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A new species of *Megacricetodon* (Cricetidae, Rodentia, Mammalia) from the Middle Miocene of northern Junggar Basin, China

SHUNDONG BI,[1] JIN MENG,[2] AND WENYU WU[3]

ABSTRACT

Dental, mandibular, and postcranial specimens of *Megacricetodon yei* n. sp., are described. The new specimens, including the complete dentition, mandible, and partial forelimb and hindlimb, represent the most complete materials known for the genus, provide valuable information concerning the interspecific variation of the genus, and lead to the reassessment of the suprageneric position of *Megacricetodon*.

Megacricetodon yei is characterized by having medium-size, clearly split anterocone of M1, presence of the labial spur of the anterolophule and the posterior spur of the paracone in some M1s, medium to long mesoloph in M1-2, frequent occurrences of double protolophules, transverse or posteriorly directed metalophule of M2, and single anteroconid of the m1. *Megacricetodon yei* is more closely related to *Megacricetodon* (= *Aktaumys*) *dzhungaricus* than to any other species of *Megacricetodon*, but is more derived than the latter. Based on the new information, the validity of the genus *Aktaumys* is discussed.

The postcranial features of *Megacricetodon yei* show clear adaptations for terrestrial habits, but as in many ground-dwelling rodents living in burrows, it could also climb or dig. The associated fauna has been correlated to Tongxin fauna from the adjacent part of China and the Belometchetskya fauna of north Caucasus, equivalent to early Middle Miocene age, or MN 6 correlative. The stage of evolution of *Megacricetodon yei* is consistent with the faunal correlation.

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INTRODUCTION

Cricetid rodents of the genus *Megacricetodon* are among the most abundant mammalian species in the Old World Cenozoic fauna. Fahlbusch (1964) first recognized *Megacricetodon* as a subgenus of the genus *Democricetodon*, which he established at the time, but later researchers have elevated the subgenus to the genus level (Mein and Freudenthal, 1971a). The genus *Megacricetodon* is species-rich. To date, more than 25 fossil species have been recognized from the Miocene of Europe and Asia. Despite their great diversity and widespread distributions, all the species of *Megacricetodon* are represented primarily by isolated teeth, often collected by screen washing. Very few cranial and postcranial bones are known. In addition to numerous specimens of dentitions, here we describe the best preserved postcranial skeletal materials known for this genus from the northern Junggar basin, Xinjiang, China. The Junggar materials shed new light on the interspecific variation and anatomy of *Megacricetodon* and help to clarify several taxonomic issues of the genus.

The northern Junggar basin of China has yielded many fossiliferous localities, of which Tieersihabahe-Chibaerwoyi Cliff (TCC) is an extremely rich locality. Fossil mammals in this area were first discovered in 1982 by a field team from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences. Subsequently, fossil mammals, mainly large mammals, were described, including carnivores (Qi, 1989), artiodactyls (Ye, 1989), proboscideans (Chen, 1988), lagomorphs (Tong, 1989), and rodents (Wu, 1988).

Our field investigations, run from 1995 through the present, have greatly improved the documentation of Tertiary strata in this area. Based on these new discoveries, Ye et al. (2001a, 2001b, 2003) redefined the stratigraphical units of TCC, in ascending order, as: (1) the Eocene-Oligocene Ulunguhe Formation, (2) the Late Oligocene Tieersihabahe Formation, (3) the Early Miocene Suosuoquan Formation, (4) the Middle Miocene Halamagai Formation, and (5) the late Middle Miocene Kekemaideng Formation. The materials described here were collected from the Halamagai Formation between the Tieersihabahe section and Chibaerwoyi section in 1998 and 2000. The bones were excavated mainly from a mudstone lens (about 2 m^2) imbedded in grayish medium-grained sandstone. Dozens of maxillae and mandibles with complete dentitions, 25 isolated teeth, and about 27 postcranial elements were recovered. Although no articulated elements were found, the ratio of the specimens, morphology, and size suggest that they belong to the same species. Numerous specimens of a distinctively larger taxon, *Cricetodon* n. sp. were also recovered from the same spot and have been described by Bi (2005). Comparisons are specifically made to *Cricetodon* from Tieersihabahe since it represents the most complete skeletal materials of extinct cricetids known to date.

MATERIALS AND METHODS

Terminology for dental morphology is after Mein and Freudenthal (1971a). Because their terminology has been well known, we prefer not to include a diagram to illustrate the tooth structure. Positional abbreviations of teeth follow the common alphanumeric convention of using uppercase versus lowercase letters to identify maxillary or mandibular teeth, respectively, and numbers to indicate their placement in the tooth row (for example, M1 and m1). The cranial and postcranial skeletal terminologies, wherever appropriate, follow those by Howell (1926), Rinker (1954), Cooper and Schiller (1975), Carleton and Musser (1989), Carleton and Olson (1999), and Gebo and Rose (1993).

Teeth and mandibles were imaged and measured using a Nikon SMZ 8 microscope set at 20 × magnifications, and measurements were recorded to the nearest 0.01 mm. The SEM photographs of some teeth were taken from uncoated specimens using a Hitachi scanning electron microscope. All postcranial measurements were taken to 0.05 mm using digital calipers. IVPP is the abbreviation of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

SYSTEMATIC PALEONTOLOGY

ORDER RODENTIA BOWIDICH, 1821

SUBORDER MYOMORPHA BRANDT, 1855

SUPERFAMILY MUROIDEA ILLIGER, 1811

FAMILY CRICETIDAE ROCHEBRUNE, 1883

SUBFAMILY CRICETINAE STEHLIN & SCHAUB, 1951

GENUS *MEGACRICETODON* FAHLBUSCH, 1964

Megacricetodon yei, n. sp.

HOLOTYPE: IVPP V15349.1, a fragmentary right maxilla with M1–M3 (fig. 3)

REFERRED MATERIAL: IVPP V15349.2, a fragmentary right maxilla with M1–M3; V15349.3, a right M1; V15349.4, a right M2; V15349.5-6, 2 right M3; V15349.7, a left maxilla with M1–M3; V15349.8, a left maxilla with M1–M3; V15349.9, a left maxilla with the zygomatic plate and M1; V15349.10–11, 2 left M2; V15349.12–13, 2 left M2; V15349.14–15, 2 left M3; V15349.16–19, 4 right upper incisors; V15349.20–22, 3 left upper incisors; V15349.23, an almost complete left mandible except the broken angular process; V15349.24, a left fragmentary mandible with the incisor and m1–3; V15349.25, a left fragmentary mandible with m1–m3; V15349.26, a left fragmentary mandible with the incisor and m1–m3; V15349.27, a left fragmentary mandible with m1–m3; V15349.28, a left fragmentary mandible with the incisor; V15349.29, a left fragmentary mandible with the incisor and m1–m2; V15349.30, a left fragmentary mandible with the incisor, m1, and m3; V15349.31, a left fragmentary mandible with m2; V15349.32, a left fragmentary mandible with m1–m2; V15349.33-34, 2 left m1; V15349.35, a left m2; V15349.36–37, 2 isolated m3; V15349.38, a right fragmentary mandible with the incisor and m1–m3; V15349.39, a right fragmentary mandible with the incisor and m2; V15349.40, a right fragmentary mandible with the incisor and m1–m3; V15349.41, a right fragmentary mandible with m2–m3; V15349.42, a right fragmentary mandible with m1–m2; V15349.43, a right fragmentary mandible with m2–m3; V15349.44,a right fragmentary mandible with m1–m2; V15349.45–46, 2 right m3; V15350.1, a baculum; V15350.2–3, 2 almost complete right humeri except the broken proximal end; V15350.4, a left humerus except broken proximal end; V15350.5–6, 2 distal portions of left humeri; V15350.7, proximal portion of a right ulna; V15350.8–10, 3 proximal portions of left ulnae; V15350.11–12, 2 distal left ulnar ends; V15350.13, a complete right femur except the broken distal end; V15350.14–17, 4 fragmentary right femurs; V15350.18–19, 2 fragmentary left femurs. V15350.20–21, 2 complete right tibiae except the broken proximal end; V15350.22–23, 2 complete left tibiae except the broken proximal end; V15350.24–26, 3 fragmentary left tibiae; V15350.27, a right calcaneus.

LOCALITY AND AGE: Site XJ 98018 (46° 40.128′ N, 88°30.846′ E) at the Tieersihabahe locality in the northern Junggar Basin of China. The first sand bed of the Halamagai Formation, early Middle Miocene.

ETYMOLOGY: The species name, *yei*, is in honor of our colleague, professor Jie Ye, for his contribution to the study of Cenozoic stratigraphy and mammals in northern Xinjiang and discovery of the locality.

REPOSITORY: The specimens are housed in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing.

DIAGNOSIS: A *Megacricetodon* species of medium size, M1 with clearly split anterocone, presence of the labial spur of the anterolophule and the posterior spur of the paracone in some M1s, medium to long mesoloph in M1–2, frequent occurrences of the double protolophules in M2 of the collection, M2 metalophule transverse or posteriorly directed, m1 anteroconid simple, mesolophid of medium length in m1–2, and presence of the entepicondylar foramen in the humerus.

DIFFERENTIAL DIAGNOSIS: Differs from *Megacricetodon* (= *Aktaumys*) *dzhungaricus* in having slightly smaller size; better bifurcated M1 anterocone; shorter mesoloph in M1 and M2; fewer occurrences of the labial spur of the anterolophule in M1; fewer occurrences of double protolophule and metalophule in M2. Differs from any other known species of *Megacricetodon* in having the following combination of features: well-bifurcated M1 anterocone; presence of a labial spur of the anterolophule in many M1s, double protolophules in most M2s, the presence of the posterior spur of paracone, and long mesoloph in M1 and M2, and single m1 anteroconid.

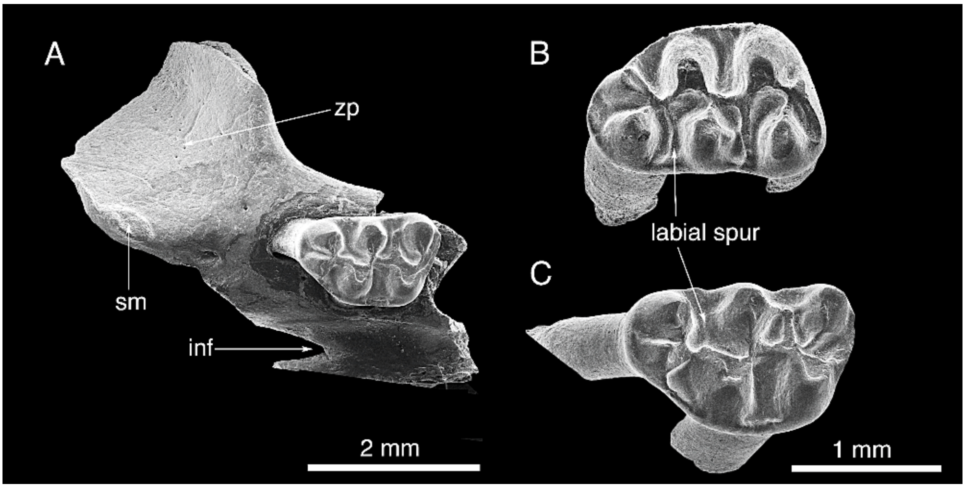

Fig. 1. SEM images of a left fragmentary maxilla with the M1 and two isolated M1s of *Megacricetodon yei* n. sp. showing variations. **A**, ventral view of the maxilla (IVPP V15349.9); **B**, occlusal view of a right M1 (V15349.3); **C**, occlusal view of a left M1 (V15349.10). Arrows point to labial spur of the anterolophule in both B and C. Abbreviations: **inf**, incisive foramen; **sm**, the oval patch for the superficial masseter; **zp**, zygomatic plate.

DESCRIPTION

Maxilla: Of the cranial elements, only the left fragmentary maxilla is preserved in IVPP V15349.9 (fig. 1). The zygomatic plate is broad and has a well- defined fossa on the ventral surface for the origin of the anterior part of the muscle masseter lateralis profundus. The anterior margin of the plate is partially broken, but the oval patch for the superficial masseter is preserved; it is prominent and located immediately posteroventral to ventral end of the anterior margin. The posterior margin of the plate extends anterior to M1. The posterior portion of the incisive foramen is preserved, of which the posterior edge levels with the protocone of M1, as in the *Cricetodon*, but differing from those in most living cricetines (*Cricetus* and *Mesocricetus*) in which the incisive foramen terminate anterior to M1.

Upper teeth: Seven upper incisors are preserved. Its anterior surface is gently convex and smooth. The enamel wraps slightly around onto both lateral and medial surface, but extends farther on the lateral surface than on the medial one (fig. 2). The cross section of the incisor is oval.

Eight complete M1s are in the collection and five of them are preserved in the maxilla (fig. 1, 3, 4). M1 is the largest upper cheek tooth with three roots, a major lingual one and two minor buccal ones; the root supporting the anterocone extends slightly anteriorly. The occlusal outline is longer than wide and

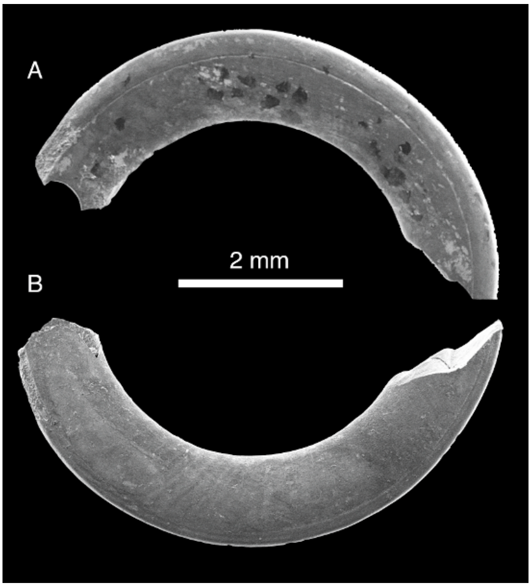

Fig. 2. Upper right incisor of *Megacricetodon yei* (IVPP V15349.16). **A**, lateral view; **B**, lingual view.

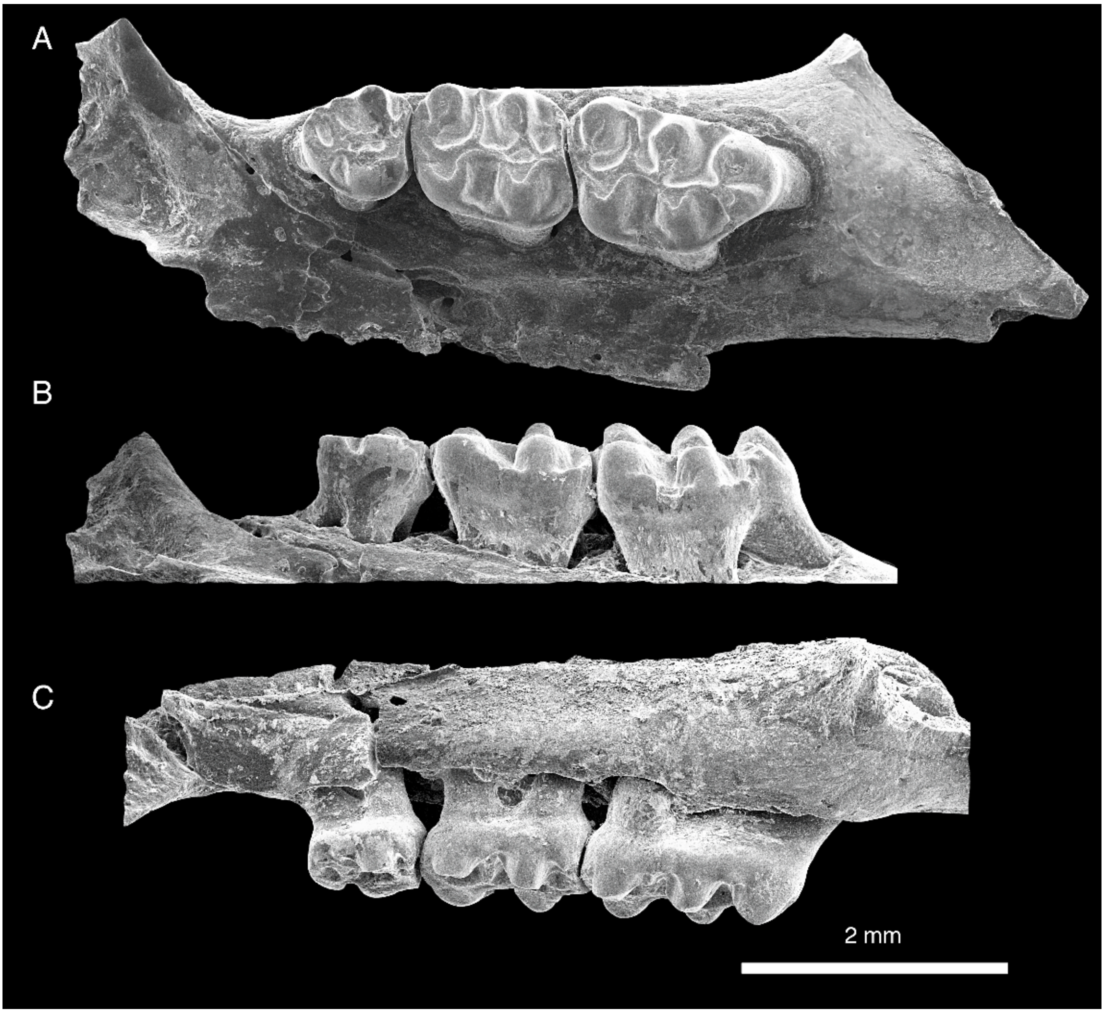

Fig. 3. Occlusal (**A**), lingual (**B**), and labial (**C**) views of upper cheek teeth of *Megacricetodon yei* (IVPP V15349.1; holotype).

slightly widens posteriorly. The anterocone is divided by a deep, longitudinal groove into labial and lingual conules, of which the former is larger. There is a low ledge on its anterior face in five of eight specimens. The anterolophule is connected to the lingual conule in six of eight specimens or extends to a point between the two conules in two M1s. The low labial spur of the anterolophule is long and transverse in two specimens, of medium length and joins the base of the paracone in two specimens, and absent in the remaining specimens. The posterior spur of the paracone is present, connecting to the mesoloph in three specimens. The mesoloph is of medium length in one specimen but is long and reaches the labial border of the occlusal surface in seven specimens. The entomesoloph is strong, reaching the lingual border of the occlusal surface only in one specimen (fig. 4A). The metalophule is directed posteriorly, joining the posteroloph immediately behind the hypocone. The posteroloph is long, extending to the posterolabial part of the metacone. A

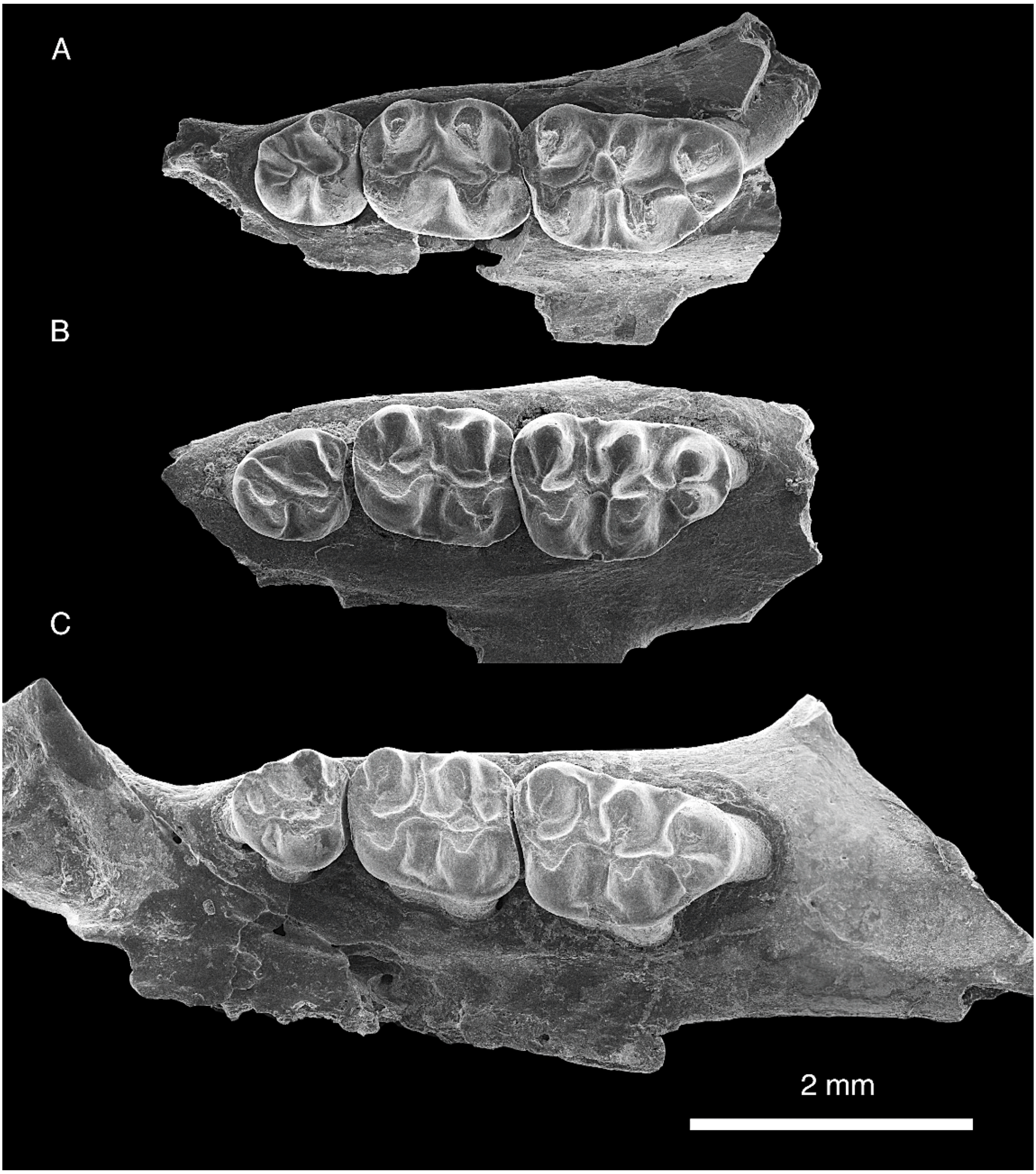

Fig. 4. Upper cheek teeth of *Megacricetodon yei* (IVPP V15349.2, V15349.7, V15349.1). Occlusal view of upper cheek teeth showing variations owing to age and wear among individuals. Image B was flipped horizontally to facilitate comparison.

cingulum is usually developed and inflated to form a small cuspate between major cusps. The sinus is transverse.

Seven M2s are in the collection. The M2 is also triple-rooted and its occlusal outline is subquadrate (fig. 3, 4). The lingual and labial branches of the anteroloph are well developed and are of about equal lengths. In three M2s, the protolophule is doubled; in the remaining four, only the anterior protolophule is present and projects anterolingually. The single metalophule extends anterolingually in one M2, transversely in two M2s, and posterolingually joining the posterior arm of the hypocone in four M2s (fig. 4). The mesoloph is long in five specimens and is of medium length in the remaining two. In two M2s, the posterior spur of the paracone is present and connects to the mesoloph. The sinus is transverse.

Eight M3s are in the collection. The M3 is much smaller than M1–2 and is also triple-rooted. The labial anteroloph is well developed in all M3s, but the lingual one is present only in two specimens. The protocone and paracone are prominent, but the posterior cusps are reduced. The metalophule extends anterolingually to connect the longitudinal crest. An axioloph originating from the longitudinal crest is directed anteriorly and connects to the protolophule in two M3s (fig. 3). The hypocone and metacone are nearly merged into the posteroloph, which encircles the posterior sinus.

MANDIBLE: IVPP V15349.23 is a nearly complete mandible except for the broken angular process (fig. 5A, B, C). The lower incisor is displaced from the alveolus and protrudes more anterodorsally than its original position. The original position of the incisor is preserved in V15349.24 (fig. 5D, E, F). The dentary is thin; its ventral rim is convex under m1 and is concave under the last two molars. The anterior slope of the diastema is gently curved, whereas its posterior slope, anterior to m1, is steep. The length of diastema is 3.1 mm, less than that of the lower tooth row. On the lateral surface of the mandible, the masseteric crests are weaker than those of *Cricetodon*; the superior and inferior crests converge anteriorly as a V shape, with its apex terminating at the level of the anterior root of m1. An oval mental foramen is at the position anteroventral to the m1; it opens anterolaterally and is best seen in lateral view. On the medial surface of the mandible, the large mandibular foramen lies anterovental to the base of the condyloid process. The ascending ramus is lateral and oblique to the tooth row, similar to that of *M. similis* (the only other *Megacricetodon* species preserving the medial side of the mandible) and extant cricetines (*Cricetus* and *Mesocricetus*), but differing from that of *Cricetodon*. In *M. yei*, *M. similis*, and extant cricetines (*Cricetus* and *Mesocricetus*), the coronoid process is falciform and very pronounced, with its tip higher than the condyloid process. In contrast, the coronoid process is reduced and its tip is slightly below or about the same level with the condyloid process in *Cricetodon*. The sigmoid notch is deep, distinctive from the shallow notch in *Cricetodon*. The capsular process of the lower incisor alveolus is conspicuous, lying below the base of the coronoid process. In dorsal view, the condyloid process is longitudinally long in a teardrop shape with its anterior tip bending slightly medially. The angular process is missing from all the specimens. But judged from the breakage, the angular notch is broad and somewhat oval. The pterygoid fossa for the insertion of the medial pterygoid muscle is deep.

LOWER TEETH: Nine lower incisors are preserved in mandibles. The lower incisor is delicate compared to the upper incisor. It extends posteriorly under the cheek teeth and terminates posteriorly at the level below the base of the coronoid process. The tip of the lower incisor is slightly lower than the occlusal surface of the cheek teeth (fig. 5F). The enamel extends only to the labial side, covering about one third of the labial surface. The incisor is oval in cross section, but the anterior and medial sides are flat. The anterior surface is smooth and has no longitudinal ornaments. The wear facet of the incisor tip is long (fig. 7C).

Fourteen m1s are present (fig. 6). The lower molars are all double-rooted. The m1 anteroconid is a high, conical cusp and situated on the longitudinal axis of the tooth. Both the labial and lingual anterolophids are well developed and reach the base of the protoconid and metaconid, respectively. The anterolophulid extends from the labial side of the anteroconid and is connected to the anterior arm of the protoconid. The metalophulid and hypolophulid extend slightly anterolabially. The mesolophid is absent in seven, of medium length in four, and long and reaches the lingual edge of the tooth in three specimens. The ectomesolophid is absent except for a weak one present in one specimen. The sinusid is transverse. The long posterolophid closes the posterosinusid.

Sixteen m2s are in the collection. The labial anterolophid is long and connected to the base of the protoconid. The lingual anterolophid is

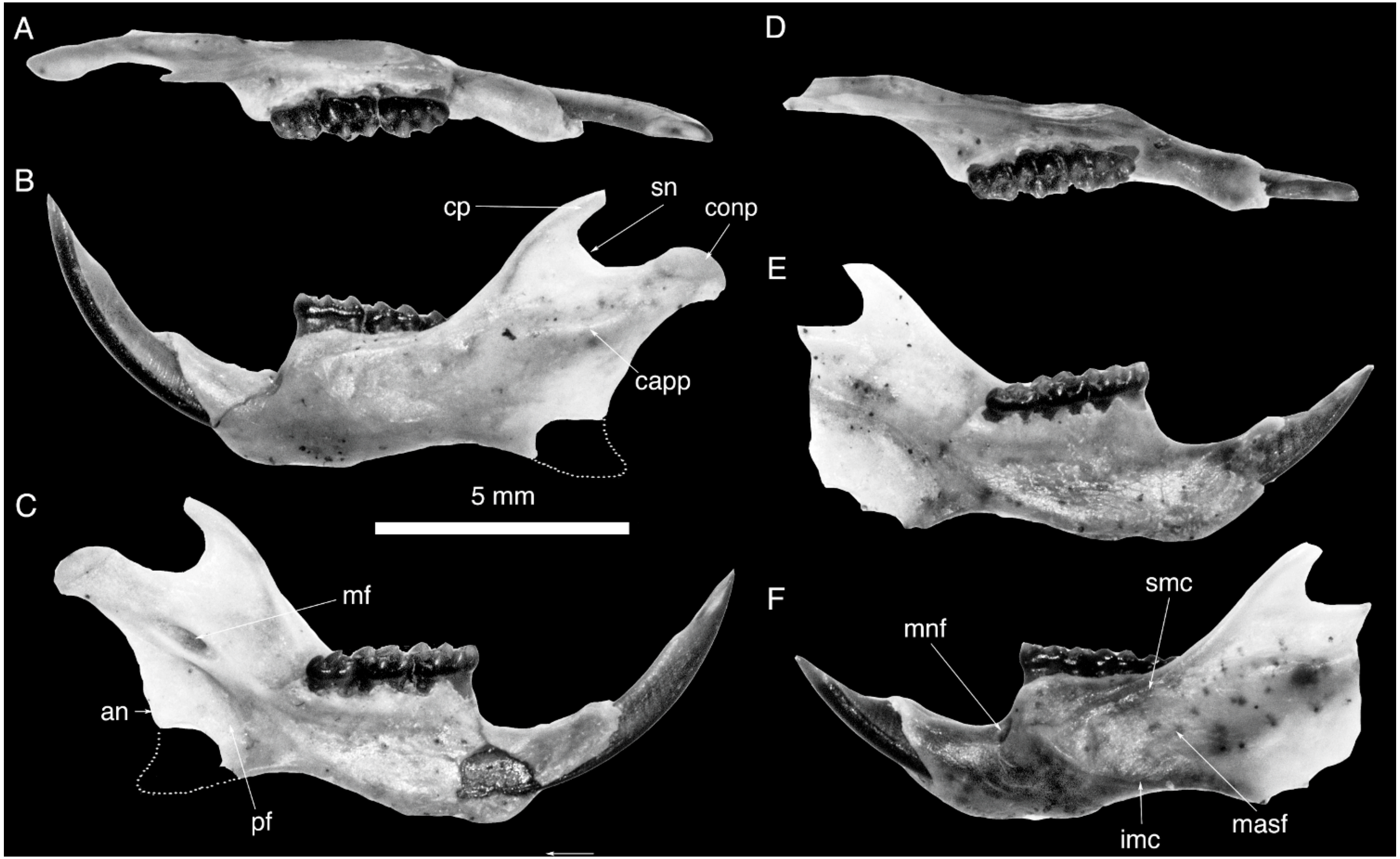

Fig. 5. Left mandible of *Megacricetodon yei*. **A–C**, occlusal, labial, and lingual views of IVPP V15349.23; **D–F**, occlusal, lingual, and labial views of IVPP V15349.24 show incisor in situ. Abbreviations: **an**, angular notch; **capp**, capsular process; **conp**, condyloid process; **cp**, coronoid process; **imc**, inferior masseteric crest; **masf**, masseteric fossa; **mf**, mandibular foramen; **mnf**, mental foramen; **pf**, pterygoid fossa; **smc**, superior masseteric crest; **sn**, sigmoid notch.

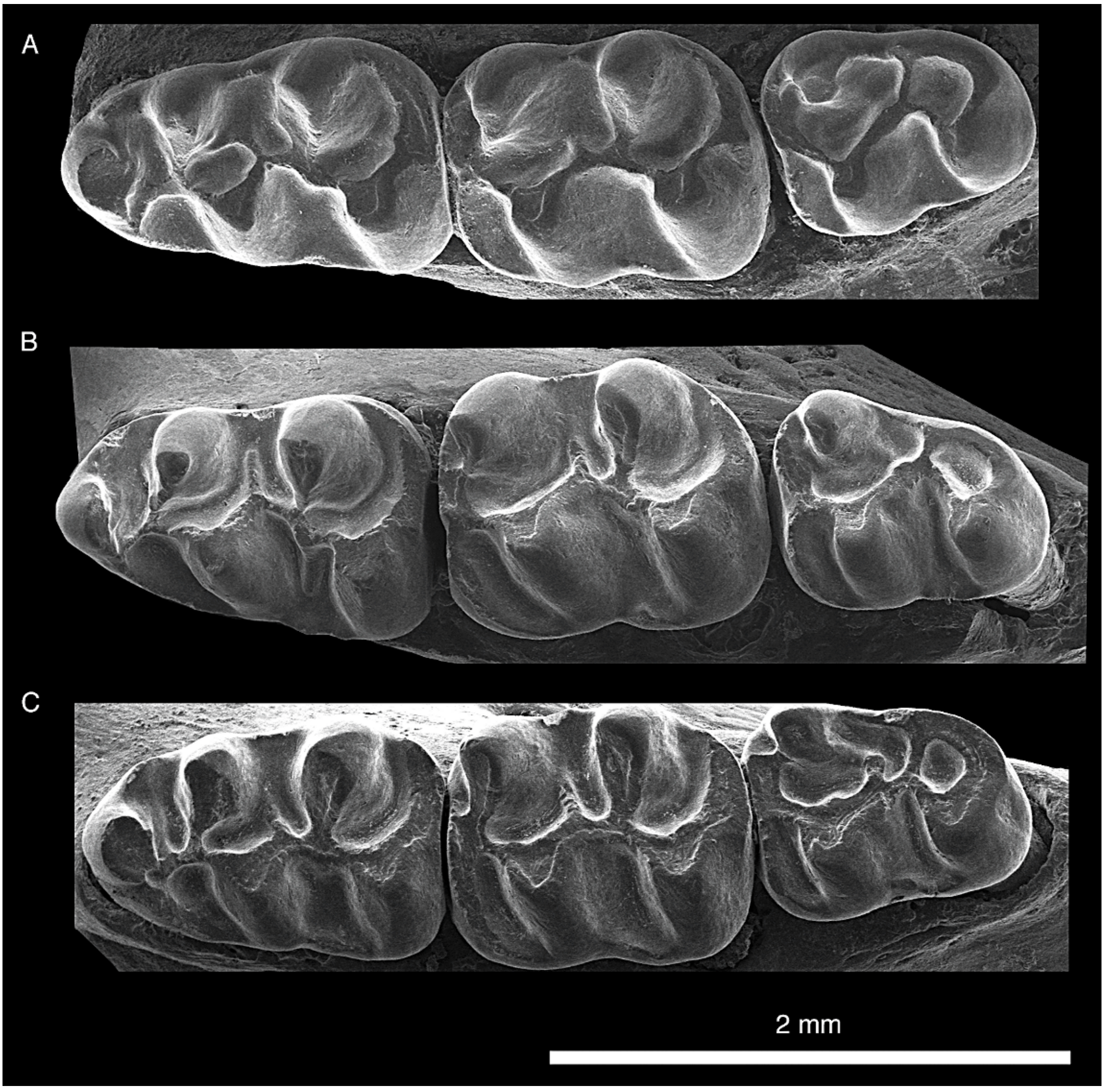

Fig. 6. Occlusal views of a left lower incisor and cheek teeth of *Megacricetodon yei* (A: IVPP V15349.23; B: V15349.25; C: V15349.24). Occlusal view of lower cheek teeth show variations owing to age and wear among individuals.

short or absent in 14, except a strong one present in one specimen. The metalophulid and the hypolophulid are directed slightly anterolabially. The mesolophid is of medium length in nine, and short or absent in six specimens. The ectomesolophid is absent. The posterolophid is strong and descends to the base of the entoconid. The wear of the lower m2 from a relatively old individual (IVPP V15349.24) is illustrated in figure 7A and B. The SEM image shows that the occlusal surface, particularly the enamel ridges, bears numerous pits and some striations. There is no shearing facet on the lingual and posterior sides of the tooth, suggesting that grinding was its primary function during mastication. The orientation of the striations indicates a primarily anteroposterior movement of the lower jaw during mastication, with a minor component of lateral shift.

Fourteen m3s are in the collection. The labial anterolophid is long and descends to join the

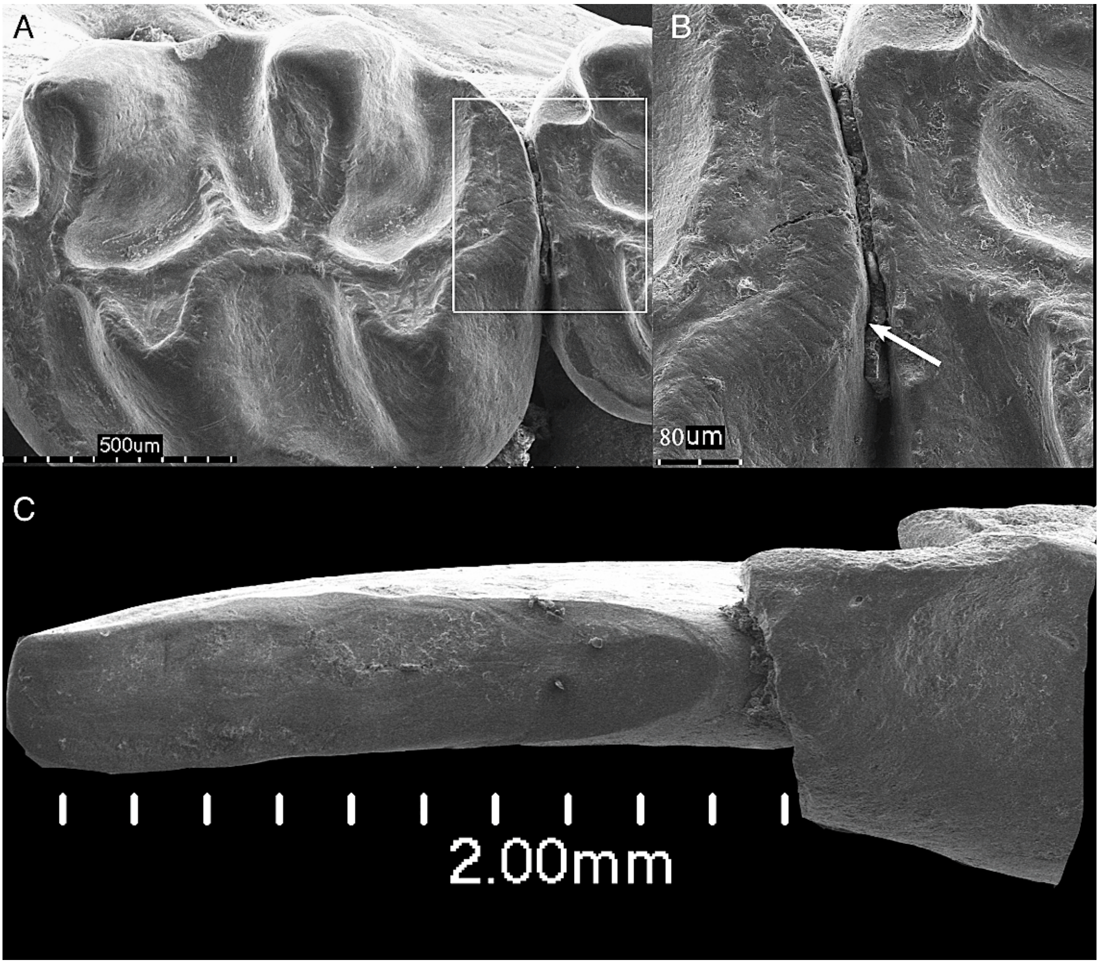

Fig. 7. Occlusal view of m2 and i1 of *Megacricetodon* (IVPP V15349.24). The box in A is enlarged in B. The arrow in B indicates the orientation of the wear striations.

base of the protoconid, but the lingual one is short or absent. The mesolophid is of medium length in three, but absent in 10 specimens. The transverse hypolophulid reaches the longitudinal crest anterior to the hypoconid. The posterolophid is connected to the entoconid and encloses the posterosinusid. The entoconid is reduced. A lingual cingulid almost connects the entoconid and the metaconid.

BACULUM: The baculum has a relatively long shaft with an anchorlike base (IVPP V15350.1; fig. 8). On each side of the base is a distally directed spike to which the corpora cavernosum attaches. The shaft is wider than deep and expands slightly distally. In lateral view, the two ends of the baculum bend dorsally. The tip, to which the cartilaginous tissue adheres, is broken.

HUMERUS: The humerus is represented by three immature specimens and two fragmentary distal ends. The proximal end was detached from all the immature specimens at the proximal epiphyseal line, so that the shape and extent of the head, greater tubercle, and lesser tubercle cannot be determined. The remaining length of the humerus measures 10.9 mm from the proximal epiphyseal line to the distal articular surface, and 2.7 mm wide between the lateral and medial edges at the distal end (IVPP V 15350.2).

The humeral shaft is straight, with a wide distal end, large medial epicondyle, and prom-

Fig. 8. Baculum of *Megacricetodon yei* (IVPP V 15350.1). **A**, ventral view; **B**, dorsal view; **C**, lateral view.

inent brachial crest (fig. 9). The deltoid crest, which marks the insertion of the deltoid and several related muscles (panniculus carnosus, pectoralis profundus anterior, pectoralis superficialis, and brachialis), is set on the anterior margin of the shaft and bends slightly laterally, its point of maximum projection approximately 40% of the shaft's length from the preserved proximal end. The crest is triangular and as elevated as that of *Cricetodon*. The medial ridge is not observed in *M. yei* and extant cricetines such as *Cricetus* and *Mesocricetus*, whereas it is distinct in many humeri of *Cricetodon*.

The distal epiphysis closely resembles that of *Cricetodon* and is transversely expanded and anteroposteriorly flattened, with a large distomedially projected medial epicondyle. There is no distinct ridge separating the capitulum from the trochlea. The spindlelike capitulum is broad anteriorly and tapers posteromedially. The trochlea is shallowly grooved; its articular surface diminishes anteriorly but expands posteriorly. The medial trochlear rim is sharply angled and projected distally. The radial fossa is wide and well developed. The olecranon fossa is shallow. A well-delineated pit is present between the medial epicondyle and trochlea, probably for the attachment of the ulnar collateral ligament.

On the medial aspect of the medial epicondyle there is a well-developed muscle scar for the flexor muscles of the carpus and digits. The entepicondylar foramen is large and located above the medial epicondyle, as in most living genera of the Cricetinae, but absent in *Mesocricetus* and *Cricetodon*. The brachial crest for the insertion of the brachialis, brachioradialis and extensor muscles of the wrist extends proximally 35% of the humeral length. The crest resembles that of *Mesocricetus* and *Cricetus*, but is more prominent and flares posterolaterally more than in *Cricetodon*. The lateral epicondyle is weakly developed and is the distal end of the brachial crest.

ULNA: The ulna is represented by four proximal and two distal fragments. The olecranon process is moderately developed and deflected slightly anteriorly (fig. 10A, B), as in *Cricetodon*. On its proximal aspect there is a distinct groove for the tendon of triceps longus. The trochlear notch is well developed with an anteriorly oriented anconeal process and an anterodistally directed coronoid process. The notch is somewhat less open than in *Cricetodon*. The triangular radial notch is flat and faces anterolaterally, being transversely narrower than in *Cricetodon*. Just distal to the coronoid process along the medial aspect of the shaft is a pronounced brachial ridge, upon which the brachialis is inserted.

The diaphysis is slender and mediolaterally compressed; its medial surface is slightly convex and the lateral surface is more deeply grooved than that of *Cricetodon*. The distal epiphysis is rounded, bearing a faint styloid process (fig. 10C, D).

FEMUR: Seven fragmentary femurs are preserved, and the one that is complete except for detachment of the distal epiphysis (IVPP V15350.13) is illustrated in figure 11. The preserved femur of V15350.13 measures 14.6 mm long from the great trochanter to

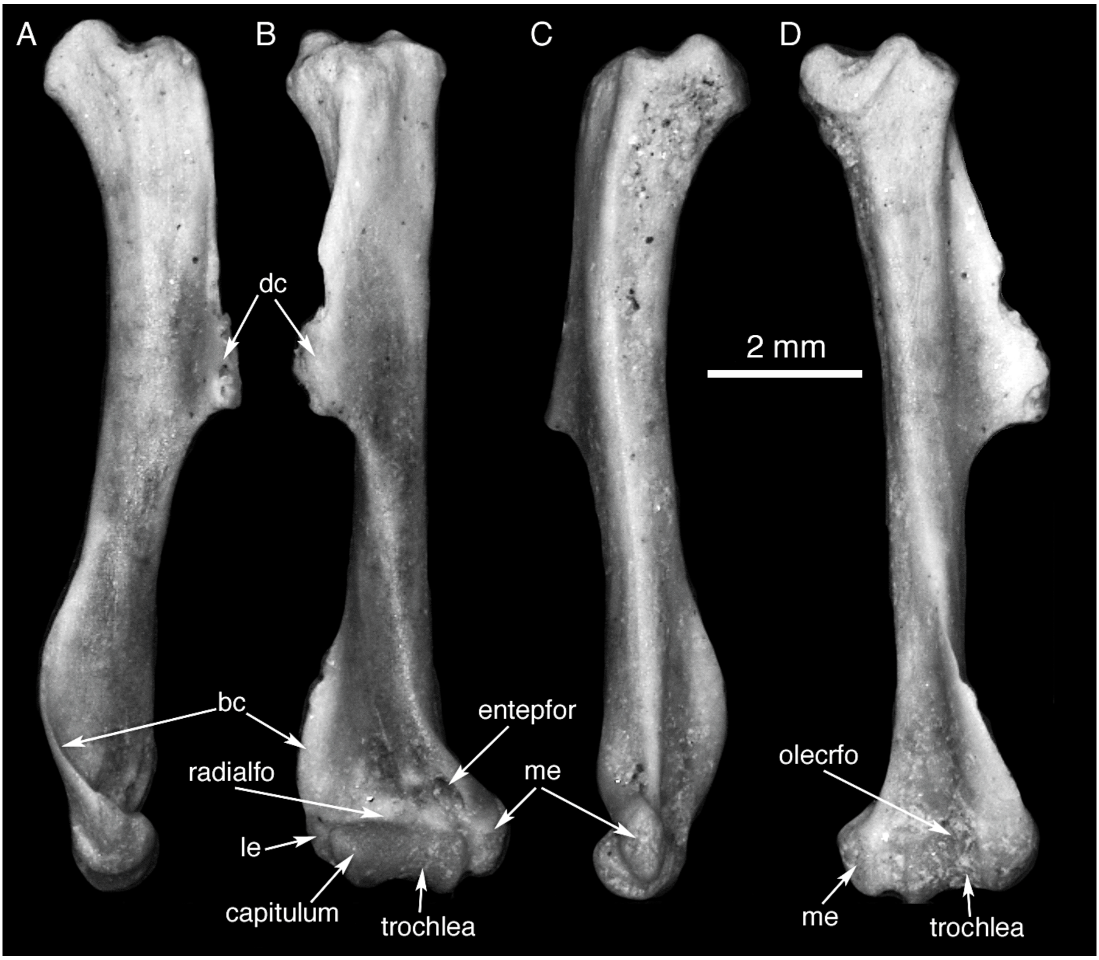

Fig. 9. Right humerus of *Megacricetodon yei* (IVPP V15350. 2). **A**, lateral view; **B**, anterior view; **C**, medial view; **D**, posterior view. Abbreviations: **bc**, brachial crest; **dc**, deltoid crest; **entepfor**, entepicondylar foramen; **le**, lateral epicondyle; **me**, medial epicondyle; **olecrfo**, olecranon fossa; **radialfo**, radial fossa.

the distal epiphyseal line and 2.65 mm wide at the distal epiphyseal line. The femur is similar to that of *Cricetodon* except for having a slightly weaker third trochanter. The head is semispherical and the articular surface does not extend onto the femoral neck; on its medial central articular surface there is a well-defined fovea for the attachment of the ligamentum capitis femoris. The neck is elongate, set at about 130° to the shaft. The greater trochanter rises nearly vertically from the shaft, and is higher than the head; its proximal end exhibits a large muscle scar for the insertion of deep gluteal muscles. The intertrochanteric fossa, the attachment site for obturator muscles, is very deep. The lesser trochanter, the attachment site for the quadratus femoris and iliopsoas, projects medially to the lateral edge of the femoral head. The third trochanter is moderately developed in contrast to the prominent one in *Cricetodon*. It is triangular and lies opposite and just distal to the lesser trochanter. The midshaft is somewhat anteroposteriorly flattened and slightly expanded distally. There is little or no anteroposterior curvature along the shaft.

The distal epiphysis is detached from the distal epiphyseal line, indicating that the specimen belongs to an immature individual. The preserved portion of the distal end

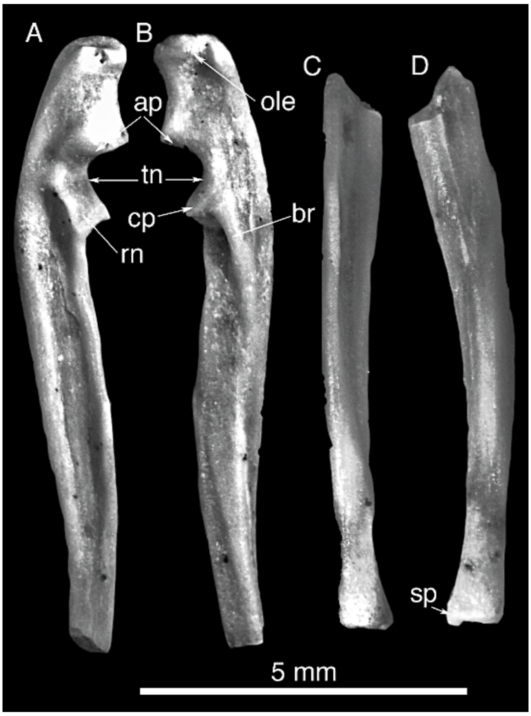

Fig. 10. Right proximal portion (IVPP V15350.7) and left distal portion (V15350.11) of the ulna of *Megacricetodon yei*. **A**, lateral view; **B**, medial view; **C**, lateral view; **D**, medial view. Abbreviations: **ap**, anconeal process; **br**, brachial ridge; **cp**, coronoid process; **ole**, olecranon; **rn**, radial notch; **sp**, styloid process; **tn**, trochlear notch.

indicates a relatively narrow and deep patellar fossa.

TIBIA: Seven fragmentary tibiae are in the collection. The proximal epiphysis is not preserved in any specimen. The tibia of IVPP V15350.22 measures 16.6 mm from the proximal epiphyseal line to the distal; slightly longer than that of the femur. In lateral view, it exhibits a sigmoid profile: its proximal end is deflected posteriorly whereas its distal end is bowed anteriorly (fig. 12).

The tibial crest appears sharp and extends distally about 30% of the preserved tibial length. It is situated less laterally than in *Cricetodon*, so that the lateral tibial fossa for the origin of the tibialis anterior is not as deeply excavated as in *Cricetodon*. The medial aspect of the proximal tibia is relatively flat owing to the absence of any muscle attachment. Posteriorly on the proximal part of the shaft, both lateral and medial edges are prominent, enfolding a deep posterior tibial fossa for the origin of the tibialis posterior.

The distal tibia is mediolaterally compressed. The articular surface of the distal end is divided into a lateral and a medial articular facet by a distinct median ridge. The lateral articular facet is broad and faces slightly laterally, as in *Cricetodon* whereas the medial one faces distally, as in *Cricetodon*, but is shallower than the latter. The medial malleolus is distinct. The posterior tibial process is large and lies behind the medial articular facet. Between the two processes lie the badly defined sulci for the tendons of muscles tibialis posterior and flexor digitorum longus. On the posterior aspect of the distal epiphysis is a broad and well-defined sulcus, which is probably left by the tendon of muscle flexor tibialis.

FIBULA: Only portion of fused fibula is preserved. Judged from the breakage, starting from a point about two thirds distal along the tibia, the fibula fuses with the tibia over a distance of several millimeters, and then the two diverge again distally to form the medial and lateral malleolus (fig. 12).

CALCANEUS: A right calcaneus (IVPP V15350.27) is perfectly preserved (fig. 13). The calcaneus is 4.0 mm long and 2.6 mm wide from the peroneal process to the medial tip of the sustentaculum. The calcaneal tubercle is long and extends distally half the calcaneal length. In dorsal view, it is transversely compressed with a slightly expanded proximal end. A broad groove for the attachment of the Achilles tendon separates the lateral and more proximally projecting medial margin of the proximal aspect of the tubercle. The calcaneoastragalar facet is convex and smoothly rounded. Proximolateral to the protuberance that bears the calcaneoastragalar facet is a distinct tubercle for the calcaneofibular ligament. The sustentacular facet is flat and faces dorsally. The sulcus calcaneus separating the sustentacular facet from the calcaneoastragalar facet is narrow and poorly defined. The sustentaculum talus is prominent and projects medially. The peroneal process of *M. yei* is more proximodistally expanded and displaced more proximally than that of *Cricetodon*. It is shelflike and almost at

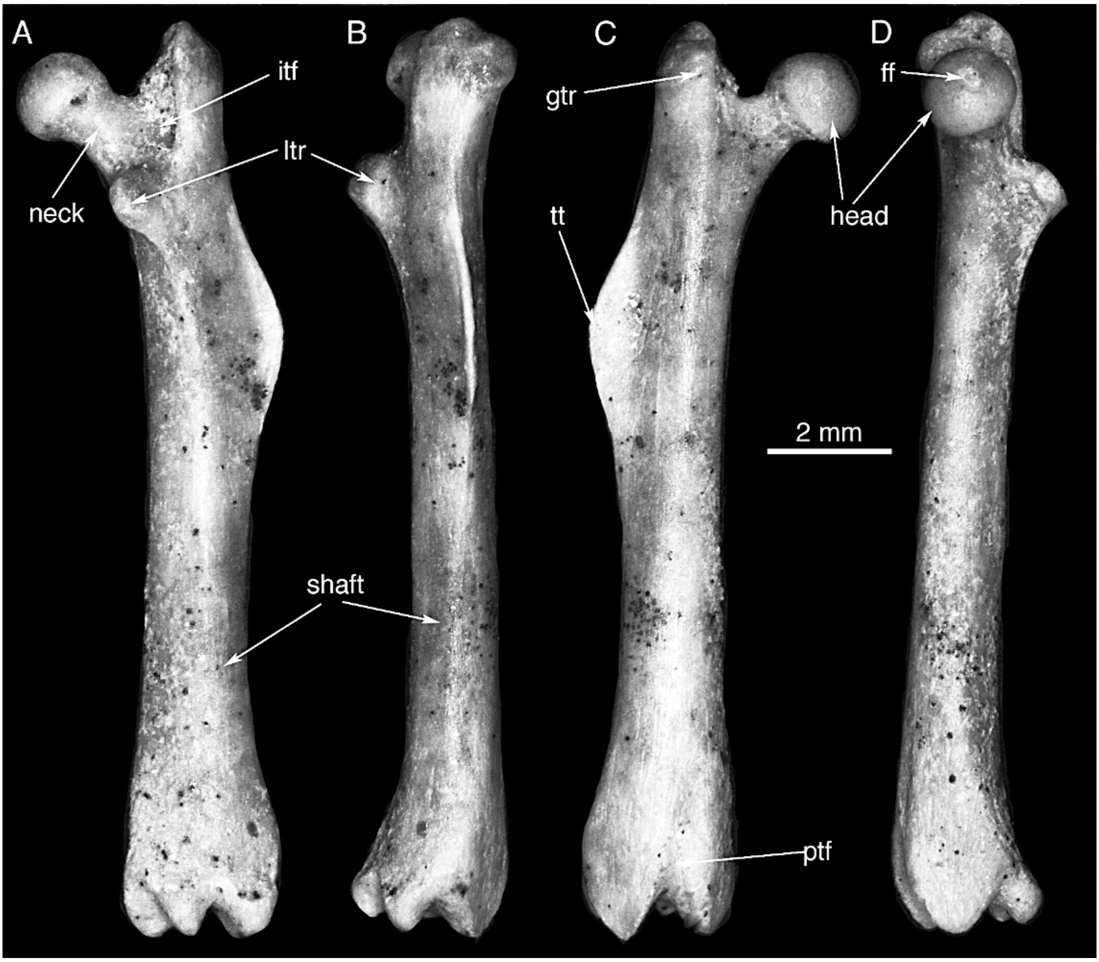

Fig. 11. Right femur of *Megacricetodon yei* (IVPP-V15350.13). **A**, posterior view; **B**, lateral view; **C**, anterior view; **D**, posterior view. Abbreviations: **ff**, femoral fovea; **gtr**, greater trochanter; **itf**, intertrochanteric fossa; **ltr**, lesser trochanter; **ptf**, patellar fossa; **tt**, third trochanter.

the same level as the sustentaculum talus. The groove for the passage of the muscle peroneus longus is poorly delineated in contrast to the deep one in *Cricetodon*.

In distal view, the calcaneocuboid facet is gently concave and oriented almost 90° to the long axis of the calcaneus, whereas it is obliquely oriented in *Cricetodon.* The anterior plantar tubercle is faint, and positioned medial to the calcaneocuboid facet. Between the anterior plantar tubercle and the calcaneocuboid facet lies a broad groove for the tendon of the muscle flexor hallucis longus, which extends proximally to the sustentaculum talus.

COMPARISON

A direct comparison of *Megacricetodon yei* with *Aktaumys dzhungaricus* (Kordikova and de Bruijn, 2001) from adjacent Aktau Mountain clearly indicates these two species are closely related and belong to the same genus (see discussion below for generic allocation). They are similar in sharing many features, including the split anterocone of M1, presence of labial spur of the anterolophule in some M1s, presence of double protolophules in some M2s, long mesoloph in M1 and M2, single anteroconid of m1, and well-developed mesolophid in m1 and m2. However, *M. yei* differs from *A. dzhungar-*

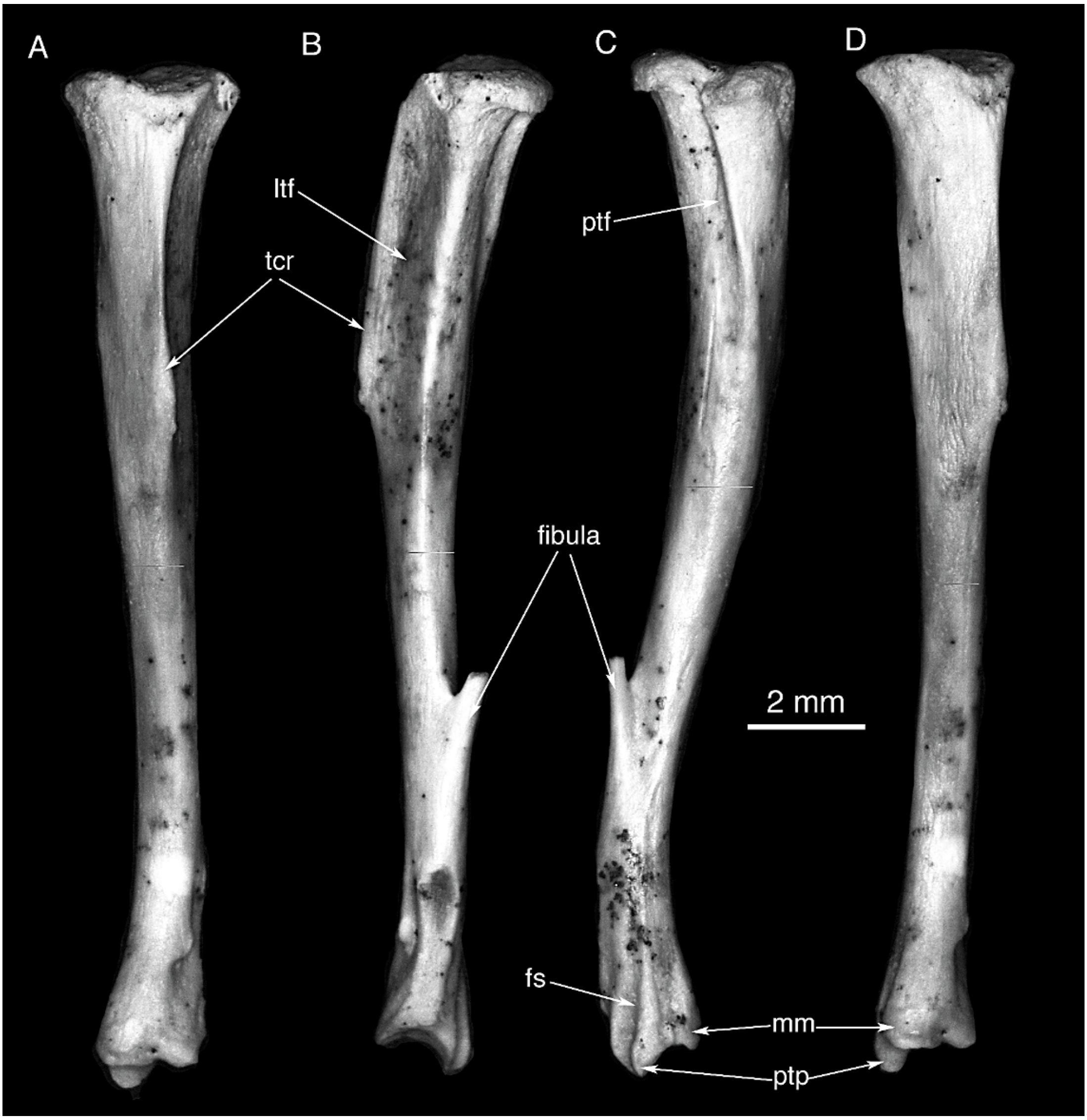

Fig. 12. Left tibia of *Megacricetodon yei* (IVPP V15350.22). **A**, anterior view; **B**, lateral view; **C**, posterior view; **D**, medial view. Abbreviations: **fs**, flexor sulcus; **ltf**, lateral tibial fossa; **mm**, medial malleolus; **ptf**, posterior tibial fossa; **ptp**, posterior tibial process; **tcr**, tibial crest.

icus by being slightly smaller and having a more clearly bifurcated anterocone, a shorter mesoloph in M1 and M2, fewer occurrences of the labial spur of the anterolophule in M1, fewer occurrences of double protolophules and single metalophule in M2 , and fewer occurrences of the ectomesolophid in m1.

Other *Megacricetodon* species from China include *M. sinensis* from Chetougou Formation of Qinghai Province (Qiu et al., 1981) and Tunggur Formation of Inner Mongolia (Qiu, 1996), *M. pusillus* from Tunggur Formation of Inner Mongolia (Qiu, 1996), and *M.* aff. *collongensis* from Xiacaowan Formation of Jiangsu (Li et al.,1983). *M. yei* is larger than all of these species. In addition, *M. yei* is distinct from them in having a longer mesoloph in M1 and M2, a labial spur of anterolophule in M1, a

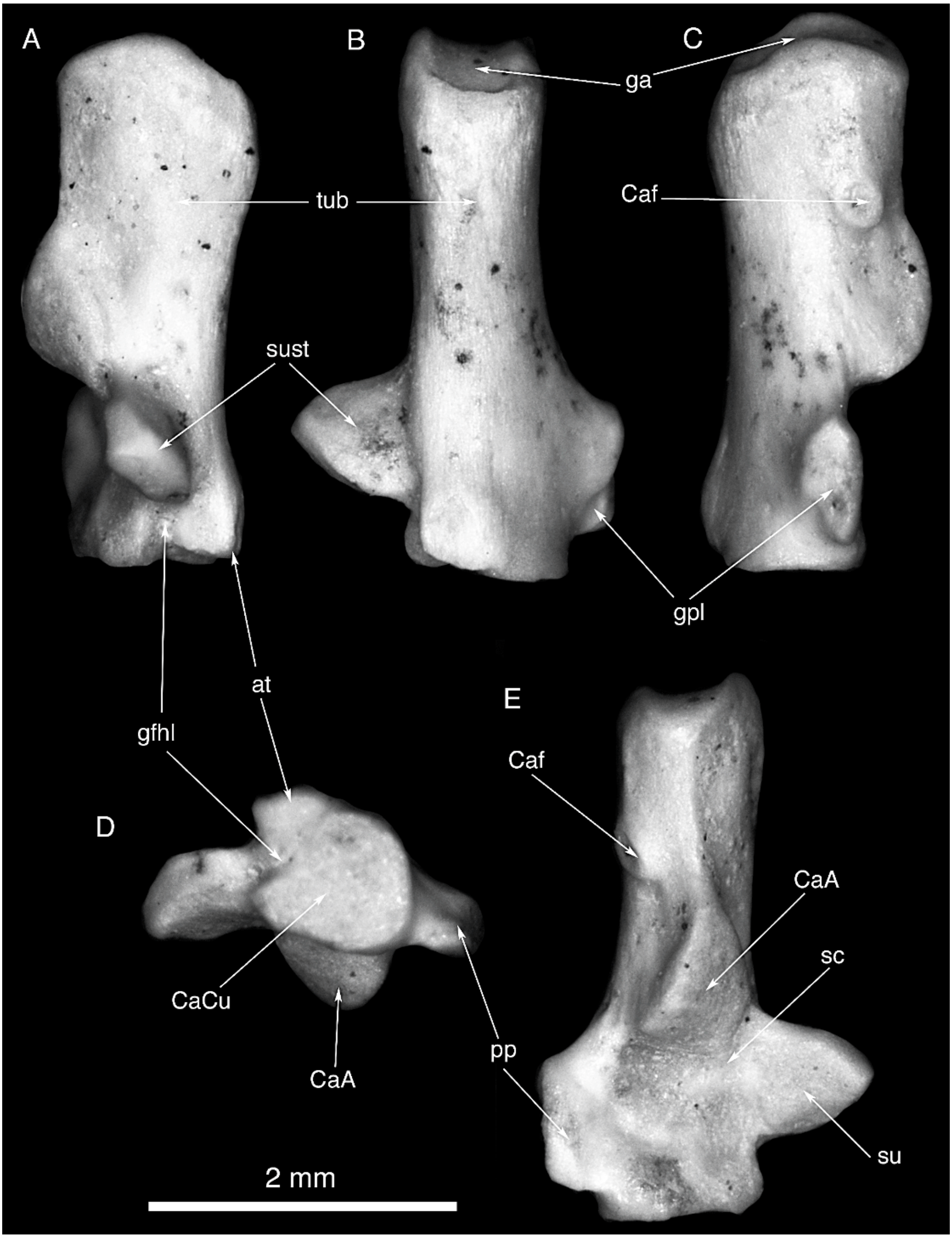

Fig. 13. Right calcaneus of *Megacricetodon yei* (IVPP V15350.27). **A**, medial view; **B**, ventral view; **C**, lateral view; **D**, distal view; **E**, dorsal view. Abbreviations: **at**, anterior plantar tubercle; **CaA**, calcaneoastragalar facet; **CaCu**, calcaneocuboid facet; **Caf**, the tubercle for the calcaneofibular ligament; **ga**, groove for the Achilles tendon; **gfhl**, groove for the flexor hallucis longus; **gpl**, groove for the peroneus longus; **pp**, peroneal process; **sc**, sulcus calcaneus; **su**, sustentacular facet; **sust**, sustentaculum talus; **tub**, calcaneal tuber.

TABLE 1

Measurements of upper teeth of *Megacricetodon yei*

Inventory No.	LM1–M3	LM1	WM1	LM2	WM2	LM3	WM3
V15349.1	3.63	1.63	1.08	1.18	1.06	0.78	0.86
V15349.2	3.52	1.61	1.14	1.11	1.05	0.78	0.80
V15349.3		1.56	1.03				
V15349.4				1.20	1.01		
V15349.5						0.85	0.81
V15349.6						0.90	0.81
V15349.7	3.52	1.59	1.02	1.13	1.01	0.71	0.70
V15349.8	3.46	1.58	0.99	1.16	0.95	0.68	0.70
V15349.9		1.64	1.01				
V15349.10		1.54	0.94				
V15349.11		1.55	1.01				
V15349.12				1.20	1.05		
V15349.13				1.09	0.95		
V15349.14						0.79	0.81
V15349.15						0.82	0.85

L = length; W = width in mm.

TABLE 2

Measurements of lower teeth of *Megacricetodon yei*

Inventory No.	i1D	i1W	Lm1-m3	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3	DMm1	DMm3
V15349.23	0.93	0.43	3.69	1.48	1.35	1.18	0.89	0.98	0.75	3.04	1.73
V15349.24	0.96	0.45	3.56	1.40	0.91	1.10	0.95	0.92	0.80	3.07	1.86
V15349.25			3.86	1.48	0.95	1.24	1.01	0.98	0.83	3.08	1.83
V15349.26	0.85	0.43	3.60	1.39	0.91	1.10	0.95	0.93	0.74	2.89	1.63
V15349.27			3.73	1.42	0.95	1.16	1.04	1.01	0.89	3.01	1.61
V15349.28	0.93	0.58									
V15349.29	1.03	0.49		1.49	0.95	1.23	1.03				
V15349.30	1.02	0.50		1.40	0.89			0.83	0.76	2.95	
V15349.31						1.26	1.05				
V15349.32				1.41	0.81	1.11	0.84				
V15349.33				1.52	0.96						
V15349.34				1.44	0.94						
V15349.35						1.19	0.97				
V15349.36								1.00	0.79		
V15349.37								0.89	0.68		
V15349.38	0.93	0.45	3.76	1.34	0.86	1.19	0.88	0.94	0.71	3.08	1.73
V15349.39	0.86	0.45				1.14	0.89			2.99	1.70
V15349.40	1.05	0.46	3.65	1.40	0.93	1.13	0.95	0.99	0.82	3.37	1.59
V15349.41						1.22	0.85	1.01	0.80		1.72
V15349.42				1.38	0.83	1.15	0.90			2.99	
V15349.43						1.16	0.95	0.89	0.78		
V15349.44				1.51	0.89	1.09	0.95				
V15349.45								0.88	0.71		
V15349.46								0.91	0.79		

L = length; W = width; D = depth in mm; DMm1 and DMm3 = mandibular depth at m1 and m3.

well-developed posterior spur of paracone in M1, double protalophules in M2, a longer mesolophid in m1 and m2, and an elongate m3.

Megacricetodon yei is comparable in size to several European species, such as *M. similis* Fahlbusch, 1964, *M. rafaeli* Daams and Freudenthal, 1988, and *M. lopezae* García Moreno, 1986. *M. yei* differs from *M. similis* by the deeply split anterocone of M1, the higher frequency of posteriorly directed metalophule in M2, the simple m1 anteroconid, and longer mesolophids on lower cheek teeth. *M. yei* differs from *M. rafaeli* by possessing the deeply split anterocone, the presence of labial spur in some M1s, and the simple anteroconid of m1. *M. yei* differs from *M. lopezae* in having a longer mesoloph of the upper molars, the double protolophules of M2, a simple anteroconid of m1, and a longer mesolophid in m1–2.

Megacricetodon andrewsi, from Paşalar, Turkey (Pelaez-Campomanes and Daams, 2002), differs from *M. yei* in having an incompletely bilobed anterocone on M1 and bilobed anteroconid on m1 as well as in lacking the labial spur of the anterolophule and the anteriorly or transversely directed metalophule of M2.

DISCUSSION

VALIDITY OF THE GENUS *AKTAUMYS*: The genus *Aktaumys* was named by Kordikova and de Bruijn (2001) based on isolated teeth recovered from the Aktau Mountains, Southeastern Kazakhstan. The genus contains only the type species, *Aktaumys dzhungaricus*. According to Kordikova and de Bruijn (2001), *Aktaumys* was differentiated from *Megacricetodon* in having the following characters: (1) long, transverse mesolophs(ids) in the first and second upper and lower molars; (2) a long labial spur of the anterolophule in most M1; (3) double protolophules in all M2 (in the material that we were able to study, courtesy of Dr. Hans de Bruijn, most, but not all, M2s have this feature) and double metalophules in most M2s; and (4) a shorter, more triangular, occlusal surface in the m1. The authors suggested that the main differences precluding Kazakhstan materials from being allocated to *Megacricetodon* are double protolophules and metalophules in most M2s (Kordikova and de Bruijn, 2001). We observed subtle differences between *M. yei* and *Aktaumys* in the overall dental morphology and their geographical occurrence is relatively close, about 150 miles apart. The morphological similarities and geographical vicinity indicate that these two species should be placed into the same genus. In *M. yei*, double protolophules of M2 are present in 43% (3 out of 7) of the specimens, and the anterolingually directed single protolophule occurs in 57% (4 out of 7) of the specimens. The presence of double protolophules of M2 also varies greatly within *Megacricetodon*. In some species, such as *M. andrewsi*, *M. ibericus*, and *M. crusafonti*, double protolophules are uncommon (0%–10%), but can be as high as up to 63% in others, such as *M. minor* (Daams and Freudenthal, 1988). Because the variation of double protolophules is common in *Megacricetodon*, this character does not distinguish *Aktaumys* from *Megacricetodon*.

The same pattern is also true for the double metalophules of M2. In *Aktaumys dzhungaricus*, double metalophules are present in many M2s but the exact percentage has not been available. In *M. yei* only a simple metalophule is present in the collection. In other species of *Megacricetodon*, however, there is a considerable variation in this character. Most species have a transverse or posteriorly projecting, simple metalophule, whereas in *M. collongensis*, for instance, 30% of the M2s have the double metalophules. The available evidence suggests that the double metalophules are variable within the species of *Megacricetodon*. Because none of the morphological differences listed above is unique for *Aktaumys*, we consider that the generic name *Aktaumys* a junior synonym of *Megacricetodon*.

TAXONOMY OF *MEGACRICETODON* IN CRICETIDAE: The suprageneric classification of the *Megacricetodon* has long been controversial. Mein and Freudenthal (1971a) placed the genus *Megacricetodon* in the subfamily Cricetodontinae with the tribe Megacricetodontini. Rieg (1972) considered that *Megacricetodon* has a closer affinity with the subfamily Cricetinae rather than with Cricetodontinae on the basis of dental similarities. Although this idea has been shared by various authors (Fahlbusch, 1996; Kälin, 1999), it has never been universally accepted. McKenna and Bell (1997), for instance, placed *Megacricetodon* in its own subfamily, Megacricetodontinae. Mein and Freudenthal's (1971a) classification relies on only a few cranial and postcranial characters, frequently surveyed from just one or a few species. The cranial character of the genus *Megacricetodon*, however, is based only on undescribed materials in the collection of the Museum of Natural Science in Lyon; no interspecific variation has been documented in publication. Uncertainties about the relationships of the subfamily Cricetinae and Cricetodontinae primarily resulted from the use of some characters, such as the incisive foramina and the entepicondylar foramen of the humerus, that have not been fully known within relevant species.

It is known that the subfamily Cricetodontinae has the incisive foramina penetrating the palate beyond the anterior borders of the first molars and that the subfamily Cricetinae is characterized by short incisive foramina, which end before the anterior border of the first molar. The incisive foramina of *M. yei* extend further back, to the protocone of M1, as reported by Mein and Freudenthal (1971a), corroborating their conclusion that *Megacricetodon* would be placed in the subfamily Cricetodontinae. However, Reig (1972) suggested that the relative development of the incisive foramina is variable at the generic level and is not useful above the generic level.

Mein and Freudenthal (1971a) used the entepicondylar foramen of the humerus as a diagnostic character to distinguish the subfamily Cricetodontinae from the Cricetinae. They pointed out that in the Cricetodontinae the entepicondylar foramen is absent, whereas all genera of Cricetinae have this foramen in the humerus. The entepicondylar foramen, however, is variable within the genus *Megacricetodon*. Unlike the undescribed specimens in the collection of Lyon examined by Mein and Freudenthal (1971a), the large entepicondylar foramen occurs in all humeri of *M. yei*. Therefore this character does not appear to be particularly useful for distinguishing species of *Megacricetodon*.

Based on the cranial and postcranial characters, Mein and Freudenthal (1971a) interpreted the dental similarities between the Cricetodontinae and the Cricetinae as convergence. However, one can argue equally well that the available cranial and postcranial features result from parallel evolution. While considering the craniomandibular, dental, and postcranial features as a whole, we think *Megacricetodon* is better placed within the subfamily Cricetinae, as suggested by Reig (1972). *Megacricetodon* lacks the characteristic features of *Cricetodon*, such as the longitudinal ridges on the anterior surface of the lower incisor. In contrast, the enamel surface of *Megacricetodon* is smooth and resembles those of *Democricetodon* and living genera of the Cricetinae. The mandible of *Megacricetodon* is also similar to those of *Democricetodon* and living genera of the Cricetinae, and differs from that of *Cricetodon*. The coronoid process is very pronounced and its tip is obviously higher than the condyloid process as in recent cricetines, whereas in *Cricetodon* the coronoid process is minute and its tip is about the same level or slightly lower than the condyloid process. The sigmoid notch is deep in contrast to the shallow notch in *Cricetodon*.

SPECIES OF MEGACRICETODON: The species assigned to the genus *Megacricetodon* have been unstable historically, making their taxonomy and phylogenetic reconstruction complicated. Future research may reveal many synonyms of named taxa, as pointed out by Kälin (1996). In Europe, 20 species have been recognized (Kälin, 1996), of which the oldest representative is *M. primitivus* from the European Neogene land mammal zone MN4 (Freudenthal, 1963) and the youngest, *M. ibericus* is from MN9 (Schaub, 1925). Several evolutionary lineages have been established, such as *M. minor–M. debruijni* and *M. primitivus–M. collongensis–M. crusafonti–M. ibericus* in Western Europe and *M. bavaricus–M. germanicus–M. lappi* in central Europe (Daams and Freudenthal, 1988). Major evolutionary trends seen in European species include size increase, bifurcation of the m1 anterconid, and reduction of the mesoloph(id). Although most European species could be fit into these lines as various evolutionary stages, some, such as *M. rafaeli*, may have evolved independently. In Turkey, *M. andrewsi* is from Paşalar (MN6) (Pelaez-Campomanes and Daams, 2002). This species is most closely related to the European *M. rafaeli* and *M. similis*, and is morphologically intermediate between these two species.

Compared to the European species, the evolution of the Asiatic species of *Megacricetodon* presents a different picture. In general, the size of the Asian species decreases and the m1 anteroconid remains unsplit through time. *M. dzhungaricus* from the Aktau (MN4) is the oldest record among known species of *Megacricetodon* in Central Asia. *M. yei* was recovered from the Halamagai Formation of the Tieersihabahe locality, and the Halamagai fauna from that locality suggests an age of the early Middle Miocene, equivalent to MN6. In comparison with *M. dzhungaricus*, *M. yei* displays several derived characters: (1) the anterocone more clearly divided; (2) a shorter mesoloph in M1 and M2; (3) fewer occurrences of double protolophules in M2; and (4) absence of double metalophules in M2. In view of the geographic proximity we think *M. dzhungaricus* may be considered to be a direct ancestor of *M. yei* and may represent a lineage distinct from European species. It is also worth noting that the *M. dzhungaricus–M. yei* lineage is characterized by a decrease in size.

M. sinensis was originally described from Chetougou Formation of Qinghai, China (Li and Qiu, 1980; Qiu, Li, and Wang, 1981) and also occurs in Tunggur (MN8), Inner Mongolia (Qiu, 1996). The second species from Tunggur is *M. pusillus*, which is very similar to *M. sinensis* in size and morphology and may prove to be a synonym of *M. sinensis*. Based on their sizes and ages, one may entertain the idea that *M. sinensis* and *M. pusillus* could have derived from the *M. dzhungaricus–M. yei* lineage. However, the bifurcated anterocone, the presence of the posterior spur of the paracone, the protolophule of M2, and the shape of m1 suggest that *M. dzhungaricus* and *M. yei* represent a distinct lineage from other Chinese species of the genus.

The evolution of the *Megacricetodon* is complex and displays a mosaic pattern. Although evolutionary trends of European species have been widely used in regional biostratigraphical correlation, Wessels et al. (2001) cautioned that the correlations might apply only to local sequences. The new materials we present here indicate that Asian lineages evolved independent of the European species, echoing the caution of Wessels et al. (2001).

BIOCHRONOLOGY

The Halamagai Formation contains more than five fossil beds, but the fossil mammals were recovered mainly from the two lower beds. Ye et al. (2001a, b) published the most updated faunal list for fossils collected from these beds and concluded that the faunas from different beds are all similar in composition, and cannot be differentiated in age; it was therefore assumed that fossils collected from these beds within the Halamagai Formation represent one fauna.

Preliminary study has identified the following taxa associated with *M. yei* from the Halamagai Formation of the Tieersihabahe locality: Insectivora (*Schizogalerix duolebulejinensis*, *Mioechinus* ? aff. *M. gobiensis*); Chiroptera (Chiroptera gen. et sp. indet.); Primates (*Pliopithecus bii*, *Pliopithecus* sp.); Lagomorpha (*Plicalagus junggarensis*, *Sinolagomys* sp., *Alloptox gobiensis*); Rodentia (*Sinomylagaulus halamagaiensis*, *Cricetodon* n. sp., *Eutamias* sp., *Atlantoxerus giganteus*, *A. junggarensis*, *Palaeosciurus* sp., Petauristinae gen. et spp. indet. 1 et 2, *Steneofiber depereti*, *Anchitheriomys tungurensis*, *Tachyoryctoides* sp.); Carnivora (*Nimravus* ? sp., *Pseudaelurus cuspidatus*, *Protictitherium intermedium*, *P.* sp. [small], *Thalassictis chinjiensis*, *Simocyon* sp. [small], *Gobicyon* sp., *Oligobunis* ? sp.); Proboscidea (*Zygolophodon* ? *junggarensis*, *Zygolophodon* ? sp., *Gomphotherium* cf. *G. shensiensis*, *Gomphotherium* sp.); Perissodactyla (*Chilotherium* sp., *Aceratherium* sp. , *Anchitherium* cf. A . *aurelianense*); Artiodactyla (*Lagomeryx* sp., *Stephanocemas* aff. *S. thomasoni*, *Micromeryx* sp., *Palaeomeryx* sp., *Eotragus halamagaiensis*, Bovidae gen. et sp. indet.).

Ye et al. (2001b) correlated the Halamagai fauna with the Tongxin fauna from the adjacent part of China and the Belometchetskya fauna of north Caucasus. This suggests that the Halamagai fauna correlates best to the European Neogene land mammal zone MN6 (Qiu et al., 1999; Pickford et al., 2000). Representatives of *Megacricetodon* have been considered as a good biostratigraphic markers in local sequence (Wessels et al., 2001). Geographical occurrence of *M. yei* and *Megacricetodon* (= *Aktaumys*) *dzhungaricus* is so close so that these two species bear significantly on the biostratigraphy of the region. *M. yei* is more advanced than *M.*

dzhungaricus from the Chul'adyr Formation of Aktau Mountains (MN4), and is therefore indicative of a later appearance, probably MN5/6. This concurs with the estimation that the Halamagai fauna is early Middle Miocene age, roughly MN 6 equivalent.

PALEOBIOLOGICAL RECONSTRUCTION

Modern species of the family Cricetidae are primarily terrestrial in habits; most forms either scamper, jump, or burrow, but a number of species are semiarboreal or semiaquatic. Similar to *Cricetodon* from Tieersihabahe, *M. yei* exhibits a number of postcranial features observed in recent terrestrial cricetines. As noted in the description, the deltoid crest of the humerus, which serves for the insertion of the pectoralis and deltoid muscle, is pronounced in *M. yei* and reflects powerful shoulder flexion in parasagittal movements. The spindle-shaped capitulum, the posteriorly concaved trochlea with prominent lateral and medial edges, and the continuation of the capitulum and the trochlea restrict movements more to the parasagittal plane during terrestrial quadrupedal walking and running in *M. yei* (Jenkins, 1973; Harrison, 1989); these are characters, common to extant cricetids, that promote stabilities at the elbow joint by restricting radial rotation while allowing flexion and extension in the parasagittal plane.

The medial epicondyle is the site of origin for the wrist and digital flexors (e.g., flexor digitorum profundus muscle) (Sargis, 2002a). Hence, a strong medial epicondyle may represent a powerful flexion of the digits during grasping of branches, or digging (Taylor, 1974; Hildebrand, 1985; Sargis, 2002a). As in the living cricetines, such as *Mesocricetus* and *Microtus* (good runners, climbers, and diggers), the medial epicondyle is well developed in *M. yei*, which probably indicates a mixture of climbing and digging abilities. The brachial crest, which serves as the insertion sites for the brachialis, brachioradialis, and extensor muscles, is distinct in *M. yei* and stronger than that in *Cricetodon*, indicating more sophisticated climbing and digging abilities.

The flat and anterolaterally oriented radial notch is indicative of a limited range of the pronation and supination at the elbow as in ground-dwelling mammals. The radial notch in *M. yei* is transversely narrower than in *Cricetodon*, suggesting more capacity for supination.

On the femora, a broad muscle scar of the greater trochanter and a laterally expanded third trochanter in *M. yei* reflect a well-developed gluteus muscle mass, which provides the powerful extension and abduction of the thigh for propulsion during terrestrial running. The more proximal projection of the greater trochanter of *M. yei* is another indicator of terrestrial habits of the animal. It restricts the mobility of the hip joint and particularly limits the range of abduction. This, in turn, makes the parasagittal hind-limb movements of terrestrial locomotion more efficient (Sargis, 2002b).

The prominent tibial crest for the patellar ligament of the quadriceps femoris indicates that muscles acting to extend knee joint are well developed. The emphasis on extension, reconstructed for *M. yei*, is typical of runners (Muizon, 1988; Szalay and Sargis, 2001). On the distal end of the tibia, the posterior tibial process of *M. yei* is relatively long. This is clearly related to efficiency in terrestrial locomotion because a relatively long posterior tibial process restricts mobility at the upper ankle joint, so that only parasagittal movements are possible at this joint (Sargis, 2002b).

In conclusion, *M. yei* was basically a terrestrial rodent with a propensity for climbing or digging. Compared to *Cricetodon* from Tieersihabahe, *M. yei* exhibits more specializations toward climbing, such as stronger brachial crest and transversely narrower radial notch.

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