

THE MID-TERTIARY  
CTENODACTYLIDAE  
(RODENTIA, MAMMALIA)  
OF EASTERN AND CENTRAL ASIA

BANYUE WANG

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## ABSTRACT

The mid-Tertiary Ctenodactylidae, a profusely ramified rodent of eastern and central Asia, is thoroughly revised based on collections from the Hsanda Gol Formation made in the 1920s by the Third Asiatic Expedition of the American Museum of Natural History, as well as on relatively recently collected material from China. *Leptotataromys*, *Murat Khanomys*, and *Roborovskia* are all synonyms of *Tataromys*. The species formerly referred to *Tataromys* are divided into four genera: *Tataromys*, *Yindirtemys*, *Bounomys*, and *Euryodontomys*, new genus. Thus *Tataromys* includes only four species: *T. plicidens*, *T. sigmodon*, *T. minor*, and *T. parvus*, new species. Some species referred to *Tataromys* [*T. grangeri*, *T. deflexus*, *T. suni*, *T. gobiensis*, *T. cf. T. plicidens*, *T. cf. T. sigmodon* of Bohlin (1946) and Zhai (1978), *T. cf. T. grangeri*, and some *Tataromys* species] are assigned to *Yindirtemys*. *T. bohlini* (partim) and *T. ulantatalensis* are allotted to *Bounomys*. *T. cf. T. sigmodon* and *T. bohlini* (partim) of Huang (1985) belong to a new genus, *Euryodontomys*.

The mid-Tertiary Ctenodactylidae of Asia falls into four lineages, here considered as four sub-

families. *Tataromyinae* includes *Tataromys*, *Yindirtemys*, and *Bounomys*; *Karakoromys* is considered not only a valid genus, but also the representative of a subfamily, *Karakoromyinae*, which is composed of *Karakoromys* and *Euryodontomys*; *Ctenodactylinae* includes *Sayimys*, some other fossil genera from the Neogene and Pleistocene, and the living ctenodactylids. This subfamily is thought to be more closely related to the *Karakoromyinae* than to the *Tataromyinae*. The family *Distylomyidae* is here reduced to subfamily rank, *Distylomyinae*, the sister group of the *Ctenodactylinae*. Among the four subfamilies, the *Tataromyinae*, which abruptly flourished during the mid-Tertiary, became extinct by the end of the middle Miocene. On the other hand, the *Ctenodactylinae* survived and migrated into southern Asia, the Mediterranean area, and North Africa. Now they still survive and live only in North and East Africa.

Evolution, radiation, migration, and extinction of the Ctenodactylidae are discussed. The main influential factors are interpreted to be climatic and topographic changes within the Palearctic Region from Eocene through Miocene times.

## INTRODUCTION

The family Ctenodactylidae, in which there are four living genera, is anatomically characterized by the following combination of characters: an hystricomorphous skull and a sciurognathous lower jaw, which has a well-developed lower masseteric crest, nonmolariform premolars, and incisor enamel with multiseriate microstructure. At present, the family is confined to North and East Africa. However, abundant fossils from early Oligocene through early Miocene ages have been found in eastern and central Asia, where they were diverse and abundant, becoming dominant among the rodents at times. Because of the fossil abundance, high diversity, and rapid evolution, they are particularly important for the biostratigraphy of the mid-Tertiary in Asia (Bohlin, 1946; Kowalski, 1974; Li and Qiu, 1980; Wang et al., 1981; Huang, 1985; Qiu and Gu, 1988; Qiu and Qiu, 1990, 1995; Wang, 1992; Wang and Wang, 1989, 1991; Wang et al., 1994).

The study of Asian ctenodactylids has been conducted along with various geologic

surveys of the Asian Tertiary. In 1922, the Third Asiatic Expedition of the AMNH found the locality Hsanda Gol in the Tsagan Nor basin, Mongolia, a locality that became famous for its richness and variety of fossils, especially micromammals including ctenodactylids. The first Asian Oligocene ctenodactylids (*Tataromys plicidens*, *T. sigmodon*, and *Karakoromys decessus*) were described by Matthew and Granger (1923). Later, Teilhard de Chardin (1926), Bohlin (1937), and Wood (1937) described fossil ctenodactylids from China and India. At that time, the Ctenodactylidae were thought to be the unique family of the superfamily Ctenodactyloidea and to include only four living genera (Simpson, 1945). The newly described fossil forms were considered to be either ?Eomyidae (Matthew and Granger, 1923) or near Theridomyidae (Teilhard de Chardin, 1926; Simpson, 1945). Bohlin (1946) first referred them to the family Ctenodactylidae based on his detailed and thorough analysis of a large number of ctenodactylid fossils from Shar-

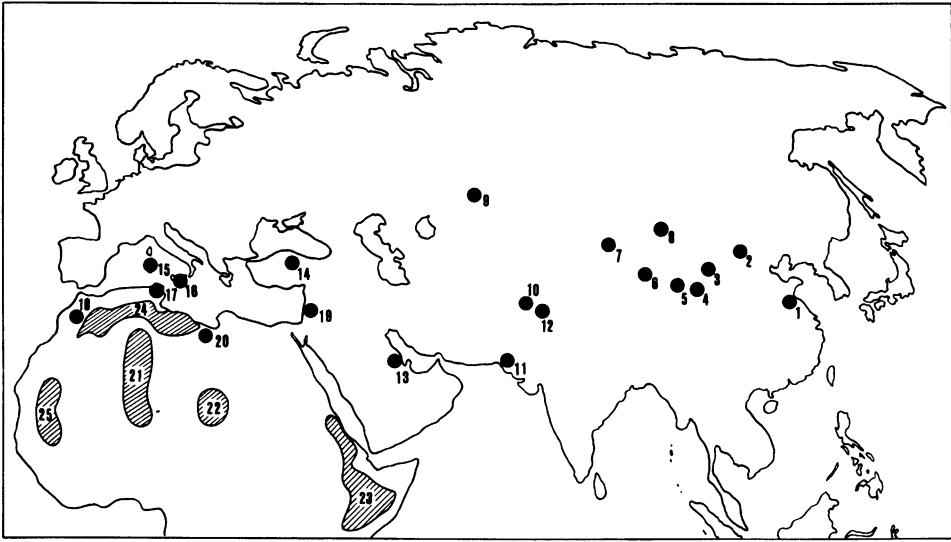


Fig. 1. Distribution of the Ctenodactylidae including recent genera (shaded; after Jaeger, 1971: fig. 1). In China: 1. Sihong, Jiangsu. 2. Tunggur District, Sonid Zuoqi, Nei Mongol. 3. Saint Jacques, Qianlishan District, and Ulantatal and Kekeamu, Nao'ertao Area, Nei Mongol. 4. Lanzhou, Gansu. 5. Xiejia, Qinghai. 6. Danghe, Gansu. 7. Turfan Basin and Junggar Basin, Xinjiang. In other areas: 8. Various localities of Mongolia. 9. Various localities of Kazakhstan. 10. Banda Daud Shah, Attoch District, Pakistan. 11. Sind, Pakistan. 12. Haritalyangar, India. 13. Al Hofuf, Saudi Arabia. 14. Gemerek, Turkey. 15. Sardinia, Italy. 16. Sicily, Italy. 17. North of Testour, Tunisia. 18. Beni Mellal and Irhoud, Morocco. 19. Israel. 20. Libya. 21 and 22. *Massouteria*. 23. *Pectinator*. 24. *Ctenodactylus*. 25. *Felovia*.

galtein Gol and Taben-buluk, Gansu (= Kansu) Province, China. Since his landmark studies, our knowledge of the ctenodactylids has greatly increased. Wood (1977) initiated an in-depth study of the family from a phylogenetic viewpoint. Dawson et al. (1984) analyzed the whole Ctenodactyloidea and included three families in it: the Ctenodactylidae, Cocomyidae, and Yuomyidae. Other paleontologists who studied the Asian mid-Tertiary ctenodactylids are N. S. Shevyreva (1971b, 1994a, 1994b), C. C. Black (1972), K. Kowalski (1974), R.-j. Zhai (1978), S. Sen and H. Thomas (1979), C.-k. Li and Z.-d. Qiu (1980), H. de Bruijn et al. (1981, 1989), X.-s. Huang (1985), Z.-x. Qiu and Z.-g. Gu (1988), and O. G. Bendukize (1993). Up to the present, 13 genera (*Tataromys*, *Karakoromys*, *Yindirtemys*, *Sayimys*, *Leptotataromys*, *Woodomys*, *Terrarboreus*, *Akzharomys*, *Distylomys*, *Prodistylomys*, *Prosayimys*, *Muratkhanyomys*, and *Roborovskia*), including more than 30 species, have been reported from the early Oligocene through Miocene of North China, Mongolia,

Kazakhstan, Pakistan, India, Saudi Arabia, Turkey, Israel, and Libya (fig. 1).

While studying fossil rodents from Nei Mongol (Inner Mongolia), the author found that the classification of mid-Tertiary ctenodactylids of Asia was in great disarray. For example, *Tataromys* included species with four different types of cheek teeth, which are considered to belong to four genera—*Tataromys*, *Yindirtemys*, *Bounomys*, and *Euryodontomys*, new genus. On the other hand, different genera (*Tataromys* and *Leptotataromys*) have the same type of cheek teeth.

A careful comparison reveals that the basic distinctions in tooth morphology of the ctenodactylids are to be found in the shape of the cusps and lophs; that is, whether they are compressed and straight or swollen and crescentic. Unfortunately, these features become obscure with wear. In most cases, once the basic pattern of the dentition is recognized, taxonomic confusion can be easily clarified.

This paper begins with a discussion of the synonymy of *Tataromys* and *Leptotataromys* and of relevant problems, on the basis of spec-

imens from the Hsanda Gol Formation at the AMNH. It then turns to review all Asian mid-Tertiary ctenodactylids, accompanied by description of the specimens recently collected by staff of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP). The review leads to the conclusion that the Ctenodactylidae may be subdivided into four subfamilies mainly on the basis of tooth morphology.

## MATERIALS AND METHODS

The material studied here includes (1) specimens from Saint Jacques, Qianlishan District, and Nao'ertao Area, Nei Mongol, China, by the Sino-Soviet Expedition (1959) and other teams from IVPP in 1977–1979, 1987, and 1988; (2) specimens collected from the Hsanda Gol Formation of Mongolia by the Third Asiatic Expedition of the AMNH in 1922 and 1925, in the AMNH, Naturhistorisches Museum, Basel, and IVPP; and (3) specimens described by Bohlin (1937, 1946) from Shargaltein Gol and Taben-buluk, Gansu; by Zhai (1978) from the Turfan Basin, Xinjiang; by Li and Qiu (1980) from Xiejia, Xining Basin, Qinghai; and by Huang (1985) from Ulanatal area, Nei Mongol. Remarks on fossils from other parts of Asia are based on casts and literature.

The terminology of the cusps and lophs used in this study (figs. 2, 3) follows the standard rodent dental terminology of Wood and Wilson (1936) with minor modifications. Bohlin (1946) called the two anterior cusps of p4 in *Tataromys* mesoconid and mesolophid. I agree with Wood (1977: 126–127) that the Ctenodactylidae have no mesoconid and mesolophid, and the two anterior cusps of p4 are protoconid and metaconid. Bohlin's mesoconid and mesolophid in the molars are the two parts of the posterior arm of the protoconid (= metalophid of de Bruijin and Rümke, 1974, and Wood's metalophid II or posterior arm of the protoconid): the "mesoconid" is the swollen middle part and the "mesolophid" is the lingual one. Bohlin (1946: 86–87) called the ridge connecting the entoconid with the ectolophid anterior to the hypoconid hypolophid I, and the connecting ridge behind the hypoconid hypolophid II. Huang (1985: 28) termed the ridge connecting the entoconid with the ecto-

lophid hypolophid I and that joining the hypoconid with the ectolophid hypolophid II. To my knowledge, the ridge from the entoconid never directly meets the hypoconid in ctenodactylids, and thus cannot be called hypolophid if we adhere to the standard of Wood and Wilson (1936). Here it is simply called the "arm of the entoconid." Likewise, the ridges from the hypoconid and the hypoconulid are here called arms of the hypoconid and hypoconulid. The buccal cusp of P4, Bohlin's metacone, is considered here to be the paracone, as in Li et al. (1989). The mure of Wood and Wilson (1936) and Schaub's (1925) Längsgrat is here identified as the entoloph. In the description of the skull, I have followed, as far as possible, the terminology of J. H. Wahlert (1974) and Li et al. (1989).

Only the specimens collected from the Hsanda Gol Formation, kept in the AMNH and IVPP, and recently collected by staff of the IVPP from other localities, and specimens of rearranged taxa, kept in IVPP, were measured and calculated. Except for the specimens of *Yindirtemys deflexus* and *Y. suni*, all the specimens were measured with a Wild M7A microscope. For the statistical treatment the original measurements of Bohlin (1946) were used.

In the descriptions, frequency of a character variant is expressed as a ratio, with the upper number indicating presence of the variant and the lower number the total number of specimens examined. Thus, 15/21 indicates that out of 21 specimens, 15 have the variant described.

Taken as a whole, the biostratigraphic sequences are taken from those of Qiu and Qiu (1995) and Wang (in press), except the Lanzhou fauna, which has to be altered in age assignment according to new data.

Abbreviations for repositories or localities are: AMNH, American Museum of Natural History; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; LDV, Vertebrate Section, Department of Geology, Lanzhou University; NMB, Naturhistorisches Museum, Basel; PIN, Paleontological Institute, Academy of Sciences of the USSR; Sh., Shargaltein Gol, Gansu, China; T.b., Taben-buluk, Gansu, China; Z.Pal., Palaeozoological Institute of the Polish Academy of Sciences. Ta-



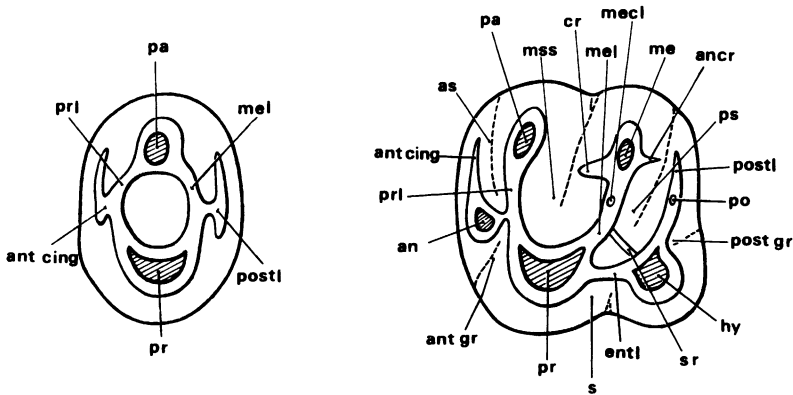


Fig. 2. Terminology of cusps and lophs of P4 (left) and upper molar (right) in ctenodactylids. Abbreviations: **an**, anterocone; **ancr**, antecrochet; **ant cing**, anterior cingulum (= anteroloph); **ant gr**, anterior groove; **as**, anterosinus; **cr**, crochet; **entl**, entoloph; **hy**, hypocone; **me**, metacone; **mecl**, metaconule; **mel**, metaloph; **mss**, mesosinus; **pa**, paracone; **po**, posterocone; **postl**, posteroloph (= posterior cingulum); **post gr**, posterior groove; **pr**, protocone; **pri**, protoloph; **ps**, posterosinus; **s**, sinus; **sr**, short ridge.

bles of measurements (in mm) of the dentition utilize the positional abbreviations: L, length; W, width; Wtr, width of trigonid; Wta, width of talonid. For statistical treat-

ment, abbreviations used are: N, number of specimens; Min, minimum; Max, maximum; Aver, average; S, standard deviation; V, variance.

## SYSTEMATICS

### SUPERFAMILY CTENODACTYLOIDEA TULLBERG, 1899

#### FAMILY CTENODACTYLIDAE ZITTEL, 1893

**EMENDED DIAGNOSIS:** Rodents with skull hystricomorphous, jaw sciurognathous, with coronoid process from high to reduced, condyle from high to low, strongly developed lateral crest forming ventral border of insertion of the muscle masseter medialis; incisor enamel multiseriate where known; dental formula 1/1, 0/0, 1/1-?0, 3/3; cheek teeth brachydont to hypsodont; P4 and p4 nonmolariform, smaller than molars, and may be lost early in life; dP4 and dp4 molariform; molars increase in size posteriorly; upper molar pattern based on quadrate arrangement with hypocone, becoming bilobate; lower molars with large hypoconulid lobe, becoming tri- or bilobate.

**REMARKS:** Included here are four subfamilies: Tataromyinae, Karakoromyinae, Distylomyinae, and Ctenodactylinae. They range in age from early Oligocene to Recent, and

geographically from Asia, the Mediterranean islands, and Africa.

Initially, the family Ctenodactylidae included only four living genera (Simpson, 1945). Even after Bohlin's assignment of the Oligocene genera to the Ctenodactylidae in 1946, Schaub (1958: 780) and Lavocat (1961: 52) still separated the fossil ctenodactylids as a distinct family and formally used the family name Tataromyidae, which was attributed to Bohlin (1946) but in fact was a step Bohlin hesitated to take. As pointed out by Dawson (1964: 14-15), Black (1972: 240), and Wood (1977: 122), there is no justification for the use of the family Tataromyidae, and in any case the family should not be credited to Bohlin. Although the term "Tataromyidae" was used by Bohlin (1946: 133-134) several times, it was always in quotation marks. In the same monograph he formally attributed the fossil genera to the Ctenodactylidae and stated that "the similarity between *Sayimys* and *Ctenodactylus* is so great that it seems superfluous to separate the fossil from the living Ctenodactylidae"

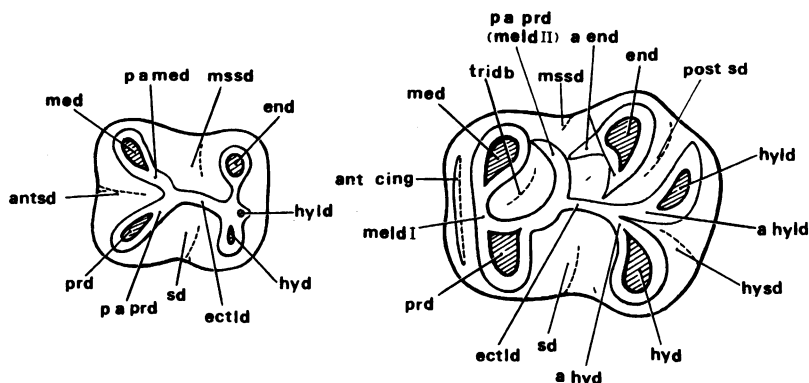


Fig. 3. Terminology of cusps and lophs of p4 (left) and lower molar (right) in ctenodactylids. Abbreviations: **a end**, arm of entoconid; **a hyd**, arm of hypoconid; **a hyld**, arm of hypoconulid; **ant cing**, anterior cingulum; **antsd**, anterosinusid; **ectld**, ectolophid; **end**, entoconid; **hyd**, hypoconid; **hyld**, hypoconulid; **hysd**, hyposinusid; **med**, metaconid; **meld I**, metalophid I; **meld II**, metalophid II; **mssd**, mesosinusid; **p a med**, posterior arm of metaconid; **p a prd**, posterior arm of protoconid; **postsd**, posterosinusid; **prd**, protoconid; **sd**, sinusid; **tridb**, trigonid basin.

(Bohlin, 1946: 8, 75, 133). I agree with Wood (1977: 122) that "Bohlin was not trying to erect a family Tataromyidae, but was using a convenient familiar reference term."

After Bohlin's (1946) inferences on the relationships between the fossil and living ctenodactylids and the redefinition of the family by Dawson et al. (1984), the concepts of the Ctenodactylidae became much clearer.

#### SUBFAMILY TATAROMYINAE LAVOCAT, 1961

TYPE GENUS: *Tataromys* Matthew and Granger, 1923

INCLUDED GENERA: *Yindirtemys* Bohlin, 1946, and *Bounomys* Wang, 1994.

GEOLOGICAL RANGE: Early Oligocene to middle Miocene.

GEOGRAPHIC DISTRIBUTION: Eastern and central Asia.

DIAGNOSIS: Skull high and narrow with flat roof, long facial and short cranial regions, rostrum long and robust, nasal long, lower branch of anterior zygomatic root of maxilla located above P4, sphenopalatine foramen within maxilla, choana far behind M3; mandible high and robust, with high coronoid process and condyle, masseteric fossa shallow, extending forward to below m1, with lower masseteric crest separated into two parts (a horizontal anterior crest and a posterior ridge extending to angular process), mental foramen below p4; cheek teeth from brachydont to moderately high-crowned; up-

per molars having four transverse lophs, metaloph complete and joining protocone, protocone V-shaped with well-developed posterior arm extending posterobuccally; M1 and M2 lacking entoloph, sinus deep, oblique posterobuccally and directed to posterosinus; on lower molars posterior arm of protoconid complete, shifting anteriorly, with its buccal part fused with metalophid I, and trigonid basin usually closed.

REMARKS: The Tataromyinae, as originally defined by Lavocat (1961), included *Tataromys*, *Karakoromys*, and *Africanomys*. The latter two genera are now referred to the Karakoromyinae and Ctenodactylinae, respectively, because they are markedly different from Tataromyinae in morphology (see below). On the other hand, *Yindirtemys* and *Bounomys* share with *Tataromys* derived features of the skull, mandible, and dentition. Therefore, I exclude *Karakoromys* and *Africanomys* but include *Yindirtemys* and *Bounomys* in the subfamily Tataromyinae.

#### *Tataromys* Matthew and Granger, 1923

*Tataromys* Matthew and Granger, 1923: 5.  
*Leptotataromys* Bohlin, 1946: 107. Schaub, 1958: 781.

*Muratkhanyomys* Shevyreva, 1994b: 116. NEW SYNONYMY.

*Roborovskia* Shevyreva, 1994b: 119. NEW SYNONYMY.

TYPE SPECIES: *Tataromys plicidens* Matthew and Granger, 1923.

INCLUDED SPECIES: *Tataromys sigmodon* Matthew and Granger, 1923, *T. minor* (Huang, 1985), and *T. parvus*, new species.

GEOLOGICAL RANGE: Early Oligocene to early Miocene.

GEOGRAPHIC DISTRIBUTION: North China, Mongolia, and Kazakhstan.

DIAGNOSIS: Dorsal part of the frontal shorter than nasal, interparietal large and triangular in form, temporal fossa large, temporal crest distinct but lacking temporal foramen, orbit large and situated completely lateral to frontal, masticatory and buccinator foramina separated, palate comparatively wide, maxilla long and palatine shifted posteriorly, posterior palatine foramen located at maxillary-palatine suture opposite to M2, choana wide; cheek teeth brachydont to moderately high-crowned, with compressed cusps and thin lophs; P4 protoloph straight or slightly curved, anterior cingulum weakly developed; on upper molars protoloph transverse and slender; p4 with long and lingually situated ectolophid and wide, U-shaped mesosinusid and sinusid; on lower molars trigonid short, posterior arm of protoconid narrow, with no swollen middle and short lingual joining with metaconid, trigonid basin small, closed or absent, ectolophid straight and lingually situated, mesosinusid wide and shallow, sinusid deep, hypoconid, entoconid, hypoconulid flat, and anterior cingulum absent.

DISCUSSION: (1) Synonymies of *Tataromys*. *Tataromys* was first described by Matthew and Granger in 1923. The genoholotype, *Tataromys plicidens*, is a palate with right and left P4–M3 (AMNH 19082) from the Hsanda Gol Formation. Although they listed other upper and lower jaws (AMNH 19081, 19083, and 19084) as paratypes, only the upper cheek teeth of the holotype were figured. The lower molars were described in the diagnosis (1923: 6): “The lower molars reverse this pattern in the usual manner but the arrangement is less regular.” In describing the other species, *T. sigmodon*, they kept silent about its lower teeth.

Teilhard de Chardin (1926) reported *Tataromys* cf. [*T.*] *plicidens* (uncorrected syntax in using “cf.”, for comments see Lucas, 1986, and Estes, 1987), *T. deflexus* new spe-

cies, *Tataromys* sp., and *Karakoromys*(?) [sp.] from Saint Jacques, Nei Mongol, China. Except for *Karakoromys*(?) [sp.], which was represented by one m3, all were represented by upper teeth. In 1937 Bohlin described some ctenodactylids from Shargaltein Gol, Gansu, China, including *Tataromys* cf. [*T.*] *plicidens*, *Karakoromys* cf. [*K.*] *decessus*, and “*Karakoromys*” sp. His *Tataromys* cf. [*T.*] *plicidens* consisted of both upper and lower teeth (figs. 89–99). However, the upper teeth are markedly different from those of the typical *Tataromys* defined by Matthew and Granger. The other material referred by Bohlin (1946) to *Tataromys* (*T. grangeri*, *T.* cf. [*T.*] *sigmodon*, and *T.* cf. [*T.*] *plicidens*) are more similar to *Yindirtemys deflexus* than to *Tataromys plicidens*. Bohlin (1946) established a new genus, *Leptotataromys*, based on the specimen Sh. 35 from Shargaltein Gol, which was originally identified as “*Karakoromys*” sp. by Bohlin (1937: 42–43).

Since then, *Leptotataromys* has been widely used. However, it is very difficult to distinguish *Leptotataromys* from *Tataromys*. This led to confusion in the classification of the *Tataromys* group. For example, within the genus *Tataromys* there are three groups that differ in upper cheek tooth morphology, represented by *Tataromys plicidens*, *T. deflexus*, and *T. bohlini*. On the other hand, *Leptotataromys* (*L. gracilidens* and *L.* cf. [*L.*] *gracilidens* described by Huang, 1985) have similar upper teeth to some species of *Tataromys* (*T. plicidens* and *T. sigmodon* of Matthew and Granger in 1923), as mentioned by Huang (1985: 34–35). The lower teeth of *Tataromys sigmodon* and *T.* cf. [*T.*] *grangeri* described by Kowalski (1974) resemble those of *Leptotataromys*, whereas those of *Tataromys* cf. *T. sigmodon* of Zhai (1978) and *Tataromys gobiensis* and *Tataromys deflexus* by Kowalski (1974) are similar to those of Bohlin’s *Tataromys* cf. [*T.*] *plicidens* (= *Yindirtemys ambiguus*) and *T. grangeri* (= *Yindirtemys grangeri*). In other words, the three latter species are different from *Leptotataromys* (= *Tataromys*), but similar to *Yindirtemys* in lower molar morphology (see table 1). *Karakoromys decessus* described by Kowalski (1974) includes two different groups of lower teeth: *Leptotataromys*-type (= *Tataromys*) (Z.Pal. MgM-III/48, Pl.



TABLE 1  
Synonyms of Some Mid-Tertiary Ctenodactylids of Asia

Matthew and Granger 1923	Teilhard de Chardin 1926	Bohlin 1937	Bohlin 1946	Kowalski 1974	Huang 1985	This paper
<i>T. plicidens</i>	<i>T. sp.</i> <i>K(?) sp.</i>			<i>T. plicidens</i>	<i>L. cf. L. gracili-</i> <i>dens</i> <i>L. gracilidens</i> (par- tim)	<i>T. plicidens</i>
<i>T. sigmodon</i>	<i>T. cf. T. pli-</i> <i>cidens</i>	" <i>K.</i> " <i>sp.</i>	<i>L. gracilidens</i>	<i>T. sigmodon</i>	<i>L. gracilidens</i> (par- tim)	<i>T. sigmodon</i>
				<i>T. cf. T. gran-</i> <i>geri</i> <i>K. decessus</i> (partim)	<i>L. minor</i> <i>T. bohlin</i> (partim)	<i>T. minor</i>
		<i>K. cf. K. de-</i> <i>cessus</i>	<i>K. cf. K. de-</i> <i>cessus</i>			<i>T. parvus</i> , new species
			<i>T. grangeri</i> <i>Y. woodi</i>			<i>Y. grangeri</i>
	<i>T. deflexus</i>			<i>T. deflexus</i>		<i>Y. deflexus</i>
				<i>T. gobiensis</i>		<i>Y. gobiensis</i>
		<i>T. cf. T. pli-</i> <i>cidens</i>	<i>T. cf. T. plici-</i> <i>dens</i> (par- tim)			<i>Y. ambiguus</i> , new species
			<i>T. cf. T. plici-</i> <i>dens</i> (par- tim)			<i>Y. cf. Y. ambiguus</i>
			<i>T. cf. T. sig-</i> <i>modon</i>			<i>Y. sp.</i>
					<i>T. bohlini</i> (partim)	<i>B. bohlini</i>
					<i>T. ulantatalensis</i> <i>L. gracilidens</i> (par- tim)	<i>B. ulantatalensis</i>
					<i>T. cf. T. sigmodon</i>	<i>E. ambliatus</i> , new genus and spe- cies
					<i>T. bohlini</i> (partim)	<i>E. exiguus</i> , new species

*T.* = *Tataromys*, *L.* = *Leptotataromys*, *Y.* = *Yindirtemys*, *B.* = *Bounomys*, *E.* = *Euryodontomys*, *K.* = *Karakoromys*.

XLIX, fig. 6) and *Karakoromys*-type. Stehlin and Schaub (1951: 290–291) referred a mandible with p4–m3 (NMB 21624), originally named *Karakoromys decessus*, from the Hsanda Gol Formation to *Tataromys* cf. [*T.*] *sigmodon*. However, they suspected that this specimen may be a species of *Leptotataromys*.  
My study of the Nei Mongol material reveals that the upper and lower cheek teeth of *Tataromys deflexus* and Bohlin’s *T. cf. T. plicidens* are very similar in having swollen

cusps and crescentic lophs. On the other hand, the upper teeth of *Tataromys plicidens* match the lower teeth of *Leptotataromys* rather than those of Bohlin’s *Tataromys* cf. *T. plicidens* in having compressed cusps and thin lophs. The question arises whether the lower teeth of *Leptotataromys* are, in fact, those of *Tataromys*? To answer this, I checked all the specimens of *Tataromys* from the Hsanda Gol Formation in the AMNH. A skull associated with the lower jaw (AMNH 21658) shows upper cheek teeth typical of

*Tataromys plicidens* in having compressed cusps and thin lophs, but lower cheek teeth typical of *Leptotataromys* in having much more slender cusps and lophids, small trigonid, and lingually situated ectolophid. In the collection of the IVPP, a skull associated with lower jaw (IVPP V 10534.1) was also found with the same features. These show that *Leptotataromys* is a junior synonym of *Tataromys*, as will be discussed in detail below.

Shevyreva (1994b) described two new genera, *Murat Khanomys* and *Roborovskia*, from the lower Oligocene Buran Formation of the Zaysan Depression, Kazakhstan. According to her figures and description (ibid.: 151–155; figs. 1, 2), both are identical with *Tataromys* in morphology as follows: the lower jaw has a well-developed lower masseteric crest extending to m1, but no upper crest; the mental foramen is under p4; the cheek teeth have compressed cusps and thin lophs, V-shaped protocone, long, lingually located ectolophid; p4 with U-shaped mesosinusid and sinusid; lower molars with reduced trigonid basin. It must be concluded that *Murat Khanomys* and *Roborovskia* are junior synonyms of *Tataromys*.

(2) Species of *Tataromys*. *Tataromys* was known to include more than 14 species (*T. plicidens*, *T. cf. T. plicidens*, *T. sigmodon*, *T. cf. T. sigmodon*, *T. deflexus*, *T. grangeri*, *T. cf. T. grangeri*, *T. gobiensis*, *T. suni*, *T. ulan-tatalensis*, *T. bohlini*, *T. boreas*, *T. raeda* and *Tataromys* spp.), whereas *Leptotataromys* included three species (*L. gracilidens*, *L. cf. L. gracilidens*, and *L. minor*); *Murat Khanomys* contains three species (*M. velivolus*, *M. kulgayniae*, and *M. dzhanarae*) and *Roborovskia* has one species (*R. collega*). The last seven species should be referred to *Tataromys* if *Leptotataromys*, *Murat Khanomys*, and *Roborovskia* are junior synonyms of *Tataromys*. This would leave 21 named species in *Tataromy*. However, *Leptotataromys gracilidens*, *Murat Khanomys velivolus*, and *Tataromys boreas* are proved to be junior synonyms of *Tataromys sigmodon*; *M. kulgayniae* and *R. collega* are junior synonyms of *T. plicidens*; Huang's *L. cf. [L.] gracilidens* is to be referred to *Tataromys plicidens*; *M. dzhanarae* and *T. raeda* are too poorly known to be discussed here. On the other

hand, some species formerly referred to *Tataromys* (including *T. deflexus*, *T. cf. T. plicidens*, *T. cf. T. sigmodon*, *T. grangeri*, *T. cf. T. grangeri*, *T. gobiensis*, *T. suni*, *T. ulan-tatalensis*, *T. bohlini*, and *Tataromys* sp.) should be excluded from *Tataromys* as discussed below. As a result, *Tataromys*, in my opinion, contains only four valid species: *T. plicidens* Matthew and Granger, 1923, *T. sigmodon* Matthew and Granger, 1923, *T. minor* (Huang, 1985), and *T. parvus*, new species.

### *Tataromys plicidens* Matthew and Granger, 1923

Figures 4–10, 11A, B, D, Figures 40, 41B, C (added in proof, pp. 87 and 88); tables 2, 3

*Tataromys plicidens* Matthew and Granger, 1923: 5–6, fig. 6. Stehlin and Schaub, 1951: 125, fig. 179. S. Schaub, 1958: 780–781, fig. 208. Mellett, 1968: 6, 10. Kowalski, 1974: 163–164, pl. 48, fig. 3. Huang, 1982: 340–341, 347. Wang, 1994: 37–38, figs. 2:1a, 1b, 3A, B, D.

*Tataromys* sp. Teilhard de Chardin, 1926: 28, fig. 15C. NEW SYNONYMY.

*Karakoromys*(?) Teilhard de Chardin, 1926: 27–28, 31, fig. 15D. NEW SYNONYMY.

?*Karakoromys decessus* (partim): Teilhard de Chardin and Leroy, 1942: 25. NEW SYNONYMY.

*Tataromys plicidens* (partim): Teilhard de Chardin and Leroy, 1942: 25, 89. NEW SYNONYMY.

?*Karakoromys* sp. Teilhard de Chardin and Leroy, 1942: 89. NEW SYNONYMY.

*Leptotataromys gracilidens* (partim): Huang and Wang, 1984: 39–48, table 1. Huang, 1985: 32–35, 38. NEW SYNONYMY.

*Leptotataromys* cf. *gracilidens* Huang, 1985: 35, 38, pl. 2, figs. 2–4. Russell and Zhai, 1987: 292, 355. NEW SYNONYMY.

*Murat Khanomys kulgayniae* Shevyreva, 1994b: 117–119, figs. 2b, v. NEW SYNONYMY.

*Roborovskia collega* Shevyreva, 1994b: 120, fig. 2zh. NEW SYNONYMY.

HOLOTYPE: A palate with right P4–M3 (AMNH 19082), from the Hsanda Gol Formation of Loh, Mongolia, and figured by Matthew and Granger, 1923: fig. 6.

PARATYPE: Upper and lower jaws [AMNH 19081 (I failed to observe this specimen. I am not sure if it belongs to *T. plicidens* or not.), 19083, 19084].

REFERRED SPECIMENS: AMNH 21622, 21658, 22087, 22088, 56631, 84203, 84204,

85408; Z.Pal. MgM-III/44; PIN 3463/24, 2979/1704; Spec. no. 3463/25; IVPP V 7345.76, IVPP V 7346.1–11, V 10534.1–45, V 10535.1–6, V 10536.1–5, V 10537.1–13, V 10538.1–3, V 10539.1–3, V 12041.1, V 12041.2, and other specimens from Saint Jacques described by Teilhard de Chardin (1926: figs. 15C, D).

**GEOLOGICAL RANGE:** Late early Oligocene, upper part of the Ulantatal Formation, the Hsanda Gol Formation and Buran Formation, and late(?) Oligocene.

**GEOGRAPHIC DISTRIBUTION:** Saint Jacques [IVPP locs. 77046.5 (V 10535), 77046.1 (V 10536), 77046 (V 10537), 77046(4) (V 10538), 77049.8 (V 10539), and other localities (V 10534)] and Ulantatal (V 7345.76, V 7346, V 12041), Nei Mongol, China; Loh, Tsagan Nor Basin, and Khatan Khayrkhan, Mongolia; and Zaysan Depression, Kazakhstan.

**EMENDED DIAGNOSIS:** *Tataromys* of medium size; sphenopalatine foramen above junction of M1 and M2; cheek teeth moderately high-crowned, with compressed cusps and lophs; P4 anterior cingulum low; upper molars with slightly curved metaloph, distinct anterocone, mesosinus wide U-shaped, anterosinus and posterosinus transverse; on M3 metaloph meets hypocone; lower molars having very short trigonid with or without small closed basin, hypoconulid usually joining entoconid or both entoconid and hypoconid on m1 and meeting hypoconid on m2 and m3.

**DESCRIPTION:** **Skull:** The two known skulls (IVPP V 10534.1 and AMNH 21658) are both damaged and crushed in the auditory and jugal region. The skull is in many ways intermediate between those of *Cocomys* and the living ctenodactylids (*Ctenodactylus*, *Pectinator*, *Massouteria*, and *Felovia*), but has some autapomorphic features as well. One of the most striking features is the outline of the skull, which is high and narrow, with a flattened roof, except for the downward curvature at anterior end of the nasals. In general outline the skull is more similar to that of *Paramys* than to any other known ctenodactylids. The facial region is longer than the cranial region. The ratio of the facial length (from the anterior end of the nasals to the postorbital process) to the cranial length (from the postorbital process to the occipital

crest) is 1.47 to 1.56, higher than in *Cocomys* but lower than in the living ctenodactylids (1.86–2.26). Probably related to the enlargement of the infraorbital foramen and the attachment of the medial masseter muscle, the rostrum is long, robust, and, in dorsal view, widens slightly anteriorly. In contrast, it is thin and parallel-sided in the living ctenodactylids, but short and tapering anteriorly in *Cocomys*. The orbital region is long.

**Dorsal view** (fig. 4): The nasals are long and taper posteriorly to meet the frontal at about the level of the anterior margin of the orbit, more posteriorly extended than in the living ctenodactylids but more anterior than in *Cocomys*. As in other ctenodactylids, the premaxillae have narrow and posteriorly prolonged dorsal processes. *T. plicidens* is closer to *Ctenodactylus* than to *Cocomys* in this respect. The dorsal part of the frontal is proportionately short, shorter than the nasal, whereas in *Cocomys* and *Ctenodactylus* it is about the same length as the nasal. The anterior end of the frontal is narrower than its posterior end, with the lateral margins convergent anteriorly as in the living ctenodactylids but unlike *Cocomys*. The large orbit is intermediate in position and size between *Cocomys* and the living ctenodactylids: the upper margin of the orbit is wholly composed of frontal in *Tataromys plicidens*, but formed by the anterior part of frontal in *Cocomys* and by both the frontal and parietal in the living ctenodactylids. The postorbital process is blunt. The postorbital constriction is distinct and extended to the parietal posteriorly. The parietal–frontal suture is convex posteriorly at the middle, extends toward the postorbital process, and then abruptly turns posterolaterally before reaching the process. The parietal–interparietal sutures form a parabola convex anteriorly. The parietal is short medially. As in *Cocomys*, the interparietal is large and roughly triangular. The temporal fossae are very large, much larger than in *Cocomys* and the living ctenodactylids. The temporal crests, extending from the postorbital process to the occipital crest, are prominent and concave laterally, but do not merge. The shortest distance between them is 6 mm (AMNH 21658) and 9 mm (IVPP V 10534.1). The interparietal–occipital suture parallels the occipital crest. The external



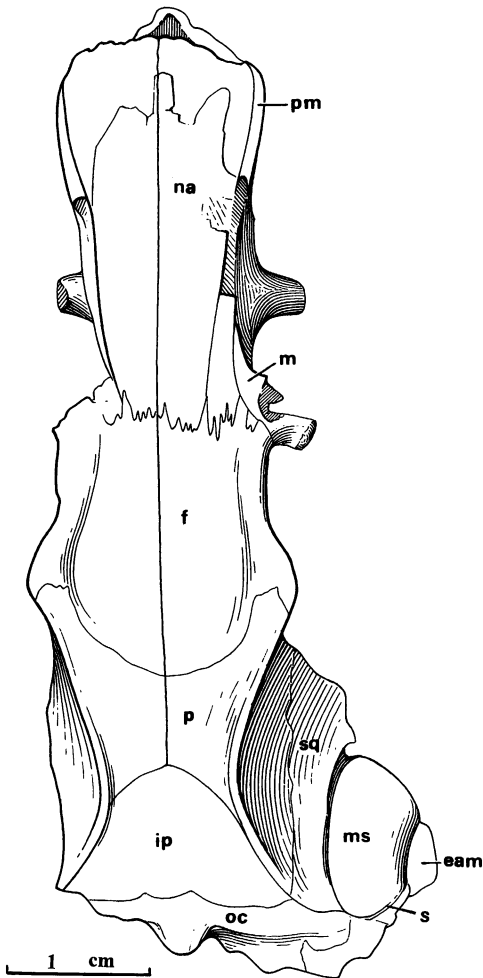


Fig. 4. Dorsal view of *Tataromys plicidens* skull (IVPP V 10534.1). Abbreviations: aa, anterior alveolar foramen; ab, auditory bulla; as, alisphenoid; bu, buccinator foramen; eam, exterior acoustic meatus; eth, ethmoid foramen; f, frontal; fo, foramen ovale; foa, foramen ovale accessorius; in, incisive foramen; ip, interparietal; m, maxillary; ms, mastoid; msc, masticatory foramen; na, nasal; oc, occipital; op, optic foramen; os, orbitosphenoid; p, parietal; pl, palatine; pm, premaxillary; ppl, posterior palatine foramen; s, septum; spf, sphenofrontal foramen; spl, sphenopalatine foramen; spn, sphenoidal fissure; sq, squamosal.

occipital protuberance protrudes posteriorly. The parietal-squamosal sutures are straight and about parallel. The temporal surface of the squamosal (= Tullberg's Processus supramastoideus des Os squamosum) is a nar-

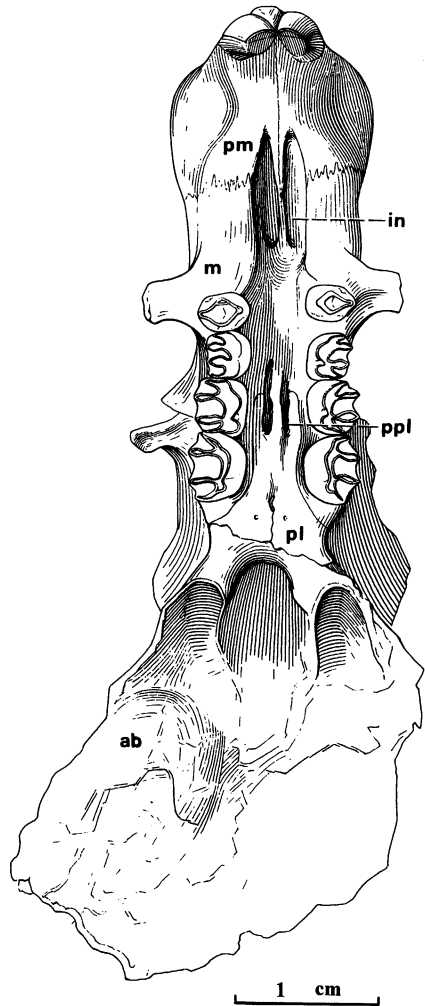


Fig. 5. Ventral view of *Tataromys plicidens* skull (IVPP V 10534.1). For abbreviations see fig. 4.

row long strip that is wider anteriorly. The extremely large tympanic bulla protrudes posterolaterally.

**Ventral view** (fig. 5): As in *Ctenodactylus* and other living ctenodactylids, the incisive foramen of *Tataromys plicidens* is large. The ratio of length of incisive foramen to that of the diastema is high (0.71–0.73). The premaxillary-maxillary suture intersects the incisive foramen near the midpoint. Only the inferior root of the zygomatic process of the maxilla is preserved. It is a little more anterior than in *Cocomys*, having the anterior surface anterior to P4 and the posterior one slightly

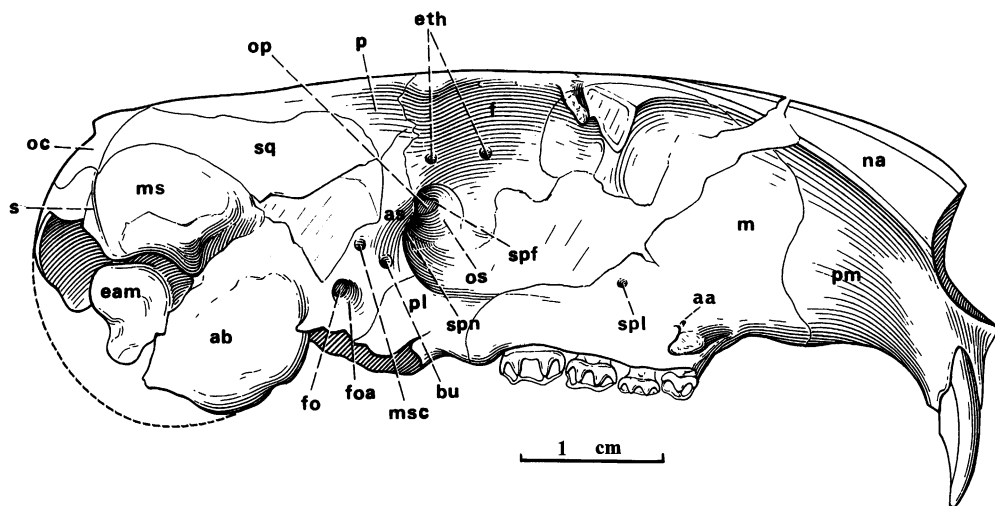


Fig. 6. Lateral view of *Tataromys plicidens* skull (IVPP V 10534.1). For abbreviations see fig. 4.

behind the paracone of P4. On the ventral surface there is a small rugged area that may be interpreted to anchor the superficial branches of the masseter muscle. The two tooth rows are about parallel or slightly convergent anteriorly. The palate is narrower than in *Cocomys* and *Ctenodactylus* but wider than in *Yindirtemys*. The width of the palate between the rows is almost equal to that of the tooth row. Unlike in *Cocomys* and the living ctenodactylids, the palatal process of the maxilla is long and the palatine shifts posteriorly. The two large posterior palatine foramina are opposite M2, with grooves extending forward to the level of M1, then merging as one groove. The lateral maxillary-palatine suture extends back along the lingual side of M2 and M3 and turns laterally behind M3. No posterior maxillary notch or foramen is visible. On the palatine there is a pair of small foramina between the two M3. As in *Ctenodactylus*, the choana opens far behind M3, more posteriorly than in *Cocomys* and *Sayimys* and wider than in *Yindirtemys ambiguus* (Sh 785) and *Bounomys*. The large, deep pterygoid fossae are located behind the anterior border of the choana, with a long epipterygoid extending posteriorly to the bulla.

**Lateral view** (fig. 6): The anterior end of the nasal is retracted behind the anterior end of the premaxilla and I2. The anterior nasal

aperture opens anterodorsally. This is similar to that in *Ctenodactylus* but different from those of *Cocomys* and other living ctenodactylids. The upper incisors are less curved than in *Cocomys*, *Yindirtemys*, and the living ctenodactylids. Their anterior tips extend downward instead of posteroventrally. On the lateral wall of the rostrum formed by the premaxilla and maxilla there is a large fossa, with its surface somewhat roughened, possibly for the attachment of the anterior part of the medial masseter muscle. Only roots are partly preserved of the zygomatic arch and the anterior orbital rim. As in the living ctenodactylids, the infraorbital foramen is large and faces anterodorsally. The superior ramus of the zygomatic process of the maxilla branches off above M2, much behind the inferior ramus. Unlike Sh 785 of *Yindirtemys ambiguus*, no distinct groove can be observed on the alveolar process of the maxilla above the tooth row. However, the sphenopalatine foramen above the junction of M1 and M2, mentioned by Bohlin (1946: 77) in Sh 785, is present. This foramen is entirely surrounded by the maxilla. The small anterior alveolar foramen is situated on the dorsal surface of the inferior root of the zygomatic process of the maxilla. The dorsal palatine foramen is not preserved. Relative to the cheek teeth, the major foramina of the orbital wall (the optic, ethmoid, and sphenoidal fissure) are located considerably farther back. Two ethmoid foramina are situ-

ated entirely within the orbital lamina of the frontal and behind M3. The optic foramen is large and posteriorly positioned relative to M3. The anterodorsal part of the alisphenoid extends around the squamosal to meet the parietal and exclude a squamosal-frontal contact. In contrast with *Cocomys* and *Ctenodactylus*, both the buccinator and masticatory foramina are present in the alisphenoid. They are separated, with the former being anteroventral to the latter. The foramen ovale and foramen ovale accessorius are large and ventral to the masticatory foramen.

**Auditory region:** The auditory region is posteriorly located as in *Cocomys* and the living ctenodactylids. Unfortunately, the only part preserved, the bullae of AMNH 21658 and the right bulla of IVPP V 10534.1, are damaged and crushed. As far as the preserved part is concerned, as in the living ctenodactylids it is large and composed of two parts. The dorsal part, above and behind the external auditory meatus, is the mastoid (= Tullberg's (1899) *Petromastoideum*). This part is very large, extending forward almost to the zygomatic process of the squamosal and back beyond the occipital surface. It is covered by the occipital posteromedially. On the dorsal surface of the mastoid there is a distinct groove extending transversely from the external auditory meatus to the squamoso-occipital suture. Inside the mastoid, opposite to the groove, there is a septum separating the mastoid into two subparts. The lower part (= Tullberg's *Bullae osseae*), just below the external auditory meatus, may be the auditory bulla made of the epitympanic bone. It is larger than in *Ctenodactylus*. The ossified external auditory meatus is broken in the fossil, but its imprint is partly preserved. It is directed outward. The petrosal is partly preserved. On the cranial side the internal auditory meatus is large and separated by a transverse crest into two parts: the opening of the facial canal and the ventral vestibular area.

**Mandible:** Of all the material available for study, the left and right halves of the mandibles are all separate. Apparently they were not firmly coalesced and remained movable during the animal's lifetime. The lower jaw is typically sciurognathous. The anterior end of the angular process arises

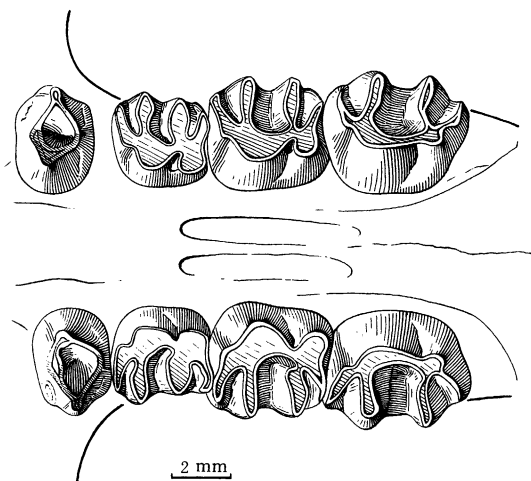


Fig. 7. Occlusal view of upper cheek teeth of *Tataromys plicidens* (IVPP V 10534.1).

from below the alveolus for the incisor. The body of the mandible is high and robust, with a convex buccal side and concave lingual one. Unlike *Cocomys*, the masseteric fossa in *Tataromys* is shallow and reaches forward to below m1; there is a distinct lower masseteric crest but no upper one. The lower masseteric crest is divided into two parts: the anterior part is usually more or less horizontal and may provide the attachment for the anterior part of the medial masseter muscle; the posterior one extends to the angular process. The mental foramen is just beneath the posterior part of p4, at about the same level as the anterior part of the masseteric fossa. The ascending ramus is damaged. Judging from the part preserved, it is high, with high coronoid process and condyle.

**Dentition:** The dental formula is 1/1, 0/0, 1/1, 3/3. The upper and lower incisors have the cross-sectional form of an equilateral triangle. The surface of the enamel is wrinkled. The upper incisors are wider and have more curved labial sides than the lowers, and have a distinct longitudinal groove along the medial side.

The cheek teeth increase in size to the posterior. The cusps are compressed and the lophs well developed, but slender.

P4 is usually obliquely implanted in the upper jaw. The buccal cusp, the paracone, and the protocone are compressed anteroposteriorly. The protoloph and metaloph are



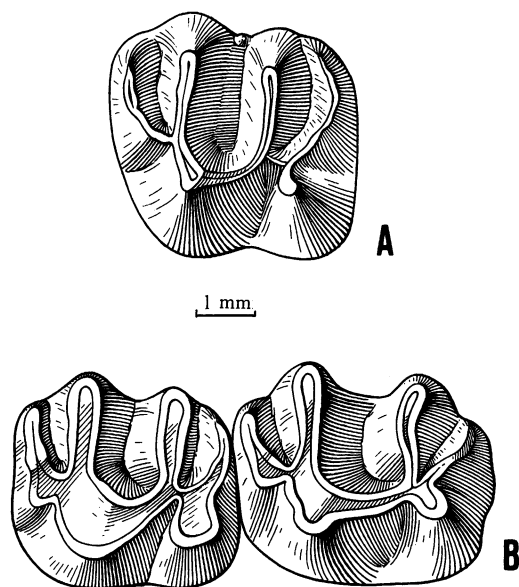


Fig. 8. Occlusal view of upper molars of *Tataromys plicidens*. A. Left M2 (IVPP V 10536.1). B. Left M2 and M3 (IVPP V 10534.5).

complete, the former usually being less curved than the latter. The anterior cingulum is very low or even absent, without lingual extension. The better developed posterior cingulum is high, usually joins the metaloph at its middle, and has both buccal and lingual extensions.

M1 and M2 are roughly quadrate in occlusal view. The paracone and metacone are compressed anteroposteriorly. The protocone is larger than the hypocone, V-shaped, with a posterior arm extending posterobuccally. The four transverse lophs (protoloph, metaloph, anterior cingulum, and posteroloph) are slender and nearly parallel to each other. In heavily worn specimens the metaloph seems to be swollen and an "entoloph" seems to be present. However, in unworn or slightly worn specimens (fig. 8), the metaloph forms a long, compressed, and curved crest, with a transverse buccal extension and a lingual extension extending anterolingually to meet the protocone (= posterior arm of protocone). In other words, the posterior arm of the protocone unites directly with the metaloph to form a continuous loph. There is no true entoloph connecting the protocone and the hypocone. The so-called entoloph is composed of the posterior arm of the protocone (= the

lingual part of the metaloph) and a short ridge connecting the metaloph with the posteroloph. The anterior cingulum joins the protoloph. The anterocone and anterior groove are distinct. The mesosinus is usually a wide U-shape. The anterosinus and posterosinus are transverse and compressed anteroposteriorly. The sinus is deep, oblique posterobuccally, and opposite the posterosinus.

M3 is roughly quadrate in occlusal view, with shorter lingual and posterior sides. The protocone is an obtuse L-shape, with a well-developed but longitudinal posterior arm joining the hypocone. The metaloph reaches the hypocone. The short posteroloph extends posterobuccally and is separated from the hypocone by a distinct posterior groove. The posterosinus is short and opens widely. The sinus is shallow, wide, and not as oblique as in other molars.

p4 is quadrate in occlusal view. The protoconid is slightly larger than the metaconid and forms a rectangle with the latter. The ectolophid varies from high and well developed to weak and low, but in all cases it is long and slightly more lingually situated than the anterior groove. Both the mesosinusid and sinusid are a wide U-shape. The former is much shallower than the latter. The entoconid is as large as the metaconid. The hypoconid is a transverse crest continued with the entoconid and does not form any distinct cusp.

m1 is relatively narrower and longer than m2 and m3. On the lower molars the trigonid is short. No anterior cingulum is present. The protoconid and metaconid are compressed anteroposteriorly. The metalophid I is complete but slender and slightly concave anteriorly. The metalophid II is complete, slender, shifts anteriorly, and appears to fuse with the metalophid I buccally. The angle between metalophids I and II is usually acute. The trigonid basin is usually small or may be absent, especially on m3 (m1, 2/21; m2, 2/17; m3, 8/12). When absent, obviously only one metalophid is present. The ectolophid is lingually positioned, with a shallow, wide mesosinusid and a deep, transverse sinusid. The entoconid, hypoconid, and hypoconulid are more or less compressed. The arm of the entoconid extends anterobuccally. On m2 and m3 the arm of the hypoconulid always meets the arm of the

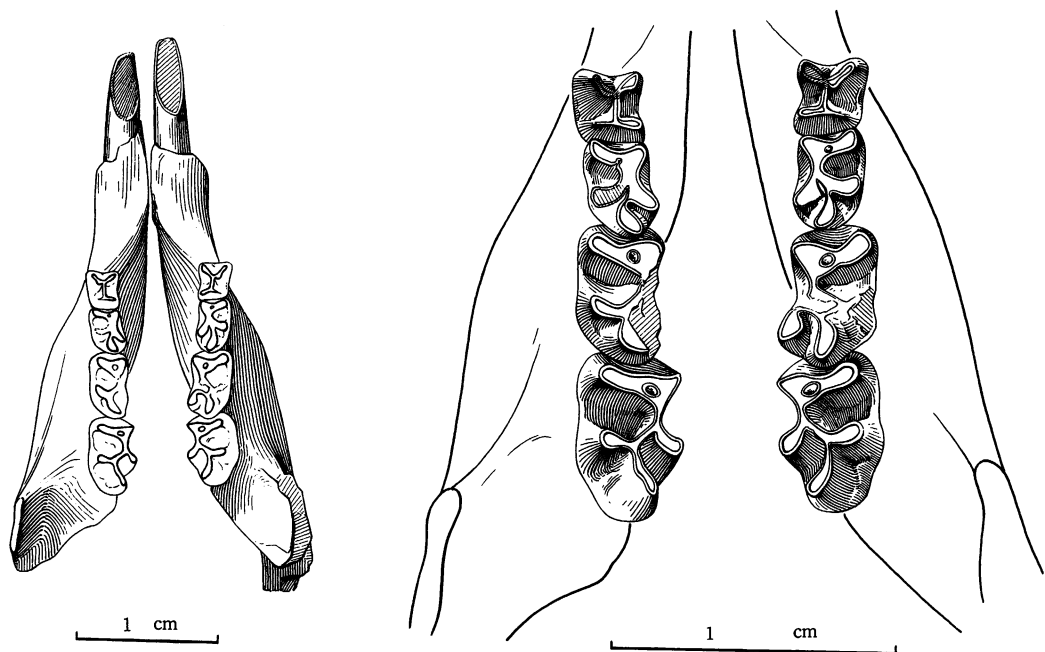


Fig. 9. Occlusal view of lower jaws with cheek teeth of *Tataromys plicidens* (IVPP V 10534.1).

hypoconid and has a shallow hyposinusid. The connection is obscure on worn m1 (6/21). On less worn m1 (15/21), it is variable: in some (8/15), including the left m1 of IVPP V 10534.1, the arm of the hypoconulid joins the arm of the entoconid rather than that of the hypoconid, and the hyposinusid is deep transversely; in others (7/15),

including the right m1 of IVPP V 10534.1, the arm of the hypoconulid connects with the arms of both the entoconid and hypoconid to form a closed central basin.

DIMENSIONS: See tables 2 and 3.

DISCUSSION: It is noteworthy that all the upper jaws described here are identical in morphology with the holotype of *Tataromys*

TABLE 2  
Measurements (in mm) of Upper Teeth of *Tataromys plicidens*

		N	Min	Max	Aver	S	V
P4-M3	L	18	12.16	14.88	13.12	0.73	0.53
M1-3	L	20	9.92	11.52	10.57	0.50	0.25
P4-M2	L	21	8.48	10.56	9.10	0.53	0.28
P4-M1	L	26	4.83	6.16	5.52	0.34	0.11
M1-2	L	26	6.00	7.36	6.60	0.33	0.11
M2-3	L	26	7.16	8.64	7.71	0.46	0.21
P4	L	33	2.08	2.88	2.51	0.21	0.04
P4	W	31	2.72	3.76	3.27	0.23	0.05
M1	L	32	2.58	3.36	3.02	0.19	0.03
M1	W	27	2.56	3.44	3.02	0.20	0.04
M2	L	36	3.20	4.16	3.69	0.22	0.05
M2	W	36	3.04	4.08	3.53	0.26	0.07
M3	L	28	3.36	4.64	3.99	0.30	0.09
M3	W	29	3.04	4.16	3.67	0.25	0.06

TABLE 3  
Measurements (in mm) of Lower Teeth of *Tataromys plicidens*

		N	Min	Max	Aver	S	V
p4-m3	L	12	12.80	15.12	13.82	0.72	0.52
m1-3	L	15	10.56	12.80	11.38	0.64	0.41
p4-m2	L	14	8.96	10.40	9.59	0.41	0.17
p4-m1	L	12	5.44	6.08	5.79	0.21	0.04
m1-2	L	21	6.56	8.00	7.18	0.40	0.16
m2-3	L	25	7.52	9.44	8.13	0.44	0.19
p4	L	16	2.40	2.88	2.64	0.16	0.03
p4	W	16	1.92	2.56	2.28	0.20	0.04
m1	L	27	3.04	3.86	3.45	0.19	0.03
m1	W	24	2.08	2.72	2.42	0.17	0.03
m2	L	36	3.52	4.72	4.04	0.23	0.05
m2	W	34	2.56	3.36	3.01	0.17	0.03
m3	L	28	4.00	5.12	4.39	0.29	0.08
m3	W	30	2.80	3.68	3.15	0.20	0.04

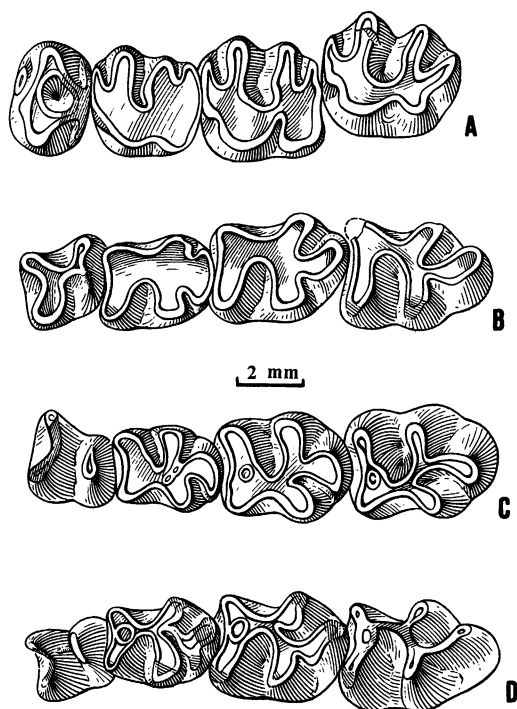


Fig. 10. Occlusal view of cheek teeth of *Tataromys plicidens*. A, B. Upper and lower cheek teeth of same individual (AMNH 21658). C. Right lower cheek teeth (IVPP V 10534.16). D. Left lower cheek teeth (IVPP V 10537.17).

*plicidens*. Clearly they are to be assigned to *Tataromys plicidens*. However, what would the lower cheek teeth look like? Naturally, the lower cheek teeth that match the uppers may be referred to *Tataromys*. However, the lower cheek teeth matching the above-described uppers were referred to *Leptotataromys* by previous authors (Bohlin, 1946; Huang and Wang, 1984; Huang, 1985). A closer comparison of the species of *Tataromys* reveals that the lower cheek teeth formerly referred to *Tataromys* are highly heterogeneous. Some specimens, such as *T. sigmodon* and *T. cf. [T.] grangeri* described by Kowalski (1974), are of *Leptotataromys*-type morphology. Others, such as *T. cf. T. plicidens*, *T. cf. T. sigmodon*, *T. grangeri*, *T. gobiensis*, *T. suni*, *T. bohlini*, and *T. ulantatalensis*, bear quite different morphology. It is critical to reexamine characters of the lower jaw from the point of view of taxonomy. There are three options: (1) The lower cheek teeth belong to *Leptotataromys* and the upper

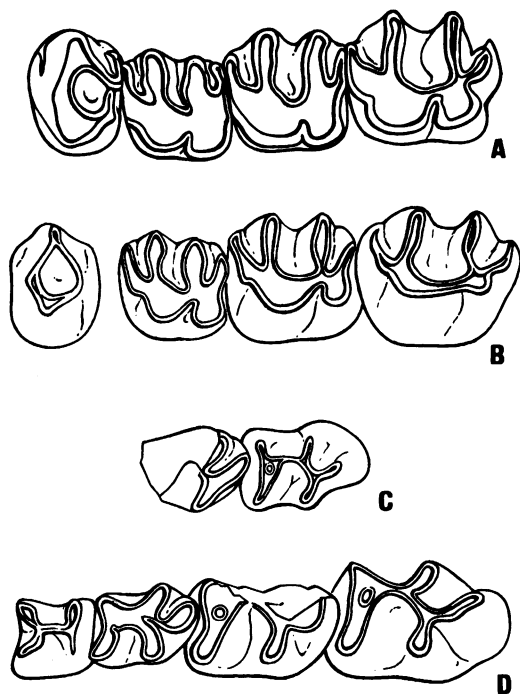


Fig. 11. Comparison of the cheek teeth of *Tataromys* (after Wang, 1994: fig. 3). A. *Tataromys plicidens*, P4-M3 (AMNH 19082, holotype), after Matthew and Granger, 1923, fig. 6, reversed. B. *T. plicidens*, P4-M3 (IVPP 10534.1). C. *T. sigmodon*, m2 and m3 (Sh. 35, holotype of *Leptotataromys gracilidens*), after Bohlin, 1937, fig. 101. D. *T. plicidens*, p4-m3 (the same individual as V 19534.1). All  $\times 6$ .

ones to *Tataromys*. In this case, the upper and lower jaws, despite having compatible features and occluding well, belong to different genera. The lower cheek teeth of *Tataromys* should be different from those of *Leptotataromys* as Bohlin (1946) suggested. (2) *Leptotataromys* is chosen as the name bearer for both the upper and lower cheek teeth, as Huang (1985) did. In doing so, the upper teeth of the same type have to be assigned to two genera. (3) All the upper and lower cheek teeth belong to *Tataromys*. In this case, *Leptotataromys* is a junior synonym of *Tataromys*. With these problems in mind, I carefully studied all specimens from the Hsanda Gol Formation in the AMNH, including the holotype and paratypes and the new material collected recently in China. Fortunately, two specimens of skulls in as-

sociation with lower jaws (IVPP V 19534.1 and AMNH 21658) helped in solving the problem (figs. 10, 11, 40, 41B, C). Their upper teeth are identical with those of *Tataromys*, but the lower ones are typical of *Leptotataromys*. Thus, the upper teeth of *Tataromys* and the lower ones of *Leptotataromys* belong to the same animal. Because *Tataromys* has priority (Matthew and Granger, 1923) over *Leptotataromys* (Bohlin, 1946), the third option is the obvious choice. In other words, *Leptotataromys* is a junior synonym of *Tataromys*.

Teilhard de Chardin (1926) described a right m3 as belonging to *Karakoromys*(?) [sp.] and a left M3 as *Tataromys* cf. [*T.*] *plicidens*. Bohlin (1946) considered Teilhard de Chardin's *Karakoromys*(?) [sp.] to be a large species of *Leptotataromys*. Huang (1985) described *Leptotataromys* cf. [*L.*] *gracilidens* from Ulantatal, Nei Mongol, China, and transferred the specimen referred to *Karakoromys*(?) [sp.] by Teilhard de Chardin (1926) to *L.* cf. [*L.*] *gracilidens*. Judging from the size and morphology, it seems to me that Huang's *Leptotataromys* cf. [*L.*] *gracilidens* and Teilhard de Chardin's *Karakoromys*(?) [sp.], and probably the M3 of *Tataromys* cf. [*T.*] *plicidens* all belong to *Tataromys plicidens*.

Of the material from the Ulantatal area, the specimen (IVPP V 7345.76) described by Huang (1985) as m2 and m3 of *Leptotataromys gracilidens* is a lower jaw with m1 and m2. It is referred to *Tataromys plicidens* here, based on the size and morphology of the teeth.

Shevyreva (1994b) described two new species, *Murat Khanomys kulgayniae* and *Roborovskia collega*, from the lower Oligocene Buran Formation. According to the measurements given by Shevyreva, the size of the two forms are within the range of *Tataromys plicidens*.

*Tataromys sigmodon* Matthew and Granger, 1923

Figures 11C, 12–14, Figure 41A (added in proof); tables 4, 5

*Tataromys sigmodon* Matthew and Granger, 1923: 6. Teilhard de Chardin and Leroy, 1942: 25, 89. Mellett, 1968: 6, 10. K. Kowalski, 1974: 164, pl. 48, fig. 4. Wang et al., 1981: 27, 29–30. Wang, 1994: 37–38, fig. 3C.

*Tataromys* cf. *plicidens* Teilhard de Chardin, 1926: 27–28, fig. 15A; pl. IV, fig. 1. NEW SYNONYMY.

“*Karakoromys*” Bohlin, 1937: 42–43, figs. 101, 102; pl. I, fig. 35.

*Leptotataromys gracilidens* B. Bohlin, 1946: 107–108, pl. II, fig. 30. Wood, 1977: 125, fig. 30.

*Tataromys* (?*Leptotataromys*) cf. *sigmodon* Stehlin and Schaub, 1951: 290–291, fig. 497. NEW SYNONYMY.

*Tataromys* spp. (partim) Huang, 1982: 340–341, 347.

*Leptotataromys gracilidens* (partim): Huang and Wang, 1984: 39–48. Huang, 1985: 32–35, 38, fig. 3; pl. II, figs. 5–9. Russell and Zhai, 1987: 292, 355, 365, 395.

*Leptotataromys* cf. *gracilidens* Qiu and Gu, 1988: 207, 212, pl. II, fig. 7. NEW SYNONYMY.

*Murat Khanomys velivolus* Shevyreva, 1994b: 117, figs. 1m, 2a. NEW SYNONYMY.

*Tataromys boreas* Shevyreva, 1994b: 120, figs. 2i, k. NEW SYNONYMY.

HOLOTYPE: A palate with right and left P4–M3 (AMNH 19079), from the Hsanda Gol Formation of Loh, Mongolia.

REFERRED SPECIMENS: AMNH 19078, 19080, 85750; Sh. 35; Z.Pal. MgM-III/45–46; PIN 2979/1707–1709, spec. no. 2979/1705, IVPP V 7345.1–16, V 7345.20, V 7345.21, V 7345.23–47, V 7345.49–75, V 7345.77–105, V 10540.1–7, V 10541.1–11, V 10542.1–4, V 10543.1–9, V 12042, V 12043.1–25, V 12045.1–8, and V 12046; and LDV 860910.

GEOLOGICAL RANGE: Late early Oligocene: upper member of the Wulanbulage Formation, upper part of the Ulantatal Formation, the Hsanda Gol Formation, the Buran Formation. Late Oligocene: the Shargaltein beds of the Baiyanghe Formation and the lower part(?) of the Xianshuihe Formation.

GEOGRAPHIC DISTRIBUTION: Saint Jacques [IVPP locs. 77046.1 (V 10541), 77046(4) (V 10542), 77046.5 (V 12042) and other localities (V 10540)], Ulantatal (V 7345, V 12043, V 12045, V 12046) and Qianlishan District [IVPP loc. 78018 (V 10543)] of Nei Mongol, Shargaltein Gol, and Lanzhou of Gansu (LDV 860910), China; Loh, Tatal Gol, and Nareen Bulak, Mongolia; Zaysan Depression, Kazakhstan.

EMENDED DIAGNOSIS: Smaller than *Tataromys plicidens* in size; sphenopalatine foramen located above M1; P4 metaloph ex-

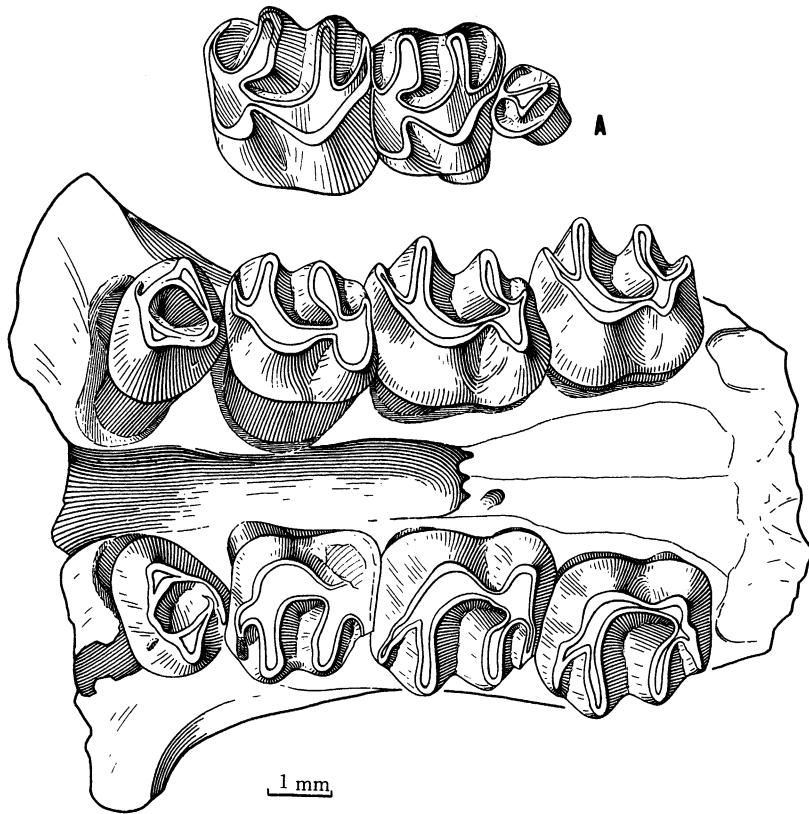


Fig. 12. Occlusal view of upper cheek teeth of *Tataromys sigmodon*. A. DP3, dP4 and M1 (V 12043.1). B. Upper cheek teeth (AMNH 19079, holotype).

tending more posteriorly, complete or incomplete, anterior cingulum usually joining protoloph, lingual part of posterior cingulum weak or lacking; on upper molar mesosinus L-shaped and posterosinus short, metaloph strongly curved, meeting posteroloph on M1 and M2, posteriorly oblique and joining posteroloph on M3; on lower molars trigonid relatively longer, usually with slightly larger closed basin, hypoconulid usually joining arm of hypoconid.

**DESCRIPTION:** Size is smaller, about 70% of that of *Tataromys plicidens*. As in *T. plicidens*, the two tooth rows are parallel or converge forward slightly. The width of the palate between the tooth rows is nearly equal to that of the tooth row. The posterior palatine foramina are medial to M2, with grooves extending forward. Two pairs of small foramina are usually present, one opposite to M3 and the other anterior to the choana. The ventral ramus of the zygomatic process of the

maxilla extends laterally and slightly posteriorly. On its ventral surface a distinct crest, originating from a tubercle at the medial end, runs laterally along the anterior margin. It provides the attachment for the superficial and lateral branches of the masseter muscle. The sphenopalatine foramen is above M1. The roots of the upper incisors reach to above P4 and M1. On the lower jaw the lower masseteric crest reaches to below the posterior part of m1. The upper crest is absent. The mental foramen is under the anterior of m1 or the posterior of p4.

The cheek teeth increase in size from P4 (p4) to M3 (m3). They resemble those of *T. plicidens* in basic morphology, but are smaller and have better developed but slender lophs.

On P4 the protoloph usually joins the paracone (15/20) or reaches its anterior slope (5/20), unlike in *T. plicidens*. The posterior arm of the paracone is straighter, extends rel-

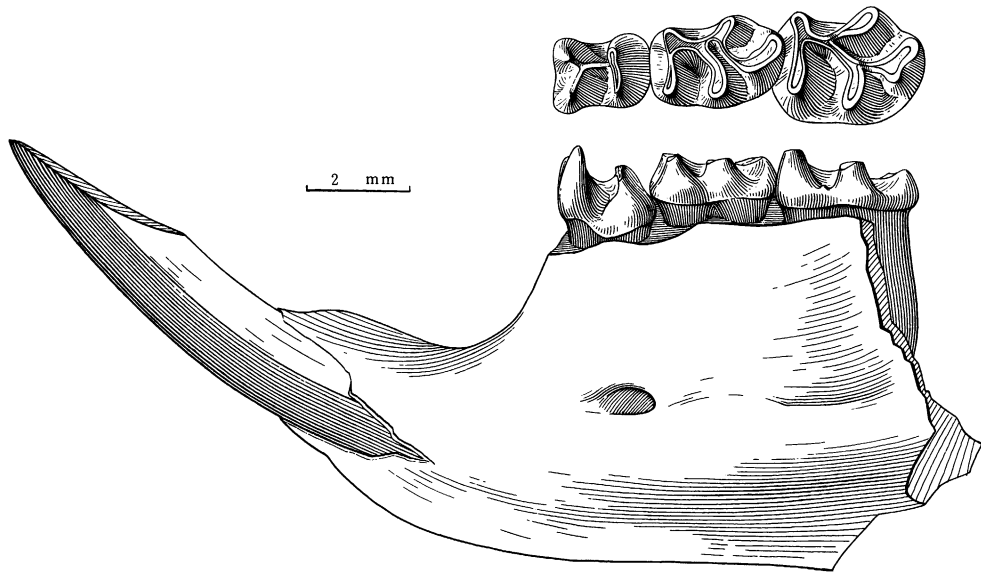


Fig. 13. Left lower jaw with i2 and p4-m2 (IVPP V 10541.1) of *Tataromys sigmodon*. Top: Occlusal view of p4-m2. Bottom: Buccal view of lower jaw.

actively posteriorly, and meets (12/20) or does not meet (8/20) the posterior arm of the protocone or posteroloph. The anterior cingulum usually connects with the protoloph (16/20) and has no lingual part. The lingual part of the posterior cingulum is very weak (5/20) or absent (15/20).

The upper molars have slender lophs and transverse protoloph. As in *T. plicidens*, the anterior cingulum joins the protoloph and has a distinct anterocone. However, the metaloph is more strongly curved than in *T. plicidens* and meets the posteroloph. The posterior arm of the protocone is longitudinal. The mesosinus is L-shaped and the posterosinus is short. The sinus is deep, oblique, and opposite to the posterosinus. On M3 the sinus is shallow and less oblique than other molars.

p4 is also similar to that in *T. plicidens*. The trigonid and talonid are about equal in width. The anterosinusid is a wide V-shape. A distinct accessory cusp may occur within it (IVPP V 7345.36, 39). The ectolophid is long, high, and lingually located. The hypoconid forms a continuous transverse ridge with the entoconid.

**Lower molars:** As in *T. plicidens*, the metalophid I is complete, high, and concave anteriorly. Metalophid II shifts anteriorly and joins the metaconid. The trigonid is slightly

longer than in *T. plicidens*. The closed trigonid basin is usually slightly larger than in *T. plicidens*, but shallow, and decreases in size from m1 to m3. It may be divided into two very small basins or even be absent (2/42 of m1). The hypoconulid always connects with the arm of the hypoconid on m2 and m3. On m1 (differing from *T. plicidens*) in most specimens (38/42) the hypoconulid joins the arm of the hypoconid as in m2 and m3. In only four specimens (IVPP V 7345.54, V 7345.73, V 10541.1, V 10541.9) is it different—it may join the arm of the entoconid, forming a long hyposinusid and a shallow posterosinusid (2/42), or it may meet both hypoconid and entoconid, enclosing a small, central basin at the lingual end of the hyposinusid (2/42) as in *T. plicidens*. Two m1s, in which the hypoconulid connects the entoconid, lack a trigonid basin (IVPP V 10541.1 and V 10541.9). Although the four m1s are similar to those of *T. plicidens* in morphology, they are too small to be referred to the latter in size. I tentatively consider them to illustrate intraspecific variation in *T. sigmodon*.

**DIMENSIONS:** Tables 4 and 5.

**DISCUSSION:** *Leptotataromys gracilidens* was the type species of *Leptotataromys*, described by Bohlin (1946) on the basis of a



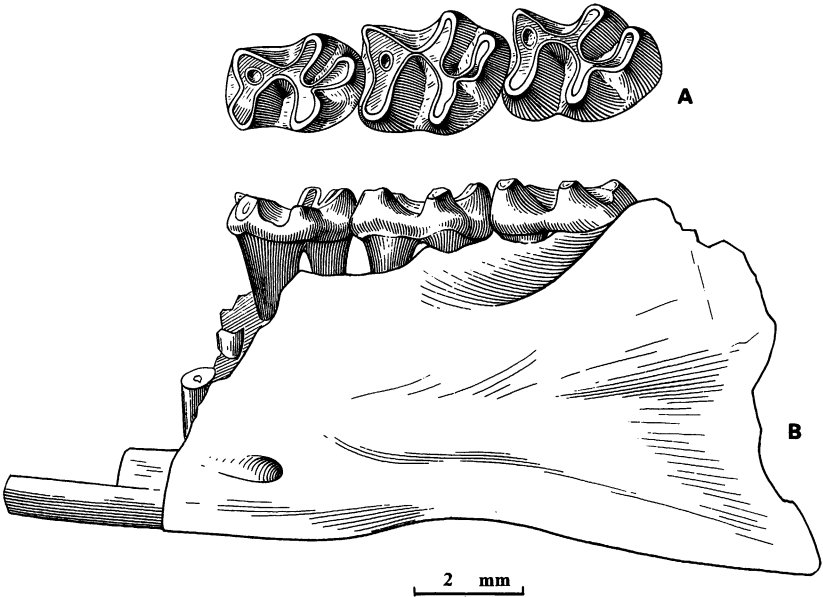


Fig. 14. Left lower jaw with i2 and m1–m3 (AMNH 85750) of *Tataromys sigmodon*. A. Occlusal view of m1–m3. B. Buccal view of lower jaw.

lower jaw fragment with m2 and broken m3 (Sh. 35) from Shargaltein Gol. Huang (1985) referred most of his specimens from the Ulantatal, Nei Mongol, to *Leptotataromys gracilidens*. As discussed above, because *Leptotataromys* is proved the junior syn-

onym of *Tataromys*, its type species is to be referred to *Tataromys*. At first glance, the type specimen (Sh. 35) of *L. gracilidens* seems larger than the type specimen (AMNH 19079) of *Tataromys sigmodon*. However, the sample described by Huang and Wang (1984) and Huang (1985) from the Ulantatal area shows that the species is variable in size, and both Sh. 35 and AMNH 19079 fall with-

TABLE 4  
Measurements (in mm) of Upper Teeth of *Tataromys sigmodon*

		N	Min	Max	Aver	S	V
P4-M3	L	18	8.69	10.40	9.68	0.46	0.21
M1-3	L	33	6.92	8.64	7.79	0.44	0.20
P4-M2	L	22	6.08	7.36	6.81	0.36	0.13
P4-M1	L	23	3.28	4.80	4.11	0.33	0.11
M1-2	L	37	4.32	5.44	5.02	0.26	0.07
M2-3	L	44	4.72	6.29	5.57	0.39	0.15
P4	L	29	1.44	2.08	1.72	0.17	0.03
P4	W	28	1.84	2.56	2.24	0.20	0.04
M1	L	41	1.84	2.72	2.34	0.17	0.03
M1	W	38	1.93	2.72	2.29	0.16	0.03
M2	L	51	2.27	3.04	2.78	0.19	0.03
M2	W	49	2.13	3.04	2.68	0.16	0.03
M3	L	48	2.32	3.20	2.87	0.24	0.06
M3	W	47	2.24	2.96	2.65	0.16	0.03
dP3	L	1			0.96		
dP3	W	1			1.12		
dP4	L	1			2.13		
dP4	W	1			2.24		

TABLE 5  
Measurements (in mm) of Lower Teeth of *Tataromys sigmodon*

		N	Min	Max	Aver	S	V
p4-m3	L	12	8.80	11.09	10.08	0.61	0.37
m1-3	L	28	7.20	9.28	8.25	0.50	0.25
p4-m2	L	18	6.40	7.81	7.06	0.33	0.11
p4-m1	L	19	4.00	5.92	4.35	0.43	0.19
m1-2	L	47	4.80	6.08	5.43	0.30	0.09
m2-3	L	50	4.96	6.72	5.97	0.40	0.16
p4	L	29	1.44	2.27	1.87	0.17	0.03
p4	W	29	1.28	1.92	1.57	0.15	0.02
m1	L	51	2.40	3.04	2.65	0.15	0.02
m1	W	48	1.60	2.13	1.87	0.13	0.02
m2	L	76	2.56	3.36	3.05	0.18	0.03
m2	W	73	1.92	2.56	2.32	0.15	0.02
m3	L	64	2.56	3.68	3.16	0.26	0.07
m3	W	62	1.76	2.62	2.27	0.16	0.03

in the range of size variation of *L. gracilidens* from Ulantatal. In addition, *L. gracilidens* of Bohlin (1946) and Huang (1985) and *T. sigmodon* of Matthew and Granger (1923) and Kowalski (1974) are much the same in their tooth structure. Thus, *L. gracilidens*, based on its holotype, is a junior synonym of *Tataromys sigmodon*.

Shevyreva's (1994b) *Muratkhanomys velivolus* and *Tataromys boreas* are identical with *Tataromys sigmodon* in size and tooth morphology, especially in having a curved metaloph on M2. The two species are most likely junior synonyms of this species.

*Tataromys minor* (Huang, 1985)

Figures 15A, B, 16A, 17; tables 6, 7

?*Leptotataromys* Mellett, 1968: 6. NEW SYNONYMY.

*Karakoromys* (?= *Leptotataromys*) cf. *Karakoromys* sp. Mellett, 1968: 10. NEW SYNONYMY. *Tataromys* cf. *grangeri*: Kowalski, 1974: 165, pl. 48, fig. 5. NEW SYNONYMY.

*Karakoromys decessus* (partim): Kowalski, 1974: 166–167, pl. XLIX, figs. 1, 2, 6, 8. NEW SYNONYMY.

*Tataromys grangeri* (partim): Huang, 1982: 340–341, 347. NEW SYNONYMY.

*Tataromys* spp. (partim) Huang, 1982: 340–341, 347. NEW SYNONYMY.

*Tataromys bohlini* (partim) Huang, 1985: 29–31. NEW SYNONYMY.

*Leptotataromys minor* Huang, 1985: 36, 38, fig. 4. Russell and Zhai, 1987: 292, 355. NEW SYNONYMY.

*Leptotataromys*? sp. Russell and Zhai, 1987: 306, 355. NEW SYNONYMY.

**HOLOTYPE:** A fragment of right ramus with m1 (IVPP V 7347), from the upper part of the Ulantatal Formation in the Ulantatal area, Alxa Zuoqi, Nei Mongol, China, and figured by Huang (1985: fig. 4).

**REFERRED SPECIMENS:** AMNH 19075, 22076–22078, 84208; Z.Pal. MgM-III/47/1, MgM-III/48, MgM-III/49/1–2, MgM-III/51/10; IVPP V 7350.3, V 10544, V 10545, V 10546.1–45, V 10547.1, V 10547.2, V 10548.1–V 10548.56, V 10549.1–V 10549.3, V 10550.1–V 10550.5, V 10551.1–4, V 10552, V 12047.1–5, V 12048.1, V 12048.2, and V 12052.

**GEOLOGICAL RANGE:** Late early Oligocene; upper member of the Wulanbulage Forma-

tion, upper part of the Ulantatal Formation, and the Hsanda Gol Formation.

**GEOGRAPHIC DISTRIBUTION:** Ulantatal area (V 7347, V 7350.3, V 12047, V 12048), Saint Jaques [IVPP locs. 77046 (V 10545), 77046(1) (V 10546), 77046(4) (V 10547), 77049.2 (V 10548), 78020 (V 10549)] and Qianlishan District [IVPP loc. 78018 (V 10550; upper level, V 10551; top level, V 10552)], Nei Mongol, China, and Tatal Gol, Boongeen Gol, Khatan Khayrkhan, Mongolia.

**EMENDED DIAGNOSIS:** Small and primitive *Tataromys*; sphenopalatine foramen located above M1; lower jaw slender; cheek teeth brachydont, with distinct main cusps and low, narrow lophs; anterior cingulum usually absent on P4, usually isolated and with prominent anterocone on upper molar; on P4 posterior arm of paracone usually free and extends relatively posteriorly; on M1 and M2 mesosinus widely V-shaped, metaloph very low, thinning lingually and directed to posterior arm of protocone, protocone acute V-shape, sinus deep, oblique posterobuccally and often connected with posterosinus; on M3 metaloph free or bending posteriorly to join with posteroloph or hypocone, posterocone and posterior groove prominent; on lower molars arm of entoconid low, slender, oblique, and arm of hypoconulid low.

**DESCRIPTION:** The alveolar process of the maxilla is low and the zygomatic process arises from the anterior margin of P4. The sphenopalatine foramen is located above the anterior part of M1.

The lower jaw is slender, but otherwise similar to that in other species of *Tataromys*.

The cheek teeth are brachydont, slender, with distinct and slightly compressed main cusps and slender, low lophs, and increase in size posteriorly.

**P4:** The posterior arm of the paracone usually extends posterolingually and is free (6/9). In a few cases it joins the posterior arm of the protocone (1/9) or posterior cingulum to form a complete metaloph (2/9). The distinct protocone usually has a posterior arm extending to the posterior cingulum (6/9). The protoloph is complete but low. The anterior cingulum is usually absent. The posterior cingulum is low, without a lingual part. Two P4s (V 10546.1 and V 10548.35) have

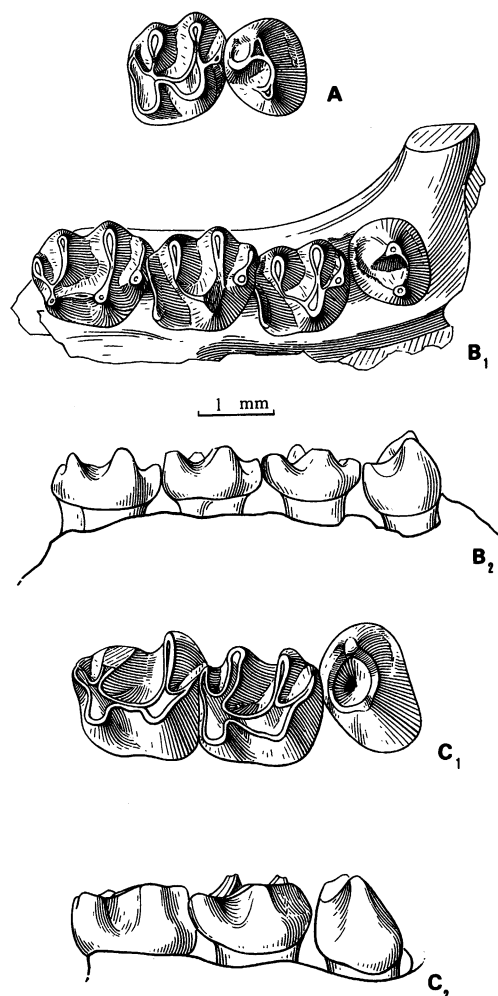


Fig. 15. *Tataromys minor* and *T. parvus*, new species. A, B. *Tataromys minor*. A. Occlusal view of right P4-M1 (V. 10545). B. Right maxillary with P4-M3 (AMNH 22077). B<sub>1</sub>. Occlusal view. B<sub>2</sub>. Lingual view. C. *T. parvus*, P4-M2 (Sh. 38, holotype). C<sub>1</sub>. Occlusal view. C<sub>2</sub>. Lingual view.

a distinct cusp on the posteroloph, which may represent a hypocone.

On M1 and M2 the paracone and metacone are distinct and extend transversely. The protoloph is well developed. The acute V-shaped protocone has a narrow posterior arm extending posterobuccally to meet the metaloph (36/48), or even the posteroloph (12/48). Unlike other species of *Tataromys*, in *T. minor* the low metaloph thins lingually and extends to join, or almost to join, the posterior arm of the protocone, forming an

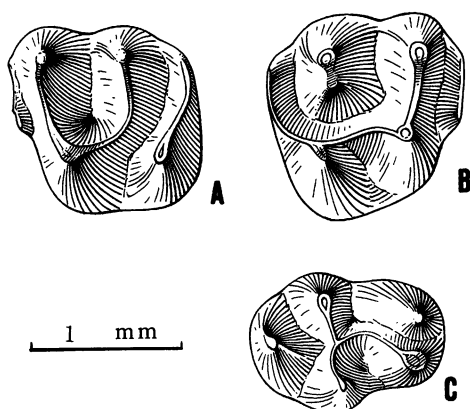


Fig. 16. Occlusal view of deciduous teeth (dP4 and dp4) of *Tataromys minor* and *Karakoromys decessus*. A. *Tataromys minor*: left dP4 (IVPP V 10548.2). B, C. *Karakoromys decessus*. B. Right dP4 (IVPP V 10576.19). C. Right dp4 (IVPP 10576.137).

oblique anterolingually directed loph (39/45). The mesosinus is usually a transversely V-shape. The smaller hypocone often protrudes more lingually than the protocone. The straight posteroloph occasionally has a distinct cusp at the middle (12/46), which can be called posterocone. The entoloph is absent. The deep V-shaped sinus runs obliquely posterobuccally to be opposite to, or unite with, the posterosinus to form a wide valley. Contrary to the condition in the other species of *Tataromys*, on most M1 and M2 (42/44) of *T. minor* the anterior cingulum is isolated and does not join the protoloph until it is heavily worn. A prominent anterocone is present.

Differing from M1 and M2, M3 has an entoloph. The metaloph usually bends posteriorly to link with the hypocone (5/17), or even with the posteroloph behind the hypocone (9/17). On three M3s (V 10548.31, V 10548.33 and V 10546.23) it is free. The mesosinus is roughly U-shaped. The posteroloph is shorter than on M1 and M2. Sometimes there is a distinct posterocone at the buccal end (25/63) and a deep posterior groove between the hypocone and posterocone. The wide, shallow sinus is usually symmetrical, separated from the posterosinus.

dP4 (fig. 16A), represented by five specimens, is molariform and nearly trapezoidal

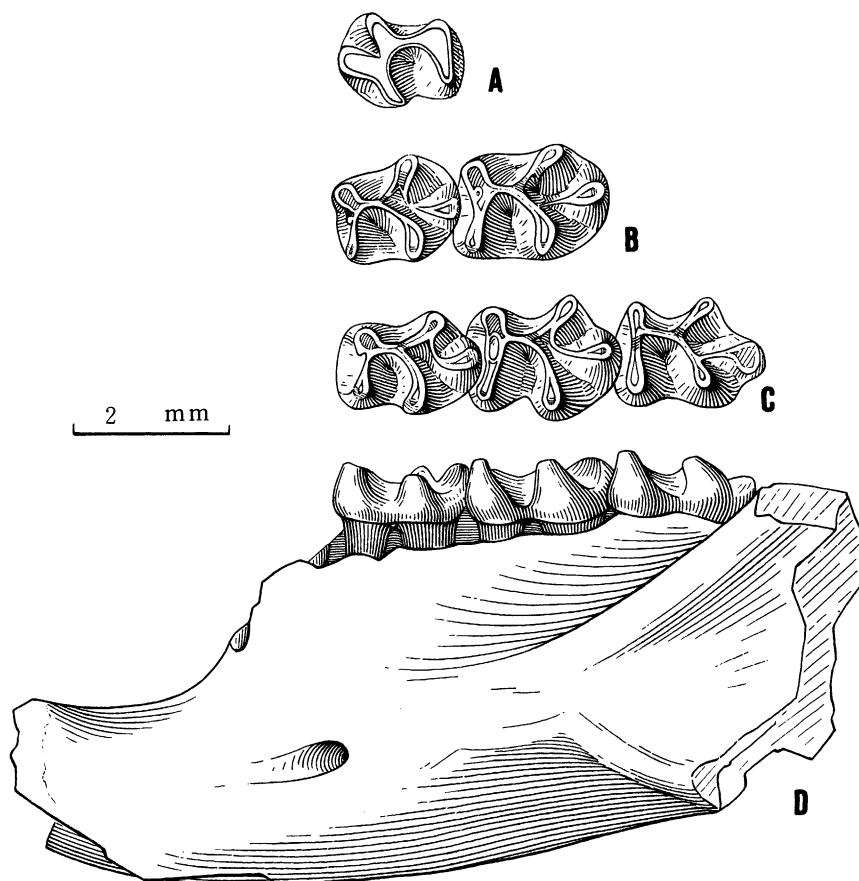


Fig. 17. *Tataromys minor*. A. Occlusal view of right m1 (V 7347, holotype), after Huang (1985, fig. 4). B. Occlusal view of m1-m2 (AMNH no. 19075). C, D. Left lower jaw with i2 and m1-m3 (AMNH 84208). C. Occlusal view of m1-m3. D. Buccal view of lower jaw.

in occlusal view. The distinct paracone and metacone are equal to each other in size. The proto-loph and metaloph are low and narrow, but complete and converge to the protocone. As in M1 and M2, the V-shaped protocone has a well-developed oblique posterior arm, and the entoloph is absent. The hypocone is slightly smaller than the protocone and is linked with the long posteroloph. The sinus and posterosinus are connected to form a wide valley separating the posteroloph from the metaloph. On only one specimen (IVPP V 10548.4) is there a very weak short ridge connecting the metaloph with the posteroloph. The anterior cingulum is distinct but very low. All dP4s have an anterior wear facet, showing that dP3 was present during their lifetime.

i2 is narrow, roughly triangular in cross

section, and extends to below m3. Enamel covers about one-third of both the lateral and the medial sides, with wrinkles on the surface.

The anterior part of p4 is similar to that in *T. plicidens* and *T. sigmodon*, but the talonid is less well developed, much narrower than the trigonid. The entoconid is lower than the metaconid. The hypoconid is absent to weakly developed as a low transverse crest. No vestige of hypoconulid has been seen.

As in the other species of *Tataromys*, the trigonid of the lower molars is short, with the protoconid and metaconid compressed anteroposteriorly, and has a very small, closed trigonid basin. The straight, narrow metalophid II shifts anteriorly to fuse, more or less, with metalophid I buccally, forming an acute angle between them. The straight ectolophid

TABLE 6  
Measurements (in mm) of Upper Teeth of  
*Tataromys minor*

		N	Min	Max	Aver	S	V
P4-M3	L	2	4.76	5.04	4.90	0.20	0.04
M1-3	L	3	3.94	5.08	4.35	0.64	0.40
P4-M2	L	2	3.36	3.61	3.49	0.18	0.03
P4-M1	L	3	1.97	2.50	2.23	0.27	0.07
M1-2	L	3	2.54	3.53	2.89	0.56	0.31
M2-3	L	3	2.79	3.61	3.09	0.45	0.20
P4	L	9	0.82	1.17	1.02	0.11	0.01
P4	W	9	1.11	1.56	1.38	0.15	0.02
M1	L	21	1.15	1.72	1.38	0.15	0.02
M1	W	21	1.12	1.80	1.38	0.17	0.03
M2	L	27	1.39	2.05	1.66	0.20	0.04
M2	W	27	1.27	2.05	1.56	0.21	0.04
M3	L	16	1.34	2.01	1.58	0.17	0.03
M3	W	16	1.07	1.85	1.43	0.19	0.04
dP4	L	5	1.05	1.23	1.15	0.08	0.007
dP4	W	5	1.09	1.23	1.15	0.07	0.004

is lingually situated. The arm of the entoconid extends obliquely anteriorly. The entoconid, hypoconid, and hypoconulid are high, oblate, and about equal to each other in size.

The m1 has a narrower trigonid than the talonid. The weakly developed metalophid I is usually complete but low medially (13/14) and occasionally incomplete (AMNH 84208). Metalophid II is complete (13/14). The closed trigonid basin may be very small (11/14) or absent (2/14). The low entoconid arm runs obliquely anterobuccally. The hypoconulid extends longitudinally, with a low arm. Its connection with other elements is also variable: it may join the arm of the hypoconid (7/15), the arm of the entoconid (3/15), both the hypoconid and entoconid (1/15), or may be entirely free (3/15). Correspondingly, the posterosinusid and the hyposinusid are also variable. The former may be deeper or shallower than the latter; they may connect with each other or be separated by a closed basin.

On m2, unlike m2 of other species of *Tataromys* but like m1 of *T. minor*, the connection of the arm of the hypoconulid with other elements is also variable: on most m2 (8/11) it joins the hypoconid, but on AMNH 84208 it joins the entoconid, whereas in the rest (2/11) the hypoconulid is isolated and has a free anterior arm.

TABLE 7  
Measurements (in mm) of Lower Teeth of  
*Tataromys minor*

		N	Min	Max	Aver	S	V
m1-3	L	3	4.60	6.07	5.35	0.74	0.54
p4-m1	L	1			3.12		
m1-2	L	5	3.20	3.89	3.61	0.29	0.08
m2-3	L	5	3.12	4.40	3.81	0.56	0.31
p4	L	10	1.03	1.31	1.14	0.09	0.008
p4	W	10	0.90	1.23	0.99	0.10	0.009
m1	L	20	1.41	2.01	1.74	0.17	0.03
m1	W	20	1.00	1.48	1.29	0.12	0.02
m2	L	19	1.56	2.46	1.90	0.24	0.06
m2	W	19	1.23	1.72	1.48	0.14	0.02
m3	L	13	1.49	2.30	1.94	0.29	0.09
m3	W	13	1.07	1.72	1.39	0.23	0.05
dp4	L	1			1.71		
dp4	W	1			1.03		

m3 has a narrower talonid than the trigonid. The trigonid basin is small or absent. The hypoconulid usually unites with the hypoconid (7/10), occasionally with the hypoconid and entoconid, or may be free, but never joins only the entoconid.

Size of the cheek teeth and the direction of the metaloph in upper molars differ slightly between the specimens from IVPP locs. 77046.1 and 77049.2. The cheek teeth from the former are generally smaller than those from the latter and the metaloph of the upper molars is usually more transverse than in the latter. Because they overlap in size and show transitional characters, intraspecific variation probably accounts for the differences.

DIMENSIONS: Tables 6 and 7.

DISCUSSION: Mellett (1968) suggested that some of the small specimens from the Hsanda Gol Formation might belong to *?Leptotataromys*, *Karakoromys* (*?= Leptotataromys*), or to cf. *Karakoromys* sp. Kowalski (1974) disagreed, but assigned some specimens (Z.Pal. MgM-III/47/1-5) collected from Khatan Khayrkhan, Mongolia, to *Tataromys* cf. [*T.*] *grangeri*. More recently, Huang (1985: 36, 38) described a new species of *Leptotataromys*, *L. minor*, on the basis of a right lower jaw fragment with m1 (IVPP V 7347), diagnosing it as "Lower molars identical to those of *L. gracilidens* morphologically, but smaller, m1 being 1.7 mm in length and 1.1 mm in width." He pointed

out that it was not impossible that all the specimens of both Kowalski's *Tataromys* cf. [T.] *grangeri* and Mellett's *Leptotataromys* belong to his *Leptotataromys minor* (Huang, 1985: 36).

Because *Leptotataromys minor* is identical with *Tataromys* in basic tooth morphology, it is here considered a species of *Tataromys*, *T. minor*. So far no upper jaw of this species has ever been found in association with its lowers. At loc. 77046.1 of Saint Jacques, Nei Mongol, where the overwhelming majority of the lower cheek teeth are referable to *T. minor*, many upper cheek teeth have also been found. They are similar to those of typical *Tataromys* in morphology and match the lower ones of *T. minor* in size and morphology. They are here considered to represent the upper dentition of *T. minor*.

In addition to the small size, *Tataromys minor* differs from the other two species of *Tataromys* in having brachydont teeth, with distinct cusps, but lower and weaker lophs, isolated anterior cingulum on upper molars, M1 and M2 usually having an acute V-shaped protocone, a weak, anterolingually oblique metaloph, a transverse V-shaped mesosinus, and a wide valley composed of posterosinus and sinus. All these characters are primitive in the Tataromyinae. *Tataromys minor* seems to represent a small and primitive species of *Tataromys*.

Kowalski (1974) referred some specimens collected by the Polish-Mongolian Paleontological Expedition from the Hsanda Gol Formation to *Karakoromys decessus*. Judging from the figures given by Kowalski (1974: pl. XLIX), some of the upper teeth (Z.Pal. MgM-III/49/1-2, pl. XLIX, figs. 1, 2) look more like those of *Tataromys minor* rather than *Karakoromys decessus*. The features that *Tataromys minor* and the specimens of Kowalski commonly shared are the following: the cheek teeth having V-shaped protocone, complete metaloph joining with protocone, and deep, posterobuccally oblique sinus. Some of the lower cheek teeth of his *Karakoromys decessus* (for example, Z.Pal. MgM-III/48 and Z.Pal. MgM-III/51/10, Pl. XLIX, figs. 6, 8) are also similar to those of *Tataromys* rather than to *Karakoromys decessus*, especially in short trigonid, small and closed trigonid basins, and lingually situated

ectolophids. It seems advisable to transfer them into *Tataromys minor*.

Of the specimens described by Huang as *Tataromys bohlini*, IVPP V 7350.3 is also identical with *Tataromys minor* in basic morphology.

### *Tataromys parvus*, new species

Figures 15C, 18; table 8

*Karakoromys* cf. *decessus* B. Bohlin, 1937: 41-42, fig. 100; taf. 1, fig. 34. Teilhard de Chardin and Leroy, 1942: 89. Bohlin, 1946: 244, figs. 21a, 22. Lavocat, 1961: 53, fig. 9. C. Russell and Zhai, 1987: 365, 395. NEW SYNONYMY. ?*Karakoromys decessus* (partim); Teilhard de Chardin and Leroy, 1942: 25. NEW SYNONYMY.

HOLOTYPE: A fragment of maxilla with right P4-M2 and left P4-M1 (Sh. 38), from the Shargaltein beds of the Baiyanghe Formation of Shargaltein Valley, the south end of the Danghe (= Tang-ho), Gansu, China, and figured by Bohlin (1937: fig. 100).

REFERRED SPECIMENS: Two P4s (IVPP V 10553.1, V 10553.2), five M1/2s (V 10553.3, V 10553.4, V 10554.1, V 10554.2, and V 10556), one M3 (V 10553.5), two p4s (V 10553.6, V 10553.7), one m1 (V 10553.8), and two m1/2s (V 10555.1 and V 10555.2).

GEOLOGICAL RANGE: Late early Oligocene: upper member of the Wulanbulage Formation. Late Oligocene: Shargaltein Beds of the Baiyanghe Formation and the Yikebulage Formation.

GEOGRAPHIC DISTRIBUTION: Shargaltein Valley, Danghe, Gansu, and Qianlishan District [IVPP locs. 78018 (V 10553; upper level, V 10554; top level, V 10555) and 79012 (V 10556)], Nei Mongol, China.

DIAGNOSIS: Close to *Tataromys minor* in size; sphenopalatine foramen located above P4; cheek teeth higher crowned, with compressed, indistinct main cusps, higher and slender lophs, anterior cingulum joining protoloph; P4 with complete protoloph and metaloph; M1-3 having well-developed protoloph, strongly curved metaloph linked to posteroloph, obtuse V-shaped protocone with a rather longitudinal posterior arm, shallow anterosinus and posterosinus, wide L-shaped mesosinus, shallow oblique sinus, and no anterocone.

ETYMOLOGY: *Parvus*, small in Latin.



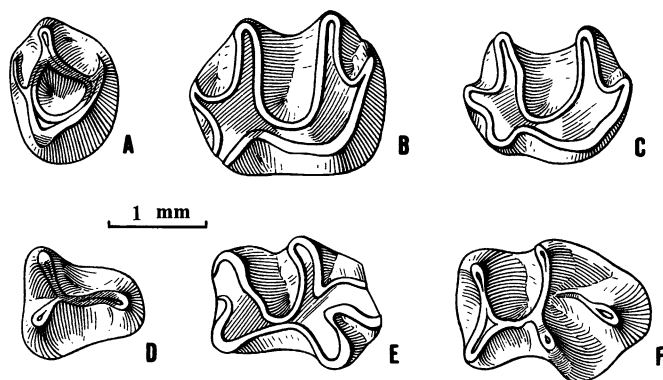


Fig. 18. Occlusal view of cheek teeth of *T. parvus*, new species. A. Left P4 (IVPP V10553.2). B. Right M2 (IVPP V 10556). C. Right M3 (IVPP V 10553.5). D. Right p4 (IVPP V 10553.7). E. Right m1 (IVPP V 10553.8). F. Right m2 (IVPP V 10555.1).

**DESCRIPTION:** The two dental rows are about parallel to each other. The palatine between them is relatively wide. The sphenopalatine foramen is above P4, more anterior than in other species of *Tataromys*. The cheek teeth are small, high-crowned, with slender, anteroposteriorly compressed main cusps, and high, slender lophs.

P4 has complete protoloph and metaloph and a close trigon basin. The anterior and posterior cingula are prominent, join protoloph and metaloph respectively, but have no lingual part.

The paracone and metacone on M1 and M2 are strongly compressed anteroposteriorly. The protoloph is straight and high. As in *T. sigmodon*, the metaloph is high and bends posteriorly to join the posteroloph. The protocone is a wide V-shape. The narrow anterior cingulum, although rather short, links with the protoloph. No anterocone is visible. The anterosinus and posterosinus are shallow. The former is much compressed anteroposteriorly, but the latter is more widely open buccally. The mesosinus is approximately L-shaped and bends posteriorly. The posterior arm of the protocone extends slightly longitudinally, reaching the posteroloph. The sinus extends obliquely to the posterosinus, but it is shallow and never connects with the latter. M3 has an entoloph, a shallow sinus, and a short posteroloph.

p4 is similar to that of other species of *Tataromys*, but the entoconid is variable in direction, either transverse or oblique postero-

lingually. The hypoconid is much reduced. As in other species of *Tataromys*, in *T. parvus* the trigonid of lower molars is short and the straight, long ectolophid is lingually situated. The hypoconulid joins the arm of the hypoconid.

**DIMENSIONS:** Table 8.

**DISCUSSION:** Sh. 38 was reported by Bohlin (1937: 42) as *Karakoromys* cf. [*K.*] *decessus* and described as "Die Grösse stimmt recht gut mit *Karakoromys decessus* überein, die dem Typusexemplar entsprechende Oberkieferzahnreihe dürfte aber etwas länger als die des Stückes Sh. 38 gewesen sein. Die Zähne sind denen von *Tataromys* sehr ähnlich, sie sind aber, auch wenn man von der geringeren Grösse absieht, zierlicher gebaut als bei *Tataromys* und die Synklinalen der Molaren sind auffallend weit; derselbe Unterschied scheint auch betreffs des Unterkiefergebisses zu bestehen."

Although Sh. 38 is close to *Karakoromys decessus* in size, its cheek teeth, as pointed out by Bohlin, are similar to those of *Tataromys* rather than to those of *Karakoromys decessus* in having compressed main cusps, high and narrow lophs, a V-shaped protocone, etc. In addition, the lower cheek teeth described above, which match the upper cheek teeth in morphology, are also close to *Tataromys*, as can be seen in features such as having a short trigonid basin and straight and lingually situated ectolophid. Therefore, Sh. 38 and the specimens described here

TABLE 8  
Measurements (in mm) of Cheek Teeth of *Tataromys parvus*, new species

		Sh 38 (type)		V	V	V	V	V	V	V	V	V	V
		right	left	10553.1	10553.2	10553.5	10554.1	10554.2	10556	10553.6	10553.7	10553.8	10555.1
P4-M2	L	4.43											
P4-M1	L	2.79	2.79										
M1-2	L	3.28											
P4	L	1.15	1.07	1.07	1.07								
P4	W	1.64	1.64	1.6	1.48								
M1	L	1.56	1.56										
M1	W	1.52	1.48										
M2	L	1.76					1.74	1.64	1.83				
M2	W	1.64					1.48	1.15	1.56				
M3	L					1.64							
M3	W					1.23							
p4	L									1.15	1.23		
p4	W									0.90	1.07		
m1/2	L											1.64	1.89
m1/2	W											1.31	1.34

seem to belong to *Tataromys* rather than to *Karakoromys*.

In *Tataromys*, the species *T. parvus* is easily distinguished from *Tataromys plicidens* and *T. sigmodon* by its much smaller size. It differs from *Tataromys minor*, of the same size, by the cheek teeth being higher crowned and more crested, with compressed main cusps and well-developed lophs; upper cheek teeth with a prominent anterior cingulum joining protoloph; upper molars having a strongly curved metaloph meeting posteroloph, curved L-shaped mesosinus, shallow posterosinus and anterosinus, and no anterocone.

*Yindirtemys* Bohlin, 1946

TYPE SPECIES: *Tataromys grangeri* Bohlin, 1946.

INCLUDED SPECIES: *Yindirtemys deflexus* (Teilhard de Chardin, 1926), *Y. gobiensis* (Kowalski, 1974), *Y. suni* (Li and Qiu, 1980), *Y. birgeri* Bendukidze, 1993, *Y. ambiguus*, new species, *Y. cf. Y. ambiguus*, *Y. xiningensis*, new species, and *Yindirtemys* sp.

GEOLOGICAL RANGE: Late Oligocene to early Miocene.

GEOGRAPHIC DISTRIBUTION: North China, Mongolia, and Kazakhstan.

EMENDED DIAGNOSIS: Small to large-sized ctenodactylid, palate very narrow; cheek

teeth brachydont, uppers having crowns higher lingually than buccally, lowers moderately high; on cheek teeth main cusps swollen and bulbous, lophs swollen; P4 protoloph and metaloph complete, equally developed; upper molars anterocone large, metacone with antecrochet; p4 ectolophid short; lower molars having anterior cingulum, posterior arm of protoconid swollen and crescentic, trigonid basin relatively large, ectolophid situated at the middle, entoconid, hypoconid and hypoconulid crescentic in shape.

DISCUSSION: *Yindirtemys* was first described by Bohlin (1946). He gave the diagnosis as follows: "Small tataromyoid rodents with isolated anteroloph, shallow lingual re-entrant and the two posterior buccal re-entrants divided into an outer portion, open buccally, and an inner portion forming a lake. Roots as in *Tataromys*." The genus had been known to be represented by only one species, *Y. woodi*, based on a single tooth, M3, until 1991, when it was proved that *Y. woodi* was a young synonym of *Yindirtemys grangeri* (original *Tataromys grangeri*; see Wang, 1991, and below). As mentioned above, some species formerly referred to *Tataromys*, such as *Tataromys deflexus*, *T. gobiensis*, *T. suni*, *T. cf. T. plicidens*, *T. cf. T. sigmodon*, and *Tataromys* sp. of Li and Qiu (1980) are morphologically different

from typical *Tataromys*. As mentioned by Wang (1994), the derived characters shared by these taxa are the narrow palate, swollen main cusps and lophs; presence of antecrochet from metacone on upper molars; short and less lingually placed ectolophid, distinct anterior cingulum, large trigonid basin, swollen and crescentic posterior arm of protoconid on lower molars. All of these are also shared by *Yindirtermys grangeri*, but not by *Tataromys*. They were transferred from *Tataromys* to *Yindirtermys* (Wang, 1991, 1994).

In 1993, Bendukidze described two species of *Yindirtermys*, *Y. sajakensis* and *Y. birgeri*, from early Miocene of Kazakhstan. Unfortunately, detailed comparison is impossible because no specimen is available at hand.

*Yindirtermys grangeri* (Bohlin, 1946)

Figure 19

*Tataromys grangeri* Bohlin, 1946: 91–94, figs. 16g–i, k, 19:31, 21b, c, c', 29b; pl. II, figs. 15, 19, 28; pl. III, fig. 3. Qiu and Gu, 1988: 206, 211, pl. II, figs. 8, 9.

*Yindirtermys woodi* Bohlin, 1946: 108–109, fig. 29a, a', a"; pl. II, fig. 16. Wood, 1977: 126, fig. 2p. Bendukidze, 1993: 60–68.

*Tataromys* cf. *grangeri* Wang et al., 1981: 27, 29, 31.

*Yindirtermys grangeri*: Wang, 1991: 296–302, figs. 1, 2. Wang, 1994: 37.

**HOLOTYPE:** A right lower jaw with i2 and p4–m3 (T.b. 586a), from the Baiyanghe Formation of Taban-buluk, Danghe, Gansu, China, and figured by Bohlin (1946: figs. 16g–i, k, 19:31; pl. II, fig. 28; pl. III, fig. 3).

**REFERRED SPECIMENS:** T.b. 207, 561, 569, 576, 577, 580, 588–590, 592, 593a–d; IVPP V 7963–7969; LDV 860908.

**GEOLOGICAL RANGE:** Late Oligocene: the Yikebulage Formation, Baiyanghe Formation, and lower part(?) of the Xianshuihe Formation.

**GEOGRAPHIC DISTRIBUTION:** Taban-buluk and Lanzhou, Gansu, and Qianlishan District [IVPP locs. 78016 (V 7968, V 7969) and 79012 (V 7963–V 7967)], Nei Mongol, China; Kazakhstan.

**EMENDED DIAGNOSIS:** A small-sized *Yindirtermys*; upper molars with well-developed anterocone, paracone, and metacone; M1 and M2 having transverse metaloph joining protocone, transverse mesosinus, weak short

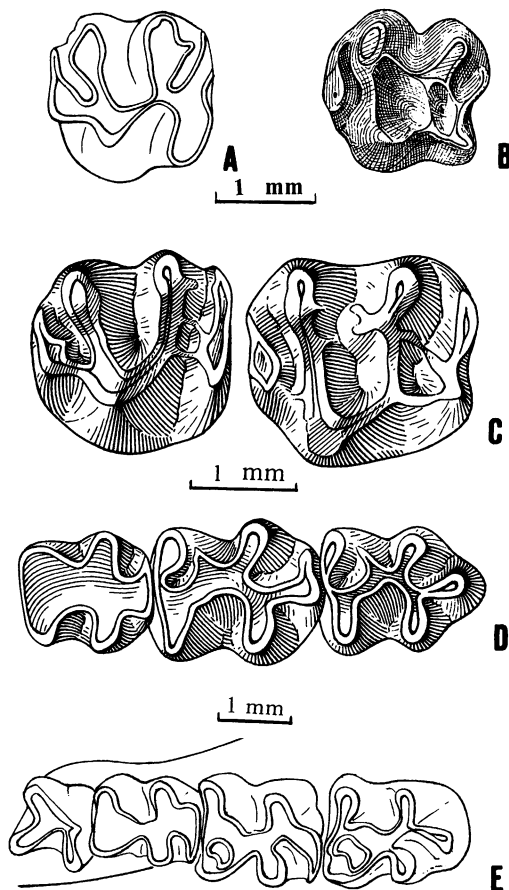


Fig. 19. Occlusal view of cheek teeth of *Yindirtermys grangeri*. A. Left M2 (T.b. 593b), after Bohlin, 1946, fig. 29b. B. Left M3 (T.b. 577, holotype of *Yindirtermys woodi*), after Bohlin, 1946, fig. 29a". C. Left M2–M3 (IVPP V 7963), after Wang, 1991, fig. 1:5. D. Left m1–m3 (IVPP V 7968), after Wang, 1991, fig. 2:1. E. Right p4–m3 (T.b. 586a, holotype of *Tataromys grangeri*), after Bohlin, 1946, fig. 19:31.

ridge connecting posteroloph with metaloph; M3 having isolated anterior cingulum and entoloph, anterolingually extended metacone with an anterior ridge and a posterior ridge reaching posteroloph; lower molars having complete metalophid II, closed trigonid basin, slightly lunar-shaped entoconid, hypoconid, and hypoconulid.

**DISCUSSION:** *Yindirtermys grangeri* was first described by Bohlin (1946) as a species of *Tataromys*, based on all upper cheek teeth, except M3, and lower jaws with complete dentition from the late Oligocene deposits of

Taben-buluk, Gansu. In the same monograph, based on one M3 from the same level of the same locality, Bohlin erected a new genus and species, *Yindirtemys woodi*. Because the two forms could not be directly compared with each other, they were treated separately. Recently, more specimens of *Yindirtemys* were collected from the late Oligocene Yikebulage Formation in Nei Mongol. Among them a left maxillary fragment with M2 and M3 (IVPP V 7963) was found to be similar to *Tataromys grangeri* in the pattern of M2 and also similar to *Yindirtemys woodi* in the structure of M3. The distinctions of *Yindirtemys woodi* from *Tataromys grangeri* used by Bohlin (1946) are, in fact, those between M3 and the anterior molars (M1 and M2) of same species. *Yindirtemys woodi* (Bohlin, 1946: 108–109) was considered a junior synonym of *Tataromys grangeri* (ibid.: 91–94), based on page priority and better material of *Tataromys grangeri*. However, as an added complication, *Tataromys grangeri* differs from typical *Tataromys* in tooth morphology. Particularly, the cusps and lophs are all swollen; upper molars have antecrochet; lower molars have anterior cingulum, swollen posterior arm of the protoconid, large trigonid basin, and medially located ectolophid; M3 is complex. According to the Article 68(e) of the International Code of Zoological Nomenclature (1985), we have to use *Yindirtemys* as a valid genus. Therefore, the species *Tataromys grangeri* (= *Yindirtemys woodi*) is the type species of *Yindirtemys* (Wang, 1991).

Wang (1991) inaccurately reported that *Yindirtemys grangeri* had no anterior cingulum on the lower molars. In fact, the anterior cingulum is present on the lower molars, but variable in size, from weak to distinct.

*Yindirtemys deflexus* (Teilhard de Chardin, 1926)

Figures 20, 21A; tables 9, 10

*Tataromys deflexus* Teilhard de Chardin, 1926: 28, 31, fig. 15B; pl. IV, fig. 3. Teilhard de Chardin and Leroy, 1942: 25, 89. Stehlin and Schaub, 1951: 125, fig. 181. Mellett, 1968: 6, 10. Kowalski, 1974: 160–161, pl. XLVII, fig. 1. Wang et al., 1981: 29.

*Tataromys* sp. Stehlin and Schaub, 1951: 289, fig.

496. Schaub, 1958: 781, fig. 211. NEW SYNONYMY.

*Yindirtemys sajakensis* Bendukidze, 1993: 60–63, pl. 20, figs. 2–7; pl. 21, fig. 1. NEW SYNONYMY.

*Yindirtemys deflexus*: Wang, 1994: 37, figs. 2a–b.

**HOLOTYPE:** A fragment of maxilla with right M2 and M3, from Saint Jacques, Nei Mongol, China, and figured by Teilhard de Chardin (1926: fig. 15B).

**REFERRED SPECIMENS:** AMNH 21644, 21688, 81328, 85110–85156, 85158–85174; Z.Pal. MgM-III/40; NMB 13; IVPP V 5898–V 5912, V 5914, V 5916, V 5922, V 5923, V 5925–V 5928, V 10557, V 10558, V 10559.1–5, V 10560.1, V 10560.2, V 10561.1–7, V 10562.1–3, V 11278–V 11280.

**GEOLOGICAL RANGE:** Early(?) Oligocene, the Hsanda Gol Formation and late Oligocene, the Yikebulage Formation.

**GEOGRAPHIC DISTRIBUTION:** Saint Jacques [IVPP locs. 77046 (4) (V 10558), 77046.5 (V 10559), 77048 (V 10560), and other localities (V 10557)] and Qianlishan District [IVPP locs. 78016 (V 5898–V 5912, V 5914, V 5916, V 5922, V 5923, V 5925–V 5928, V 10561) and 79020 (V 10562)], Nei Mongol, China, and Tatal Gol, Tsagan Nor Basin, Mongolia.

**DIAGNOSIS:** “Les dents sont notablement plus grandes que celles de *T. plicidens* (longueur M3–M2 = 10.5 au lieu de 6); mais surtout leur dessin est sensiblement différent. Le paralophe et le métalophe, au lieu d’être transverses, sont fortement infléchis en avant; et le métacône émet un crochet qui, rejoignant un anté-crochet issu du paracône, détermine un (puits) d’émail sur les dents moyennement usées. Le bourrelet cingulaire antérieur est assez fortement développé pour esquisser un troisième lobe sur la muraille interne de la dent” (Teilhard de Chardin, 1926: 28).

**DESCRIPTION:** The upper tooth rows are parallel or slightly convergent anteriorly. Unlike *Tataromys*, the palate between the rows is very narrow, much narrower than the width of the cheek teeth. The posterior palatine foramina are opposite M2 and the choana is far behind M3, as in *Tataromys*. The mental foramen is below p4 and the lower masseteric crest reaches to below m1 and is divided into two parts.

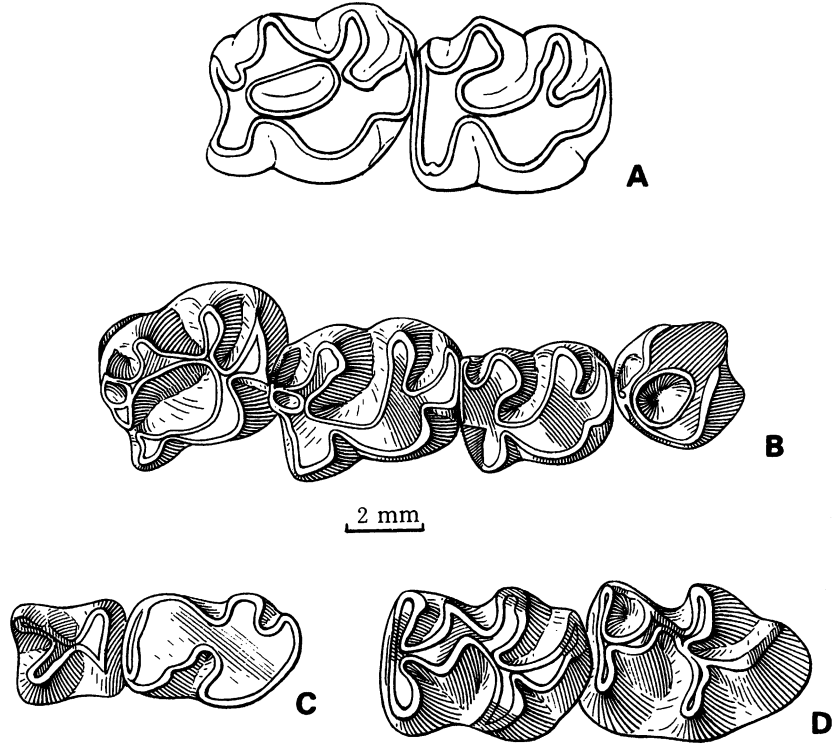


Fig. 20. Occlusal view of cheek teeth of *Yindirtemys deflexus*. A. Right M2-M3, (holotype), after Teilhard de Chardin, 1926, fig. 5B. B. Right P4-M3 (IVPP V 5899). C. Left p4-m1 (AMNH 85154). D. Left m2-m3 (AMNH 85150).

P4 is obliquely implanted in the upper jaw. The paracone is swollen. Protoloph and metaloph are equally developed and curved. The anterior and posterior cingula are connected with the protoloph and metaloph, respective-

ly, and have distinct lingual parts. The antecrochet from the metaloph (usually present) reaches the posteroloph to form a small basin.

The upper molars have swollen paracone

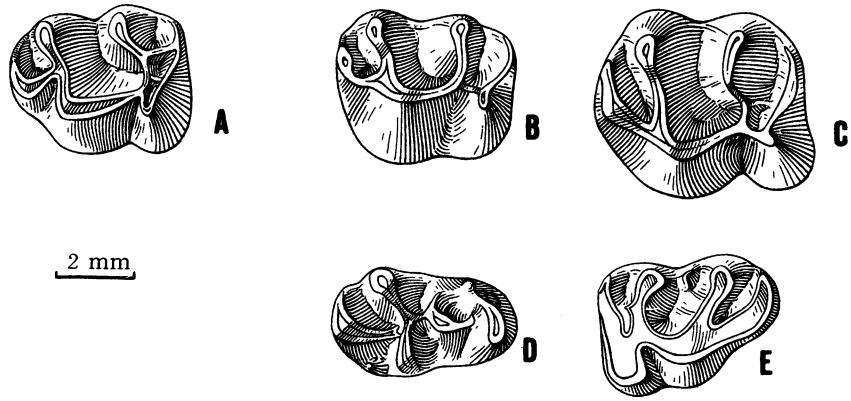


Fig. 21. Occlusal view of deciduous teeth (dP4 and dp4) and upper molars of *Yindirtemys deflexus* and *Y. suni*. A. *Y. deflexus*: left M2 (IVPP V10559.2). B-E. *Y. suni*: B. Left M1 (IVPP V 10564.31). C. Left M3 (IVPP V 5993.28). D. Right dp4 (IVPP V 10564.44). E. Right dP4 (IVPP V 10564.34).

TABLE 9  
Measurements (in mm) of Upper Teeth of  
*Yindirtemys deflexus*

		N	Min	Max	Aver	S	V
P4-M3	L	14	15.80	18.34	16.94	0.87	0.76
M1-3	L	23	12.80	15.14	13.69	0.86	0.47
P4-M2	L	12	11.04	12.75	11.69	0.51	0.26
P4-M1	L	10	6.50	7.50	7.05	0.41	0.16
M1-2	L	28	8.00	9.58	8.71	0.46	0.21
M2-3	L	36	8.30	10.98	9.97	0.59	0.35
P4	L	13	2.70	3.20	2.95	0.17	0.03
P4	W	12	2.20	4.46	3.55	0.51	0.26
M1	L	27	3.38	4.60	3.89	0.30	0.09
M1	W	18	2.90	3.90	3.28	0.28	0.08
M2	L	48	4.20	5.44	4.86	0.31	0.10
M2	W	42	3.60	4.48	4.08	0.23	0.05
M3	L	41	4.20	5.70	5.11	0.38	0.14
M3	W	35	3.80	4.90	4.44	0.27	0.07

and metacone. The protoloph is oblique posterolingually. One of the particular features is that the metaloph bends strongly posteriorly in the middle to form an anteriorly facing curve. The lingual end of the metaloph seems to join the posteroloph, but on less worn specimens it joins the posterior arm of the protocone, forming a continuous and strongly curved loph as in *Tataromys sigmodon* (fig. 21A). It differs from *T. sigmodon*, but resembles *Yindirtemys grangeri* in that there is an antecrochet extending from the metaloph to the posteroloph, thus separating the posterosinus into two parts—a lingual closed basin and a short buccal one, open buccally. The anterior cingulum is well developed and the anterocone is large. There is a distinct anterior groove between the anterocone and protocone. The posterosinus is short. On M1 and M2, the anterosinus and mesosinus are L-shaped, bending posteriorly. The deep sinus is oblique posterobuccally. One of the remarkable features on M3 is that the crochet from metacone is well developed and reaches the antecrochet from the protoloph to enclose an enamel basin in the mesosinus. The antecrochet from the metacone on M3 is usually well developed, reaching the posteroloph (15/19), and occasionally is very weak (2/19) or absent (2/19).

The lower cheek teeth have a very short and medially situated ectolophid.

On p4, the ectolophid varies from high and

TABLE 10  
Measurements (in mm) of Lower Teeth of  
*Yindirtemys deflexus*

		N	Min	Max	Aver	S	V
p4-m3	L	9	17.20	19.94	18.48	0.90	0.81
m1-3	L	16	14.20	17.32	15.29	0.86	0.75
p4-m2	L	11	11.75	12.83	12.42	0.35	0.12
p4-m1	L	11	6.90	7.54	7.15	0.23	0.05
m1-2	L	30	8.32	11.30	9.39	0.62	0.38
m2-3	L	30	10.20	12.80	11.37	0.62	0.39
p4	L	15	2.70	3.34	3.05	0.20	0.04
p4	W	12	2.50	3.08	2.73	0.18	0.03
m1	L	31	3.54	4.76	4.24	0.28	0.08
m1	W	25	2.70	3.50	2.95	0.17	0.03
m2	L	51	4.46	5.96	5.38	0.30	0.09
m2	W	49	3.14	4.12	3.75	0.24	0.06
m3	L	37	5.40	7.26	6.16	0.44	0.19
m3	W	38	3.54	4.38	4.00	0.22	0.05

well developed to absent. The mesosinusid and sinusid are acutely V-shaped. The hypoconid is usually weakly developed. The hypoconulid may be absent (6/10) or present (4/10).

The lower molars have an anterior cingulum and large trigonid. Metaconid and protoconid are swollen. Metalophid I is slightly convex anteriorly. The buccal part of the posterior arm of the protoconid fuses with that of the metalophid I and seems to extend from the middle of the latter. The middle part is swollen and more crescentic. The more oblique lingual part extends anterolingually to the metaconid enclosing a large trigonid basin. The entoconid, hypoconid, and hypoconulid are crescentic. The arm of the entoconid is not so transverse, but bends anteriorly, meeting the ectolophid in front of the hypoconid. The hypoconid (close behind the entoconid) is usually curved and has an oblique arm and a sharp buccal end extending anteriorly over the entoconid. The hypoconulid is always connected with the hypoconid.

DIMENSIONS: Tables 9 and 10.

DISCUSSION: Bendukidze (1993) described a new species, *Y. sajakensis*, from Kazakhstan. Its only distinct feature is that it is smaller in size than *Y. deflexus*. However, *Y. sajakensis* is still within the range of the variation of *Y. deflexus*.

The differences between *Y. deflexus* and



other species of *Yindirtemys* (*Y. grangeri*, *Y. gobiensis*, *Y. suni*, *Y. ambiguus*, *Y. xiningensis*, and *Yindirtemys* sp.) are obvious in the upper tooth morphology. The main features of *Yindirtemys deflexus* are more swollen main cusps and lophs, anteriorly oblique protoloph, more strongly anteriorly curved metaloph on upper molars, and well-developed crochet connecting metaloph with protoloph on M3. In addition, *Y. deflexus* differs from *Y. suni* in having a developed anterior cingulum on P4 and having a developed antecrochet on upper molars. It differs from *Y. grangeri*, *Y. ambiguus*, *Y. xiningensis*, and *Yindirtemys* sp. in being larger. *Y. deflexus* differs from *Y. birgeri* in being larger and having more swollen cusps and more oblique transverse lophs.

However, distinctions of the lower cheek teeth between *Y. deflexus* and other large species of *Yindirtemys* do not seem to be completely clarified. Kowalski (1974: 162) stated that "Distinction of species in the large forms of *Tataromys* (= *Yindirtemys* in this paper) is very difficult," and "the similarity of the structure of teeth of lower jaws does not allow to determine to which one the mandibles belonged." A detailed comparison of these large forms reveals some differences that set *Y. deflexus* apart from *Y. gobiensis* and *Y. suni*. Consistent with the upper teeth, the lower teeth of *Y. deflexus* have more oblique transverse lophs; oblique lingual part of the posterior arm of protoconid; crescentic hypoconid with an oblique arm and a sharp buccal end that extends more anteriorly; a bent arm of the entoconid; and a large, closed trigonid basin. In comparison with other species of *Yindirtemys*, these features seem to be derived, and *Yindirtemys deflexus* thus may represent an advanced species of *Yindirtemys*.

Stehlin and Schaub (1951: 289, fig. 496) and Schaub (1958: 781, fig. 211) referred a left lower jaw with p4-m3 (NMB 13) from the Hsanda Gol to *Tataromys* sp. According to the features—such as large closed trigonid basin; swollen protoconid and metaconid; swollen, crescentic posterior arm of protoconid; developed anterior cingulum; medially situated ectolophid; and sharp, oblique and extending rather anteriorly hypoconid—the lower cheek teeth are quite different from

those of *Tataromys*, but similar to those of *Yindirtemys* and identical with *Y. deflexus* in size. Thus, it likely belongs to *Yindirtemys deflexus*.

*Yindirtemys deflexus* was reported to have been found in the early Oligocene Hsanda Gol Formation and Saint Jacques and the late Oligocene Yikebulage Formation of Nei Mongol (Teilhard de Chardin, 1926; Mellett, 1968; Kowalski, 1974; Wang et al., 1981). However, its early Oligocene occurrence is seriously doubted. First, *Yindirtemys deflexus* seems to be an advanced form. Secondly, the assignment of the deposits yielding *Yindirtemys deflexus* to the early Oligocene is questionable. Mellett (1966, 1968: 9) mentioned that with one exception all the specimens of this species came from the same locality (field number 536) that yielded *Tachyoryctoides*, a locality distinct from (apparently younger than) the locality that yielded the bulk of the Hsanda Gol fauna. Kowalski (1974: 149–150, 160) also pointed out that *Yindirtemys deflexus* and *Tachyoryctoides obrutchewi* were found exclusively in the upper part of the profile at Tatal Gol. Until now, *Tachyoryctoides* has been known to occur only in younger strata: the late Oligocene Baiyanghe Formation of Gansu, the Suosuoquan Formation of Xinjiang, as well as the Yikebulage Formation of Nei Mongol, the early Miocene Xiejia Formation of Qinghai and Urtu Formation of Nei Mongol, and the uppermost Oligocene deposits in Kazakhstan, which are stratigraphically above deposits yielding a fauna equivalent to that of the Hsanda Gol Formation. In China, *Yindirtemys deflexus* is known to occur in two areas: Saint Jacques and the Qianlishan District. It is clear that in the Qianlishan District all specimens of *Yindirtemys deflexus* are known to occur in the late Oligocene Yikebulage Formation only. They have never been found in the early Oligocene Wulanbulage Formation. Saint Jacques is the type locality of *Yindirtemys deflexus*. Unfortunately, its provenance cannot be exact. Some specimens described here as *Yindirtemys deflexus* were also collected from Saint Jacques by the Sino-Soviet Paleontological Expedition (1959) and a field team of IVPP (1977, 1979). Only three localities [IVPP locs. 77046.5, 77046(4), and 77048] are con-

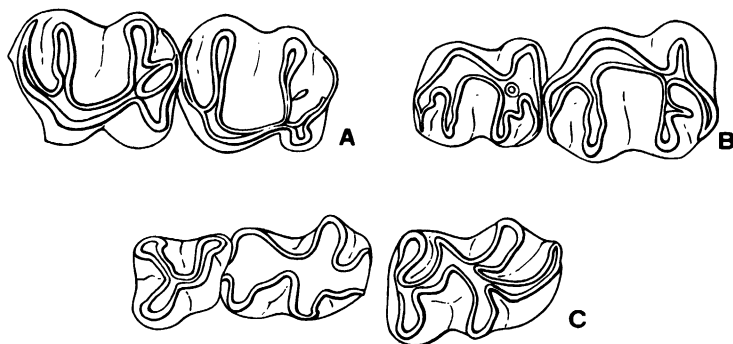


Fig. 22. Occlusal view of cheek teeth of *Yindirtemys gobiensis*. A. Left M2-M3 (Z.Pal. MgM-III/41/1, holotype; L, 8.5 mm), after Kowalski, 1974, p1. XLVII, fig. 2. B. Right M1-M2 (Z.Pal. MgM-III/41/2; L, 7.8 mm), after Kowalski, 1974, p1. XLVII, fig. 3. C. Left p4-m2 (Z.Pal. MgM-III/42/3; L, 10.6 mm), after Kowalski, 1974, p1. XLVIII, fig. 2.

firmed to yield *Yindirtemys deflexus*. However, because the geological structure is complex in this area, their exact horizon in the geological section is uncertain. As far as the fauna is concerned, the other fossils from loc. 77046.5 include *Amphechinus* sp., *Desmatolagus pusillus*, *D. robustus*, *D. gobiensis*, *Sinolagomys kansuensis*, *Ordolagus teilhardi*, *Cricetops dormitor*, *Tsaganomys altaicus*, *Tachyoryctoides* sp., *Yindirtemys ambiguus*, *Tataromys plicidens*, and *T. sigmodon*. This fauna seems mixed in age and requires study, but some forms, such as *Tachyoryctoides* sp. and *Yindirtemys ambiguus*, are known from the late Oligocene, and *Tataromys sigmodon* occurs in the late Oligocene Lanzhou fauna. Loc. 77046(4) is similarly of unclear age. The fauna of loc. 77048 seems younger in age based on *Yindirtemys ambiguus*, *Promeniscomys sinensis*, and *Pseudotheridomys asiaticus*. *Pseudotheridomys* is known in late Oligocene (MP28-MP30) in Europe and late Oligocene to early Miocene (middle Arikareean to early Hemingfordian) in North America. *Meniscomys* (Meniscomyinae) begins in the Arikareean in North America, but *Promeniscomys sinensis* is more primitive than *Meniscomys*. The age of loc. 77048 may be late Oligocene. The evidence consistently shows *Yindirtemys deflexus* to be of late Oligocene age.

*Yindirtemys gobiensis* (Kowalski, 1974)

Figure 22

*Tataromys gobiensis* K. Kowalski, 1974: 162-163, pl. XLVII, figs. 2-5; pl. XLVIII, figs. 1, 2.

*Yindirtemys gobiensis*: Wang, 1994: 37.

**HOLOTYPE:** A skull fragment with left M2, M3, and right M3 (Z.Pal. MgM-III/41/1), from Khatan Khayrkhan, Gobi Desert, Mongolia, and figured by Kowalski (1974: Pl. XLVII, fig. 2).

**REFERRED SPECIMENS:** Z.Pal. MgM-III/41/2-4, MgM-III/42, and MgM-III/43.

**GEOLOGICAL RANGE:** Late(?) Oligocene, upper part(?) of the Hsanda Gol Formation.

**GEOGRAPHIC DISTRIBUTION:** Khatan Khayrkhan and upper part of Boongeen Gol, Khaitch Bulak, Mongolia.

**DIAGNOSIS:** "Large form of the genus *Tataromys* (M2-M3 in the holotype 8.5 mm). The valleys of upper molars transversal. There is no trace of a crest connecting proto- and metaloph and of a formation of fossette in the center of the teeth. The deep postero-external valley in M1-M3 is divided by a longitudinal crest descending from the metacone and isolating its medial part into a fossette. In M1 a small fossette develops from the medial part of the anteroexternal valley" (Kowalski, 1974: 162).

**DISCUSSION:** *Yindirtemys gobiensis* was described by Kowalski (1974) as a species of *Tataromys*, based on several fragments of skull and lower jaws. These upper teeth are, to a certain degree, similar to *Tataromys* (especially *T. plicidens*) in having unswollen cusps and lophs and transverse buccal part of metaloph. One of the distinctive features of these teeth is that they have an antecrochet from the metaloph, which is not present in

*Tataromys* but is known in some *Yindirtemys*. On the other hand, the lower cheek teeth are identical to those of *Yindirtemys*. Because no skull and lower jaw were found in direct association, there are two possibilities: either they belong to the same species or they represent different taxa. If they belong to one species, as Kowalski (1974) thought, and the antecrochet from the metacone is considered as a derived feature in *Yindirtemys*, they are to be referred to *Yindirtemys*. Otherwise, the upper teeth would remain as *Tataromys*, but the lower jaws would be transferred to *Yindirtemys*. Because the similarities between *Tataromys plicidens* and *Yindirtemys gobiensis* are primitive features, I tentatively agree with Kowalski (1974) in putting them together, but assign them to *Yindirtemys*, pending new material.

According to Kowalski's report (1974), *Yindirtemys gobiensis* was collected with *Cyclomylus lohensis* from the upper part of Boongeen Gol. *Cyclomylus lohensis* is known to occur in both the upper and lower parts of Tatal Gol. The fauna from the lower part of Boongreen Gol includes *Anomoemys lohicululus*, *Tsaganomys altaicus*, *Karakoromys decessus*, *Cricetops dormitor*, and *Eucricetodon asiaticus*. Among them, *Anomoemys lohicululus*, *Karakoromys decessus*, *Cricetops dormitor*, and *Eucricetodon asiaticus*, which are known only from the early Oligocene, do not occur in the upper part of Boongreen Gol. Thus, the upper part of Boongreen Gol and *Yindirtemys gobiensis* may be of late Oligocene age.

*Yindirtemys suni* (Li and Qiu, 1980)

Figures 21B–E, 23; tables 11, 12

*Tataromys suni* Li and Qiu, 1980: 205–206, 212, fig. 7; pl. I, fig. 3. Wang et al., 1981: 27, 29, 34. Qiu and Gu, 1988: 204–206, 211, pl. II, figs. 1–4, 10.

*Yindirtemys suni*: Wang, 1994: 37.

**HOLOTYPE:** A right maxilla with P4–M3 (IVPP V 5992), from the Xiejia Formation of Xiejia, Qinghai, and figured by Li and Qiu, 1980: fig. 7; pl. I, fig. 3.

**REFERRED SPECIMENS:** IVPP V 5993.1–47; V 10563.1–3, V 10564.1–15, V 10564.17–46, V 10565.1–16, LDV 860902–860907. AMNH 85175 and 85176.

**GEOLOGICAL RANGE:** Late Oligocene Yikebulage Formation and lower part (?) of Xianshuihe Formation, as well as early Miocene Xiejia Formation.

**GEOGRAPHIC DISTRIBUTION:** Qianlishan District [IVPP locs. 78016 (V 10563), 79012 (V 10564), and 79017 (V 10565)], Nei Mongol; Xiejia (V 5992, V 5993), Qinghai; and Lanzhou (LDV 860902–860907), Gansu, China, and Tsagan Nor Basin of Mongolia.

**EMENDED DIAGNOSIS:** Large species of *Yindirtemys*; upper cheek teeth having swollen cusps; P4 posterior cingulum developed; upper molars with transverse, nearly straight protoloph and metaloph, transverse mesosinus, well-developed anterocone, weakly developed antecrochet from metaloph; p4 hypoconid reduced, but always with a hypoconulid; lower molars with large open trigonid basin, round and obtuse hypoconid, and entoconid with transverse arm.

**DESCRIPTION:** The tooth rows parallel each other. The width of the palate between the rows is narrower than that of the tooth row. The cheek teeth are brachydont, but uppers with crown on lingual side higher than on buccal one and lowers having moderately high crown.

On P4 the protoloph is less curved than the metaloph. The anterior cingulum is usually weak or absent. The posterior cingulum is developed nearly into a crest and connected with the metaloph by one or two short ridges.

On upper molars the paracone, metacone, and transverse lophs are more or less swollen. The protocone is V-shaped. The protoloph and metaloph are transverse and join the protocone. A short ridge connects the metaloph with the posteroloph. The anterior cingulum is short and the anterocone is well developed. The buccal sinuses are transverse. The lingual sinus is deep, oblique posterobuccally, and opposite the posterosinus on M1 and M2. Unlike other species of *Yindirtemys*, the antecrochet from metaloph is weak (7/39) or absent. On M3 the metaloph turns slightly posteriorly to join the hypocone. The sinus is shallower than that in M1 and M2 and slightly oblique posteriorly. The posteroloph is short.

DP4 (figs. 21E, 23B) is similar to the molars, but longer, with a narrower anterior side.

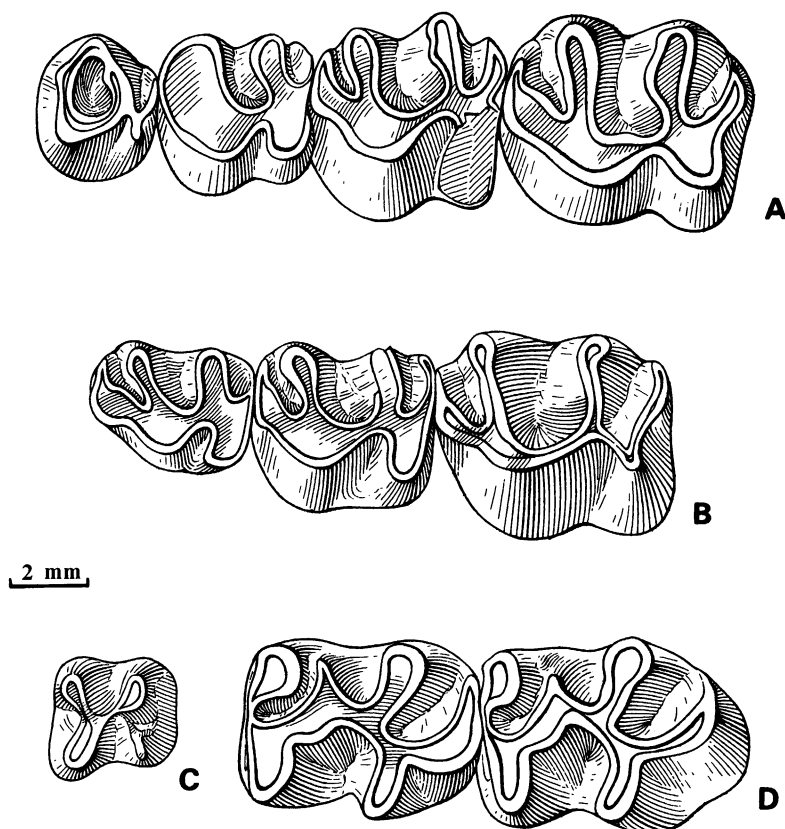


Fig. 23. Occlusal view of cheek teeth of *Yindirtemys suni*. A. Left P4-M3 (IVPP V 5992, holotype). B. Left dp4-M2 (IVPP V 10564.36). C. Left p4 (IVPP V 5993.33). D. Left m2-m3 (IVPP V 5993.30).

The anterocone is well developed. The better developed anterior cingulum and the proto-loph are oblique anterobuccally. The curved metaloph joins the protocone. The anterosinus is wide. The ridge connecting the anterocone with the protoloph may be distinct (IVPP V 10564.32), weak (IVPP V 10564.36), or absent. The mesosinus is a wide V-shape, and the mesostyle may be distinct (3/5) or indistinct (2/5). The sinus is deep and opposite the posterosinus. The antecrochet from the metaloph is weak (IVPP V 10564.34) or absent. There is no wear facet on the anterior surface of dp4, so it is not certain whether dp3 is present in *Y. suni*.

On p4 the protoconid and metaconid are distinct and the ectolophid is short and medially situated. The hypoconulid is always present as a crest. The lower molars are similar to those of *Yindirtemys deflexus*, but the lingual part of the posterior arm of the pro-

toconid is usually transverse. The large trigonid basin usually opens lingually. The hypoconid, entoconid, and hypoconulid are swollen but less crescentic than in *Y. deflexus*. The hypoconid has an obtuse, round buccal end and a transverse arm, which forms a right angle with the ectolophid, located almost in the same transverse line as the entoconid.

Dp4 (fig. 21D) is narrow and long. The metaconid extends posterolingually, shortly behind the protoconid. The buccal part of the posterior arm of the protoconid extends more or less longitudinally and the lingual part is widely separated from the metaconid. The trigonid basin is open lingually.

DIMENSIONS: Tables 11 and 12.

DISCUSSION: *Yindirtemys suni* was first described as a species of *Tataromys* by Li and Qiu (1980) on the basis of material from the early Miocene Xiejia Formation, Xining Ba-

TABLE 11  
Measurements (in mm) of Upper Teeth of  
*Yindirtemys suni*

		N	Min	Max	Aver	S	V
P4-M3	L	3	18.25	20.90	19.88	1.43	2.04
M1-3	L	8	13.70	17.40	15.81	1.47	2.16
P4-M2	L	5	12.25	15.20	14.40	1.23	1.51
P4-M1	L	5	7.50	9.46	8.71	0.80	0.64
M1-2	L	14	8.45	11.10	10.07	0.99	0.97
M2-3	L	11	9.80	13.30	11.60	1.07	1.13
P4	L	14	3.24	4.10	3.60	0.27	0.07
P4	W	14	3.56	4.70	4.02	0.37	0.14
M1	L	23	3.26	6.10	4.48	0.64	0.41
M1	W	22	3.27	5.40	3.96	0.47	0.22
M2	L	23	4.90	6.90	5.68	0.60	0.36
M2	W	23	4.10	6.00	4.95	0.49	0.24
M3	L	17	4.40	6.90	5.73	0.61	0.37
M3	W	17	4.32	6.10	5.16	0.48	0.23
dP4	L	5	4.00	4.50	4.36	0.22	0.05
dP4	W	5	3.00	3.30	3.16	0.13	0.02

TABLE 12  
Measurements (in mm) of Lower Teeth of  
*Yindirtemys suni*

		N	Min	Max	Aver	S	V
p4-m3	L	4	21.00	25.24	23.76	1.91	3.65
m1-3	L	6	17.20	20.80	18.70	1.25	1.55
p4-m2	L	8	12.50	17.10	14.46	1.48	2.20
p4-m1	L	8	7.26	10.40	8.36	1.06	1.13
m1-2	L	12	9.00	12.50	10.81	1.04	1.08
m2-3	L	12	12.20	15.60	13.45	0.97	0.94
p4	L	15	3.00	4.80	3.73	0.44	0.20
p4	W	13	2.60	4.30	3.34	0.42	0.18
m1	L	23	3.90	5.70	4.71	0.52	0.27
m1	W	20	3.07	4.00	3.49	0.31	0.09
m2	L	23	5.04	7.30	6.03	0.53	0.28
m2	W	19	4.02	5.70	4.60	0.55	0.31
m3	L	24	6.30	8.90	7.18	0.65	0.42
m3	W	24	4.00	5.50	4.89	0.43	0.18
dp4	L	2	4.10	4.50	4.30	0.28	0.08
dp4	W	2	2.80	3.10	2.95	0.21	0.05

sin, Qinghai. According to them, *Yindirtemys suni* was considered close to *Tataromys plicidens* in morphology and possibly the descendant of the latter. The upper teeth are not dissimilar to those of *Tataromys* in having more transversely directed transverse lophs and simpler structure. However, *Y. suni* shares with *Yindirtemys* such features as narrow palate, swollen cusps and lophs, lower molars with anterior cingulum, swollen and crescentic posterior arm of the protoconid, large trigonid basin, and short and medially situated ectolophid. All of these features are derived, whereas the similarities between *Yindirtemys suni* and *Tataromys* are primitive. *Tataromys suni* was transferred from *Tataromys* to *Yindirtemys* (Wang, 1994).

Within the genus *Yindirtemys*, *Y. suni* is most similar to *Y. gobiensis*. The distinctive features of *Y. suni* are the following: the upper teeth have swollen cusps, the anterocone is well developed, the antecrochet from the metaloph is less developed, and p4 has a hypoconulid. *Y. suni* differs from *Y. grangeri*, *Y. ambiguus*, *Y. xiningensis*, and *Yindirtemys* sp. in being larger and having a transverse and less curved metaloph and less developed antecrochet. It differs from *Y. deflexus* in having more transverse, less curved proto-loph and metaloph, transverse mesosinus, simpler M3, more transverse lingual part of

the posterior arm of the protoconid, open trigonid basin, round and obtuse hypoconid, and more transverse arm of the entoconid.

Judging from their morphology (more transversely oriented posterior arm of the protoconid, open trigonid basin, round and obtuse hypoconid with a more transverse arm), two lower jaws from Hsanda Gol Formation (AMNH 85175 and 85176), which were named *Tataromys* sp. on the labels, also possibly belong to *Y. suni*. The beds yielding the two specimens in Tsagan Nor Basin may also be late Oligocene or even later in age based on the known temporal distribution of *Y. suni* in China.

*Yindirtemys ambiguus*, new species  
Figure 24; tables 13, 14

- Tataromys* cf. *plicidens* Bohlin, 1937: 40–41, figs. 87–99; Taf. I, figs. 29–33. Stehlin and Schaub, 1951: 289, fig. 495. Schaub, 1958: 780, fig. 209. NEW SYNONYMY.
- Tataromys plicidens* (partim): Teilhard de Chardin and Leroy, 1942: 25. NEW SYNONYMY.
- Tataromys* cf. *plicidens* (partim): Bohlin, 1946: 95–107, figs. 16a–e, j, l–q, 17, 18, 19:1–27, 29, 30, 33–35, 37, 38, 20; pl. I, figs. 34–37; pl. II, figs. 1–13, 17, 20, 21, 23–27; pl. III, figs. 1, 2; pl. V; pl. VIII, figs. c–f. NEW SYNONYMY.
- Tataromys plicidens*: Wood, 1977: 123, 125, figs. 2O, 3N. NEW SYNONYMY.

HOLOTYPE: A palate with right P4–M3 and

TABLE 13  
Measurements (in mm) of Upper Teeth of  
*Yindirtemys ambiguus*, new species

		N	Min	Max	Aver	S	V
P4-M3	L	7	11.50	15.52	14.08	1.42	2.01
M1-3	L	6	10.50	12.50	11.71	0.82	0.67
P4-M2	L	10	8.00	11.04	9.90	0.93	0.87
P4-M1	L	15	4.90	6.72	5.68	0.58	0.34
M1-2	L	13	6.00	7.90	7.18	0.57	0.32
M2-3	L	7	7.00	9.40	8.26	0.97	0.93
P4	L	25	2.08	3.36	2.55	0.33	0.11
P4	W	25	2.50	3.84	2.98	0.34	0.11
M1	L	24	2.50	3.52	3.06	0.29	0.08
M1	W	24	2.10	3.68	2.80	0.43	0.18
M2	L	25	3.20	4.80	3.95	0.51	0.26
M2	W	24	2.90	4.20	3.58	0.43	0.18
M3	L	20	3.40	5.00	4.18	0.47	0.23
M3	W	21	3.00	4.16	3.62	0.36	0.13
dP4	L	2	3.00	3.20	3.10	0.14	0.02
dP4	W	2	2.00	2.10	2.05	0.07	0.005

TABLE 14  
Measurements (in mm) of Lower Teeth of  
*Yindirtemys ambiguus*, new species

		N	Min	Max	Aver	S	V
p4-m3	L	9	12.50	15.80	14.34	1.28	1.65
m1-3	L	7	10.40	13.10	11.90	1.09	1.18
p4-m2	L	5	8.50	10.72	9.88	0.96	0.93
p4-m1	L	9	5.10	6.56	5.60	0.43	0.19
m1-2	L	13	6.00	8.20	7.22	0.79	0.63
m2-3	L	11	7.80	9.70	8.97	0.62	0.39
p4	L	19	2.10	3.00	2.54	0.25	0.06
p4	W	19	1.80	2.70	2.23	0.23	0.05
m1	L	22	2.50	3.80	3.34	0.31	0.09
m1	W	21	1.90	2.90	2.38	0.25	0.06
m2	L	26	3.20	4.64	4.17	0.38	0.14
m2	W	28	2.30	3.90	3.09	0.36	0.13
m3	L	18	3.80	5.80	4.81	0.56	0.31
m3	W	19	2.50	4.00	3.34	0.35	0.12
dp4	L	2	2.50	3.50	3.00	0.71	0.50
dp4	W	2	1.40	1.70	1.55	0.21	0.05

left M2 and M3 (Sh. 281), from the Shargaltein beds of the Baiyanghe Formation of Shargaltein Valley, south end of Danghe, Gansu, China, and figured by Bohlin (1937: fig. 87).

REFERRED SPECIMENS: Tb. 212, 224, 236, 248, 557, 558, 566a, 566c, 568, 569a,b, 570a,b, 571a,b, 572a, 574, 575, 576a-d, 582, 583, 585, 587, 588, 589a-c, 590a-f, 591a-e, 592a-c, 593a-j; Sh. 59, 60, 67, 74, 99-105, 107, 108, 110, 144, 145, 147, 150, 221-223, 226, 257, 269, 282, 322, 500, 534, 608, 703, 705, 706, 708, 710, 712, 713, 715, 717, 719, 720, 731, 737, 752, 773, 777-779, 781, 782, 785, 786, 788, 790-793; IVPP V 5913, V 5915, V 5917-V 5921, V 5924, V 5929, V 5930, V 5932-V 5934, V 10566, V 10567, and V 10568.1-4.

GEOLOGICAL RANGE: Late Oligocene Baiyanghe Formation and Yikebulage Formation.

GEOGRAPHIC DISTRIBUTION: Saint Jacques [IVPP locs. 77046.5 (V 10566) and 77048 (V 10567)] and Qianlishan District [IVPP loc. 78016 (V 5913, V 5915, V 5917-V 5921, V 5924, V 5929, V 5930, V 5932-V 5934, V 10568)], Nei Mongol, and Shargaltein Gol and Taben-buluk, Danghe, Gansu, China.

DIAGNOSIS: Medium-sized species of *Yindirtemys*, cheek tooth cusps and lophs mod-

erately swollen; upper molar anterocone distinct; metaloph strongly curved, mesosinus posteriorly curved, posterosinus short; M3 lacking crochet connecting paracone with metacone; on lower molar lingual part of the posterior arm of the protoconid slightly oblique, trigonid basin usually open.

ETYMOLOGY: *Ambiguus*, Latin, changeable and uncertain.

DIMENSIONS: Tables 13 and 14.

DISCUSSION: Most of the specimens from Danghe, Gansu, described by Bohlin (1937, 1946) as *Tataromys* cf. [*T.*] *plicidens* are included here in this species. As described by Bohlin (1946: 83), in this species the metacone and paracone bend forward; there is often an antecrochet on the metacone, which sometimes reaches the posteroloph after wear and forms a small enamel island at the lingual end of the posterosinus; on the lower molars there is an anterior cingulum, a swollen middle part of the posterior arm of the protoconid (= Bohlin's mesoconid). In addition, the palate is very narrow and the lower molars have short, nearly medially situated ectolophid, large trigonid basin, and crescentic entoconid, hypoconid, and hypoconulid. All these features show that the specimens from Gansu are distinguished from *Tataromys* but agree with *Yindirtemys*. Indeed, these specimens vary in size, in the degree



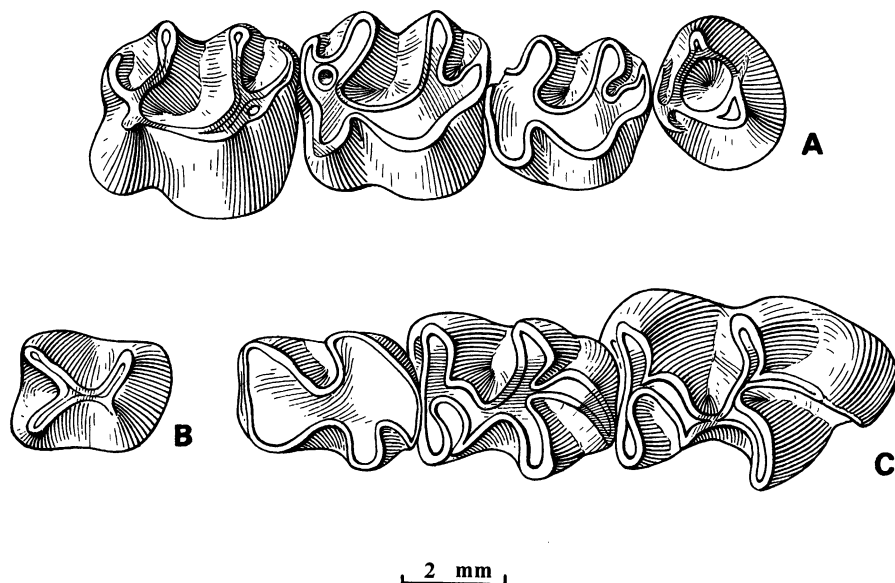


Fig. 24. Occlusal view of cheek teeth of *Yindirtemys ambiguus*, new species. A. Right P4–M3 (Sh. 281, holotype). B. Left p4 (T.b. 276a). C. Right m1–m3 (T.b. 589b).

of obliquity and curvature of the lophs, especially the metaloph and the posterior arm of protoconid, and in the form of the trigonid basin. However, as mentioned by Bohlin (1946), it is difficult to separate them according to these variable characters. I tentatively refer all of them, except T.b. 566b and T.b. 577, to the new species *Yindirtemys ambiguus*.

Some specimens from Saint Jacques and the Yikebulage Formation are identical with *Y. ambiguus* in size and tooth proportion. They also are referred to this species.

*Yindirtemys ambiguus* differs from both *Y. grangeri* and *Y. deflexus* in usually having an open trigonid basin on lower molars. Differences from *Y. grangeri* are its larger size and upper molars having more strongly curved metaloph. It differs from *Y. deflexus* in being smaller, having less swollen cusps and lophs, and its M3 lacks a crest connecting the protoloph with the metaloph. *Y. ambiguus* differs from *Y. gobiensis* and *Y. suni* in being smaller and in having upper molars with more strongly curved metaloph, a curved mesosinus, and a shallow posterosinus. It differs from *Y. birgeri* in upper molar having more oblique, curved transverse lophs and in lacking connection between protoloph and metaloph on M3.

#### *Yindirtemys* cf. *Y. ambiguus*

Some specimens of Bohlin's *Tataromys* cf. [*T.*] *plicidens* (T.b. 566b and T.b. 577) from Taben-buluk, Gansu, are similar to those of *Y. ambiguus* in having higher crowns and in general morphology of the cheek teeth. However, the two lower molars have a well-developed longitudinal anterior arm of the entoconid, which meets the posterior arm of the protoconid, and a reduced transverse arm of the entoconid.

#### *Yindirtemys xiningensis*, new species

Figure 25; table 15

*Tataromys* sp. Li and Qiu, 1980: 206, 213.

**HOLOTYPE:** A fragment of maxilla with left M1 and M2 (IVPP V 5994.1), from the Xiejia Formation, Xining Basin, Qinghai, China.

**REFERRED SPECIMENS:** IVPP V 5994.2–4.

**HORIZON AND LOCALITY:** Early Miocene, the Xiejia Formation, Xiejia (IVPP loc. 78027), Qinghai, China.

**DIAGNOSIS:** Medium-sized *Yindirtemys*; on upper molars crown on lingual side of protocone distinctly higher than other part, anterior cingulum isolated, anterocone well developed, paracone and metacone bulbous, antecrochet of metacone present, protoloph and metaloph low and curved, convergent to

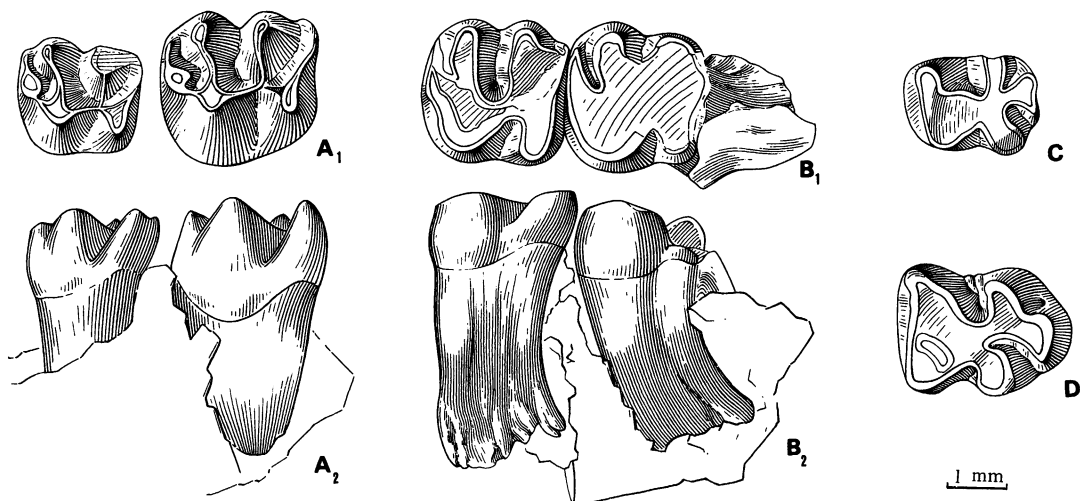


Fig. 25. Cheek teeth of *Yindirtemys xiningensis*, new species. **A.** Left M1–M2 (IVPP V 5994.1, holotype). A<sub>1</sub>. Occlusal view. A<sub>2</sub>. Lingual view. **B.** Left M2–M3 (IVPP V 5994.2). B<sub>1</sub>. Occlusal view. B<sub>2</sub>. Lingual view. **C.** Occlusal view of right m1 (IVPP V 5994.3). **D.** Occlusal view of right m3 (IVPP V 5994.4).

protocone, mesosinus U-shaped; on lower molars posterior arm of protoconid complete and trigonid basin closed.

**ETYMOLOGY:** *Xining*, the name of the basin where the specimens were collected.

**DESCRIPTION:** On M1 the paracone and metacone are well developed, bulbous in form. The protocone is the strongest cusp, with the lingual side of its crown extending dorsally much higher than the other parts. It is V-shaped in occlusal view, with a posterior arm extending posterobuccally. The protoloph is low and curved. The metacone of the holotype is damaged. The metaloph is transverse and narrow lingually, meeting the posterior arm of the protocone to form a lower continuous curved loph. The hypocone is equal to the protocone in size and is positioned just behind the latter. The posteroloph is the highest loph on M1. The anterior cingulum is low, isolated, and with a well-developed anterocone, which is about the size of the paracone. The mesosinus is U-shaped. The anterosinus is a narrow S-shaped valley and the posterosinus is wide and deep. The broad sinus is oblique posterobuccally and opposite the posterosinus. M1 possesses three roots: two small buccal roots (anterior one larger) and a large lingual one, with its lingual surface convex.

M2 is similar to M1, but much larger. The metaloph is as well developed as the protocone and forms a continuous curve. The metacone is larger than the paracone, with a well-developed antecrochet extending almost to the posteroloph, closing the posterosinus.

Only one M3 is known. It is close to M2 in size. Because most of its crown (IVPP V 5994.2) is damaged. Knowledge of its morphology is very limited. It has three roots, but unlike M1 and M2, the lingual one has a shallow groove on the lingual surface and the posterior buccal one is larger than the anterior and extends posterodorsally.

Only one m1 and one m3 are known, both heavily worn. The short ectolophid is located near the middle of the tooth. m1 has an anterior cingulum. The round hypoconid and entoconid are opposite each other. m3 is much larger than m1, with a large closed trigonid basin. The entoconid meets the ectolophid anterior to the hypoconid. The hypoconulid joins the hypoconid. The sinusid is oblique posterolingually and larger than the mesosinusid. The posterosinusid is curved and larger than the hyposinusid.

**DIMENSIONS:** Table 15.

**DISCUSSION:** Li and Qiu (1980) reported *Tataromys* sp. from the early Miocene Xiejia Formation of Xining Basin, Qinghai. Having

TABLE 15  
Measurements (in mm) of Cheek Teeth of  
*Yindirtemys xiningensis*, new species

		V	V	V	V
		5994.1	5994.2	5994.3	5994.4
		(type)			
M1-2	L	4.80			
M2-3	L		4.48		
M1	L	2.08			
M1	W	1.76			
M2	L	2.56	2.40		
M2	W	2.24	2.40		
M3	L		2.16		
M3	W		2.56		
m1	L			2.08	
m1	W			1.60	
m3	L				2.72
m3	W				1.92

noticed similarities between their specimens and *Yindirtemys*, they tentatively referred them to *Tataromys* based on size, which was considered close to that of *Tataromys sigmodon*. They thought that both the maxillae (IVPP V 5994.1 and V 5994.2) had M1 and M2. Closer observation revealed that only the type specimen (IVPP V 5994.1) has M1 and M2. The other specimen (IVPP V 5994.2) bears M2 and M3 because no trace of alveolus behind the last tooth is visible, and, like other M3, the roots of the last tooth bend posteriorly.

As described above, the molars of *Yindirtemys xiningensis* are quite different from those of *Tataromys* in morphology. For example, the upper molars have a well-developed paracone, metacone, and antecrochet of metacone; the lower molars have anterior cingulum, large trigonid basin, and medially situated ectolophid. All these derived features are shared by *Yindirtemys*. Although it is also similar to *Bounomys* in some features, *Y. xiningensis* has higher crowns, a better developed antecrochet of the metacore, and lacks a longitudinal arm of the entoconid, one of the derived features for *Bounomys*. Thus, *Y. xiningensis* belongs to *Yindirtemys*.

*Yindirtemys xiningensis* is different from other species of *Yindirtemys* in having weak transverse lophs on the upper molars. It is smaller than *Y. deflexus*, *Y. gobiensis*, *Y. suni*, *Y. ambiguus*, *Yindirtemys* sp., and *Y. birgeri*.

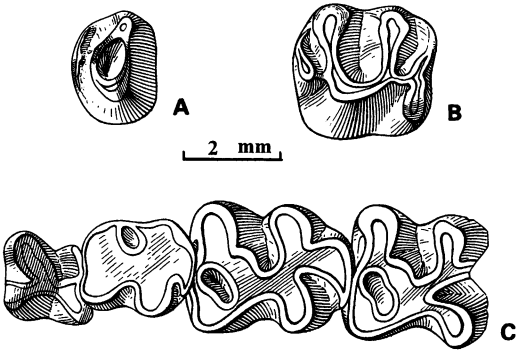


Fig. 26. Occlusal view of cheek teeth of *Yindirtemys* sp. A. Left P4 (IVPP V 10569.2). B. Left M2 (IVPP V 10569.1). C. Right p4-m3 (Tb. 570).

Furthermore, it differs from *Y. deflexus* and *Y. ambiguus* in having less curved metaloph, wide U-shaped mesosinus, deep transverse posterosinus on upper molars; less crescentic entoconid, hypoconid, and hypoconulid on the lower molars. It differs from *Y. gobiensis* and *Y. suni* in having closed trigonid basins on the lower molars and from *Y. deflexus* and *Y. birgeri* in lacking a connection between protoloph and metaloph on M3. Finally, it differs from *Y. grangeri* in being larger and in having better developed antecrochet of metacone and a wide U-shaped mesosinus.

*Yindirtemys* sp.

Figure 26

*Tataromys* cf. *sigmodon* Bohlin, 1946: 94-95, figs. 16f, 19:32; pl. II, fig. 29. Zhai, 1978: 128.

Two isolated teeth [a left M2 (IVPP V 10569.1) and a left P4 (IVPP V 10569.2)] were collected from the late Oligocene Yikebulage Formation, IVPP loc. 78016, Qianlishan District, Nei Mongol, China. They share with *Yindirtemys* the following derived features: on upper cheek teeth crown on lingual side higher than on buccal one, upper molars having distinct and swollen paracone and metacone, and a distinct metacone antecrochet. They are referred to the genus *Yindirtemys*. They are intermediate in size between *Y. ambiguus* and *Y. xiningensis* (P4: L, 1.68 mm; W, 2.16 mm; M2: L, 2.88 mm; W, 2.64 mm).

Among species of *Yindirtemys*, the two teeth are most similar to those of *Y. xin-*

*gensis* and *Y. gobiensis* in morphology. They differ from the former in being larger, cheek teeth having better developed and straight transverse lophs, anterior cingulum joining the protoloph, and weaker anterocone and antecrochet. They differ from the latter in being much smaller and having less well-developed antecrochet on M2. They may represent a large *Y. xiningensis* or an intermediate form between *Y. xiningensis* and *Y. gobiensis*.

Bohlin (1946) and Zhai (1978), respectively, referred T.b. 570 from Taben-buluk and V 4372 from the upper part of the Taoshuyuanzi Formation of Turfan Basin, Xinjiang, to *Tataromys* cf. [*T.*] *sigmodon* mainly based on size. These specimens are also similar to *Yindirtemys* rather than to *Tataromys sigmodon* in tooth morphology, such as the higher crown, swollen posterior arm of the protoconid, large and closed trigonid, medially situated ectolophid, and the presence of an anterior cingulum. In addition, they match the upper teeth described above in size and in having well-developed lophs. All the specimens referred to *Tataromys* cf. [*T.*] *sigmodon* mentioned above may belong to *Yindirtemys* sp.

#### *Bounomys* Wang, 1994

TYPE SPECIES: *Tataromys bohlini* Huang, 1985.

INCLUDED SPECIES: *Bounomys ulantatalensis* (Huang, 1985).

GEOLOGICAL RANGE: Late early Oligocene.

GEOGRAPHIC DISTRIBUTION: The Ulantatal area and Saint Jacques, Nei Mongol, and Haiyuan, Ningxia, China.

DIAGNOSIS: A ctenodactylid of small to medium size; incisive foramen large; palate broad; sphenopalatine foramen located above junction of P4 and M1; cheek teeth brachydont and moderately bunodont, main cusps distinct or swollen, and lophs weak; on upper molars anterocone developed, anterior cingulum isolated or joining protoloph, protocone V-shaped, protoloph and metaloph low, narrow at middle and joining protocone, mesosinus transverse, entoloph absent, short ridge connecting metaloph and posteroloph weak or absent, posterosinus long, variably connected with sinus; on p4 ectolophid long,

situated buccal to anterior groove; on lower molars posterior arm of protoconid complete, fusing with metalophid I on buccal part, and with strong swollen middle part, trigonid basin large, closed, ectolophid situated in middle of tooth, entoconid bulbous in shape, usually with double weak arms; anterior arm always present and transverse arm reduced to a weak crest or absent, arm of hypoconulid weak and low, anterior cingulum weak or absent.

ETYMOLOGY: *Bounomys* = bouno + mys; *bounos*, Greek, hill; referring to the bunodont cheek teeth.

DISCUSSION: Huang (1985) described two species of *Tataromys*: *T. ulantatalensis* and *T. bohlini*, from the upper part of the Ulantatal Formation of the Ulantatal area, Alxa Zuoqi, Nei Mongol. The two forms are very similar to each other, but quite different from typical *Tataromys* in upper jaw and tooth morphology (see Diagnosis). They are clearly to be excluded from *Tataromys*. On the other hand, they also differ from *Yindirtemys* and *Karakoromys* in having more bunodont cheek teeth and the form of entoconid. In addition, they differ from *Yindirtemys* in having a broader palate and brachydont cheek teeth, in lacking antecrochet of metacone on the upper molars, and in having weakly developed anterior cingulum on the lower molars. They differ from *Karakoromys* in upper teeth having a V-shaped protocone, metaloph joining with protocone, well-developed anterocone, and lacking the entoloph, lower molars having a complete swollen posterior arm of protoconid fusing with the buccal part of the metalophid I, and closed trigonid basin.

#### *Bounomys bohlini* (Huang, 1985)

Figure 27, 28; tables 16, 17

*Tataromys grangeri* (partim): Huang, 1982: 340–341, 347 (Huang, pers. comm., 1993).

*Tataromys bohlini* (partim) Huang, 1985: 29–31, fig. 2; pl. I. figs. 4–7. Russell and Zhai, 1987: 292, 355.

*Bounomys bohlini*: Wang, 1994: 37–38, fig. 3a–b.

HOLOTYPE: A fragment of skull associated with lower jaw with complete dentition (IVPP V 7348), from the upper part of the Ulantatal Formation of the Ulantatal area,

Alxa Zuoqi, Nei Mongol, China, and figured by Huang (1985: fig. 2; pl. I, fig. 4).

PARATYPE: A fragment of a skull with right and left P4–M3 (IVPP V 7349).

REFERRED SPECIMENS: IVPP V 7350.1, V 7350.2, V 10570.1, V 10570.2, V 10571, V 10572.1–4, V 12049.1, V 12049.2.

GEOLOGICAL RANGE: Late early Oligocene, upper part of the Ulanatal Formation.

GEOGRAPHIC DISTRIBUTION: Saint Jacques [IVPP locs. 77046 (V 10570), 77047 (V 10571) and 78020 (V 10572)] and the Ulanatal area (V 7348–V 7350, V 12049), Nei Mongol, China.

DIAGNOSIS: “A small *Tataromys*, size about those of *T. grangeri* or *Karakoromys decessus*; anteroloph not connected with protocone; external valley straight and not bent backwards interiorly on the upper molars. Lower molars similar to those of *T. ulantatalensis* morphologically, but without accessory longitudinal crests on the lingual side; hypolophid poorly developed and entoconid rather isolated” (Huang, 1985: 38).

DESCRIPTION: Most of the facial part of the skull is preserved. The skull is high and narrow, with a flattened dorsal surface. The rostrum is high, with a broad, slightly concave lateral surface. The very large infraorbital foramen faces slightly dorsally. The anterior root of the zygomatic process of the maxilla extends from P4. The orbit is also large. The sphenopalatine foramen is above the junction of P4 and M1, more anteriorly located than in *Tataromys plicidens*. The incisive foramen is exceptionally large, much more than in *Tataromys*, and almost as long as the diastema, extending from behind I2 to P4, or even to M1. As in *Tataromys*, the premaxillary–maxillary suture intersects the midpoint of the incisive foramen. The width of the palatine between the dental rows is nearly equal to that of the cheek teeth, and the posterior palatine foramina are opposite M2. The choana is far behind the M3.

The lower jaw is thick. As in *Tataromys* and *Yindirtemys*, the mental foramen is below p4. The shallow masseteric fossa reaches below m1, but lacks an upper masseteric crest. The lower masseteric crest is separated into two parts—the anterior one, short and horizontal under m1 and m2; the posterior one, strong and extending posteroventrally.

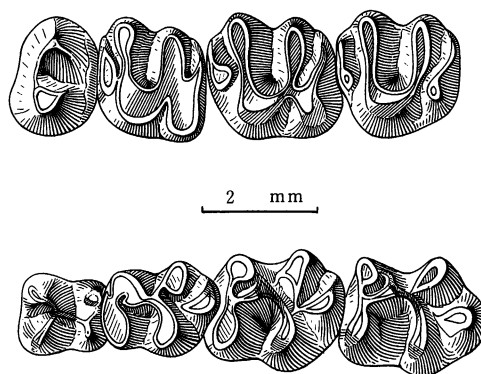


Fig. 27. Occlusal view of cheek teeth of *Bounomys bohlini* (IVPP V 7348, holotype). (Top: Left P4–M3). Bottom: Left p4–m3.

The incisor extends posteriorly below m3. The ascending ramus rises outside m3.

The upper incisor is triangular in cross section and has a weakly wrinkled surface enamel.

The cheek teeth are brachydont and bunodont. On P4 the anterior cingulum is weak or absent. The protoloph is low, but complete. The metaloph is also low. It is either free or may join the posterior arm of the protocone. The posterior cingulum is present, but low. On the upper molars the paracone and metacone are distinct. Both the protoloph and metaloph are low, but always complete, converging to the protocone to form a continuous V-shaped ridge. The short ridge between metaloph and posteroloph is weak or even absent. The broad, deep sinus, oblique posterobuccally, usually connects with the deep posterosinus to form a wide valley. The short anterior cingulum is isolated and has a well-developed anterocone.

On p4 the trigonid is wider and higher than the talonid. The protoconid is larger and higher than the metaconid. They form roughly a right angle. The entoconid is conical in shape, lower than the metaconid. The ectolophid is also low and narrow, but long. The hypoconid forms a low and narrow transverse loph. The sinusid and mesosinusid are broadly U-shaped.

The lower molars increase in size posteriorly. The main cusps are strong and conical. The posterior arm of the protoconid is crescentic and appears an extension from the middle of metalophid I to the metaconid. It

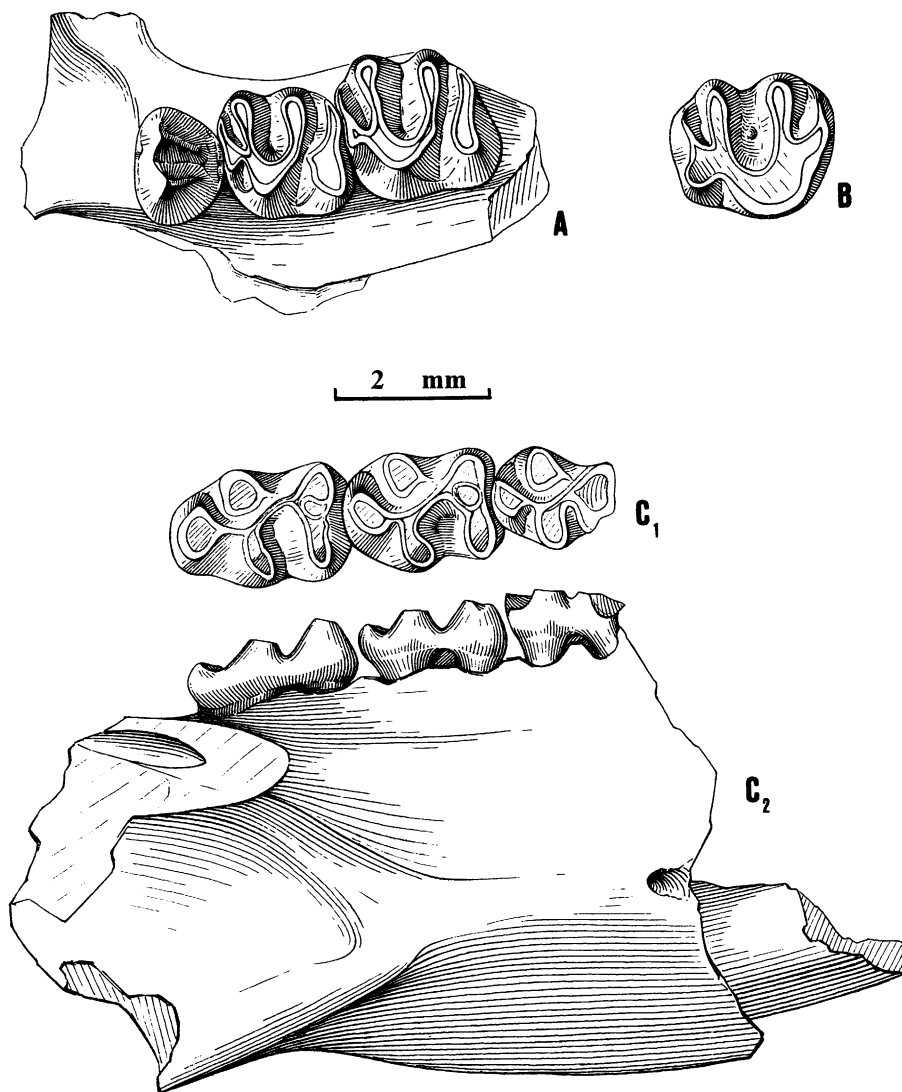


Fig. 28. *Bounomys bohlini*. A. Occlusal view of left P4-M2 (IVPP V10572.1). B. Occlusal view of right M3 (IVPP V 10572.3). C. Right lower jaw with m1-m3 (IVPP V 10572.4). C<sub>1</sub>. Occlusal view of m1-m3. C<sub>2</sub>. Buccal view of lower jaw.

may also be the result of fusion of the buccal part of the posterior arm of the protoconid with that of metalophid I. The trigonid basin is closed. In some specimens the posterior arm of the protoconid is interrupted and separated from metalophid I so that the trigonid basin opens buccally. The short ectolophid is medially situated. A peculiar feature is that the entoconid forms an isolated rounded cone, with a low, weak anterior arm (= Huang's lingual longitudinal crest). On some m2 (4/7) and m3 (1/7) the entoconid

has a transverse arm (= Bohlin's hypolophid II or Huang's hypolophid I), reaching or almost reaching the arm of the hypoconulid to enclose a central basin. The arm of the hypoconulid is also low, weak, and reaches the arm of the hypoconid on m2 and m3, but on m1 it is usually free (4/5), only occasionally joining the hypoconid (1/5). Therefore, on m1 the hyposinusid is usually deep and extends almost to the lingual side to connect with the posterosinusid.

V 7350.1 is special in that the p4 has a dis-

TABLE 16  
Measurements (in mm) of Upper Teeth of  
*Bounomys bohlini*

		N	Min	Max	Aver	S	V
P4-M3	L	4	6.15	7.30	6.71	0.64	0.41
M1-3	L	5	4.92	5.82	5.40	0.41	0.17
P4-M2	L	6	4.10	5.41	4.73	0.50	0.25
P4-M1	L	7	2.46	3.49	2.96	0.38	0.14
M1-2	L	7	3.03	3.94	3.47	0.32	0.10
M2-3	L	5	3.53	4.02	3.82	0.26	0.07
P4	L	8	0.98	1.48	1.25	0.21	0.04
P4	W	5	1.23	1.97	1.59	0.27	0.07
M1	L	8	1.31	1.99	1.66	0.21	0.05
M1	W	6	1.48	2.05	1.78	0.18	0.03
M2	L	7	1.64	2.13	1.90	0.17	0.03
M2	W	7	1.56	2.09	1.82	0.23	0.05
M3	L	6	1.72	2.16	1.95	0.19	0.04
M3	W	6	1.60	2.05	1.85	0.19	0.04

tinct hypoconulid and the molars have a distinct accessory crest extending lingually from the hypoconid. Because the nature of the variation is unclear, I tentatively assign it to *B. bohlini*.

DIMENSIONS: Tables 16 and 17.

DISCUSSION: Huang (1985) considered that *Bounomys bohlini* (= Huang's *Tataromys bohlini*), *Karakoromys decessus*, and *Yindirtemys grangeri* (= Huang's *Tataromys grangeri*) are similar to one another in size and basic morphology and possibly belong to one species. As mentioned above and by Wang (1994), *Bounomys bohlini* merits not only specific separation but also generic separation on the basis of tooth morphology.

*Bounomys ulantatalensis* (Huang, 1985)

Figure 29; tables 18, 19

*Tataromys* spp. (partim) Huang, 1982: 340–341, 347.

*Tataromys ulantatalensis* Huang, 1985: 28–29, fig. 1; pl. I, figs. 1–3. Russell and Zhai, 1987: 292, 355.

*Leptotataromys gracilidens* (partim): Huang, 1985: 32–35. Russell and Zhai, 1987: 292, 355.

NEW SYNONYMY.

*Bounomys ulantatalensis*: Wang, 1994: 37–38.

HOLOTYPE: A lower jaw fragment with i2 and p4–m3 (IVPP V 7341), from the upper part of the Ulantatal Formation of Ulantatal area, Alxa Zuoqi, Nei Mongol, China, and figured by Huang (1985: fig. 1; pl. I. fig. 1).

TABLE 17  
Measurements (in mm) of Lower Teeth of  
*Bounomys bohlini*

		N	Min	Max	Aver	S	V
p4-m3	L	2	7.46	7.71	7.59	0.18	0.03
m1-3	L	4	5.82	6.31	6.13	0.22	0.05
p4-m2	L	2	5.41	5.58	5.50	0.12	0.01
p4-m1	L	2	3.36	3.44	3.40	0.06	0.003
m1-2	L	4	3.94	4.10	4.00	0.08	0.006
m2-3	L	5	4.18	4.51	4.38	0.12	0.02
p4	L	2	1.48	1.56	1.52	0.06	0.003
p4	W	2	1.31	1.31	1.31	0	0
m1	L	5	1.89	2.01	1.94	0.06	0.004
m1	W	4	1.44	1.56	1.49	0.05	0.003
m2	L	6	2.09	2.46	2.25	0.12	0.02
m2	W	6	1.64	1.97	1.79	0.12	0.02
m3	L	6	2.13	2.38	2.30	0.09	0.008
m3	W	6	1.56	1.80	1.69	0.11	0.01

PARATYPE: A lower jaw fragment with dp4–m3 (IVPP V 7342).

REFERRED SPECIMENS: IVPP V 7343.1–17, V 7345.17–19, V 7345.22, V 7345.48, V 10574, V 10575.1–12.

GEOLOGICAL RANGE: Late early Oligocene, upper part of the Ulantatal Formation.

GEOGRAPHIC DISTRIBUTION: Saint Jacques [IVPP loc. 77046.5 (10574)] and Ulantatal area (V 7341–V 7343, V 7345, V 10575), Nei Mongol, China.

EMENDED DIAGNOSIS: About 1.5 times the size of *Bounomys bohlini*; on upper molars paracone and metacone swollen, metacone larger than paracone, protoloph and metaloph short, anterior cingulum joining protoloph, sinus separated from posterosinus; lower molars usually having a large central basin closed by longitudinal anterior arm and transverse posterior arm of entoconid.

DESCRIPTION: *B. ulantatalensis* is about 50% larger than *Bounomys bohlini*. As in *Bounomys bohlini*, the width of the palatine between the dental rows is nearly equal to that of the dental row. The two posterior palatine foramina are opposite M2, with two deep grooves extending anteriorly, and at the level of the M1 fuse into one wide groove entering the incisive foramen. The root of the zygomatic process extends from P4. The dental rows converge slightly anteriorly.

As in *B. bohlini*, the lower jaw is thick. The mental foramen may be below p4 (12/

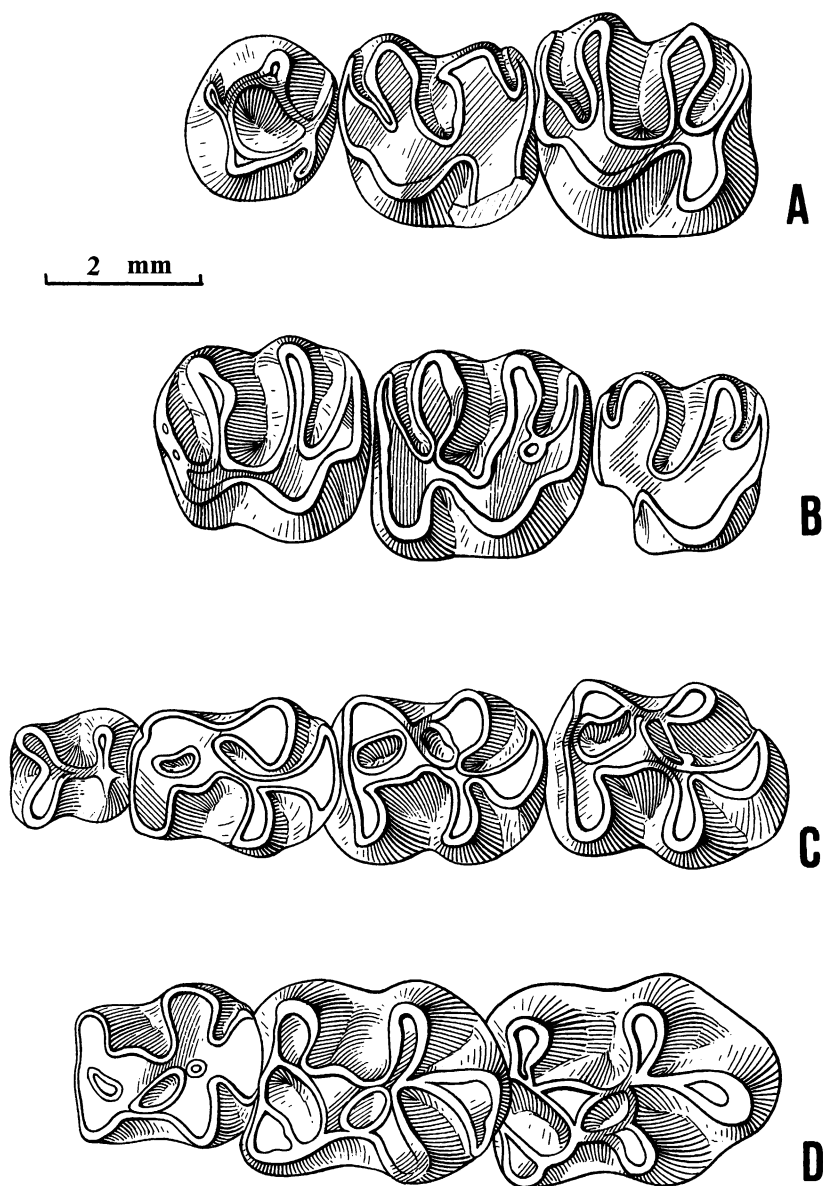


Fig. 29. Occlusal view of cheek teeth of *Bounomys ulantatalensis*. **A.** Left P4-M2 (IVPP V 10575.1). **B.** Right M1-M3 (IVPP V 7345.17). **C.** Left p4-m3 (IVPP V7341, holotype). **D.** Right m1-m3 (IVPP V10574).

17) or m1 (5/17). The masseteric fossa reaches below m1. No distinct upper masseteric crest is seen. The lower masseteric crest is separated into two parts.

P4 is oval in occlusal view. The complete protoloph and metaloph enclose the trigonid basin. The low anterior cingulum joins the protoloph, but lacks a lingual part. The well-

developed posterior cingulum joins the metaloph at the middle of the tooth.

On m1 and M2 the V-shaped protocone is the largest cusp. The paracone and larger metacone are more swollen and prominent than in *B. bohlini*. The protoloph and metaloph are low, slender, short, and join the protocone. The hypocone is large, but smaller than the proto-



cone. The long well-developed posteroloph contacts the metaloph by one or two weak short ridges. The relatively long anterior cingulum joins the protoloph. The well-developed anterocone occasionally has an accessory crest reaching the protoloph. The deep sinus is oblique posterobuccally and opposite to the posterosinus. The deep antero- and posterosinus are S-shaped.

M3 is similar to M1 and M2, but with a shorter posterior side and posteroloph. The posterior arm of the protocone and the metaloph reach the hypocone. The posterior groove is distinct and the sinus is shallow.

On p4 the trigonid is narrower than its talonid. The protoconid is usually higher and larger than the metaconid and may be connected with (4/7) or separated from (3/7) the latter. The long and high ectolophid joins the protoconid, slightly more buccally than the anterior groove. The hypoconid, a low transverse loph, usually joins the entoconid, which is lower than the metaconid. The hypoconulid may be present (4/8) or absent (4/8).

m1 is relatively long, with a narrower trigonid than talonid. The metaconid is large and round. The protoconid is slightly swollen anteroposteriorly but extends transversely. The great swollen posterior arm of the protoconid is semilunar or triangular in shape when worn. The large trigonid basin is closed. The short ectolophid is medially located. The conical entoconid is as large as the metaconid, usually with two narrow, low arms enclosing the central basin with the ectolophid. Occasionally an accessory crest is present in the basin (IVPP V 7343.8). The anterior arm of the entoconid is always present and extends longitudinally or anterobuccally to meet the posterior arm of the protoconid. The transverse arm is short, low, and usually reduced or absent (10/19). The hypoconid is similar to the protoconid in orientation and size. The crescentic hypoconulid is the largest cuspid, with a well-developed transverse arm and an anterior arm. The anterior arm is low, narrow, and usually joins the arm of the hypoconid, occasionally the entoconid (V 7343.3), or both (V 7343.11 and V 7343.13), or it may be completely free (V 7343.6). There is an accessory crest or cusp extending from the hypoconulid at the

TABLE 18  
Measurements (in mm) of Upper Teeth of  
*Bounomys ulantatalensis*

		N	Min	Max	Aver	S	V
M1-3	L	2	7.36	7.68	7.52	0.23	0.05
P4-M2	L	1			7.20		
P4-M1	L	1			4.48		
M1-2	L	4	4.80	5.28	5.00	0.20	0.04
M2-3	L	6	4.80	5.52	5.21	0.26	0.07
P4	L	1			1.84		
P4	W	1			2.16		
M1	L	5	2.24	2.56	2.34	0.14	0.02
M1	W	5	2.16	2.53	2.28	0.14	0.02
M2	L	9	2.56	2.80	2.64	0.10	0.01
M2	W	9	2.08	2.72	2.52	0.19	0.04
M3	L	6	2.24	2.88	2.59	0.24	0.06
M3	W	4	2.45	2.72	2.57	0.11	0.01

entrance of the hyposinusid on some m1 (10/17). The sinusid is a deep U-shape. The mesosinusid may be shallow broad (8/16) or V-shaped (8/16), depending on the direction of the anterior arm of the entoconid. The deep posterosinusid extends anteriorly when the transverse arm of the entoconid is reduced. The hyposinusid is usually shallower than the posterosinusid. The anterior cingulum is weak.

m2 is similar to m1, but larger, proportionately wider, with the trigonid and talonid being equal in width. The transverse arm of the entoconid is more frequently present (19/23), but is short and low. The central basin is always closed. The posterosinusid is always shorter than in M<sub>1</sub>. The form of the mesosinusid is variable from widely open to V-shaped. Occasionally a mesostylid or an accessory crest appears in it. There is also an extra crest or cusp in the hyposinusid.

m3 is larger than m2, with a more prominent posterior side. As in m1, the transverse arm of the entoconid is often reduced or absent (12/19). The anterior arm of the entoconid sometimes extends longitudinally (6/18) but more frequently obliquely to meet the posterior arm of the protoconid (5/18) or ectolophid (7/18). The hypoconulid extends longitudinally and has a shorter transverse arm.

DIMENSIONS: Tables 18 and 19.

DISCUSSION: *Bounomys ulantatalensis* was described by Huang (1985) as *Tataromys*

TABLE 19  
Measurements (in mm) of Lower Teeth of  
*Bounomys ulantatalensis*

		N	Min	Max	Aver	S	V
p4-m3	L	3	9.12	10.08	9.60	0.48	0.23
m1-3	L	10	7.20	9.12	8.35	0.60	0.36
p4-m2	L	3	6.56	6.88	6.72	0.16	0.03
p4-m1	L	5	3.36	4.48	3.95	0.41	0.17
m1-2	L	14	4.64	6.24	5.44	0.39	0.15
m2-3	L	17	5.12	6.72	6.09	0.42	0.18
p4	L	8	1.60	1.76	1.72	0.07	0.006
p4	W	8	1.28	1.65	1.50	0.12	0.01
m1	L	18	2.32	2.88	2.63	0.16	0.02
m1	W	17	1.76	2.40	1.97	0.17	0.03
m2	L	21	2.56	3.36	3.03	0.22	0.05
m2	W	21	2.08	2.61	2.36	0.13	0.02
m3	L	18	2.72	3.52	3.24	0.24	0.06
m3	W	18	2.05	2.61	2.34	0.17	0.03
dp4	L	1			2.16		
dp4	W	1			1.12		

*ulantatalensis* and diagnosed as: “Size about that of *T. sigmodon*; lower molars with accessory longitudinal lingual crests and ectolophid relatively situated in the middle.” The original material included only lower jaws. Having observed all the material of the ctenodactylids described by Huang (1985), I found that, like specimens V 10575.1 and V 10575.2, some upper jaws (IVPP V 7345.17–19, V 7345.22) formerly referred to *Leptotataromys gracilidens* by Huang (1985) are different from the core sample of the species. They show features of *Bounomys* and match well with those of the lower teeth of *B. ulantatalensis*. They differ from *B. bohlini* only in being larger, having more swollen and larger metacone and shorter metaloph, anterior cingulum joining protoloph, and in M3 having both posterior arm of protocone and metaloph reaching hypocone. Probably these specimens are the upper jaws of *B. ulantatalensis*.

Of the lower jaws referred to *Leptotataromys gracilidens* by Huang (1985), IVPP V 7345.48 is referable to *B. ulantatalensis* judging from its size and morphology.

SUBFAMILY KARAKOROMYINAE WANG, 1994

TYPE GENUS: *Karakoromys* Matthew and Granger, 1923.

INCLUDED GENUS: *Euryodontomys*, new genus.

GEOLOGICAL RANGE: Early Oligocene.

GEOGRAPHIC DISTRIBUTION: Eastern and central Asia.

DIAGNOSIS: Palate relatively wide, zygomatic process of maxilla anterior to P4, sphenopalatine foramen surrounded by maxilla; mandible robust, mental foramen below p4; shallow masseteric fossa extends to below m1 and lacks upper masseteric crest, lower masseteric crest with a well-developed horizontal anterior part and a posterior part extending to angular process; dental formula 1/1, 0/0, 1/1, 3/3; cheek teeth brachydont, robust, and relatively wide; on P4 metaloph usually incomplete, anterior cingulum weak or absent; on upper molars entoloph well developed, hypocone large, metaloph wide but incomplete, never joining protocone, sinus shallow, transverse, more or less symmetrical, anterior cingulum joining protoloph, and anterocone absent; on lower molars trigonid relatively large, posterior arm of protoconid extending relatively posteriorly, with straight buccal part, ectolophid located near medial line, lacking anterior cingulum; on m3 hypoconulid reduced.

DISCUSSION: *Karakoromys* generally looks more primitive than the Tataromyinae and Ctenodactylinae in retaining the following features: cheek teeth brachydont, main cusps distinct, metaloph incomplete, with vestige of metaconule, and short posterior arm of protoconid. It is similar to the Tataromyinae in morphology of the mandible, losing the upper masseteric crest and having the lower one bipartite. However, it is even closer to the Ctenodactylinae in the position of the ventral root of the maxillary zygomatic process and tooth morphology—proportionately wide cheek teeth, large hypocone, well-developed entoloph, and relatively posteriorly extending posterior arm of the protoconid. Because the characters common to *Karakoromys* and the Tataromyinae are primitive within the Ctenodactylidae and those commonly shared by it and the Ctenodactylinae are derived, it has closer relationships to the Ctenodactylinae than to the Tataromyinae. On the other hand, it lacks such advanced features common to all the later Ctenodactylinae, as the particularly developed hori-

zontal masseteric crest, hypsodont cheek teeth. In addition, it possesses some autapomorphic characters of its own: sphenopalatine foramen anterior to above M1, transverse and symmetrical sinus on the upper molars, reduced hypoconulid on lower molars. *Karakoromys* was considered the representative of a separate subfamily, *Karakoromyinae* (Wang, 1994).

*Karakoromys* Matthew and Granger, 1923

*Karakoromys* Matthew and Granger, 1923: 6.  
*Terrarboreus* Shevyreva, 1971b: 81–83, fig. 7.  
*Woodomys* Shevyreva, 1971b: 83–85, fig. 8.

TYPE SPECIES: *Karakoromys decessus* Matthew and Granger, 1923.

INCLUDED SPECIES: *Karakoromys* sp.

GEOLOGICAL RANGE: Early Oligocene.

GEOGRAPHIC DISTRIBUTION: Nei Mongol of China, Mongolia, and Kazakhstan.

EMENDED DIAGNOSIS: Small ctenodactylid; cheek teeth brachydont; on molars transverse lophs high, main cusps distinct but not swollen; on upper molars metaloph incomplete, usually free lingually, short ridge connecting metaloph and posteroloph very weak or absent, mesosinus usually united with the posterosinus to form a continuous U-shaped valley; on lower molars lingual part of posterior arm of protoconid short or absent, trigonid basin open, arm of entoconid transverse, entoconid, hypoconid, and hypoconulid near cone-shaped, on m3 talonid reduced.

DISCUSSION: *Karakoromys* was named by Matthew and Granger (1923). Until now the genus has been known to include only one species, *Karakoromys decessus*. Some specimens from Saint Jacques and Shargaltein Gol, which were assigned to *Karakoromys* by Teilhard de Chardin (1926) and Bohlin (1937), respectively, have been transferred to *Tataromys* (see above). Kowalski (1974: 167) doubted whether *Karakoromys* merited generic separation, when small forms of *Tataromys* were discovered. Huang (1985: 37) also thought that *Karakoromys decessus* might be a small species of *Tataromys*, or even a synonym of *Yindirtemys grangeri*.

Having compared the specimens of *Karakoromys* with all the mid-Tertiary ctenodactylids in detail, I found that *Karakoromys* was quite unique in morphology and differed

from *Tataromys*, *Yindirtemys*, and *Bounomys*. As far as the lower teeth are concerned, the main characters of *Karakoromys* are as follows: cheek teeth proportionately wide; trigonid relatively long, with large open basin; posterior arm of protoconid extending relatively posteriorly and with weakly developed lingual part, transverse arm of entoconid on lower molars, and reduced talonid on m3. In addition, *Karakoromys* differs from *Tataromys* in its less lingually situated ectolophid. It differs from *Yindirtemys* and *Bounomys* in having straight, less swollen posterior arm of protoconid, and less crescentic entoconid, hypoconid, and hypoconulid; from *Yindirtemys* further in lacking anterior cingulum on lower molars and having different dp4; and from *Bounomys* further in lacking longitudinal arm of entoconid. As for the upper jaw, *Karakoromys* also has features distinct from other ctenodactylids, if the upper jaws described here really belong to this genus (see below). The main distinguishing features of upper teeth of *Karakoromys decessus* are (1) on upper molars metaloph is robust, incomplete, never joining protocone; (2) mesosinus usually unites with posterosinus to form a U-shaped valley; (3) entoloph is present on M1 and M2; (4) hypocone is about equal to protocone; (5) sinus is more transverse, more or less symmetric and never opposite, or open to the posterosinus; (6) anterocone is absent; (7) the ventral ramus of the maxillary zygomatic process and the choana are more anteriorly located. It is evident that *Karakoromys* is not only a valid genus and species, but also represents a distinct lineage from *Tataromys*, *Yindirtemys*, and *Bounomys*.

*Karakoromys decessus* Matthew and Granger, 1923

Figures 16B, C, 30–32; tables 20, 21

*Karakoromys decessus* Matthew and Granger, 1923: 6–7, fig. 7. Bohlin, 1946: 135, fig. 37. Stehlin and Schaub, 1951: 288–290, fig. 494. Schaub, 1958: 780, fig. 207. Mellett, 1968: 6, 10. Wood, 1977: 125, fig. 3P. Wang et al., 1981: 28–29. Russell and Zhai, 1987: 321, 329. Wang, 1994: 38–40, fig. 4.

*Karakoromys decessus* (partim): Teilhard de Chardin and Leroy, 1942: 25, 89. Kowalski, 1974: 166–167, pl. XLIX, figs. 3–5, 7.

*Terrarboreus arcanus* Shevyreva, 1971b: 81–83, fig. 7. Russell and Zhai, 1987: 332, 345.

*Woodomys chelkaris* Shevyreva, 1971b: 83–85, fig. 8. Russell and Zhai, 1987: 306, 332, 345.

*Tataromys* sp. B.-y. Wang et al., 1981: 28–29. NEW SYNONYMY.

*Tataromys* spp. (partim) Huang, 1982: 340–341, 347.

?*Karakoromys decessus* Huang, 1985: 36–37.

*Karakoromys decessus*? Russell and Zhai, 1987: 292, 355.

*Karakoromys* cf. *decessus* Wang and Wang, 1991: 67–70.

*Woodomys dimetron* Shevyreva, 1994b: 116, fig. 11. NEW SYNONYMY.

TYPE SPECIMEN: AMNH 19070, lower jaw, both rami with cheek teeth and left incisor complete, from the Hsanda Gol Formation, red beds, Loh, Tsagan Nor basin, Mongolia, and figured by Matthew and Granger (1923: fig. 7).

REFERRED SPECIMENS: AMNH 19071–19074, 19077, 22079, 84209; IVPP V 7351, V 10576.1–140, V 10577.1–5, V 10578, V 10579.1–39, V 10580.1, V 10580.2, V 10581.1–3, V 10582.1–4, V 10583.1–5, V 10584.1–6, V 12044, V 12050, V 12051.1–3; PIN 478/306, 478/386, 478/387, 2259/449; MgM-III/49/3–11, MgM-III/50, MgM-III/51/2–9, MgM-III/51/11–13 and PIN 2979/2706.

GEOLOGICAL RANGE: Early Oligocene, the Wulanbulage Formation, Ulanatal Formation, Hsanda Gol Formation and Buran Formation.

GEOGRAPHIC DISTRIBUTION: Saint Jacques [IVPP locs. 77046.1 (V 10577), 77047 (V 10578), 77049.2 (V 10579), and 78020 (V 12044)], Qianlishan District [IVPP locs. 79010 (V 10580), 77011 (V 10581), and 78018 (V 10584; top level, V 10582; upper level, V 10583)], Kekeamu [IVPP loc. 88004-2 (V 10576)] and Ulanatal area (V 7351, V 12051), Nei Mongol, China; Loh, Tatal Gol, Khatan Khayrkan, Boongeen Gol, Ulan Ganga, Mongolia; Chelkar-Teniz, Aktyubinsk Area, and Kyzyl-Kak, Dzhezkazgan Area; Chaybulak-Dzhamangora Watershed, Kazakhstan.

DIAGNOSIS: Sphenopalatine foramen situated above junction of P4 and M1; on upper molars wide metaloph with or without distinct metaconule; on p4 metaconid usually isolated and hypoconulid usually distinct.

DESCRIPTION: Six fragments of maxillae are known. The incisive foramen is large and extends posteriorly to the level of P4. As in the living ctenodactylids, the ventral ramus of the zygomatic process of the maxilla is anterior to P4, more anterior than in *Tataromys*, *Yindirtemys*, and *Bounomys*. On the ventral surface of this process there is a distinct tubercle with a crest extending laterally along the anterior margin, probably for the attachment of the superficial and lateral branches of the masseter muscle. The alveolar process of the maxilla is not high. The small anterior alveolar foramen is located on the dorsal surface of the ventral ramus of the zygomatic process. The sphenopalatine foramen is entirely surrounded by the maxilla and located above the junction of P4 and M1, similar to that of *Tataromys minor*, but more anteriorly than in *T. plicidens*. The palate is wide and its width between the two dental rows is nearly equal to that of cheek teeth. The posterior palatine foramen is on the maxillary–palatine suture and opposite M1. The posterior maxillary notch is distinctly behind M3. As in *Ctenodactylus*, the anterior margin of choana is only slightly behind M3, more anteriorly situated than in *Tataromys*, *Yindirtemys*, and *Bounomys* but more posteriorly than in *Cocomys*.

The horizontal ramus of the mandible is robust and high. The mental foramen is below p4. The large masseteric fossa extends to below m1. As in the *Tataromyinae*, the upper masseteric crest is absent, whereas the lower one is well developed and subdivided into two parts: a horizontal anterior part below m1 and m2 and an oblique posterior part extending to the angular process. The ascending ramus is damaged. Its anterior margin arises lateral to m3. On the lingual side there is a distinct ridge extending back from m3. The mandibular foramen is just below it.

The lower incisor is oval in cross section, with a slightly flat medial side. Enamel covers about one-third of the lateral surface and one-quarter of the medial one. The surface of the enamel is covered by fine wrinkles.

The cheek teeth are brachydont, moderately robust, and wide relative to length. The main cusps are distinct but not swollen, whereas the lophs are well developed. The first molar is the smallest. M3 is always

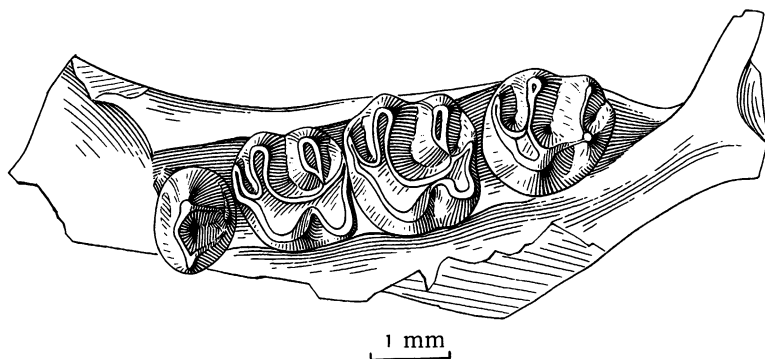


Fig. 30. Occlusal view of left upper jaw with P4–M3 (IVPP V 10576.1) of *Karakoromys decessus*.

smaller than M2 (7/7). However, m3 is variable in size: equal (2/16) to, larger than (8/16), or even smaller than m2 (6/16).

P4: The paracone is not compressed. On most of P4 the proto-loph is low and weak (11/21) or absent (5/21). On others it is high, but is slender and hardly curved when present. The metaloph is usually incomplete. The wide posterior arm of the paracone extends posterolingually and may be free (16/21) or reach the posteroloph (5/21). It never joins the posterior arm of the protocone. The posterior arm of the protocone may be free and separated from the posteroloph (9/20) or join the latter to form a continuous loph. Sometimes there is a distinct hypocone at the lingual end of the posteroloph. The anterior cingulum is usually absent (18/23), but when present it is low and weak.

The upper molars are slightly wider than long. One of the most distinctive features of *Karakoromys decessus* is that all the upper molars, including not only M3 but also M1

and M2, have a well-developed entoloph connecting protocone with hypocone. As opposed to *Tataromys*, *Yindirtemys*, and *Bounomys*, the metaloph is robust but incomplete, with a free lingual end where a vestige of the metaconule can be seen on some upper molars. In a few specimens it is connected with the hypocone or posteroloph by a thin ridge. The direction of the metaloph varies from transverse to slightly anterolingually oblique. It never joins the protocone or entoloph directly. Therefore, the mesosinus usually unites with the posterosinus to form a continuous U-shaped valley. Unlike the condition in *Tataromys minor* and *Bounomys*, the anterior cingulum links the proto-loph. There is no distinct anterocone, and no distinct posterocone on the posteroloph. On M1 and M2 the hypocone is about equal in size to the protocone. The sinus is usually transverse and symmetrical; sometimes it is slightly oblique posteriorly, but never so oblique as to be opposite or join the posterosinus as in

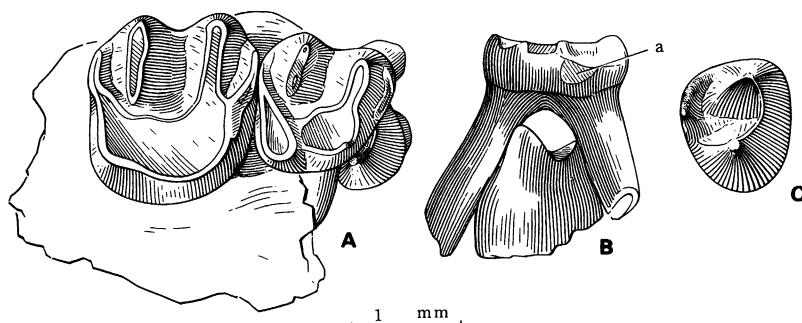


Fig. 31. Right dP4, P4, M1 (IVPP V 10581.1) of *Karakoromys decessus*. A. Occlusal view of dP4, P4–M1. B. Anterior view of dP4 and P4; a, wear facet for dP3. C. Occlusal view of P4.

*Tataromys minor* and *Bounomys bohlini*. On M3 the hypocone is smaller than the protocone and the sinus is shallow and symmetrical. The posteroloph is much shorter than that of M1 and M2.

DP4 (fig. 16B) is molariform and similar to upper molars except in having a lower, isolated anterior cingulum. Most dP4 (8/9) have a wear facet on their anterior side, showing that dP3 may have been present in this species. IVPP V 10581.1 (fig. 31) has dP4 and P4–M1. As in most dP4, there is a distinct wear facet on the anterior side, whereas P4 is typical for *Karakoromys decessus*. Apparently, *Karakoromys decessus* has two upper deciduous teeth (dP3 and dP4), but has only one permanent tooth (P4), and the P3 did not develop.

On p4 the metaconid, about equal to the protoconid in size, is lower and cuspsate. It may be isolated (7/11) or connected with the protoconid by a narrow ridge (4/11). The anterosinusid usually unites with the mesosinusid. The usually low, long ectolophid connects the posterior arm of the protoconid with the hypoconulid. Unlike in other ctenodactylid genera, the hypoconulid is usually present as a distinct cusp at the point where the ectolophid joins the arm of the entoconid. The entoconid is low. The hypoconid is usually reduced to either a low transverse crest or an isolated cusp, except in AMNH 19071, which has a large hypoconid with a distinct posterior arm.

IVPP V 10576.25 is a fragment of right lower jaw with i2 and p4. The trigonid resembles other p4 of *Karakoromys*, but the talonid is unusual. The three main cusps (entoconid, hypoconid, and hypoconulid) are low and isolated. The hypoconulid is not located in the same transverse line as the other two cusps, but behind them. The low ectolophid, slightly buccally located, connects the posterior arm of the protoconid with the hypoconid. This tooth seems more primitive than other p4 and may or may not belong to *Karakoromys decessus*. Unfortunately, no molar is preserved, although i2 and the lower jaw are similar to those of *Karakoromys* and other ctenodactylids.

On the lower molars the metaconid and protoconid are prominent, not compressed. Metalophid I is complete and straight. The

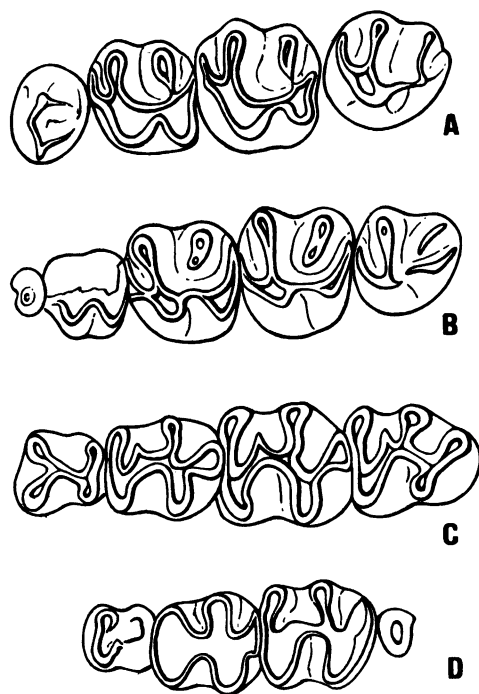


Fig. 32. Comparison of cheek teeth of *Karakoromys decessus* (after Wang, 1994, fig. 4). **A.** Left P4–M3 (IVPP V 10576.1). **B.** Left dP3, dP4, M1–M3 (no. 478/386, holotype of *Terraroboreus arcanus*). **C.** Left p4–m3 (AMNH 19070, holotype of *Karakoromys decessus*), after Matthew and Granger, 1923, fig. 7. **D.** Left p4–m2 (no. 478/387, holotype of *Woodomys chelkaris*), after Shevyreva, 1971b, fig. 8B. All  $\times 12$ .

posterior arm of the protoconid does not shift anteriorly but extends relatively posteriorly. The buccal part is straight and not swollen. The lingual part is very short or absent, not reaching the metaconid. The large trigonid basin opens posterolingually. The short ectolophid is located near the midline. The entoconid, hypoconid, and hypoconulid are more cone-shaped than crescentic. Entoconid and hypoconid are opposite each other and have more or less transverse arms. The hypoconulid always joins the hypoconid.

Dp4 (fig. 16C) is similar to the lower molars, but narrower, longer in proportions, and has more distinct main cusps and lower lophs. The trigonid is much narrower than the talonid. Both the protoconid and metaconid are isolated, with no connection between them. The posterior arm of the pro-

TABLE 20  
Measurements (in mm) of Upper Teeth of  
*Karakoromys decessus*

		N	Min	Max	Aver	S	V
P4-M3	L	1			5.68		
M1-3	L	2	4.08	4.56	4.32	0.34	0.12
P4-M2	L	3	3.92	4.24	4.11	0.17	0.03
P4-M1	L	6	2.24	2.80	2.49	0.18	0.03
M1-2	L	5	2.70	3.28	2.94	0.24	0.06
M2-3	L	3	2.72	3.40	3.08	0.34	0.12
P4	L	24	0.82	1.07	0.98	0.06	0.004
P4	W	23	1.01	1.56	1.32	0.12	0.01
M1	L	34	1.23	2.02	1.45	0.16	0.03
M1	W	34	1.28	1.89	1.54	0.14	0.02
M2	L	22	1.36	2.05	1.65	0.19	0.04
M2	W	22	1.44	2.21	1.73	0.21	0.04
M3	L	18	1.19	1.80	1.56	0.19	0.04
M3	W	18	1.15	1.76	1.55	0.16	0.03
dP4	L	8	1.04	1.28	1.14	0.08	0.007
dP4	W	8	1.04	1.28	1.18	0.08	0.006

TABLE 21  
Measurements (in mm) of Lower Teeth of  
*Karakoromys decessus*

		N	Min	Max	Aver	S	V
p4-m3	L	4	6.31	6.56	6.40	0.11	0.01
m1-3	L	7	5.29	6.07	5.52	0.29	0.08
p4-m2	L	6	4.18	4.59	4.40	0.16	0.02
p4-m1	L	6	2.46	2.79	2.66	0.13	0.02
m1-2	L	14	2.88	4.08	3.52	0.28	0.08
m2-3	L	9	3.65	4.26	3.89	0.23	0.05
p4	L	16	0.98	1.28	1.11	0.08	0.007
p4	W	15	0.84	1.12	0.94	0.09	0.009
m1	L	29	1.19	1.98	1.63	0.18	0.03
m1	W	29	1.08	1.59	1.32	0.12	0.01
m2	L	37	1.52	2.21	1.87	0.18	0.03
m2	W	38	1.24	1.85	1.57	0.14	0.02
m3	L	19	1.48	2.13	1.92	0.18	0.03
m3	W	19	1.28	1.64	1.43	0.12	0.01
dp4	L	5	1.16	1.31	1.22	0.06	0.003
dp4	W	5	0.86	0.90	0.88	0.02	0.0003

toconid may be present or absent. The low and long ectolophid may link with the posterior arm of the protoconid or may reach the posterior side of the metaconid. The hypoconulid may be isolated or may meet the hypoconid.

DIMENSIONS: Tables 20 and 21.

DISCUSSION: The type specimen of *Karakoromys decessus* is a lower jaw from the Hsanda Gol Formation. In 1974, Kowalski referred some upper and lower jaws from the early Oligocene of Mongolia to *K. decessus*. As mentioned above, his *K. decessus* was based on mixed samples. Some of these lower jaws (Z.Pal. no. MgM-III/48 and Z. MgM-III/51/10) may belong to *T. minor*. It should be born in mind that both *T. minor* and *K. decessus* are small-sized, brachydont, and their type specimens are exclusively lower jaws. Until now, no upper jaw in association with lower jaw has been collected. How to distinguish the upper cheek teeth of *T. minor* from those of *K. decessus* causes problems. In 1987, some small early Oligocene ctenodactylids were collected in Kekeamu, Alxa Zuoqi, Nei Mongol (Wang and Wang, 1991). Although the upper and lower jaws were collected separately, they were found in the same level of the same locality (IVPP loc. 88004-2). All the lower cheek teeth are of *K. decessus* type. It is logical to consider that

among the upper cheek teeth there should be some that belong to the same species as the lowers do. In fact, they match with the lower teeth of *K. decessus* very well. Therefore, we assigned these upper teeth to the same species. In this case the upper teeth of *K. decessus* also differ from those of *T. minor* and other ctenodactylids (see above).

Shevyreva (1971b) described two genera from the early Oligocene of Kazakhstan: *Woodomys* and *Terrarboreus*. *Terrarboreus* is known only by the type species, *Terrarboreus arcanus*, based on only the holotype (PIN 478/386), a maxilla with five teeth, which, according to Shevyreva, were P3–P4 and M1–M3. It appears to me that the first two teeth of PIN 478/386 should be interpreted as deciduous teeth, dP3–dP4, because they were more heavily worn than molars (fig. 32B). Being interpreted as such, the species is identical with *Karakoromys decessus* in size and morphology. The genus *Terrarboreus* and its type species, *T. arcanus*, therefore, are junior synonyms (Wang, 1994).

According to Shevyreva (1971b, 1994b), *Woodomys* included two species, *W. chelkaris* and *W. dimetron*. *Woodomys* and *W. chelkaris* were proved to be junior synonyms of *Karakoromys* and *K. decessus* (Wang, 1994). *W. dimetron*, based on only a m2 from Kazakhstan, is also identical with that

of *K. decessus* in having relatively posteriorly extending posterior arm of protoconid, with short lingual part, open trigonid basin, and transverse arms of entoconid. In addition, it is within the range of variation in size for *K. decessus*. *W. dimetron* is a junior synonym of *Karakoromys decessus*.

*Karakoromys* sp.

A right M1 or M2 (IVPP V 10585) from the early Oligocene of loc. 77049.2 of Saint Jacques, Hangjinqi, Nei Mongol, is similar to *Karakoromys* in general morphology. The tooth is proportionately wider, having distinct main cusps, well-developed entoloph, an incomplete but robust metaloph with metaconule, and more transverse and symmetric sinus, lacking distinct anterocone. It is larger (L, 2.08 mm; W, 2.08 mm) for *K. decessus*. It may represent a large individual of *Karakoromys decessus* or a distinct species.

*Euryodontomys*, new genus

TYPE SPECIES: *Euryodontomys ampliatus*, new species.

INCLUDED SPECIES: *Euryodontomys exiguus*, new species.

GEOLOGICAL RANGE: Early Oligocene.

GEOGRAPHIC DISTRIBUTION: Nei Mongol, China.

DIAGNOSIS: Cheek teeth brachydont, but higher in crown than those of *Karakoromys*, wider and shorter in proportions, on upper molars metaloph connected with posteroloph by a better developed short ridge, mesosinus large L-shaped; on lower molars posterior arm of protoconid complete, with a well-developed lingual part joining metaconid, trigonid basin large and closed, entoconid conical in shape, with narrow, slightly oblique arm, m3 short, with much reduced hypoconulid.

ETYMOLOGY: *Euryodontomys* = Eury + odonto + mys, from Greek: *eury*s, broad, wide; *odonto*s, tooth; *mys*, mouse.

COMPARISON: This animal differs from the known primitive ctenodactylids, including *Tataromys*, *Yindirtemys*, *Bounomys*, and *Karakoromys* in having a reduced m3 with vestigial and cuspidate hypoconulid. It is similar to *Karakoromys*, but different from *Tataromys*, *Yindirtemys*, and *Bounomys* in the fol-

lowing features: the cheek teeth are proportionately wider; the upper molars have entoloph, incomplete metaloph not joining the protocone, and more transversely directed sinus; on the lower molars the posterior arm of protoconid extends more posteriorly, with straighter buccal part; entoconid cone-shaped, and the sinusid is less oblique. It can also be distinguished from *Karakoromys* in its higher crowned teeth, better developed short ridge connecting metaloph with posteroloph, complete posterior arm of protoconid with better developed lingual part joining metaconid, closed trigonid basin, shorter m3 with more reduced hypoconulid. It represents a genus distinct from other ctenodactylids. Because the features shared by *Euryodontomys* and *Karakoromys* are derived, the two genera seem to have closer relationships than to *Tataromys*, *Yindirtemys*, and *Bounomys*. *Euryodontomys* may represent an advanced member of the Karakoromyinae.

*Euryodontomys ampliatus*, new species

Figure 33, table 22

*Tataromys* cf. *sigmodon* Huang, 1985: 31–32; pl. II, fig. 1. NEW SYNONYMY.

HOLOTYPE: A fragment of left lower jaw with m1–3 (IVPP V 7344), from the upper part of the Ulanatal Formation of the Ulanatal area, Alxa Zuoqi, Nei Mongol, China, and figured by Huang (1985: pl. II, fig. 1).

REFERRED MATERIAL: Two fragmentary lower jaws (IVPP V 10586, V 10587.3), left M1–3 (IVPP V 10587.1), and one fragmentary upper jaw with right P4–M1 and left M1 and M3 (IVPP V 10587.2).

GEOLOGICAL RANGE: Late early Oligocene, the upper part of the Ulanatal Formation.

GEOGRAPHIC DISTRIBUTION: Ulanatal area (V 10587), Alxa Zuoqi, and Saint Jacques [IVPP loc. 78020 (V 10586)], Hangjinqi, Nei Mongol, China.

ETYMOLOGY: *Ampliatus*, Latin, enlarged.

DIAGNOSIS: One and one-half times the size of *Karakoromys decessus*; on lower molars metaconid and entoconid large and cone-shaped, arm of entoconid relatively transverse.

DESCRIPTION: A fragment of maxilla, IVPP V 10587.2, is preserved. The palate is wide and the width between the two dental rows



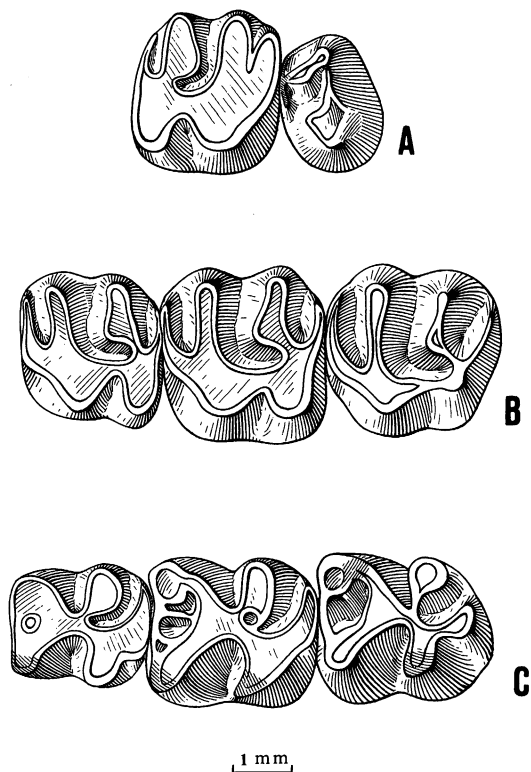


Fig. 33. Occlusal view of cheek teeth of *Eur-yodontomys ampliatus*, new genus and species. A. Right P4-M1 (IVPP V 10587.2). B. Left M1-M3 (IVPP V 10587.1). C. Left m1-m3 (IVPP V 7344, holotype).

is wider than that of the cheek teeth. The posterior part of the incisive foramen is wide and extends posteriorly to the level of P4. The ventral root of the zygomatic process of the maxilla is anterior to P4.

The lower jaw is similar to that of *K. decessus*. The mental foramen is below p4. The masseteric fossa extends below m1. The upper masseteric crest is lost and the lower one is also separated into two parts.

The cheek teeth are brachydont, slightly higher in crown than in *K. decessus*. They are wider and shorter in proportion. The first molars are the smallest. Both M3 and m3 are not enlarged and are slightly smaller than M2 and m2, respectively. The upper cheek tooth crowns are higher lingually than buccally.

P4 is obliquely implanted in the maxilla. The protocone is larger than the paracone, without a distinct posterior arm. As in *K. de-*

*cessus*, the protocone is straight and narrow. The posterior arm of the paracone is wide and extends more posteriorly than lingually to meet the posterior cingulum rather than the protocone. The trigon basin is open posteriorly. There is no distinct anterior cingulum.

The upper molars are wider than long. The protocone is the largest cusp and about triangular in form when worn. The hypocone is slightly smaller than the protocone. The entoloph is well developed. The paracone and metacone are less distinct than in *K. decessus* and equal to each other in size and morphology. The protocone is complete. The metaloph is robust, slightly oblique anterolingually and incomplete. A vestige of the metaconule may be present. The short ridge connects the metaconule with the posteroloph. The anterior cingulum is longer than the posteroloph. As in *Karakoromys*, there is no distinct anterocone. The anterosinus is longer than the posterosinus. The mesosinus is largest and L-shaped. The sinus is more transverse than oblique, and not opposite the posterosinus. M3 has a slightly narrow posterior part, and the hypocone is smaller and located slightly buccally.

On m1 the trigonid is narrower than the talonid but as long as the latter. The metaconid is distinctly cone-shaped and the protoconid is not compressed. Metalophid I is narrow and straight. The posterior arm of the protoconid is well developed and extends relatively posteriorly. It may separate into three parts: a straight buccal part, a slightly enlarged middle part, and a long lingual part. The lingual part turns forward to reach the metaconid and enclose a large trigonid basin. The short ectolophid is located near the midline. The entoconid is also cone-shaped, with a narrow, transverse arm reaching the ectolophid. The hypoconid and hypoconulid are nearly semilunar in shape. The hypoconulid joins the hypoconid. The posterosinusid is deeper than the hyposinusid. The short V-shaped sinusid and mesosinusid are opposite each other, similar in size, and slightly oblique.

m2 is similar to m1, but the trigonid is as wide as the talonid. The trigonid basin is large and has an accessory crest. In the posterosinusid there is an accessory arm that

TABLE 22  
Measurements (in mm) of Cheek Teeth of  
*Euryodontomys*, new genus

			<i>E. ampliatus</i> , new species		<i>E. exiguus</i> , new species
			V 7344 (type)	V 10586	V 7350.4 (type)
m1-3	L		8.12		4.51
m1-2	L		5.33		3.03
m2-3	L		5.66		3.12
m1	L		2.46		1.42
m1	W		2.13		1.23
m2	L		3.03	2.95	1.64
m2	W		2.62	2.54	1.39
m3	L		2.87		1.48
m3	W		2.54		1.25

			V 10587.1	V 10587.2	
				left	right
M1-3	L		8.20		
P4-M1	L			4.18	
M1-2	L		5.33		
M2-3	L		5.82		
P4	L			1.64	
P4	W			2.21	
M1	L		2.50	2.46	2.54
M1	W		2.71	2.71	2.71
M2	L		2.95		
M2	W		3.12		
M3	L		2.95		2.87
M3	W		2.95		2.87

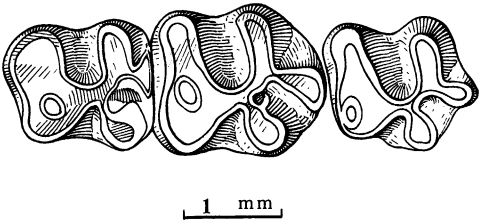


Fig. 34. Occlusal view of right m1–m3 (IVPP V 7350.4) of *Euryodontomys exiguus*, new species.

of the relevant specimens shows that V 7344 differs from *Tataromys*, *Yindirtemys*, and *Bounomys*, but is similar to *Karakoromys* in proportionately wide cheek teeth, large trigonid basin, relatively posteriorly extending posterior arm of protoconid, transverse arm of entoconid, and reduced m3. In addition, the upper cheek teeth from the Ulantatal area, which match with the lower molars of V 7344 very well, are also similar to *Karakoromys* in cheek tooth structure. However, they differ from *Karakoromys* not only in being larger in size, but also in higher crowns, upper molars with more developed short ridge, large L-shaped mesosinus, lower molar having complete metalophid II and closing trigonid basin, and a shorter m3 with a more reduced hypoconulid.

*Euryodontomys exiguus*, new species

Figure 34; table 22

*Tataromys bohlini* (partim) Huang, 1985: 29–31.  
NEW SYNONYMY.

HOLOTYPE: A right lower jaw with m1–m3 (IVPP V 7350.4).

HORIZON AND LOCALITY: Late early Oligocene, the upper part of the Ulantatal Formation, Ulantatal area, Alxa Zuoqi, Nei Mongol, China.

DIAGNOSIS: Approximately one-half size of *E. ampliatus*, lower molars with slightly oblique arm of entoconid and more reduced hypoconulid, and m3 more reduced.

ETYMOLOGY: *Exiguus*, Latin, small, short.  
DIMENSIONS: Table 22.

REMARKS: IVPP V 7350.4 was first described by Huang (1985: 29–31) as *Tataromys bohlini*. It proves to be similar to *Karakoromys* and *Euryodontomys* than to *Bounomys bohlini* in tooth morphology. Its cheek

may extend from the entoconid to the ectolophid to close a small basin (IVPP V 7344), or may be free and extend backward from the arm of the entocone (IVPP V 10586).  
m3 is similar to m2, but with a reduced talonid. The hypoconulid is cone-shaped, smaller than the other main cusps. The entoconid has only one arm. No distinct accessory crest occurs in the posterosinusid.  
DIMENSIONS: Table 22.  
DISCUSSION: IVPP V 7344 was considered as *Tataromys* cf. [*T.*] *sigmodon* by Huang (1985) although he thought that both his and Bohlin’s *T.* cf. [*T.*] *sigmodon* may represent a new species of *Tataromys*. As mentioned above, Bohlin’s *T.* cf. [*T.*] *sigmodon* is referred to *Yindirtemys* sp. Further comparison

teeth are wider, with better developed lophs, have larger trigonid, more posteriorly extending and less swollen posterior arm of protoconid, and conic-shaped entoconid. It is more similar to *Euryodontomys ampliatus* than to *Karakoromys* in having a higher crown, a better developed lingual part of posterior arm of protoconid, a closed trigonid basin, and more reduced m3. However, V 7350.4 differs from *E. ampliatus* in much smaller size (nearly one-half size of *E. ampliatus*), having more reduced and relatively smaller m3, and lower molar with more reduced hypoconulid and slightly oblique arm of entoconid.

SUBFAMILY DISTYLOMYINAE WANG, 1994

TYPE GENUS: *Distylomys* Wang, 1988.

INCLUDED GENUS: *Prodistylomys* Wang and Qi, 1989.

GEOLOGICAL RANGE: Late Oligocene to ?middle Miocene.

GEOGRAPHIC DISTRIBUTION: North China.

DIAGNOSIS: Middle-sized ctenodactylids; lower jaw robust, mental foramen near the upper margin of middle of diastema, masseteric fossa extending below dp4, without upper crest but with well-developed lower crest; dental formula:  $? / 1 \ 0 \ 1 \ 3$ ; cheek teeth hypsodont and bilobate, with or without root, bridge connecting the two prisms short and situated at the middle of the tooth, sinusid and mesosinusid deep, wide and opposite to each other, teeth covered with cement; shedding of dp4 delayed.

REMARKS: The Distylomyinae were first tentatively considered as a special and independent family, Distylomyidae, of the Ctenodactyloidea by Wang (1988). At that time it was clear that they were similar to the ctenodactylids in the lower jaw structure and the general tooth morphology, excluding the first lower cheek tooth. The problem lies in the fact that the first tooth of *Distylomys* was then considered p4. Because of its degree of molarization, it was difficult then to assign the species to the Ctenodactylidae.

Recently, the first tooth of known *Prodistylomys* jaw has been recognized as dp4 (Wang and Qi, 1989). The first tooth of *Distylomys* is similar in morphology to dp4 of *Prodistylomys*. Therefore, I now consider the first tooth of *Distylomys* dp4 rather than p4.

As in *Prodistylomys*, the shedding of dp4 may be delayed here, and p4 may never appear in *Distylomys*. Because the dp4 of ctenodactylids is molariform and the shedding of dp4 is also delayed in some ctenodactylids, such as *Sardomys* (de Bruijn and Rümke, 1974; Wood, 1977; 135), *Sayimys intermedius*, and *S. sivalensis* (de Bruijn et al., 1989), there is no obstacle to referring *Distylomys* and *Prodistylomys* to the Ctenodactylidae. The Distylomyidae was earlier considered a subfamily of the Ctenodactylidae (Wang, 1994).

### *Distylomys* Wang, 1988

TYPE SPECIES: *Distylomys tedfordi* Wang, 1988.

INCLUDED SPECIES: *Distylomys qianlishanensis* Wang, 1988.

GEOLOGICAL RANGE: Late Oligocene to ?middle Miocene.

GEOGRAPHIC DISTRIBUTION: Nei Mongol, China.

DIAGNOSIS: "Middle sized ctenodactylid, lower jaw thick, mental foramen near upper margin of middle of diastema, distinct masseteric crest extends anteriorly to below p4, sciurognathous angular process; dental formula  $/ 1 \ 0 \ 1 \ 3$ ; p4 (= dp4 here) molariform, with wide talonid; cheek teeth hypsodont, rootless and composed of two prisms; the bridge connecting the two prisms narrow; mesoflexid and ectoflexid deep and wide, opposite to each other and covered by cement; worn occlusal surface of cheek teeth smooth and concave; on posterior side enamel thin or interrupted" (Wang, 1988: 45–46).

### *Distylomys tedfordi* Wang, 1988

Figure 35; table 23

HOLOTYPE: Right lower jaw with i2 and dp4–m3 (AMNH 114262), from ?Tunggur Formation of the Tairum Nor Basin, Tunggur District, Sonid Zuoqi (= Left Banner), Nei Mongol, China, and figured by Wang (1988: fig. 2; pl. I, figs. 3–6).

HORIZON AND LOCALITY: ?Middle Miocene, ?Tunggur Formation, Tunggur District, Sonid Zuoqi, Nei Mongol, China.

DIAGNOSIS: "Lower jaw thick, talonid of cheek teeth relatively wide and short, anterior end of p4 (= dp4) pointed, metaflexid

distinct on p4 (= dp4), vestigial on m1 and disappears on m2" (Wang, 1988: 46).

DIMENSIONS: Table 23.

REMARKS: Describing *D. tedfordi*, Wang (1988: 41, 48) pointed out the contradictory fact that *D. tedfordi* from the middle Miocene was morphologically more primitive than late Oligocene *D. qianlishanensis*. The holotype of *D. tedfordi* (AMNH 114262) was reported to be collected from the Tairum Nor Basin, Tunggur District, by the Third Asiatic Expedition in 1928. In 1987 and 1988 a field team of IVPP worked in the Tairum Nor Basin and collected a large number of micromammalian fossils. Strikingly enough, no *Distylomys* was found (Qiu, 1996). Qiu mentioned that there might also be Oligocene deposits near the Tairum Nor Basin (Qiu, pers. comm.). Therefore, I doubt whether the material of *D. tedfordi* found by the Third Asiatic Expedition was really collected from the middle Miocene deposits.

*Distylomys qianlishanensis* Wang, 1988

Figure 36; table 23

HOLOTYPE: A left ramus with dp4–m2 and anterior part of m3 and a right ramus with dp4–m3, which may belong to one individual (IVPP V 7961), from the Yikebulage Formation of IVPP loc. 79017, Yikebulage, Otog Qi (= Banner), Nei Mongol, China, and figured by Wang (1988: fig. 3; pl. I, figs. 1, 2; pl. II).

OTHER SPECIMENS: A left dp4 (IVPP V 10590.1), two m2s (V 10588, V 10590.2), and two m3s (V 10589, V 10590.3).

GEOLOGICAL RANGE: Late Oligocene, the Yikebulage Formation and early Miocene, the Urtu Formation.

GEOGRAPHIC DISTRIBUTION: Qianlishan District, Otog Qi, and Urtu, Nao'ertao Area [IVPP locs. 88005-2 (V 10588), 88005-3 (V 10589), 88005-5 (V 10590)], Alxa Zuoqi, Nei Mongol, China.

DIAGNOSIS: "About one-fourth larger than *D. tedfordi*; lower jaw thick; incisor narrow; cheek teeth with narrower talonid but without any vestige of metaflexid, anterior end of p4 (= dp4) is rounded" (Wang, 1988: 46–47).

DIMENSION: Table 23.

REMARKS: Wang and Wang (1990) re-

ported additional material of *D. qianlishanensis* from the Urtu Formation of Early Miocene from IVPP loc. 88005 (= original h/2), Urtu, Nao'ertao Area, Alxa Zuoqi, Nei Mongol, China. The material is composed of isolated teeth, including one dp4, two m2, and two m3. They resemble the holotype of *D. qianlishanensis* in tooth morphology and size and show that the geological range of *D. qianlishanensis* may be longer than expected and it may survive into the early Miocene.

*Prodistylomys* Wang and Qi, 1989

TYPE SPECIES: *Prodistylomys xinjiangensis* Wang and Qi, 1989.

GEOLOGICAL RANGE: Late Oligocene to early Miocene.

GEOGRAPHIC DISTRIBUTION: Xinjiang and Nei Mongol, China.

DIAGNOSIS: "A more primitive distylomyid close to *Distylomys tedfordi* in size. Differs from *Distylomys* in following features: cheek teeth rooted; dp4 with metaflexid and metafossetid, and shorter trigonid and talonid; molar trigonid short and wide rhombus in form and talonid lozenge shaped, longer and narrower than trigonid; m1–2 with developed metaflexid and thin cement in ectoflexid and mesoflexid" (Wang and Qi, 1989: 34).

*Prodistylomys xinjiangensis* Wang and Qi, 1989

Figure 37; table 23

HOLOTYPE: A fragmentary lower jaw with i2 and dp4–m3 (IVPP V 7962) from IVPP loc. 82503, Chibaerwoyi, the north bank of the Ulungur River, Junggar Basin, Xinjiang, China, and figured by Wang and Qi (1990: fig. 1).

OTHER SPECIMENS: A broken left dp4 (IVPP V 8785.1) and a left m2 (V 8785.2).

GEOLOGICAL RANGE: Late Oligocene, the Suosuoquan Formation and early Miocene, the Urtu Formation.

GEOGRAPHIC DISTRIBUTION: Junggar Basin, Xinjiang, and Urtu, Nao'ertao Area [IVPP loc. 88009 (V 8758)], Alxa Zuoqi, Nei Mongol, China.

DIAGNOSIS: As for the genus.

REMARKS: *Prodistylomys xinjiangensis* was also listed in the early Miocene Urtu

TABLE 23  
Measurements (in mm) of Cheek Teeth of Distylomyinae

		Distylomys						Prodistylomys	
		tedfordi	qianlishanensis					xinjiangensis	
		AMNH no. 114262 (type) <sup>a</sup>	V7961 (type) <sup>a</sup>		V 10588	V 10589	V 10590.1	V 10590.2	V 7962 V 8785.2 (type) <sup>b</sup>
			right	left					
dp4-m3	L								6.72
dp4-m2	L	4.64	6.24	6.32					
m1-3	L								4.80
dp4	L	1.60	2.16	2.16			2.21		1.89
dp4	Wtr	0.88	1.28	1.28			1.23		1.15
dp4	Wta	1.12	1.44	1.44			1.39		1.39
m1	L	1.76	2.08	2.08					1.72
m1	Wtr	1.20	1.76	1.60					1.64
m1	Wta	1.36	1.76	1.76					1.56
m2	L	1.68	1.92	2.00	1.72			1.07	1.56 1.39
m2	Wtr	1.36	1.76	1.76	1.64			1.64	1.72 1.48
m2	Wta	1.44	1.76	1.60	1.80			1.64	1.39 1.29
m3	L					1.86			0.98
m3	Wtr		1.76			1.56			1.31
m3	Wta		1.60			1.39			0.98

<sup>a</sup> After Wang (1988, table 1).  
<sup>b</sup> After Wang and Qi (1989, table 1).

fauna of IVPP loc. 88009 (original h/6), Urtu area (Wang and Wang, 1990: 608). The species is represented there by two isolated cheek teeth. They are hypsodont and rooted. As in the holotype of *P. xinjiangensis*, the dp4 retains a metaflexid (= posterosinusid here). m2 is similar to that of *P. xinjiangensis* in having the trigonid wide, short and rhomboidal in shape, wider than the talonid. However, the trigonid is shorter than that in the holotype and the talonid does not show a metaflexid. As mentioned by Wang and Qi (1989), in *P. xinjiangensis* the metaflexid may become gradually shallower and finally disappear with wear, and the molars may shorten in length toward the root. Probably the m2 (V 10591.2) may be of an older individual than the holotype and the metaflexid might have been already worn off and the tooth shortened. Therefore, the two teeth may belong to the same species. If this proves true, *Prodistylomys xinjiangensis* may survive into the early Miocene.

Although the two genera were sympatric and contemporaneous, *Prodistylomys* was

certainly morphologically more primitive than *Distylomys*. Stratigraphically the beds at loc. 88009 are lower than those of loc. 88005 bearing *Distylomys qianlishanensis*. Thus, in the Urtu area *P. xinjiangensis* occurs earlier than *D. qianlishanensis*.

SUBFAMILY CTENODACTYLINAE HINTON, 1933

TYPE GENUS: *Ctenodactylus* Gray, 1828.  
INCLUDED GENERA: *Sayimys*, *Prosayimys*, *Akzharmys*, *Metasayimys*, *Africanomys*, *Testouromys*, *Sardomys*, *Pireddamys*, *Irhou-dia*, *Pellegrinia*, *Pectinator*, *Massouteria*, and *Felovia*.

GEOLOGICAL RANGE: Early Miocene to Recent.

GEOGRAPHIC DISTRIBUTION: Asia, early to late Miocene; Africa, Miocene to Recent; Sardinia, Miocene; Sicily, Pleistocene.

DIAGNOSIS: Skull relatively low, wide, with a slightly convex roof, rostrum thin, temporal fossa small, temporal crest weak; mandible relatively thin, single horizontal masseteric crest heavy, extending to low condyle, coronoid process weak or absent; dental for-

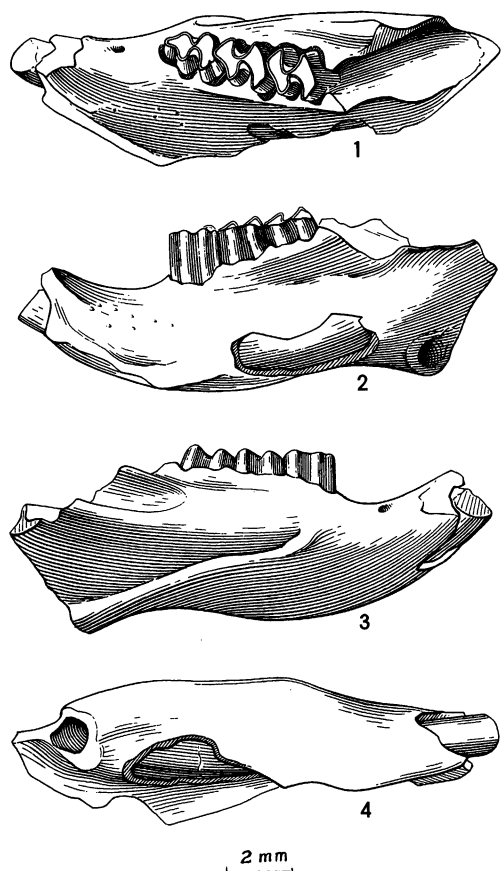


Fig. 35. Right lower jaw with dp4-m2 (AMNH 114262, holotype) of *Distylomys tedfordi*, after Wang, 1988: fig. 2. 1: Occlusal view; 2: Lingual view; 3: Buccal view; 4: Ventral view.

mula: 1/1, 0/0, 1/1-0, 3/3; cheek teeth from unilaterally hypsodont to hypsodont; P4 and p4 reduced, may be lost early in life; upper molars tending to be bilobate, entoloph present, hypocone large, sinus deep and anteriorly oblique, metaloph incomplete or joining posteroloph, anterosinus and posteroloph short or absent; lower molars tending to be tri- or bilobate, posterior arm of protoconid reduced and thin.

REMARKS: The Ctenodactylinae, the fourth subfamily of the Ctenodactylidae, include all the later ctenodactylids from Miocene to Recent. When describing *Sayimys sivalensis* (= his *Pectinator sivalensis*), Hinton (1933) established the subfamily Ctenodactylinae. Although he did not give a diagnosis and list the members of the subfamily, inclusion of

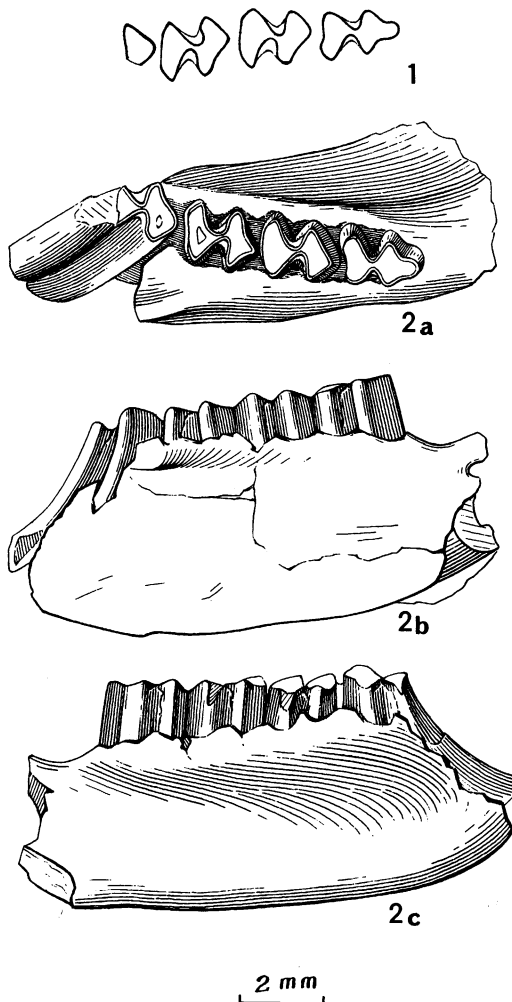


Fig. 36. *Distylomys qianlishanensis* (IVPP V 7961, holotype), after Wang, 1988: fig. 3. 1. Occlusal view of left dp4-m3. 2. Right lower jaw with dp4-m3. 2a. Occlusal view. 2b. Buccal view. 2c. Lingual view.

*Ctenodactylus* was implied. Lavocat (1961) considered "Tataromyidae" valid and subdivided it into two subfamilies: Sayimyinae, including *Sayimys* and *Metasayimys*, and Tataromyinae, including *Tataromys*, *Karakoromys*, and *Africanomys*. It is clear that he excluded all the five genera mentioned above from the Ctenodactylidae. Indeed, *Africanomys* is similar to *Karakoromys* in having an incomplete metaloph, relatively narrow cheek teeth, and less oblique sinus. However, these are primitive features for the Ctenodactylinae. On the contrary, *Africanomys* shares

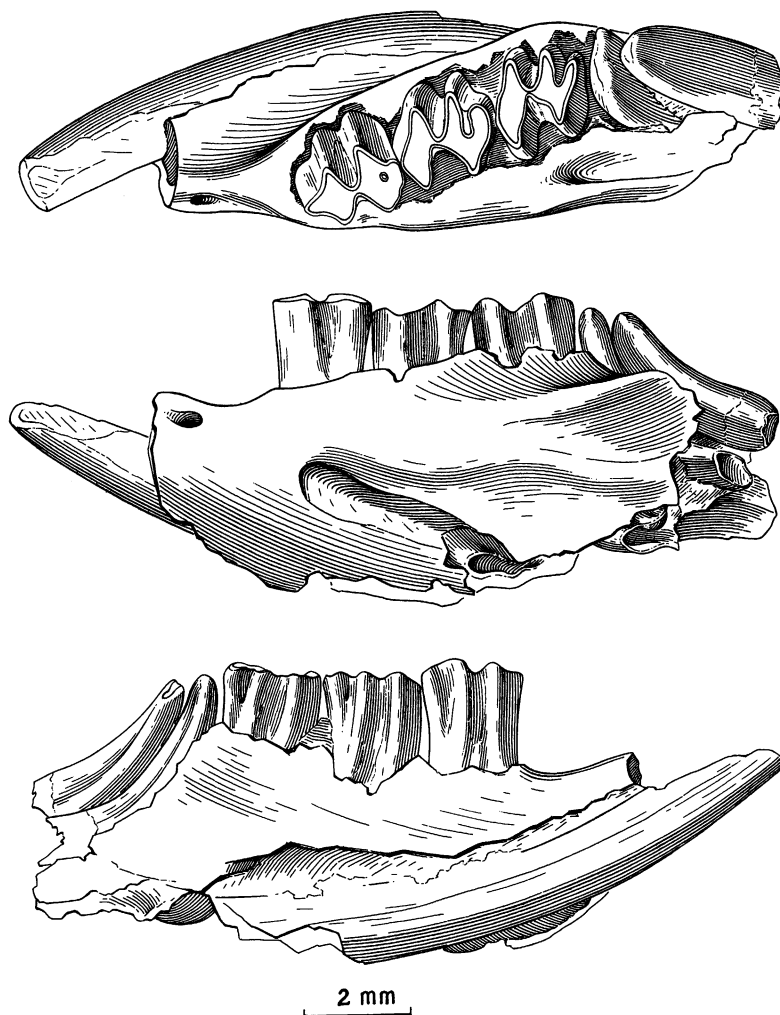


Fig. 37. Left lower jaw with dp4-m3 (IVPP V 7962, holotype) of *Prodistylomys xinjiangensis*, after Wang and Qi, 1989: fig. 1. Top: Occlusal view. Middle: Buccal view. Bottom: Lingual view.

with not only *Sayimys* and *Metasayimys* but also all other later ctenodactylids a number of derived features, such as the weak coronoid process, the single heavy horizontal masseteric crest, hypsodont cheek teeth that tend toward to bilophodonty, and reduced P4 and p4. Because they share these synapomorphies they form a group distinct from the Tataromyinae and Karakoromyinae. Because the name Ctenodactylinae was erected by Hinton in 1933, earlier than the name Sayimyinae of Lavocat (1961), the name Ctenodactylinae is used here.

Relationships among members of the Ctenodactylinae remain somewhat uncertain.

According to Wood (1977: figs. 2, 3), the Ctenodactylinae can be subdivided into at least three groups: the first is formed by *Pi-reddamys* and *Sardomys*; the second includes *Africanomys*, *Irhoudia*, and *Pectinator*; and the third is composed of all the other later ctenodactylids, including *Sayimys*.

As for the relationships of *Sayimys* to other ctenodactylids, Black (1972) considered *Africanomys* and *Sayimys* to represent two independent lines developed from a *Tataromys*-like stock. Wood (1977) supposed that *Sayimys* might be derived from *Africanomys*, which was thought structurally ancestral to *Metasayimys* and possibly had, in turn, an

ancestor, which should not be very different from *Woodomys*. In my opinion, *Africanomys* is more primitive in tooth morphology. However, the absence of anteroconid and metalophid I on dp4 seems to imply another evolutionary direction distinct from that of *Sayimys* and *Metasayimys*. In addition, the two latter genera share commonly shallow mandible, wider cheek teeth, and deeper and more oblique sinus. *Sayimys* and *Metasayimys* may represent a sister group to *Africanomys*. The latter may have closer relationships with *Irhoudia* and *Pectinator* in sharing such derived characters as transverse sinusid and lophid, and dp4 structure.

### *Sayimys* Wood, 1937

TYPE SPECIES: *Sayimys perplexus* Wood, 1937.

INCLUDED SPECIES: *S. sivalensis* (Hinton, 1933), *S. obliquidens* Bohlin, 1946, *S. intermedius* (Sen and Thomas, 1979), *S. minor* de Bruijn et al. 1981, *S. chinjiensis* Baskin, 1996, and *Sayimys* spp.

GEOLOGICAL RANGE: Miocene to Pliocene.

GEOGRAPHIC DISTRIBUTION: China, India, Pakistan, Saudi Arabia, Turkey, and Libya.

DIAGNOSIS: "Jaw shallow with very heavy masseteric crest and gently sloping coronoid; angle not continuous with lower end of masseteric fossa, but begins to diverge from corpus beneath m2; p4 quadrate with V-shaped loph and posteroexternal cingulum; molars with anterior V-shaped crests and posterior crest connected to middle of posterior arm of V" (Wood, 1937: 73).

DISCUSSION: *Sayimys* is known to be the last member of the family to occur in Asia, as well as the earliest and most primitive representative of the Ctenodactylinae. The distribution of *Sayimys* is wider than of the other ctenodactylids, occurring not only in eastern and central Asia, but also in southern Asia, southwestern Asia, and North Africa (Munthe, 1982, 1987). Its distribution provides important information on migration events within this subfamily. The available evidence shows that during the Miocene, *Sayimys* migrated from eastern and central Asia first to southern Asia, then to southwestern Asia, and finally to North Africa.

During the same time the whole family, Ctenodactylidae, began migrating westward.

*Sayimys obliquidens* and *S. intermedius* were referred to *Metasayimys* (Jaeger, 1971; Sen and Thomas, 1979) and *S. sivalensis* to *Africanomys* (Wood, 1977). In this paper I follow de Bruijn et al. (1989) in considering the foregoing three species members of *Sayimys*. Altogether *Sayimys* is known to include eight species: *S. perplexus*, *S. sivalensis*, *S. obliquidens*, *S. intermedius*, *S. minor*, *S. chinjiensis*, and two *Sayimys* spp. In eastern and central Asia only three species are known to occur: *S. obliquidens* from Gansu, China, and *Sayimys* spp. listed from early Miocene Xiacaowang Formation (= MN4) of Jiangsu by Qiu and Qiu (1990) and from mid-Tertiary of Sonid Zuoqi (= Sunitezuoqi), Nei Mongol, by Meng et al. (1996). The other five species (*S. perplexus*, *S. sivalensis*, *S. chinjiensis*, *S. intermedius*, and *S. minor*) are known from southern and western Asia. The distinction among them is obscure and their relationships ambiguous. Munthe (1980) suggested that *S. perplexus* was a junior synonym of *S. sivalensis*. This was supported by de Bruijn et al. (1981), but later de Bruijn et al. (1989) considered both species to be valid. It seems to me that Munthe's suggestion is more reasonable. *S. minor* faces the same problem. According to de Bruijn et al. (1981), *S. minor* differs from *S. intermedius* in being smaller and having a metalophid II on dp4. However, their measurements of the cheek teeth of *S. minor* are within the range of variation of *S. intermedius*. The only difference between the two species is the morphology of dp4. Probably *S. minor* is also a junior synonym of *S. intermedius*. The *Sayimys* species known from southern and western Asia are mainly based on isolated teeth, few are based on jaws. A paper on the Siwalik *Sayimys* has been published by Baskin (1996). The material so far available does not permit me to discuss the problems in more detail. Only short comments on *S. obliquidens* are given below.

### *Sayimys obliquidens* Bohlin, 1946

*Sayimys obliquidens* Bohlin, 1946: 118, 144; figs. 30b, b', b'', b''', 31A, B, 32B, E, 34A, B, 42A; pl. III, figs. 18–21; pl. IV, figs. 1–4. Stehlin and Schaub, 1951: 126–127, 291; figs. 182, 499.



Schaub, 1958: 781, fig. 212. Lavocat, 1961: 58–59. Black, 1972: 241–242. Wood, 1977: 123, 125, 129–130; figs. 2K, 3M. de Bruijn et al., 1989: 195.

*Sayimys* cf. *obliquidens* Bohlin, 1946: fig. 30a, a', a'', a'''.

*Sayimys*: B. Bohlin, 1946: 110, figs. 30c, c', c'', d, d', d'', e, e', e'', 35, 36L, M, P, Q; pl. III, figs. 8–17; pl. VIII, figs. A, B.

*Metasayimys obliquidens*: Jaeger, 1971: 123. Sen and Thomas, 1979: 35–36.

"*Sayimys*" *obliquidens*: de Bruijn et al., 1981: 96.

**HOLOTYPE**: T.b. 268b, fragment of left lower jaw with broken p4, m1, m2, and complete m3, from the Baiyanghe Formation, Taben-buluk, Danghe area, Gansu, China, and figured by Bohlin (1946: figs. 30b, b', b'', 31A, B; pl. III, figs. 19–21).

**PARATYPE**: T.b. 279b, a fragment of right lower jaw with p4–m2.

**REFERRED MATERIAL**: T.b. 254, 261, and 279a.

**HORIZON AND LOCALITY**: Early(?) Miocene, (?) the Baiyanghe Formation, Taben-buluk, Danghe area, Gansu, China.

**DIAGNOSIS**: "Size as *Sayimys perplexus*, and also otherwise very like this species, but the crista masseteric retains traces of its primitive connection with the lower border of the angular process, and the posterior half of the lower molars is as broad (or nearly as broad) as the anterior half. Metaconid transverse" (Bohlin, 1946: 118).

**REMARKS**: *Sayimys obliquidens* was established by Bohlin (1946) on the basis of the material from Taben-buluk, Gansu. Although he thought that the Gansu material varied so much that it might comprise more than one species, he did not think it necessary to give specific names to all the variants. However, there is confusion in his paper in naming some species. For example, the skull (T.b.

279a) was listed as *Sayimys* cf. [*S.*] *obliquidens* in Fig. 30a, a', a'', and a''', but the same specimen was simply named as *Sayimys* in pl. III, figs. 14–16 and pl. VIII, figs. A and B. Later, Stehlin and Schaub (1951) and Schaub (1958) called two upper jaws (T.b. 254 and 261, which were named *Sayimys* by Bohlin in fig. 30) *Sayimys obliquidens*. The study shows that the differences among the specimens mentioned above may represent individual or ontogenetic variation. In addition, the skull (T.b. 279a) matches the lower jaws of the holotype (T.b. 268b) and paratype (T.b. 279b) very well. All specimens from Taben-buluk described by Bohlin, including the two upper jaws (T.b. 254 and T.b. 261) and the skull (T.b. 279a), are here referred to *Sayimys obliquidens*.

*Sayimys obliquidens* was referred to *Metasayimys* by Jaeger (1971). As mentioned by de Bruijn et al. (1989), *Metasayimys* differs from *Sayimys* in lacking a longitudinal depression on the lower incisors, but having cement and a relatively short first syncline on the lower molars. Furthermore, in *Sayimys*, P4 and p4 are larger than in *Metasayimys*, and the posteroexternal cingulum is present on lower molars. In the abovementioned features, *Sayimys obliquidens* is obviously similar to *Sayimys*, different from *Metasayimys*, and ought to remain in *Sayimys*.

The beds containing *S. obliquidens* was considered by Bohlin (1946) to be Miocene in age (his "probably upper Miocene"). Qiu and Qiu (1990) thought that the *Sayimys-Kansupithecus* local fauna of Gansu might be correlated with early Miocene Zhangjiaping local fauna (= MN3) in age. Unfortunately, the level of the beds bearing *S. obliquidens* has not been exactly located, so the age of *S. obliquidens* is by no means settled.

## DISCUSSION

### (I) ANALYSIS OF THE FEATURES OF THE SKULL AND MANDIBLE OF *TATAROMYS*

#### 1. The most significant features of skull and mandible of *Tataromys*

##### 1) Skull hystricomorphous;

2) Skull high and narrow with flattened roof;

3) Facial region long and cranial region short;

4) Rostrum long, robust, and widens anteriorly;

5) Nasal long, decreases in width

posteriorly, and reaches to above the anterior margin of orbit;

6) Dorsal process of premaxillary narrow and prolonged, extending to the frontal at the same level as the nasal-frontal suture;

7) Dorsal part of frontal proportionally short;

8) Orbit large;

9) Orbit is located lateral to frontal, with posterior process at the posterior margin of frontal;

10) Interparietal large and triangular in form;

11) Temporal fossa large, with distinct temporal crest;

12) Anterior nasal aperture retracted;

13) Infraorbital foramen very large, facing anterodorsally;

14) Sphenopalatine foramen surrounded by maxillary;

15) Optic foramen large and far behind M3;

16) Two ethmoid foramina within frontal;

17) Alisphenoid contact parietal, separating squamosal from frontal;

18) Masticatory foramen and buccinator foramen present and separated;

19) Incisive foramen large;

20) Premaxillary-maxillary suture intersects incisive foramen at its middle;

21) Lower branch of anterior zygomatic root located above paracone of P4;

22) Palate between two tooth rows narrow;

23) Palatal process of maxillary long;

24) Palatine and posterior palatal foramen shifted posteriorly;

25) Choana located far behind M3;

26) Pterygoid fossa large and deep;

27) Epipterygoid plate contacts bulla;

28) Orbital region expanded posteriorly;

29) Auditory region located in a more posterior position of skull;

30) Bulla large and composed of mastoid part and auditory bulla, with septum;

31) Lower jaw sciurognathous;

32) Masseteric fossa shallow and extends forward to m1;

33) Upper masseteric crest lacking;

34) Lower masseteric crest extending to angular process;

35) Mental foramen below p4.

## 2. Analysis of the features of the skull and mandible of *Tataromys plicidens*

To evaluate the significance of the above-listed features in phylogenetic analysis of the

group, the early Eocene *Cocomys lingchaensis* (Li et al., 1979) has been chosen as an outgroup for comparison. The features of *Tataromys plicidens* may be subdivided into three different groups.

1) Primitive features (plesiomorphies), which are shared by both *Tataromys* and *Cocomys*, are 10, 15, 21, 26, 27, 34 and 35.

2) Derived features, which may be further subdivided into three subsets:

a) Synapomorphy of *Tataromys* and *Ctenodactylus*, which includes 1, 3, 8, 12, 13, 19, 20, 25, 30 and 33.

b) Intermediate features which are more advanced than in *Cocomys*, but less than in *Ctenodactylus*. They are:

(1) Ratio of facial region to cranial region is larger than in *Cocomys*, but smaller than in *Ctenodactylus*;

(2) Nasal extended posteriorly more than in the living ctenodactylids, less than in *Cocomys*;

(3) Position and size of the orbit are between those of *Cocomys* and the living ctenodactylids;

(4) Incisive foramen is larger than in *Cocomys*, but smaller than in *Ctenodactylus*;

(5) Masseteric fossa shallow and extends forward below m1, whereas it reaches below m3 in *Cocomys* and below p4 in *Ctenodactylus*;

(6) Upper masseteric crest is absent and lower crest extending to angular process, in *Cocomys* upper crest is present, in *Ctenodactylus* a heavy horizontal crest is present.

c) Autapomorphy of *Tataromys*, which is different from both *Cocomys* and *Ctenodactylus*, comprises 12 features (2, 4, 5, 7, 11, 14, 16, 18, 22-24, and 28).

3) Features shared by the three genera are 6, 29, and 31.

Judging from the foregoing grouping of features, it is clear that *Tataromys* has closer relationships to *Ctenodactylus* than to *Cocomys* but it represents a lineage distinct from that represented by *Ctenodactylus*.

## (II) ECOLOGY OF *TATAROMYS*

It is difficult to discuss the ecology of *Tataromys* in detail because very few skeletal

remains are known. I can only roughly postulate some aspects of their ecology on the basis of the features already known.

It is known that in desert areas the micro-mammals generally have more developed sensory organs, including large eyes, keen sense of smell, and well-developed auditory organs that help them to detect predators and other mammals and give them maximum awareness of their surroundings. *Tataromys plicidens* has large eyes and enormous tympanic bullae composed of mastoid part and auditory bulla with septum. These features show that *Tataromys* may already have more developed visual and auditory organs, adapting to wide desert or wilderness as the living ctenodactylids do. Like the living ctenodactylids, *Tataromys* has a hystricomorphous skull with a large infraorbital foramen, and large masseteric fossa with well-developed lower masseteric crest on the lower jaw. In addition, *Tataromys* has a large fossa on the lateral wall of the rostrum and a well-developed anterior part of the lower masseteric crest. It is clear that *Tataromys* has a well-developed masseter medialis muscle, especially the anterior part, and has strong capability of gnawing and chewing. However, *Tataromys* has large temporal fossa, distinct temporal ridge, and high coronoid process, which resembles those of some of the recent cricetids and sciurids, but differs from those of the living ctenodactylids. Those features reveal that *Tataromys* may have more developed temporalis muscle than the Recent ctenodactylids. In addition, the cheek tooth crown of *Tataromys* is lower than that of the Ctenodactylinae. Based on the above information we may conclude that *Tataromys* was probably more omnivorous than the living ctenodactylids, which feed solely on plant material. By living in the wide desert, wilderness, or grasslands in eastern and central Asia, *Tataromys* may eat, in addition to some plant parts (nuts, seeds, buds, foliage, flower, fruits, bulbs, etc.), insects, larvae, and possible birds' eggs, as do some the living sciurids (e.g., *Citellus*) and cricetids (such as *Cricetus*, *Cricetulus*).

### (III) RELATIONSHIPS WITHIN THE CTENODACTYLIDAE

As for the relationships of the mid-Tertiary ctenodactylids, Bohlin (1946: 133) stated

that "At least three lines of evolution can be distinguished inside this family: 1) *Karakoromys-Tataromys-Yindirtemys*; 2) *Leptotataromys*; 3) *Sayimys*, and these are specialized in such different ways that they may perhaps be considered as different sub-families," but still included the fossil forms and living ones in the same family Ctenodactylidae. Schaub is the first (1958: 780–782) who formally used the family name Tataromyidae encompassing all the abovementioned fossil forms while retaining all the extant forms in Ctenodactylidae. Lavocat (1961: 52) adopted the family Tataromyidae concept and subdivided the family into two subfamilies: Tataromyinae and Sayimyinae. Other paleontologists (Dawson, 1964: 14; Jaeger, 1971: 133; Black, 1972: 240; Wood, 1977: 122) argued that the groupings of Schaub and Lavocat were unnatural and the information then available was not enough to subdivide the family Ctenodactylidae into groups higher than the generic rank.

Shevyreva (1971b: 73–74) suggested that the Oligocene ctenodactylids might be divided into three forms: 1) *Woodomys*, the most primitive one; 2) *Tataromys*, representing the first one of the line of *Tataromys-Sayimys-Pectinator*; and 3) *Karakoromys*, the most advanced one. According to Wood (1977: 123, fig. 2; 125, fig. 3), the later ctenodactylids were derived from two forms: *Yindirtemys* (Wood's *Tataromys plicidens*) and *Karakoromys* (his *Woodomys chelkaris* and *Terarboreus arcanus*).

The accumulation of new materials led to the conclusion that probably four main evolutionary lineages existed in the mid-Tertiary of eastern and central Asia. They are demonstrated in fig. 38 and table 24. The first lineage is composed of *Tataromys*, *Yindirtemys*, and *Bounomys*. They share the following features: high, narrow skull with flattened roof, large temporal fossa and distinct temporal crest, choana located far behind M<sup>3</sup>, lower molars having complete and generally anteriorly located posterior arm of protoconid, closed trigonid basin, upper molars having V-shaped protocone, complete metaloph joining with protocone, posteriorly oblique sinus, and lacking entoloph on M1 and M2. In the second one, represented by *Karakoromys* and *Euryodontomys*, the main derived features are as follows: cheek

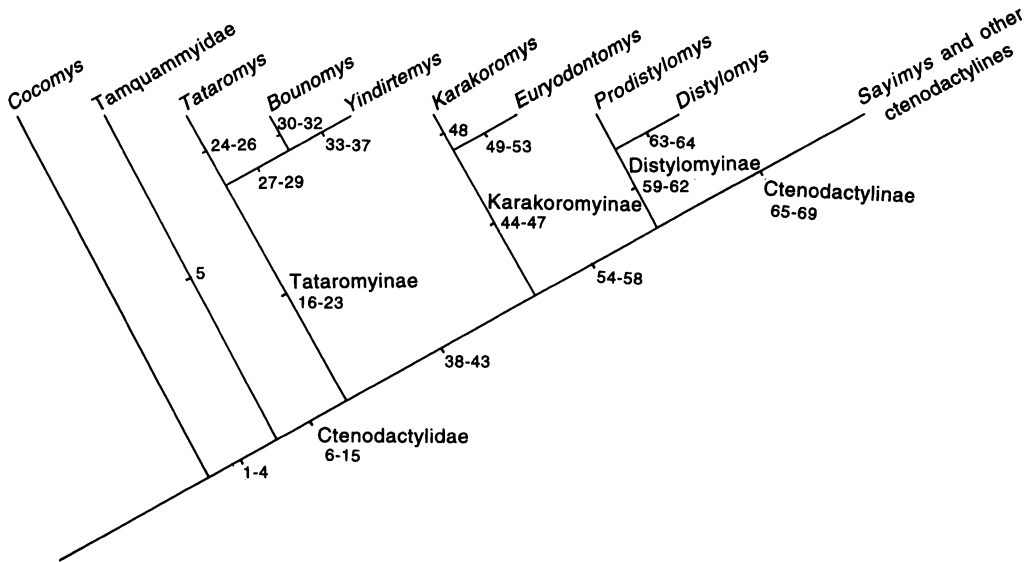


Fig. 38. Diagram of relationships among ctenodactylids. Numbers correspond to derived traits listed in table 24.

teeth proportionally wide, upper molars having developed entoloph, massive, but incomplete metaloph never joining protocone, large hypocone almost equal to the protocone in size, more or less transverse and symmetric sinus, on lower molars posterior arm of protoconid extending more posteriorly, and having relatively small m3. The synapomorphies of the third group, *Distylomys* and *Proditylomys*, are: the mental foramen is anterior to dp4; the masseteric fossa extends below dp4; the incisor extends below m2; the cheek teeth are hypsodont, covered with cement, transverse sinusid, tending to be bilobate; and the shedding of dp4 is delayed. The fourth one includes *Sayimys* and all the later (from early Miocene through Recent) ctenodactylids. They have such common derived features as a heavy and horizontal masseteric crest extending backward to condyle on lower jaw, coronoid process reduced or absent; cheek teeth becoming unilaterally or fully hypsodont; P4 and p4 reduced or even lost early in life; upper molars tending to become bilobate and having deep, anteriorly oblique sinus, metaloph joining with posteroloph, anterosinus and posterosinus short, tending to disappear; lower molars tending to be tri- or bilobate with sinusid oblique posteriorly. The four lineages are here considered as four sub-

families of Ctenodactylidae: Tataromyinae, Karakoromyinae, Distylomyinae, and Ctenodactylinae.

For a long time the relationships of the Ctenodactylinae, including *Sayimys*, to other ctenodactylids have been poorly understood. Detailed analysis of the above features leads to the following conclusion. Among the four subfamilies the Distylomyinae and Ctenodactylinae have the closest relationship and share the following synapomorphies: mental foramen located before p4 (dp4), incisor ending below m2, cheek teeth hypsodont, tending to be bilobate, and P4 and p4 reduced. These features are not shared by the Karakoromyinae and Tataromyinae. But the Karakoromyinae share other derived features with the two former subfamilies, including relatively wide cheek teeth, large hypocone, well-developed entoloph, massive but incomplete metaloph never joining with protocone, relatively posteriorly extending posterior arm of protoconid. Thus, Karakoromyinae may have closer relationships with them than with the Tataromyinae. In conclusion, the Distylomyinae and Ctenodactylinae form a sister group to the Karakoromyinae, and the three are sister to the Tataromyinae.

Within the Tataromyinae, *Yindirtemys* may represent the more advanced genus in having

TABLE 24

**Derived Characters for Ctenodactylid Cladogram (fig. 38)**

1. Hystricomorphy
2. Rostrum high
3. Masseteric fossa extends below m2
4. Arm of entoconid present
5. Arm of entoconid curved posteriorly and joins hypoconulid on m1
6. Bulla large
7. Masseteric fossa shallow and extends below m1
8. Dorsal masseteric crest absent
9. P3 lost
10. More lophodont, cusps joined by crests
11. Conule absent on M1–M3
12. Anterior cingulum higher and usually joins proto-loph on M1–M3
13. Mesoconid absent on m1–m3
14. Ectolophid short
15. Mental foramen below p4
16. Skull high, narrow, and with flattened roof
17. Temporal fossa large and temporal crest distinct
18. Choana located far behind M3
19. Metaloph complete and joins protocone on M1–M3
20. Entoloph absent on M1–M2
21. Lingual sinus oblique posterobuccally on M1–M3
22. Posterior arm of protoconid shifts anteriorly and fuses with metalophid I buccally
23. Trigonid basin closed
24. Cusps and lophs compressed
25. Trigonid short and trigonid basin small or absent
26. Ectolophid straight and linguallly situated
27. Posterior arm of protoconid with swollen middle part
28. Trigonid basin large
29. Anterior cingulum present on m1–m3
30. Lophs slender
31. Entoconid conical, with two slender arms
32. Entoloph absent on M3
33. Palate narrow
34. Crown higher linguallly than buccally on upper cheek teeth
35. Lophs and cusps swollen
36. Antecrochet of metacone present
37. Hypoconid, entoconid, and hypoconulid crescentic
38. Ventral ramus of zygomatic process of maxilla anterior to P4
39. Cheek teeth proportionally wide
40. Metaloph massive, incomplete, and does not join protocone on M1–M3
41. Hypocone large and equal in size to protocone on M1–M2
42. Entoloph developed on M1–M3
43. Posterior arm of protoconid extends relatively posteriorly
44. Sphenopalatine foramen above juncture of P4 and M1
45. Lingual sinus symmetric on M1–M2

TABLE 24—(Continued)

46. Arm of entoconid transverse
47. Hypoconulid of m3 small
48. Lingual part of posterior arm of protoconid weak to absent
49. Crown higher
50. Metaloph connected with posteroloph by distinct short ridge on M1–M3
51. Lingual part of posterior arm of protoconid reaches to metaconid
52. Trigonid large and trigonid basin closed
53. Hypoconulid further reduced on m3
54. Mental foramen before p4
55. Incisor extends posteriorly below m2
56. Hypsodont
57. Cheek teeth become tri- and bilobate
58. P4 and p4 reduced
59. Masseteric fossa extends below dp4
60. Shedding of dp4 delayed
61. Cement present
62. Buccal and lingual sinusids transverse on lower molars
63. Roots of cheek teeth lost
64. Posterosinusid lost
65. Coronoid process reduced to absent
66. Condyle low
67. Masseteric crest horizontal, strong, and extends from below P4 to condyle
68. Lingual sinus oblique anteriorly on M1–M3
69. Buccal sinusid oblique posteriorly on m1–m3

narrow palatine, higher crown cheek teeth, more swollen main cusps and lophs, distinct accessory crests, and lower molars having more oblique and crescentic hypoconid, entoconid, and hypoconulid. *Yindirtemys* and *Bounomys* may form a sister group to *Tataromys* since they share some derived features, such as lower molars having anterior cingulum, posterior arm of protoconid with a swollen middle part, and a large trigonid basin. *Tataromys* may represent a special lineage in having compressed cusps and lophs, short trigonid, small trigonid basin, and linguallly situated ectolophid.

Among *Tataromys*, *T. minor* may represent the most primitive species. *T. parvus* and *T. sigmodon* may form a sister group to other species. The evolutionary tendencies of the cheek teeth of *Tataromys* are as follows: the size increases gradually, the crown heightens gradually, the cusps and lophs are more and more compressed, and the metaloph varies from oblique anteriorly, straight, and then to convex posteriorly. *T. plicidens*

has its own autapomorphies: larger size and the posterior arm of the protoconid shifted anteriorly, resulting in shorter trigonid and smaller trigonid basin on lower molars.

In the Tataromyinae the cheek teeth show some evolutionary tendencies common to the three genera; for example, the dramatic change in the metaloph of M1 and M2. It seems possible to subdivide the change into three upgrading stages. In the first stage, represented by *Tataromys minor*, *Yindirtemys grangeri*, and *Bounomys bohlini*, the metaloph extends anterolingually and usually joins the posterior arm of protocone to form a continuous oblique ridge, which is separated from the posteroloph. Sometimes there is a low short ridge, which joins metaloph with posteroloph, but never joins hypocone with protocone directly. *Tataromys plicidens*, *Yindirtemys gobiensis*, *Y. suni*, *Y. xiningensis*, and *Bounomys ulantatalensis* represent the second stage, in which the metaloph begins to be convex posteriorly, with a transverse buccal part and a relatively longitudinally extending lingual one. In some worn M1 and M2 a distinct "entoloph" and a transverse "metaloph" appear to exist. On the fresh or slightly worn M1 and M2, however, they represent two parts of one continuous and posteriorly convex metaloph. The transverse "metaloph" is only the buccal part of the complete metaloph and the "entoloph" is mainly composed of the lingual part of the complete metaloph or posterior arm of the protocone. The short ridge connecting metaloph with the posteroloph is short and lower (figs. 8, 21B, C). In the third stage, typified by *Tataromys parvus*, *T. sigmodon*, *Yindirtemys deflexus*, and *Y. ambiguus*, the metaloph becomes more and more convex posteriorly and reaches the posteroloph at its middle part. The buccal one extends posterolingually and its lingual part extends more longitudinally so that it usually looks like "entoloph." However, it is not the true entoloph connecting protocone and hypocone as in other ctenodactylids (e.g., *Karakoromys* and *Sayimys*). The posteriorly oblique sinus on M1 and M2 is also an evidence for this (fig. 21A). Thus, the true entoloph of M1 and M2 is absent in the Tataromyinae.

Along with the evolution of the Ctenodactylidae in mid-Tertiary, the cheek teeth gen-

erally show distinct evolutionary tendencies as follows: (1) from brachydont to hypsodont; (2) from relatively bunodont to lophodont; (3) metaloph from oblique anteriorly to curved or oblique posteriorly; (4) posterior arm of protoconid tends to shift anteriorly to fuse with the metalophid I or absent, or to extend more posteriorly; (5) patterns usually tend to be simple lophs and to become tri- or bilobate; or (6) being complex by adding accessory cusps and crests in some species.

#### (IV) OLIGOCENE BIOSTRATIGRAPHIC PROBLEMS IN ASIA

##### 1. STATUS QUO OF OLIGOCENE OF ASIA

The reassessment of the Asian Oligocene in light of the new understanding of the Eocene–Oligocene boundary in recent years is still in its initial stage, although research on Oligocene mammalian faunas has a long history in Asia. Age determination and subdivision have been based mainly on intercontinental correlation. Only one of these faunas, the Hsanda Gol fauna, has been radiometrically dated and very few have been calibrated magnetostratigraphically. Most genera of the Oligocene mammals in Asia are endemic. Only a few genera are common to Asia and other continents. Biostratigraphic correlation of Asian mammalian faunas with those of North America and Europe is therefore difficult.

Geochronologically, the Asian Oligocene is traditionally considered to include three ages: early, middle, and late Oligocene (Li and Ting, 1983; Russell and Zhai, 1987; Wang, 1992). Recent research on the Eocene and Oligocene stratigraphy has advanced greatly in the world. New dating of the Eocene–Oligocene boundary, around 34 Ma (Berggren et al., 1992), has been increasingly accepted by geologists, and the North American biostratigraphy based on terrestrial mammal ages has been realigned (Swisher and Prothero, 1990; Prothero and Swisher, 1992). The Chadronian is now considered as late Eocene in age. Accordingly, the traditional Asian early Oligocene is also suggested to be transferred to late Eocene (Berggren and Prothero, 1992; Ducrocq, 1993). To verify the applicability of these new ideas to the

Asian Paleogene biostratigraphy, much work remains to be done, including restudy of the mammalian faunas in light of the recent advances in vertebrate paleontology, clarification of biostratigraphic uncertainties in classic Oligocene basins, radiometric dating, and magnetostratigraphic calibration. As far as Asian Oligocene mammalian faunas are concerned, the following comments apply.

Among the known mammalian fauna of the traditional Asian early Oligocene, five genera—*Harpagolestes*, *Forstercooperia*, *Amynodon*, *Amynodontopsis*, and *Metamynodon*—are found from late middle Eocene Duchesnean or earlier deposits in North America. Three other genera—*Ardynomys*, *Pseudocylindrodon*, and *Bothriodon*—existed in the Chadronian. When the Chadronian correlated with the late Eocene, it seems reasonable to realign the traditional Asian early Oligocene to the late Eocene as well. However, five genera—*Eucricetodon*, *Nimravus*, *Ronzotherium*, *Entelodon* and *Lophiomyx*—made their first appearance in both the traditional Asian early Oligocene and the European early Oligocene (post-Grande Coupure). This tends to contradict the above correlation with North America. A closer study reveals the following: the Asian species of *Eucricetodon* (*E. meridionalis* and *E. leptaleos*), *Nimravus* (*N. mongoliensis*), and *Lophiomyx* (*L. angarae*, *L. gobiae*, *L. shinaoensis* and *L. gracilis*) are more primitive than those from the early Oligocene of Europe, and thus may represent earlier stages of evolution (Wang and Meng, 1986; Gromova, 1959; Miao, 1982; Brunet and Sudre, 1987). *Entelodon*, originating in Asia, is known to include four species: *Entelodon* sp., *E. orientalis*, *E. gobiensis*, and *E. dirus*. These species represent quite different evolutionary stages, from a more primitive one, close to *Euenterodon* (*Entelodon* sp.), to a more advanced one (*E. dirus*). It is interesting that *E. major* from the Hsanda Gol Formation and *E. ordosius* from the Qingshuiying Formation are closer to *E. magnus* (MP 21) and *E. deguilhemi* (MP 22) of early Oligocene of Europe (Brunet, 1979). *Symphysorrhachis brevirostre* was reassigned by Heissig (1969) to *Ronzotherium*. However, it is an aberrant form, probably leading to the bizarre *Aprotodon*. The genus *Symphysorrhachis*, there-

fore, should remain separate from the European *Ronzotherium*. The above analysis seems to corroborate the idea that the traditional early Oligocene of Asia is earlier than the early Oligocene of Europe. Probably the forms mentioned above appeared later in Europe than in Asia because they could not have migrated into Europe until the early Oligocene when the Turgai Strait vanished. In addition, the dating of the basalt from the Hsanda Gol Formation, which is 31.3 and 32.0 Ma (Evernden et al., 1964), seems also supportive if the lower part of the Hsanda Gol Formation below the basalt represents the early Oligocene. Therefore, I agree with Berggren and Prothero (1992) in reinterpreting the Asian “early Oligocene” as late Eocene and the “middle Oligocene” as early Oligocene. Thus, the Asian Oligocene includes only two ages: early Oligocene and late Oligocene (Wang, in press).

## 2. BIOSTRATIGRAPHY OF THE CTENODACTYLIDAE IN ASIA

The ctenodactylid fossils are one of the most abundant and diversified rodent groups in the mid-Tertiary of eastern and central Asia. They may be used to define local biostratigraphic “zones” and seem to have good potential for establishing interregional correlation. (Li and Qiu, 1980; Wang et al., 1981; Huang, 1985; Qiu and Gu, 1988; Qiu and Qiu, 1990, 1995; Wang, 1992, in press; Wang and Wang, 1991; Wang et al., 1994)

The mid-Tertiary ctenodactylids of China are known to occur in 12 horizons of 15 localities and can be chronologically arranged. Most of the ctenodactylid fossils of Mongolia were collected from the Hsanda Gol Formation.

Mellet (1968: 9) and Kowalski (1974: 49) mentioned that the Hsanda Gol Formation might be subdivided into two parts in the locality Tatal Gol. Based on comparison with Chinese Oligocene faunas, Wang (1992: 533) suggested that the lower part of the Hsanda Gol fauna might be mostly equivalent to the late Wulanbulage fauna, and the fauna from the upper part of the Hsanda Gol Formation may be equivalent to or younger than the later period of the late Wulanbulage fauna. According to Mellett (1968) and Kowalski (1974),

*Yindirtemys deflexus* was only found with *Tachyoryctoides obrutchewi* in the upper part. The other ctenodactylids, such as *Karakoromys decessus*, *Tataromys plicidens*, *Tataromys sigmodon*, and *T. minor*, may have been collected from only the lower part of the Hsanda Gol Formation. As discussed above, *Yindirtemys deflexus* is known to be found only in late Oligocene strata in China, and *Tachyoryctoides obrutchewi* is known only from the late Oligocene and early Miocene. On the other hand, *Karakoromys decessus*, *Tataromys plicidens*, *T. sigmodon*, and *T. minor* are known to be found together in the early Oligocene Wulanbulage Formation, some localities of Saint Jacques, and the Ulantatal Formation in China. However, no *Yindirtemys* is known from these levels. Recently a joint team from Mongolia and the AMNH has proved that the Hsanda Gol Formation may be composed of two different parts (Bryant and McKenna, 1995). It is possible that the upper part of the Hsanda Gol Formation may represent or at least include Late Oligocene deposits, and the lower part may be early Oligocene and equivalent to the Wulanbulage Formation in age. However, a final conclusion cannot be drawn until all the mammalian fossils of the Hsanda Gol Formation are restudied and the radiometric dating is retested.

Two separate rodent faunas are also present in Boongeen Gol, Mongolia (Kowalski, 1974). *Karakoromys decessus* was found exclusively in the lower one, but *Yindirtemys gobiensis* was found exclusively from the upper part. It is also possible that the upper part of Boongeen Gol may represent or at least include Late Oligocene beds.

Huang (1985: 37–38) stated that the absence of typical ctenodactylids (*Tataromys plicidens* and *T. sigmodon*) of the Hsanda Gol Formation in the Ulantatal area might indicate that the Ulantatal fauna was slightly younger than the Hsanda Gol fauna, probably “late middle Oligocene.” As mentioned above, however, such forms as *Yindirtemys deflexus* and *Y. gobiensis*, which occur only in the upper part of the Hsanda Gol Formation, have not been found in the Ulantatal area, whereas some other ctenodactylids, including *Tataromys plicidens*, *T. sigmodon*, *T. minor*, and *Karakoromys decessus*, exist in both Ulantatal and the lower part of the Hsanda Gol faunas. Probably that

the Ulantatal fauna and the lower part of the Hsanda Gol fauna are roughly equivalent.

In China, *Karakoromys* occurs first in Kekamu, the lower part of the Ulantatal Formation, and the lower member of the Wulanbulage Formation, whereas *Tataromys* makes its first appearance only in the upper member of the Wulanbulage Formation. *Karakoromys* occurs earlier than other ctenodactylids, including *Tataromys*. Because I do not know exactly their occurrence in the Hsanda Gol Formation, their geological range is primarily based on the known Chinese biostratigraphy.

The biostratigraphic distribution of the ctenodactylids in Asia is given in figure 39. The horizons bearing the species of the ctenodactylids in China are drawn in bold lines. The horizons that have not been reported to yield the same species between them are shown in dashed lines. Because there are some uncertainties of the presence of the ctenodactylids in some beds in the Hsanda Gol Formation and some other localities, the geological range of the ctenodactylids in these areas are marked with question marks.

As is shown in figure 39, the Karakoromyinae, represented by two genera and four species (*Karakoromys decessus*, *Karakoromys* sp., *Euryodontomys ampliatus*, and *E. exiguus*), are the earliest forms of the family and are known to occur only in the early Oligocene. The Tataromyinae are more diversified (including three genera and 13 species) and lasted a longer time [from late early Oligocene through middle middle Miocene (Dinjiaergou, MN6; Wu, pers. comm., 1994)]. Among them, *Yindirtemys* does not appear until the late Oligocene. The Distylomyinae occur from the late Oligocene through the early Miocene. The Ctenodactylinae are represented by three genera, *Sayimys*, *Akzharomys*, and *Prosayimys*, in Asia. It appeared latest, first appearing in the early Miocene (= MN4) (Qiu and Qiu, 1990, 1995), but was more widely distributed than other Asian ctenodactylids, being known from North China (Gansu, Jiangsu, and Nei Mongol), Kazakhstan, India, Pakistan, Saudi Arabia, Turkey, and perhaps Israel. However, after the late Miocene it disappeared in Asia. Since then, no descendants of the ctenodactylids have been found in Asia.





## (V) INTERRELATIONSHIPS AMONG THE CTENODACTYLOIDEA

Initially, the taxon Ctenodactyloidea was established on the basis of a single living family (Ctenodactylidae) that included four living genera, *Ctenodactylus*, *Massouteria*, *Pectinator*, and *Felovia*, (Simpson, 1945). Later, the Chapattimyidae was erected as an ancestral family to the Ctenodactylidae by Hussain et al. (1978). Shevyreva (1983) proposed the Tamquammyidae in the Ctenodactyloidea. Dawson et al. (1984) included, in addition to the Ctenodactylidae, two new families, Cocomyidae and Yuomyidae, in the superfamily. From then on Ctenodactyloidea has been generally considered to include five families separated into two distinct lineages based on the morphology of P4 (Dawson et al., 1984; Wang, 1984; Flynn et al., 1986). The Cocomyidae, Tamquammyidae, and Ctenodactylidae form the main stem, in which P4 and p4 are non-molariform and tend gradually to be reduced or even lost, whereas the Chapattimyidae and Yuomyidae represent a side branch in having molariform P4 and p4. However, the relationships within the superfamily are still obscure.

### Taxonomic Position of the Cocomyidae

The Cocomyidae were established by Dawson et al. (1984) as a family of the Ctenodactyloidea to include *Cocomys*, *Tamquammys*, and *Tsinlingomys*. Considering hystricomorphy as the fundamental criterion for defining Ctenodactyloidea, Flynn et al. (1986) excluded the protrogomorphous *Cocomys* from the superfamily. Bryant and McKenna (1995) further thought that *Cocomys* did not have a close cladistic relationship with the Ctenodactylidae. It is true that as a more primitive rodent, *Cocomys* has more primitive features, including the auditory region. The relationship of *Cocomys* with other rodents cannot be discussed based purely on primitive features. Fortunately, *Cocomys* has several derived features, especially in tooth morphology. For instance, its upper molars have well-developed hypocone separated from metaloph; the lower molars have a strong metalophid I forming the anterior border and conspicuously large hypoconulid. All

these features are shared by later ctenodactyloids exclusively. The most interesting feature of *Cocomys* is the structure of P4 and p4, such as presence of anterior and posterior ridges between the paracone and protocone on P4, p4 having well-developed protoconid and metaconid, and a low narrow talonid with hypoconid and entoconid. These features are only shared by later ctenodactyloids, but not by any other rodents. In addition, in *Cocomys* the premaxillary has a long dorsal process, which is also shared only by later ctenodactyloids in the Rodentia. This feature was considered primitive by Li et al. (1989), but in comparison with the primitive eutherian morphotype, it seems to represent a derived state (Butler, 1985; Novacek, 1986). If it is derived, it gives additional evidence of close relationship of *Cocomys* with later ctenodactyloids. The structure of the zygomatic arch complex and infraorbital foramen is vitally important for higher classification of the Ctenodactyloidea. However, the development of these features is gradual. *Cocomys* is protrogomorphous and its infraorbital foramen is smaller than in the other Ctenodactyloidea. However, its foramen is larger than in the Asian Paleocene *Heomys* (an early rodent or rodent relative) and in other protrogomorphs, such as the primitive North American Ischyromyidae and Sciuravidae. Li et al. (1989: 182) noted that in one of the skulls of *Cocomys lingchaensis* (IVPP V 7399), there was a very weak semicircular scar just anterior to the infraorbital foramen, which might be interpreted as a scar marking origin of the muscle. If the small infraorbital foramen is primitive, the relatively large one of *Cocomys* seems to represent, at least, a slightly advanced intermediate stage, or possibly a transition from protrogomorphous to hystricomorphous skull. This means that *Cocomys* began to develop toward the hystricomorphous condition. Recently Hu (1995) described a new ctenodactyloid form, *Hohomys*, from the late early Eocene deposits of China. Its zygomatic structure is of a primitive hystricomorphous type with a medium-sized infraorbital foramen, which is larger than that of *Cocomys* but smaller than that of *Saykanomys* and *Yuomys*. This is consistent with the infraorbital foramen developing from small to large and shows that *Co-*

*comys* has closer relationships with the other ctenodactyloids than with other rodents. Therefore, I followed Dawson et al. (1984) to include the Cocomyidae in the Ctenodactyloidea (Wang, 1994).

Flynn et al. (1986) excluded *Tamquammys* and *Tsinlingomys* from the Cocomyidae and thought the Cocomyidae monotypic. Recently Hu (1995) reported a cocomyid from late early Eocene deposits of Hubei, China. It is similar to *Cocomys* in having nonmolariform p4, but different from the latter in molars with more developed lophs and hypoconulid. It may represent a new genus distinct from *Cocomys*. Therefore, the Cocomyidae is in any case not a monotypic taxon. On the contrary, Dashzeveg (1990a) subdivided the Cocomyidae into two subfamilies: Cocomyinae and Advenimurinae. The Cocomyinae included *Cocomys*, *Tamquammys*, and his new genera: *Sharomys*, *Kharomys*, *Tsagamys*, and *Ulanomys*. It seems that *Tamquammys* and *Sharomys* should be transferred from the Cocomyidae to Tamquammyidae because they have a hystricomorphous skull. On the other hand, *Kharomys* and *Ulanomys* (Dashzeveg, 1990a) seem to be synonyms of *Cocomys*, because in disagreement with Dashzeveg (1990a) the infraorbital foramen of *Kharomys* is not larger than in *Cocomys* and the tooth morphology is also similar to that of *Cocomys*. Having a molariform P4 and p4, *Tsagamys* is to be relocated from the Cocomyidae to the Chapattimyidae–Yuomyidae group. In the same manner, Dashzeveg's Advenimurinae should be excluded from the Cocomyidae. Shevyreva (1989) assigned several genera in the Tamquammyidae: *Tsagankhushumys*, *Adolomys*, and *Bumbanomys*, from the early Eocene deposits of Mongolia. According to her description and figures (figs. 2–4), these genera are similar to *Cocomys* in size and pattern of the cheek teeth. They may represent *Cocomys* or have close relationships with that genus.

#### Systematic Position of Chapattimyidae and Yuomyidae

The distinction between the Chapattimyidae and Yuomyidae has been ambiguous since their establishment (Hussain et al., 1978; Dawson et al., 1984). They are mutu-

ally inclusive. *Advenimus* and *Saykanomys* were referred to the Yuomyidae (Dawson et al., 1984; Flynn et al., 1986) or to the Chapattimyidae (Hussain et al., 1978; Wang, 1984). Shevyreva (1983, 1989) included members of both Chapattimyidae and Yuomyidae and her new genera (*Bolosomys*, *Chkhikvadzomys*, and *Esesempomys*) in the Chapattimyidae, but included *Advenimus* in her Tamquammyidae.

Indeed, the characters distinguishing the Chapattimyidae from the Yuomyidae are far from clear-cut. Most of them are gradual in nature. The morphology of P4 and p4 is commonly considered as one of the main distinguishing features, but it is variable in size and shape in both families. Perhaps both families should be combined into one family, Chapattimyidae. However, because there are some differences between the two families in tooth morphology and, more importantly, because the Chapattimyidae are mainly known from isolated teeth and our knowledge of it is not sufficient for further discussion, I tentatively kept them as separate families (Wang, 1994).

The position of the Chapattimyidae and Yuomyidae in the Ctenodactyloidea is also problematic. In the Ctenodactyloidea the Cocomyidae, Tamquammyidae, and Ctenodactylidae are thought to form the main stem, in which P4 and p4 are nonmolariform, and the Chapattimyidae and Yuomyidae represent a side branch having molariform P4 and p4. There are two possibilities. If nonmolariform P4 and p4 are primitive features for rodents, the molariform P4 and p4 could have derived from a nonmolariform P4 and p4 as in *Cocomys*. Then both lineages, with molariform P4 (p4) and nonmolariform P4 (p4), would have developed simultaneously but in different directions. If the nonmolariform P4 and p4 of *Cocomys* are derived features shared with the Tamquammyidae and Ctenodactylidae and developed in a different direction from the Yuomyidae and Chapattimyidae, the Chapattimyidae–Yuomyidae group would be separated from the Cocomyidae–Tamquammyidae–Ctenodactylidae group. This should occur before the appearance of *Cocomys*. The hystricomorphous skull common to the two groups would then be logically considered a result from parallel evolution. Wood

(1962: 252–253) hypothesized that the ancestry of rodents might have simple non-molariform P4 and p4. This hypothesis was supported by de Bruijn et al. (1982). Based on the morphology of P4 and p4 of the Asian Paleogene *Heomys*, Dawson et al. (1984: 146) and Li et al. (1989: 190) agreed with Wood's viewpoint and considered nonmolariform P4 and p4 of *Cocomys* primitive. Recently two new primitive yuomyids, *Hohomys lii* and *Bandaomys zhonghuaensis*, were reported from Early Eocene of China (Hu, 1995; Tong and Dawson, 1995). *Hohomys* has a primitive hystricomorphous skull, in which the infraorbital foramen is larger than in *Cocomys*, but smaller than other ctenodactyloids. Its P4 and p4 are molariform, but simpler than those in the Chapattimyidae and other yuomyids: its metacone of P4 appears in rudimentary form and the hypoconulid of p4 begins developing. Likewise, in *Bandaomys zhonghuaensis* P4 and p4 are molariform, but also simpler than the Chapattimyidae and other yuomyids in P4 having rudimentary metacone and p4 having slightly wider talonid and smaller and slightly cusped hypoconid. It is obvious that *Hohomys* and *Bandaomys*, being near the base of the Yuomyidae, may represent a transitional stage from the Cocomyidae to the Yuomyidae. Probably Yuomyidae–Chapattimyidae split from the Cocomyidae soon after *Cocomys* appeared, as was suggested earlier (Wang, 1994: fig. 6). Therefore, *Cocomys*, Yuomyidae, and Chapattimyidae should be included in the Ctenodactyloidea.

#### (VI) RELATIONSHIPS OF THE CTENODACTYLOIDEA TO OTHER RODENTS

For many years the protrogomorphous Ischyromyidae were generally considered as the primitive ancestral group of most later rodents (Wood, 1959, 1962, 1965). However, in the last two decades, especially after the discovery of early Eocene *Cocomys* and middle–late Paleocene *Heomys* in China, the primitive ctenodactyloids have been suggested as the most ancient and primitive group of rodents (Korth, 1984; Dawson et al., 1984; Li et al., 1989). They were thought to be either a stem group for all rodents (Hartenber-

ger, 1985, 1990), or near the root of the families including Cricetidae, Dipodidae, Protoptychidae, Simimyidae, and Theridomyoidea(?) (Vianey-Liaud, 1985), or a sister group to Pedetidae, Hystricognathi, and Cylindrodontidae (Hussain et al., 1978; Luckett, 1980).

#### Relationships with Other Primitive Rodents

As mentioned by Li et al. (1989), *Cocomys* represents the earliest record of fossil rodents in Asia and is one of the most primitive known rodents. Compared with primitive rodents of the Ischyromyidae, Sciuravidae, and Theridomyoidea, *Cocomys* does have some more primitive features and also shares some features with them, mostly symplesiomorphies (Li et al., 1989: table 2). The only derived feature common to *Cocomys* and Theridomyoidea is the enlarged infraorbital foramen. The most important fact is that *Cocomys* has its own derived features (autapomorphies): posterior prolongation of the dorsal process of the premaxillary, anteriorly located temporal fossa, partly ossified facial nerve canal, and small facial wing of the lachrymal. It is worth mentioning that the earliest record of the Ischyromyidae is from the Tiffanian (late Paleocene), older than *Cocomys*. Recently some new rodents, the Alagomyidae and Ischyromyidae, have been reported from the latest Paleocene Clarkforkian of North America and the transitional Paleocene–Eocene age and early Eocene of Asia (Dashzeveg, 1990b; Meng et al., 1994; Tong and Dawson, 1995; Dawson and Beard, 1996). It seems to corroborate the point of view that *Cocomys* cannot be the ancestral type or stem of other rodents, including the Theridomyoidea, Ischyromyidae, and Sciuravidae, although among them the Theridomyoidea may have closer relationships with the Ctenodactyloidea than the others. It is probable that, having originated from a common ancestry, the two superfamilies split and developed independently in different ways.

#### Relationships with the Hystricognathi

Studying the rodents from middle Eocene site in Pakistan, Hussain et al. (1978) first suggested that the African hystricognaths, Phiomysidae, might have derived from the

Chapattimyidae and migrated from Asia to North Africa. Luckett (1980) further thought that the Ctenodactylidae and Pedetidae might be closely related to Hystricognathi. The sister group hypothesis (between the Ctenodactyloidea and Hystricognathi) was substantiated by cladistic analysis based on biological studies (Bugge, 1985; Luckett, 1985; George, 1985). Jaeger et al. (1985) and Flynn et al. (1985) also supported the hypothesis based on the discovery of late Eocene forms from North Africa and microstructure of incisor enamel, respectively. Bryant and McKenna (1995) further thought that the living Ctenodactylidae would be the sister taxon of Hystricognathiformes, including Hystricognathi and *Tsaganomys*. However, Hartenberger (1985, 1990) argued that Hystricognathi would not be the only ctenodactylid sister group. Having emphasized the parallel evolution in the rodent features, Wood thought that the Ctenodactyloidea had no relationship with the Hystricognathi, and several of the features common to the two taxa were acquired independently (Wood, 1975, 1980, 1985).

It seems that the evidence from the fossils is not enough to support the sister group hypothesis of the Ctenodactyloidea with the Hystricognathi. The hypothesis was first proposed on tooth similarities between the chapattimyids and the African hystricognaths, *Phiomyidae* (Hussain et al., 1978). Unfortunately, however, the Chapattimyidae, except for *Birbalomys*, are represented only by isolated teeth. Their status is still problematic. The lack of mandible material in this group means that there is no test for the above hypothesis. *Protophiomys algeriensis*, which was considered as important evidence for this hypothesis (Jaeger et al., 1985), has the same problems. Because it is only known from isolated teeth, its taxonomic position is also uncertain. Jaeger et al. (1985) referred it to the *Phiomyidae*, whereas Luckett and Hartenberger (1985) indicated that cranial and mandibular evidence was lacking to corroborate its *phiomyid-hystricognath* affinities. Flynn et al. (1986) further believed that it was a chapattimyid of *baluchimyine* affinity. Likewise, the *Baluchimyinae* are known from isolated teeth. They were referred to the Chapattimyidae by Flynn et al. (1986) but

were suggested to be a member of *Hystricognathiformes* by Bryant and McKenna (1995). The material so far available shows that all the other ctenodactylids have a *sciurognathous* mandible. As mentioned before, the Ctenodactyloidea have their own evolutionary tendencies. To date I have not seen any material in the Ctenodactyloidea showing the change from the *sciurognathous* mandible to a *hystricognathous* one.

As for the microstructure of the incisor enamel, according to Martin (1992), *Cocomys* and some Eocene chapattimyids, including cf. *Birbalomys* [sp.], have pauciserial enamel, whereas the *Baluchimyinae* of the Chapattimyidae and the Ctenodactylidae have multiserial enamel. It seems that the multiserial enamel evolved twice at least in the Ctenodactyloidea if the Chapattimyidae and Ctenodactylidae do represent different lineages as mentioned by some paleontologists (Dawson et al., 1984; Wang, 1984, 1994; Flynn et al., 1986).

It appears that the hypothesis of sister group affinities between the Ctenodactyloidea and Hystricognathi remains to be tested when more complete material becomes available.

#### (VII) EVOLUTION, EXTINCTION, AND MIGRATION OF THE CTENODACTYLOIDEA

The extant ctenodactylids include four genera—*Ctenodactylus*, *Felovia*, *Massouteria*, and *Pectinator*. All live in Africa. However, as mentioned above, the ctenodactylids originated in eastern and central Asia. There they lived from Eocene through the Miocene, diversified widely, and radiated several times, becoming a flourishing group of rodents during the whole Paleogene.

*Cocomys* is known from the early Eocene of Hengdong County, Hunan Province of China. This genus is the earliest and most primitive ctenodactylid, and also the most primitive one so far known for the whole Rodentia (Li et al., 1989). Probably the Ctenodactyloidea, first represented by *Cocomyidae*, originated in eastern and central Asia at the beginning of the Eocene or earlier, in the Paleocene. By the late early Eocene the Ctenodactyloidea began their first radiation,

diversifying into two lineages: Yuomyidae–Chapattimyidae and Tamquammyidae–Ctenodactylidae. The first lineage, having molari-form P4 and p4, is widely distributed over all eastern, central, and southern Asia and is split into two families, Yuomyidae and Chapattimyidae. The Chapattimyidae spread into the India subcontinent, where they evolved until late early Miocene (Flynn et al., 1986), whereas the Yuomyidae evolved from early Eocene through late Eocene and spread widely over eastern and central Asia (Li, 1963, 1975; Dawson, 1964; Shevyreva, 1971a, 1971b; Wang (J.-w.), 1978; Wang et al., 1981; Wang and Zhou, 1982; Ye, 1983; Wang, 1984; Hu, 1995; Tong and Dawson, 1995). Meanwhile the second lineage, retaining nonmolariform P4 and p4, is only distributed in eastern and central Asia. The Tamquammyidae mainly developed from late early Eocene to middle Eocene, and the Ctenodactylidae possibly split from the former in the late Eocene or earlier.

The Ctenodactylidae became well developed in the early Oligocene in eastern and central Asia. The Karakoromyinae–Distylomyinae–Ctenodactylinae group split from the Tataromyinae in the early Oligocene or earlier, and then split again into two lineages before the late Oligocene. The Ctenodactylinae split from other ctenodactylids in the early Miocene or earlier. By the late early Miocene (about 18 Ma) the subfamily spread widely and migrated into southern and western Asia, then in the early middle Miocene (about 14 Ma) moved to the circum-Mediterranean area and North Africa. The living ctenodactylids inhabit North and East Africa (Lavocat, 1961; Jaeger, 1971; Robinson and Black, 1973; Sen and Thomas, 1979; Goldsmith et al., 1982; Flynn et al., 1986; Jacobs et al., 1989). In contrast, the Tataromyinae, which split into several lineages and became the most successful rodent group in the mid-Tertiary Asia, became extinct completely, leaving no descendant after the middle Miocene in Asia. It seems that Tataromyinae was replaced by the Ctenodactylinae. Unfortunately, the Ctenodactylinae also disappeared first in eastern and central Asia in the late middle Miocene, then in southern Asia after the late Miocene. Since then, Ctenodactylidae has been extinct in Asia.

To know the reason of the evolution and extinction of Ctenodactylidae in Asia and the migration to circum-Mediterranean area and Africa, it is necessary to understand the ecology of living ctenodactylids. The paleoecology, paleoclimatology, and paleogeography of the Palearctic Region in the mid-Tertiary must be considered first.

The four living genera of ctenodactylids live in desert or semidesert habitats at altitudes ranging from sea level to 2,400 m above sea level in North and East Africa. They never excavate or occupy burrows, but dwell in caves or rocky crevices. The living ctenodactylid ecological niche is described as long hours of sunshine, low humidity for most of the year, and a relatively high average and high maximum temperature combined with rocky outcrops and low density vegetation. They are diurnal and adapted to the hot conditions. They sunbathe a long time every day, but they do not like wetness. When the weather is cold, windy, or wet, their activity is restricted. Their fur is very soft, without stiff, straight hairs, and offers the ctenodactylids no protection from rain. When the weather is wet, their hair sticks together in tufts. To groom their extremely soft fur bloom, they often use their pectinate bristles on their hind feet to curry their fur very carefully. Their diet includes leaves, stalks, seeds, and flowers. They do not store food and reserve fat partly (George, 1974; Grzimek, 1975; Delany and Happold, 1979; Nowak and Paradiso, 1983). Clearly, some of the areas in North and East Africa are ideal habitats for them.

As mentioned above, during the Tertiary Ctenodactyloidea shows distinct evolutionary tendencies. The cheek teeth evolved from brachydont and bunodont to hypsodont and lophodont, accompanied by the tendency to become tri- or bilobe prismatic. The skull evolved from protrogomorphous to hystricomorphous. Both the orbit and bulla enlarged gradually. The masseteric fossa also enlarged gradually and the lower masseteric crest became more and more developed. The ascending ramus changed from higher to low, with the coronoid process progressively reduced. Probably along with the development of the masseter muscle and the reduction of the temporal muscle, the Ctenodac-

tyloidea developed a greater capability of gnawing and chewing, and evolved from more omnivorous to herbivorous. It seems quite likely that in Asia the ctenodactylids gradually adapted to a dry climate and broad desert or semidesert landscape as the living ctenodactylids do.

It is well known that global climate changed greatly during Tertiary. During the period from the Cretaceous through Paleocene, the climate was generally warm. In central and eastern Asia a dry subtropical belt stretching in a northwest-southeast direction was formed. The area south of this belt (i.e. South China and southern Asia) was covered predominantly by tropical evergreen forest (Tao, 1992). During the Eocene the global climate was generally characterized by higher temperature, higher humidity, and greater degree of equability of the temperature, although there was a cooling event in the late middle Eocene. The animals adapting to the warm and humid climate, such as the brontotheres, amynodonts, and anthracotheres, greatly diversified. At the beginning of the Eocene or in the late Paleocene, the primitive ctenodactylids originated and began their development in such ecological circumstances. During that period Asia might have been a single faunal province with no barrier for dispersal of mammals. The Indian Plate made its initial contact with the Laurasian Plate. The Ctenodactyloidea began their first wide radiation. The Chapattimyidae could have spread into the Indian subcontinent during this time. By the middle Eocene the Himalayas/Tethys might have become a geological barrier to hinder the interchange of mammals between northern and southern Asia (Sahni et al., 1981; Hartenberger, 1982b; Flynn et al., 1986; and Sahni, 1989). The Chapattimyidae evolved in the Indian subcontinent while the other ctenodactylids, including the Cocomyidae, Tamquammyidae and Yuomyidae, diversified in eastern and central Asia.

The late middle Eocene-early Oligocene interval was one of the most significant episodes of Tertiary climatic changes. Paleoclimatic evidence indicates global deterioration: cooling, drying, and increasing mean annual range of temperature and latitudinal temperature gradient (Wolfe, 1978; Berggren and

Prothero, 1992; Retallack, 1992). With the retreat of the Turgai Strait, eastern and central Asia became arid, evidenced by widespread red beds rich in gypsum. Drought-adapted ctenodactylids flourished and diversified, in place of archaic rodents adapted to a warm and humid climate. Throughout this period, the Himalayas/Tethys was still a circum-equatorial, deep-water passage from the Pacific to the Atlantic (Rögle and Steininger, 1984) and hindered mammalian interchange between northern and southern Asia.

In the early Miocene (about 20–18 Ma), with the further retreat of Himalayas/Tethys, the sea between northern and southern Asia vanished, but the Himalayas were not high enough to obstruct the migration of animals (Xu, 1993: 115). Exchange of mammals began. *Sayimys* and some large mammals migrated into southern Asia from northern Asia (Raza and Meyer, 1984; Flynn et al., 1986). The endemic chapattimyids, the Baluchimyinae, survived (Flynn et al., 1985, 1986) until late early Miocene (about 18 Ma), when the climate became drier and cooler, and a variety of rodents could enter southern Asia from northern Asia and replaced the Baluchimyinae (Rögle and Steininger, 1984; Jacobs et al., 1989).

The marked uplift of the Himalayas from the middle Miocene on apparently played an important role in reforming atmospheric circulation and climatic differentiation, biotic evolution, and diversification (Xu, 1993). It prevented the warm and humid air flow from going farther north, rendering the land south to the Himalayas even more wet. On the other hand, the uplifted Himalayas blocked the southward movement of the Siberian cold current, rendering the area north of it cooler and drier. Meanwhile the famous eastern Asian monsoon regime developed. In summer, the warm wet air prevailed, whereas in winter the cold current from Siberia prevailed. Both wet and cold climate were unfavorable for ctenodactylids. In the early middle Miocene (about 16 Ma), the south Asian monsoon was still weak in southern and western Asia. Especially during that period a global deteriorating climatic condition occurred. In the Siwalik sequence these events may be correlated with the radiation of the bovids and murids (Barry et al., 1985).

This might be favorable for the ctenodactylids to live in southern Asia. Therefore, by the middle Miocene *Sayimys* had become extinct in northern Asia, and could not enter the southeastern Asia due to the unfavorable conditions related to the eastern Asian monsoon regime. In southern Asia, however, *Sayimys* survived, where the climate remained hot and not very humid, until 9 Ma, when the south Asian Monsoon intensified (Ducrocq et al., 1994). With the strengthening of the monsoon and increasing humidity in southern and eastern Asia and collision of Asia with Afro-Arabia, probably a corridor for mammalian exchange opened between Asia and Africa across Arabia and Asia Minor. The ctenodactylids migrated gradually westward, moved into the circum-Mediterranean area and North Africa, via Arabia. Since then, no survivor of ctenodactylids has been found in Asia.

Around the Eocene–Oligocene boundary, with climatic change and the retreat of the Turgai Strait, a corridor for continental mammal exchange between Asia and Europe formed. A variety of mammals including several rodent families migrated into Europe from Asia at the so-called “Grande Coupure” (Stehlin, 1909). However, until now

no ctenodactyloid has been reported from the European continent except in the Mediterranean area, where some Miocene ctenodactylids invaded some islands. This is a rather puzzling problem. It seems that ecologically the climate may play a very important role. Although the climate changed from dominantly subtropical (late Eocene) to a colder, warm, and seasonal climate from the Oligocene through the Miocene time, the humidity probably did not change very much in Europe. Hence, the biotopes were predominantly rather wet in Europe (Hartenberger, 1983; Fahlbusch, 1989; Berggren and Prothero, 1992; Collinson, 1992; Legendre and Hartenberger, 1992), which may have hindered the ctenodactylids from migrating into the continent of Europe. From the late early Miocene (= MN4) onward the biotopes changed gradually. In most parts of Europe, including France and central Europe, the biotopes still remained moist and rich in vegetation, whereas in the Mediterranean area, including Spain, the biotopes became rather dry and savanna-like (Van de Weerd and Daams, 1978; Fahlbusch, 1989). That may be the reason why the ctenodactylids never entered then European continent, but some of them could move into the Mediterranean islands in the middle Miocene.

## CONCLUSIONS

(1) Recent study shows that the mid-Tertiary Ctenodactylidae of eastern and central Asia include 10 genera: *Tataromys*, *Yindirtemys*, *Bounomys*, *Karakoromys*, *Akzharomys*, *Prosayimys*, *Sayimys*, *Distylomys*, *Proditylomys*, and *Euryodontomys*, new genus. *Leptotataromys*, *Muratkhanomys*, and *Roborovskia* are junior synonyms of *Tataromys*.

The species previously referred to *Tataromys* can be divided into four genera: *Tataromys*, *Yindirtemys*, *Bounomys*, and *Euryodontomys*, new genus. *Tataromys* includes only four species: *T. plicidens*, *T. sigmodon*, *T. minor*, and *T. parvus*, new species. *Yindirtemys* is composed of eight species: *Y. grangeri*, *Y. deflexus*, *Y. gobiensis*, *Y. suni*, two new species, *Y. ambiguus* and *Y. xiningensis*, *Yindirtemys* sp., and perhaps *Y. birgeri*. *Bounomys* has two species: *B. bohlini* and *B. ulantatal-*

*ensis*. *Euryodontomys* includes two species, *E. ampliatus* and *E. exiguus*.

*Karakoromys* is not only a reliable and well-defined genus but also represents a subfamily, Karakoromyinae. *Terrarboreus* and *Woodomys* are junior synonyms of *Karakoromys*.

(2) The family Ctenodactylidae consists of four subfamilies: Tataromyinae, Karakoromyinae, Distylomyinae, and Ctenodactylinae. The Distylomyinae and Ctenodactylinae form a sister group to the Karakoromyinae, then to the Tataromyinae. The Ctenodactylidae originate in the Eocene of Asia. The Tataromyinae split from the others in the late Eocene or earlier. By the mid-Tertiary the Tataromyinae split into three lines and became the most flourishing rodent group. After the middle Miocene, this subfamily became extinct, leaving no descendants. The sister



group of the Distylomyinae and Ctenodactylinae split from Karakoromyinae before the late Oligocene. The Ctenodactylinae split from the Distylomyinae in the early Miocene or earlier, spread widely, and migrated into southern and western Asia in the late early Miocene, then moved to the circum-Mediterranean area and North Africa. By the end of the late Miocene the ctenodactylids had completely disappeared from Asia, but at present they still inhabit North and East Africa. The evolution, diversity, migration, and extinction of the Ctenodactylidae were under strong influence of the climatic and landscape changes of the Palearctic Region.

(3) The superfamily Ctenodactyloidea includes five families. The Cocomyidae represent the most primitive group and is ancestral type to other ctenodactylids. The other four families originated from *Cocomys*-like rodents and split into two lineages shortly after *Cocomys* appeared in the early early Eocene: the Tamquammyidae and Ctenodactylidae form the main stem, in which P4 and p4 are nonmolariform and have tendency to be reduced or absent; the Chapattimyidae and Yuomyidae form a side branch, in which P4 and p4 are molariform.

(4) The Hsanda Gol Formation may comprise deposits of a longer duration, including early and late Oligocene, than previously thought. *Yindirtemys deflexus* and *Yindirtemys gobiensis* might not appear until the late Oligocene, at least late early Oligocene. However, further work is needed for a final solution of this problem.

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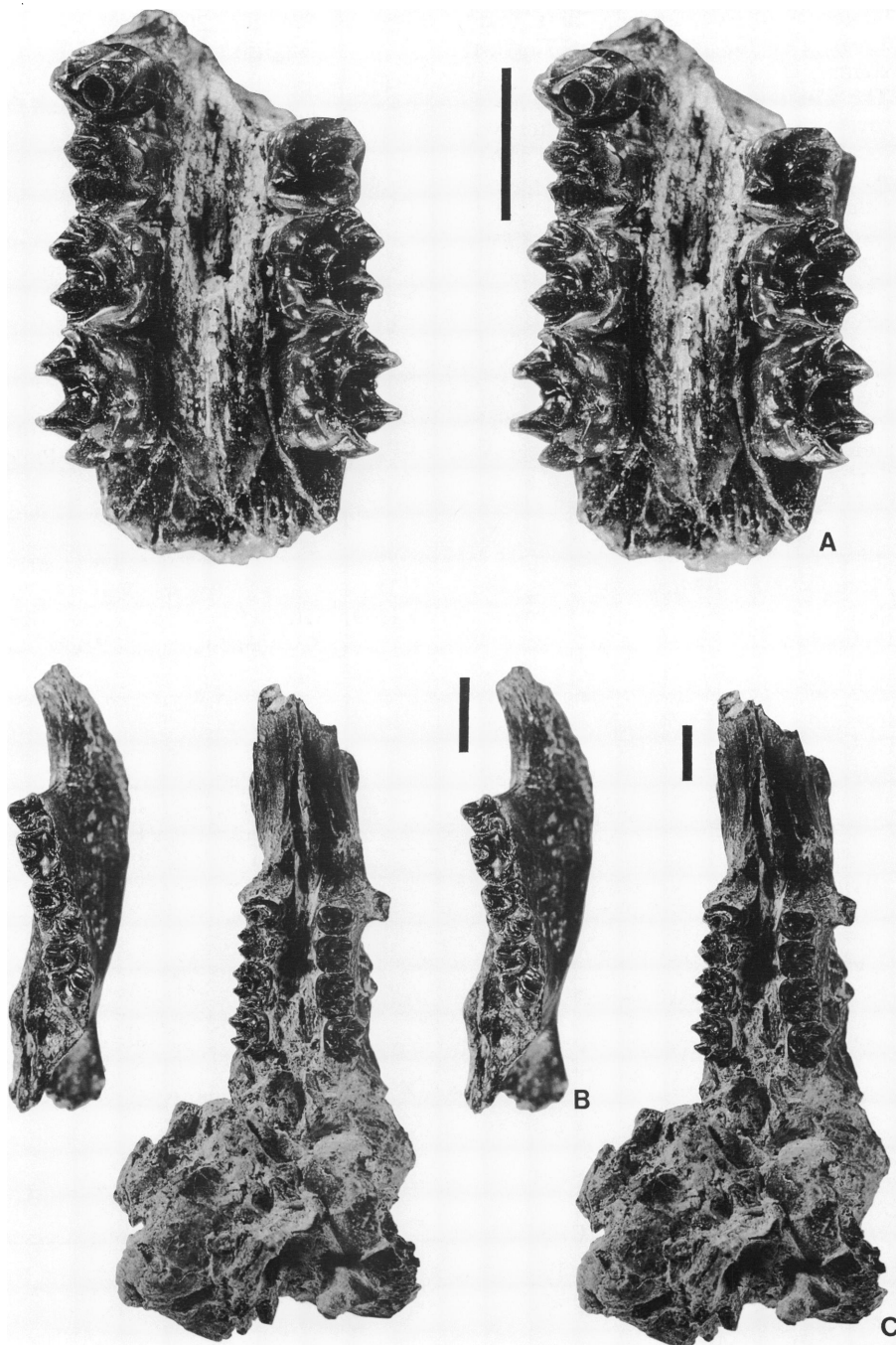


Fig. 40. *Tataromys plicidens* (in stereo). A. Occlusal view of upper jaw with right P4-M3 and left M1-3 (AMNH 19082, holotype). B, C. AMNH 21658. B. Occlusal view of left lower jaw. C. Ventral view of skull. Scales = 5 mm.

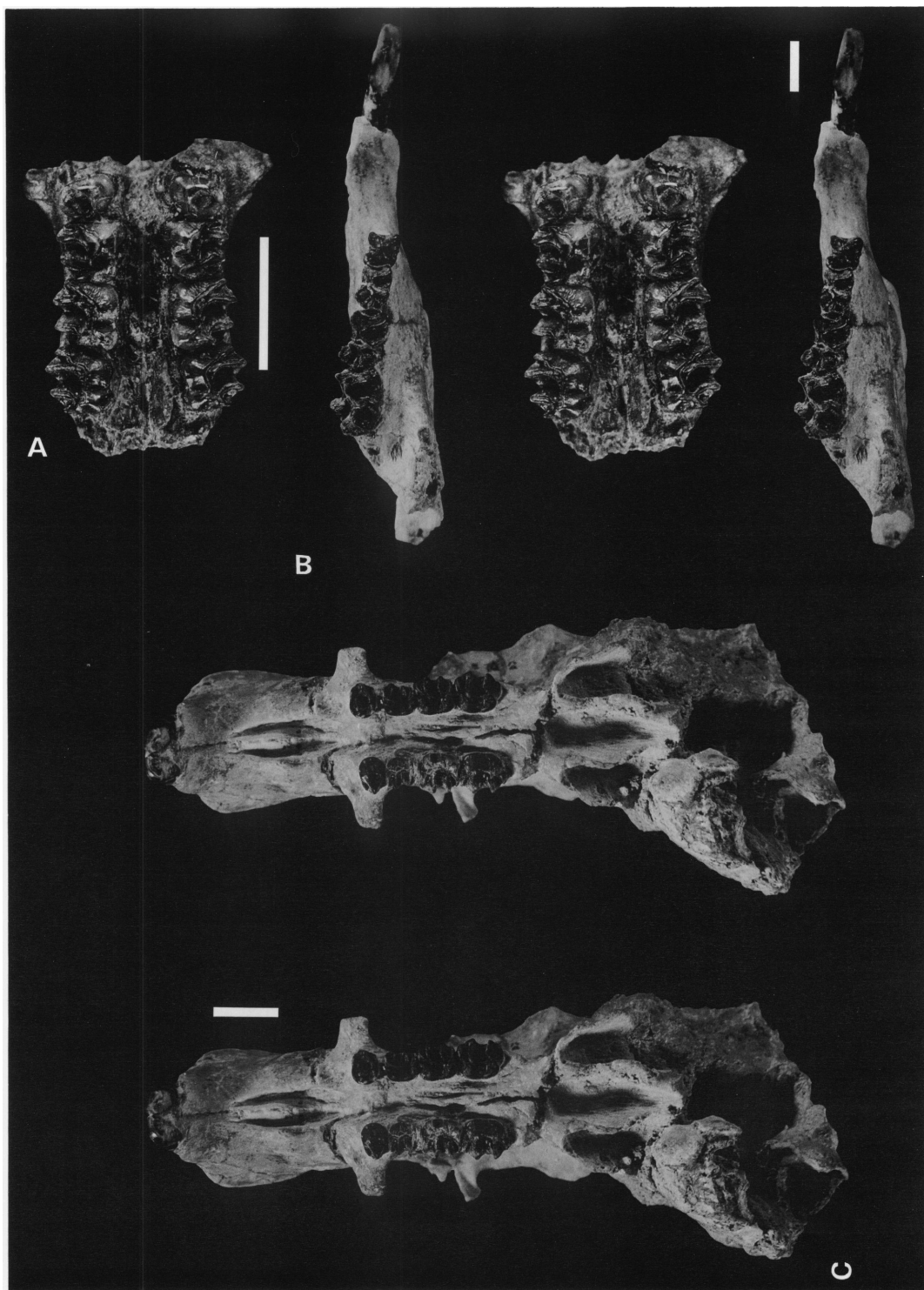


Fig. 41. *Tataromys* (in stereo). A. *T. sigmodon*. Occlusal view of upper jaw with right and left P4-M3 (AMNH 19079, holotype). B, C. *T. plicidens*. V 10534.1. B. Occlusal view of right lower jaw with p4-m3. C. Ventral view of skull. Scales = 5 mm.





