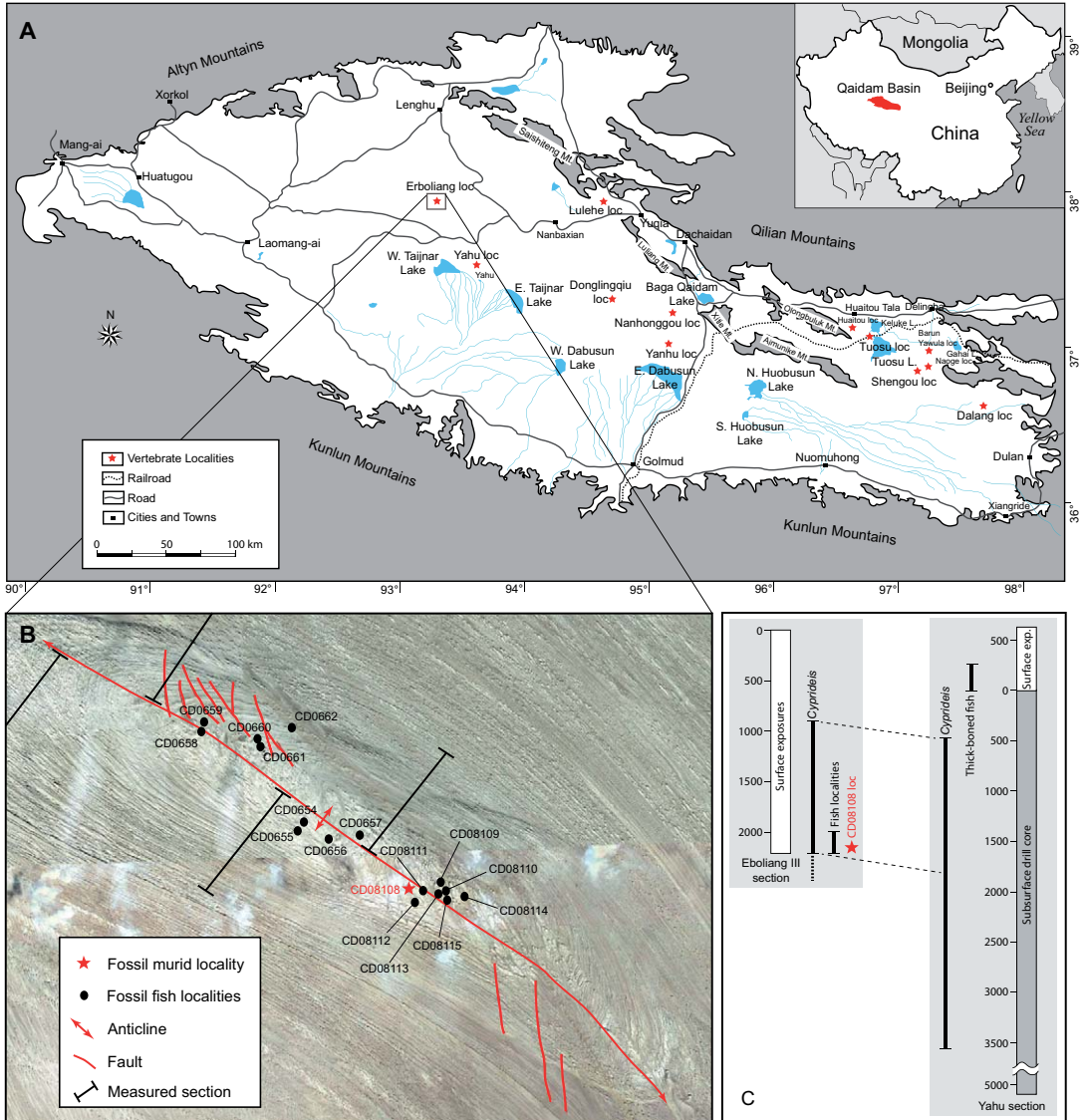


Fig. 1. (A) Map of Qaidam Basin showing major areas of vertebrate fossil-producing localities (modified from Wang *et al.* 2007: fig. 1). (B) Satellite image of the Eboliang III Anticline showing the location of the new rodent locality and other fossil fish localities. (C) Correlation of Eboliang III and Yahu sections. Yahu surface section was based on Fang *et al.* (2008: fig. 2) and occurrence of fossil fishes based on Chang *et al.* (2008), and Yahu drill section and Eboliang surface section, as well as ostracod occurrences, based on unpublished data of Sun Zhen-Cheng, archived in China University of Petroleum.

Storch, 2000. This new genus can be easily distinguished from the Pleistocene genera such as *Wushanomys* Zheng, 1993 and *Qianomys* Zheng, 1993, and extant ones such as *Rattus* Fischer von Waldheim, 1803, *Nesokia* Gray, 1842, *Bandicota* Gray, 1873, *Limnomys* Mearns, 1905, *Hadromys* Thomas, 1911, *Dacnomys* Thomas,

1916, *Diplothrix* Thomas, 1916, *Chiromyscus* Thomas 1925, *Leopoldamys* Ellerman, 1947, *Berylmys* Ellerman, 1947, *Niviventer* Marshall, 1976, *Srilankamys* Musser, 1981, *Margaretamys* Musser, 1981, and *Anonymomys* Musser, 1981. For additional comments and comparisons see Taxonomic Remarks.

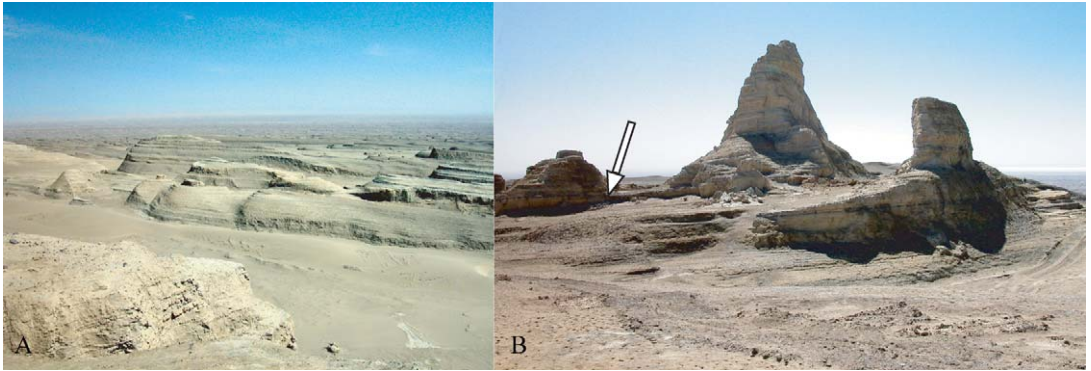


Fig. 2. (A) Eboliang exposures on the northeastern limb of the Eboliang III Anticline. Similar to that of Yahu Anticline (Wang *et al.* 2007: figs. 8–9), the wind-eroded exposures are mostly oriented along the prevailing winter northwesterly winds, coinciding with the axis of the anticline. (B) Fossil murid producing exposures at the axis of the Eboliang III Anticline. View is to the south. An arrow indicates the type locality CD08108 of *Qaidamomys fortelii* gen. & sp. nov.

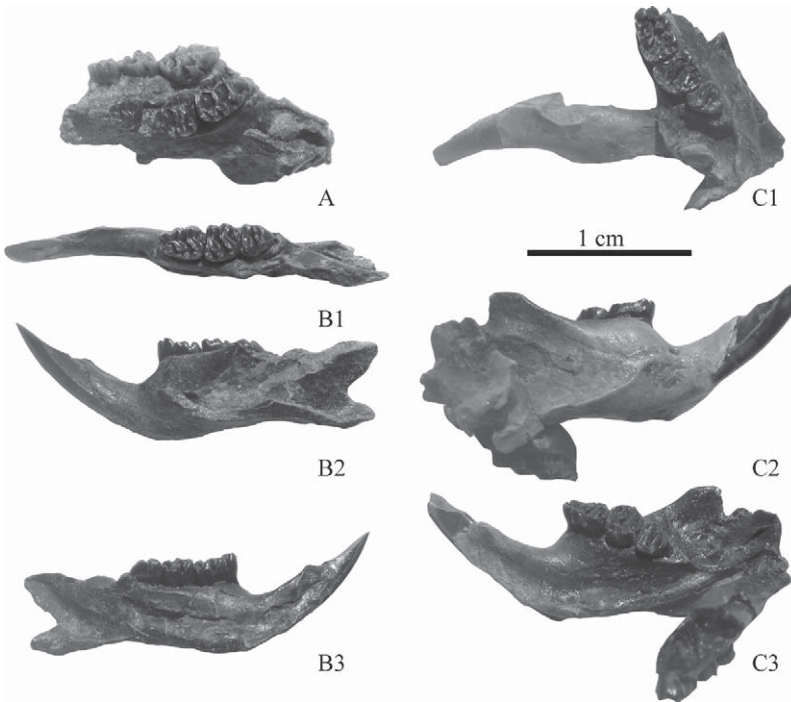


Fig. 3. Maxillary and mandibles of *Qaidamomys fortelii* gen. & sp. nov. from Eboliang III Anticline. — **A–B:** holotype (V 18853). **A:** maxilla, occlusal view; **B:** left mandible (1–3, occlusal, labial, lingual views, respectively). — **C:** paratype (V 18854) (1–3, ventral, labial and lingual views, respectively).

***Qaidamomys fortelii* Li & Wang sp. nov.**
(Figs. 3–5)

HOLOTYPE: Fragment of maxillary with nearly complete left and right dentitions, and associated lower jaws including left mandible with incisor and m1–3 and right incomplete dentition with m1–2, V 18853 (IVPP) (Figs. 3A–B, 4A–D and 5A–C). **MEASUREMENTS** (length × width, mm): upper left dentition: M1, 3.24 × 2.36; M2, 2.33 × 2.29; M3, 1.73 × 1.70; upper right dentition: M2, 2.25 × 2.30; M3, 1.68 × 1.69; lower left m1–3: diastema length, 5.0; dentition length, 6.47;

m1, 2.73 × 2.0; m2, 2.12 × 2.23; m3, 1.97 × 1.87; lower right m1–2: m1, 2.88 × 1.99; m2, 2.31 × 2.18.

PARATYPE: A pair of incomplete mandibles, left one with m1–3 and right one with incisor and m1–3, V 18854 (IVPP) (Figs. 3C and 4E–F). **MEASUREMENTS** (length × width, mm): lower left m1–3: dentition length, 6.80; m1, 3.07 × 2.10; m2, 2.12 × 2.42; m3, 1.78 × 1.88; lower right m1–3: diastema length, 4.9; dentition length, 6.60; m1, 2.76 × 1.94; m2, 2.0 × 2.46; m3, 1.79 × 2.09.

ETYMOLOGY: Dedicated to Professor Mikael Fortelius, in recognition of his outstanding work on Neogene Eurasian mammals.

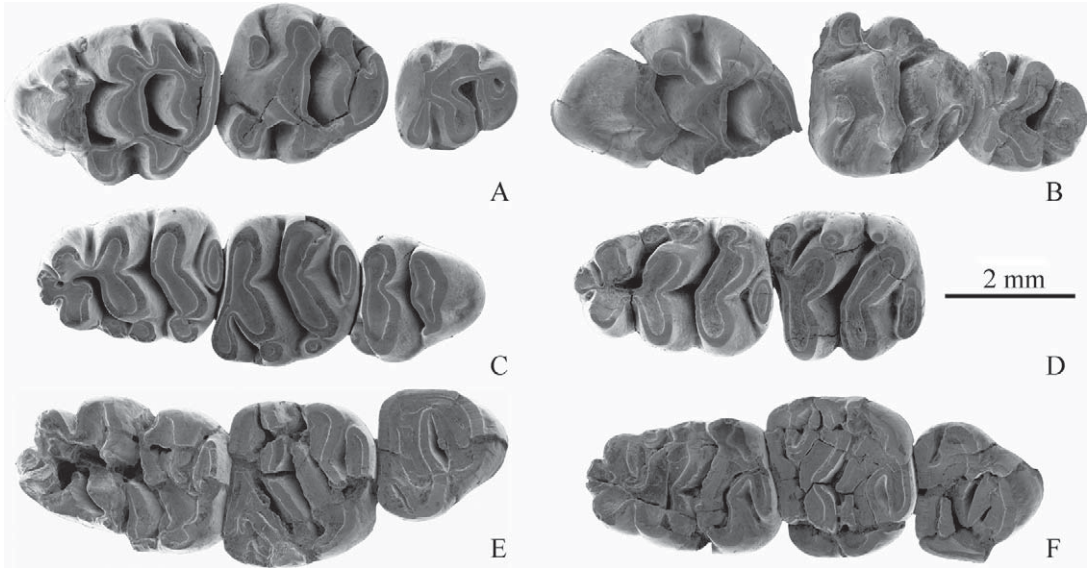


Fig. 4. Molars of *Qaidamomys fortelii* gen. & sp. nov. from Eboliang III Anticline, all in occlusal view. — **A–D:** holotype (V 18853). **A:** left M1–3; **B:** right M1–3, M1 postero-labial portion is broken; **C:** left m1–3; **D:** right m1–2. — **E–F:** paratype (V 18854). **E:** left m1–3; **F:** right m1–3.

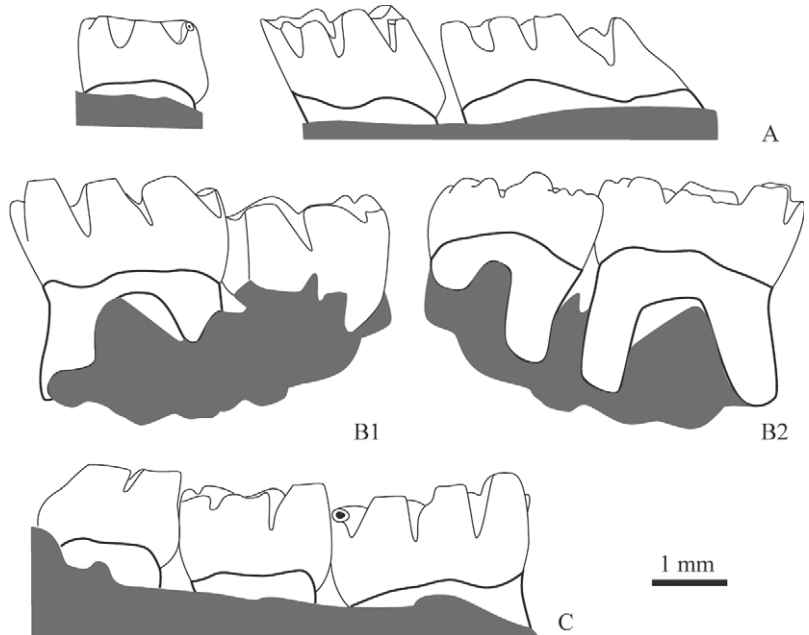


Fig. 5. Lateral views of dentitions of the holotype (V 18853) of *Qaidamomys fortelii* gen. & sp. nov. from Eboliang III Anticline. **A,** left M1–3, **B,** right m1–2, **C,** left m1–3, **A** and **B2** in labial view, **B1** and **C** in lingual view.

TYPE LOCALITY: IVPP CD08108, Eboliang III Anticline, western Qaidam Basin, Qinghai Province, China (Figs. 1–2).

STRATUM TYPICUM: Upper Youshashan Formation, the Late Miocene (early Bahean Chinese LMS/A, equivalent of Vallesian age, MN9 + 10).

DIAGNOSIS: As for the genus.

The only maxilla is poorly preserved (Fig. 3A). No useful characters can be observed from the maxilla. Fortunately, dentitions are well

preserved, except that the posterolabial portion of right M1 is damaged (Fig. 4B). Due to the strongly taphonomic distortion, the left M3 and right M1 are deviated far from their original position. Molars have robust cusps and strong ridges. The molars size decreases from M1 to M3. The labial crown heights of molars are all higher than 1.2 mm (Fig. 5A).

M1: The occlusal outline is pyriform. t1 is remarkably seated posteriorly to t3, and well connected with both t2 and t5. No t1bis and t2bis [= t0 and prestyle, respectively, in Storch (1987)] is present. The posterior spur of t3 is developed, but not connected with t5. t4 is displaced posteriorly to t6, and connected with t8 by ridge-like t7. t6 is connected with t9 through a short and high ridge. Stephanodonty is complete, i.e. t4, t5, t6, t9, t8 and t7 form a continuous garland. t12 is well developed. A deep fold can be observed between t12 and t9 (Fig. 4A–B).

M2: t1 is large-sized and connected with t5. t3 is isolated and smaller than t1 in size. t4 is displaced slightly posteriorly relative to t6, and connected with t8 through ridge-like t7. t9 is smaller than t6 and not connected with it. t12 is developed (Fig. 4A–B).

M3: The t1 is elongated labially, and connected with t5. t3 is small but distinct, and connected with t5. t4 is not connected with t8. t8 is nearly subtriangular, and connected with t6 via a distinctly developed t9. A small enamel funnel is enclosed by t9 and t8 and labially seated (Fig. 4A–B).

MANDIBLE: On the four mandibles (Fig. 3B–C), the coronoid, condyloid and angular processes are all damaged in varying degrees. The left dentary of the holotype (*V 18853*, Fig. 3B) is relatively well preserved. In labial view, the bottom of worn facet of the incisor is nearly at the same level as the molar alveoli. The anterior slope of diastema is gently curved, whereas its posterior slope, anterior to m1, is steep. A round mental foramen is seated antero-ventrally to m1 and beneath the bottom of diastema. Only the inferior masseteric crest is developed, with its apex terminating at the level of the anterior root of m1. The masseteric fossa is distinctly concave. The ascending ramus begins at the position under m2. Molars have robust main cusps, accessory cusplets and strong ridges. The molars

size decreases from m1 to m3 (Fig. 4C–F). In lingual view, the crown heights of molars are all higher than 1.2 mm, while the labial crown heights are lower than 1.0 mm (Fig. 5B–C).

m1: The occlusal outline is relatively wide. The antero-central cusp [= tma, in Storch (1987)] is very strong. It is mostly single and posterolingually connected with the lingual anteroconid (Fig. 4D–F), or double and connected with paired anteroconids (Fig. 4C). A strong ridge is developed between lingual anteroconid and metaconid, through which the nearly symmetrical anteroconid complex is always connected with the metaconid-protoconid chevron. No enclosed enamel funnel is present. There is no trace of longitudinal crest [= medial ridge, in Storch (1987)] on the entoconid-hypoconid chevron. The posterior tubercle [= cp, in Storch (1987)] is wide and robust. Accessory cusps [= cingular cusps, in Storch (1987)] are well developed. c1, c2 and c3 are robust, of which c1 is the largest one.

m2: The occlusal outline is nearly rectangular. It is the widest one of the dentition. The anterolabial cusp [= labial anteroconid in Storch (1987)] is strong and continuous with metaconid-protoconid complex. There is no trace of longitudinal crest on the entoconid-hypoconid chevron. The posterior tubercle is wide and robust. Labial accessory cusps are well developed. c1, c2 are present, and c1 is smaller than c2 (Fig. 4C–D).

m3: The occlusal outline is subtriangular. The antero-labial cusp is present and connected with metaconid-protoconid complex. A very small c1 can be observed on slightly worn tooth (Fig. 4C). The hypoconid and entoconid merge into a wide and strong cusp. The fold between metaconid-protoconid and entoconid-hypoconid complexes is enclosed on the heavily worn teeth (Fig. 4E–F).

Taxonomic remarks

Freudenthal and Martín-Suárez (1999) divided the European Miocene murid genera into seven groups. Four of them also have representations in Miocene to Pliocene of China. For example, *Progonomys sinensis* from the Bahe Formation, Lantian County, Shaanxi Province and *Huerze-*

lerimys exiguus from the Upper Youshashan Formation in eastern Qaidam Basin indicate the presence of the *Progonomys* group, and the former was regarded as the oldest murids known from China (Qiu *et al.* 2004, Qiu & Li 2008). *Hansdebruijnina perpusilla* from Baogedawula and *H. pusilla* from Ertemte, Inner Mongolia show the dispersion of the *Occitanomys* group (Storch 1987, Storch & Ni 2002). A series of species of *Apodemus*, including *A. orientalis*, *A. qiui*, *A. lii* and *A. zhangwagouensis* represent the rich records of the *Apodemus* group in China. The *Micromys* group is also flourishing, such as *M. chalceus* from Ertemte and *M. kozaniensis* from Bilike of Inner Mongolia, and *M. tedfordi* from Yushe Basin, Shanxi Province (Storch 1987, Wu & Flynn 1992, Qiu & Storch 2000). Besides the above four groups, there are some local or endemic genera occurring in Neogene of China, such as *Orientalomys* de Bruijn & van der Meulen, 1975; *Chardinomys* Jacobs & Li, 1982; *Yunomys* Qiu & Storch, 1990; *Huxiamys* Wu & Flynn, 1992; *Linomys* Storch & Ni, 2002 and *Leilaomys* Storch & Ni, 2002.

In morphology, *Qaidamomys* differs from the *Micromys* group by its distinct higher crown and strongly cusped teeth, development of the connections between t1 and t5, well developed antero-central cusp and accessory cusps on low molars. *Qaidamomys* can be easily distinguished from *Progonomys* group by its distinct higher crown and strongly cusped teeth, development of a ridge-like t7 and a strong connection between t6 and t9 on M1, and well developed antero-central cusp and accessory cusps on low molars. *Qaidamomys* shares with the *Occitanomys* group some characters, such as complete stephanodonty and connection between t1 and t5 on M1. However, *Qaidamomys* also shows some differences from *Occitanomys*. For example, in the latter genus, t7 is normally absent on M1, t12 is often reduced, antero-central cusp on m1 is weak, and longitudinal crests are well developed. *Qaidamomys* also shares with the *Apodemus* group some characters, such as the presence of t7 and well developed t12 on M1, strongly developed accessory cusps and antero-central cusp, and absence of longitudinal crests on lower molars. The differences between *Qaidamomys* and *Apodemus* are mainly on their upper molars.

Qaidamomys has strong connections between t1 and t5, t4 and t8 on M1–2, respectively, and disconnection between t6 and t9 on M2. Moreover, though *Qaidamomys* also shares with *Orientalomys* and *Chardinomys* some characters on their lower molars, the former differs from the latter two taxa by its relatively anteriorly displaced t1 and t6, absence of t7 and reduction of t12 on M1–2, and absence of longitudinal crests on lower molars. *Huaxiamys*, *Yunomys*, *Linomys*, and *Leilaomys* are all endemic Neogene genera in China. *Qaidamomys* is remarkably different to them by its diagnostic characters listed above. The origin and relationships of *Qaidamomys* are currently not well understood. It shows a unique mosaic of characters from the *Occitanomys* and *Apodemus* groups, which suggest an early divergence from the main murid stem.

Discussion

Biochronology

With the exception of the murid from CD08108 and some limb bone fragments from CD08110, vertebrate fossils from the Eboliang area consist almost entirely of cyprinid fishes, which are generally not age-diagnostic. The fossil yielding bed of CD08110 is slightly higher than that of *Qaidamomys* site CD08108 (*see* Fig. 1). The limb bone fragments including at least a right lunate, a right first phalanx II and III, respectively from CD08110 are identified as *Chalicotherium* sp. by our colleague Dr. Chen Shaokun, who is studying Chinese Neogene chalicotheres. The genus *Chalicotherium* in China has been found at a few localities, including *C. brevirostris* from the Middle Miocene Tunggur area, Inner Mongolia, *C. sp.* (*Macrotherium sp.*) from Cixian, Hebei Province, and *C. cf. C. brevirostris* from Tuosu Fauna in eastern Qaidam Basin (Colbert 1934, Chen & Wu 1976, Wang & Wang 2001). In the Qaidam Basin, sporadic additional materials of *Chalicotherium* were collected by us in recent years. They include a phalanx from the Quanshuiliang area in eastern Qaidam, and limb bone fragments from CD08110 of the Eboliang area, still poorly preserved materials possibly belonging to a single species. *Chalicotherium* often co-

occurs with *Hipparion* in Tuosu Mammal Fauna in eastern Qaidam Basin, and elsewhere in the early Late Miocene (Wang *et al.* 2007, 2011).

In ostracod biostratigraphy, the lowest occurrence of the brackish-water ostracod *Cyprideis* is near the boundary of Upper and Lower Youshashan formations at about 12–13 Ma within Qaidam Basin (Yang *et al.* 1994, Lu *et al.* 2005, Zhang *et al.* 2006, Chen *et al.* 2010). *Cyprideis* is abundantly represented in the lower 1200 m of the Eboliang sections (Fig. 1C), indicating the late Middle to early Late Miocene age.

The nearest paleomagnetic section is from the Yahu Anticline (Fang *et al.* 2008), which is along the same structural axis as the Eboliang III Anticline about 50 km to the southeast (Fig. 1A), although the Yahu Anticline is exposing a much younger part of the section as compared with that in Eboliang. An even younger magnetic section from a drill core (SG-1) to the west stops at the lower boundary of the Quaternary (Zhang *et al.* 2012). Fang *et al.* (2008) correlated the Yahu surface section to 2n through 3r of the GPTS, ~5.30–1.83 Ma. Abundant pachyostotic fishes, *Hsianwenia wui*, were recovered from the lower 220 m of the Yahu section (Chang *et al.* 2008), presumably indicating hypersaline environments. These thick-boned fishes are not present in the lower section of the Eboliang III, where our fossil fish localities occur (there are unpublished reports of other fish localities in upper part of the Eboliang section, which we did not find). The absence of pachyostotic fishes in the lower Eboliang section, as well as the lack of gypsum veins abundant in the Yahu section, suggests a stratigraphic interval below the Yahu section, i.e., before Pliocene.

The above constraints place IVPP CD08108 locality within the long interval of the Late Miocene (11.6–5.3 Ma). To further narrow down the age range, ostracod biostratigraphy still offers the only means for a consistent basin-wide correlation. Yang *et al.* (1994) published an integrated study of an ostracod biostratigraphy and a composite magnetostratigraphy from the Ganchaigou section (late Cenozoic) in western Qaidam Basin and the Lulehe section (early Cenozoic) further to the east. Seven species of *Cyprideis* occur within chrons 4Ar.2r to 5AAr (Yang *et al.* 1994: figs. 2–8), including a characteristic long normal

(C5n.2n) of ~1 million years in duration, and if their magnetic correlation is correct, it corresponds to 9.41–13.37 Ma based on ATNTS2004 (Lourens *et al.* 2004). Lu and Xiong (2009: section k in fig. 6) indicated a single occurrence of *Cyprideis* at 11–12 Ma range of their Dahonggou magnetic section, which is 175 km southeast of Eboliang III in central Qaidam Basin. *Cyprideis* occurs in the 880–2300 m range of the Eboliang section (Fig. 1C), and the lowest occurrence of this genus probably extends further down below surface exposures. Subsurface drill core at nearby Yahu Anticline has documented a much longer range for *Cyprideis* at 500 to 3500 m below the surface. Assuming a similar rate of deposition between the depositional sequences at these two nearby anticlines, it seems reasonable to correlate the lower-most occurrence of *Cyprideis* in Eboliang, where CD08108 occurs, to somewhere in the upper part of the *Cyprideis* range in the Yahu section (Fig. 1C). If this is the case, CD08108 is likely to be in the upper part of the *Cyprideis* magnetochron, i.e., in the range of ~9.4–11 Ma. We do realize, however, that the above age inference is rather circumstantial and should be viewed as a preliminary estimate.

Palaeoecology

The remains of normal-boned cyprinid fishes confirm the existence of freshwater bodies in the Eboliang lacustrine section, and the occurrence of *Chalicotherium*, commonly regarded as a browser, indicates the existence of a shrub or forest habitat near shore during the Late Miocene. It is obvious that the paleoecology of the Eboliang area of western Qaidam Basin was much more moderate than it is today. Moreover, the paleoecology in the Late Miocene lower Eboliang section was still more moderate than that of the neighboring Yahu section in Pliocene, because the thick-boned fish *Hsianwenia wui* produced from the lower Yahu section was regarded as adapted to extreme conditions resulting from the aridification of Qaidam Basin (Chang *et al.* 2008). It is notable that the high-crowned and robustly-cusped teeth of *Qaidamomys fortelii* also show adaptation to the tough and coarse food, which may hint that in

the early Late Miocene, western Qaidam Basin was already arid to a certain degree. The aridification process of Qaidam Basin likely initiated at least as early as the Late Miocene, possibly influenced by both global cooling and Tibetan Plateau uplift.

Acknowledgements

It is with great pleasure that we dedicate this paper to our friend and colleague, Mikael Fortelius, who has contributed so much to Chinese vertebrate paleontology. This paper on a new murid from Qaidam is particularly fitting because Mikael has personally helped in archival research that was instrumental to our understanding of historic collections from Qaidam Basin by Birger Bohlin. Wang Ning, Zhao Min, Shi Fuqiao and Wang Qiuyuan from the IVPP, Zhijie J. Tseng from the University of South California (now at American Museum of Natural History in New York), and Xie Guangpu from Provincial Museum of Gansu participated partly in the field work. The authors would like to express their gratitude to Prof. Qiu Zhuding and Dr. Ni Xijun for their valuable discussion on the subject. Many thanks are also due to Zhang Wending for the SEM photographs. Funding of the fieldwork and travel was provided by the Major Basic Research Projects (2012CB21904) from the Ministry of Science and Technology of China, Strategic Priority Research Program of the Chinese Academy of Sciences (XDB03020104), Chinese National Natural Science Foundation (no. 40702004), and National Science Foundation (US) (EAR-0446699, 0444073, 0958704, 1227212).

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