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New Eocene Ctenodactyloid Rodents from the Eastern Gobi Desert of Mongolia and a Phylogenetic Analysis of Ctenodactyloids Based on Dental Features

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ABSTRACT

Two ctenodactyloid rodents, *Mergenomys orientalis*, n. gen. and sp., and *Butomys prima*, n. gen. and sp., from the middle Eocene localities of the Eastern Gobi Desert of Mongolia are described. Dental features that bear phylogenetic importance for ctenodactyloids are discussed. A cladistic analysis based primarily on dental features reveals the phylogenetic positions of the two new taxa. *Mergenomys* is closely related to the clade of the Ctenodactylidae, whereas *Butomys* is possibly related to Tsinlingomyinae. The analysis indicates that several traditional taxa of ctenodactyloids, such as Cocomyidae and Yuomyidae, are paraphyletic.

INTRODUCTION

The Eocene continental deposits are exposed widely in the Eastern Gobi Desert and a number of sections were known to geologists. The localities of Mergen and Tsagan Tsav, among others, were discovered by the senior author in 1981 and several investigations have been conducted since then (fig. 1; see also Dashzeveg and Hooker, 1997; Storch and Dashzeveg, 1997). The Mergen locality (Quarry 1) is 20 km to the northwest

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of the Dzamyn Ude frontier station, 10 km to the west of the railway, and 5 km to the southwest of the Lake Doloodoi. The Tsagan Tsav locality is 22 km to the southwest of the Khubsugul sum center of the Eastern Gobi Desert and approximately 40 km to the east of the classic Ergil Obo locality.

Screen-washing of the bone-bearing deposits from the Mergen and Tsagan Tsav localities during the field seasons of 1981-83 and 1991-92 produced a considerable number of middle Eocene mammals for the first time in the Eastern Gobi Desert. Among the mammals, rodents and lagomorphs are the predominant elements. Preliminary study has identified the following taxa from the Mergen locality: rodents (*Mergenomys orientalis*, n. gen. and sp. and *Yuomys* sp.), a tupaiodontine insectivore *Zaraalestes*, a lagomorph (*Gobilagus* sp.,) and two tapiroids (*Lophialetes expenditus* and *Breviodon minutus)*. Not far from Quarry 1, the senior author collected remains of a rhinocerotoid, *Triplopus? mergenensis*, from the middle part of the Mergen section. Fossils from the Tsagan Tsav locality include ctenodactyloid rodents (*Butomys gobiensis* n. gen. and sp. and *Yuomys* sp.), a tupaiodontine insectivore (*Zaraalestes russelli* Storch and Dashzeveg, 1997), two lagomorphs (*Gobilagus* and *Shamolagus*), and a tapiroid perissodactyl (*Lophialetes expeditus*). The coexistence of *Zaraalestes* and *Lophialetes expeditus* suggest age equivalence of the fossil assemblages from the Mergen and Tsagan Tsav localities. Tapiroids and ctenodactyloid rodents also allow us to correlate the Mergen and Tsagan Tsav faunas with the well-studied Irdin Manha and Ulan Shireh faunas in the adjacent territory in China; the latter faunas are considered middle Eocene in age.

The evolution and systematics of ctenodactyloid rodents, a major Asian rodent group found throughout most of Tertiary time, have been studied by many workers (Shevyreva, 1976; Wood, 1977; Dawson et al., 1984; Korth, 1984; Flynn et al., 1986; Wang, 1994, 1997; Averianov, 1996; Tong, 1997), but issues still remain controversial. For instance, a recent study by Averianov (1996) concluded that Cylindrodontidae, Ctenodactylidae and Baluchimyinae form a monophyly, in which Cylindrodontidae and Ctenodactylidae are sister groups. Species of Cylindrodontidae are reported from Asia and North America and are protrogomorphous with uncertain phylogenetic position (Emry and Korth, 1996). Averianovs conclusion, therefore, either implies paraphyly of the ctenodactyloid rodents or suggests that the Cylindrodontidae are a subgroup within hystricomorphous ctenodactyloid rodents. Our present study will focus on those traditionally considered as ctenodactyloids and explore their relationships based on dental morphologies. Relationships of Cylindrodontidae will be investigated in another study. Among previous phylogenetic analyses of ctenodactyloid rodents, a cladistic approach employing the rule of parsimony has not been used, with the exception of Averianov (1996). However, Averianov recognizes paraphyletic and polyphyletic groups. Our analysis provides a view of the phylogenetic issues within ctenodactyloids that differs from those of previous studies.

In the description, terminology of dental structures follows Wang (1997; fig. 2).

SYSTEMATIC PALEONTOLOGY

RODENTIA BOWDICH, 1821

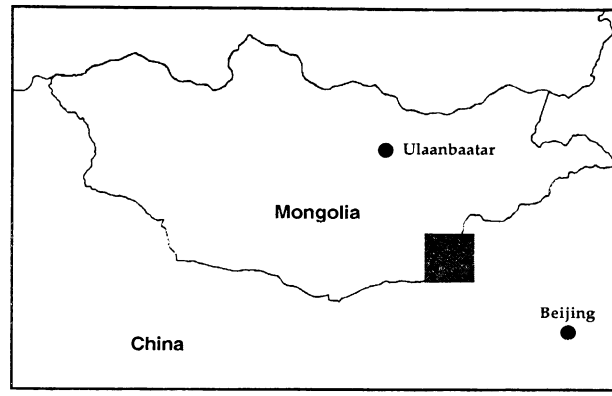
SUPERFAMILY CTENODACTYLOIDEA TULLBERG, 1899

Mergenomys, new genus

ETYMOLOGY: The name indicates the locality Mergen, with the Greek suffix *-mys* for "mouse."

TYPE SPECIES: *Mergenomys orientalis* n. sp.

DIAGNOSIS: Small ctenodactyloid. Cheek teeth quadrate, brachydont and more cuspate than lophate; masseteric fossa extending to below anterior edge of m1. Posterior root of zygomatic arch at anterior end of P4. Upper molars differing from those of other early ctenodactyloids in lacking a crest (entoloph) between protocone and hypocone (except *Viriosomys* and some yuomyids; see Tong, 1997), protoconule absent, lingual end of anterior cingulum expanded to form a small anterocone, large metaconule isolated from protocone and a large hypocone. Lower molars differing from those of early ctenodactyloids in having short but more lingually po-



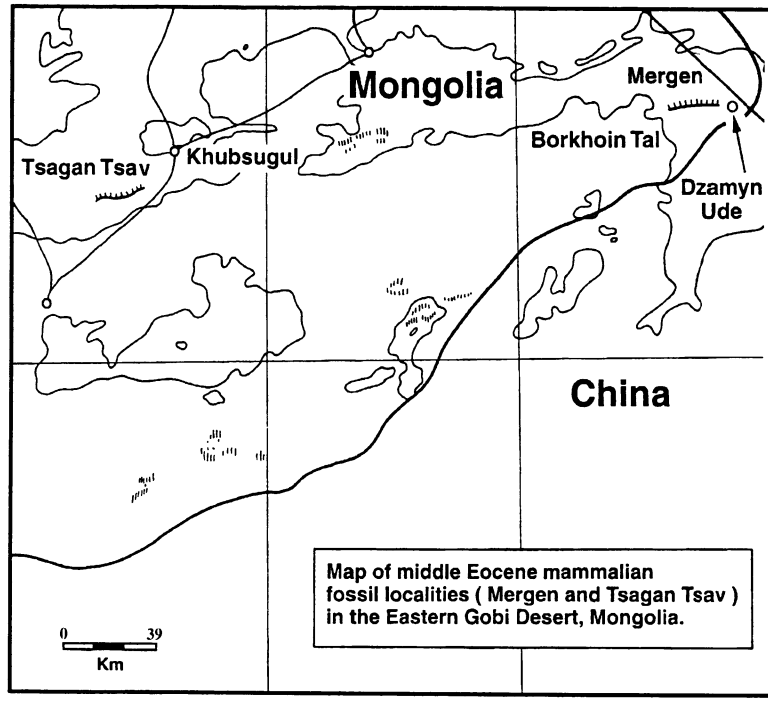


Fig. 1. Location of the Mergen and Tsagan Tsav mammalian fossil localities.

sitioned ectolophid; ectolophid connecting hypoconid and protoconid; absence of mesoconid; weak hypolophid leading from a conical entoconid to mid-ectolophid; large hypoconulid connecting the hypoconid by a weak ridge; and m1 considerably smaller than m2. Differs from ctenodactylids in being less lophodont and possessing a large metaconule and possibly having P3.

Mergenomys orientalis, new species

ETYMOLOGY: *Orientalis*, Latin: "eastern."

HOLOTYPE: PSS 41/43, a fragment of right upper jaw with dP4, M1 and M2 (fig. 3B, D).

REFERRED MATERIAL: PSS 41/23, a fragment of right lower jaw with m1-m2 (fig. 3A, C). This specimen and the type came from a small pit of the same locality.

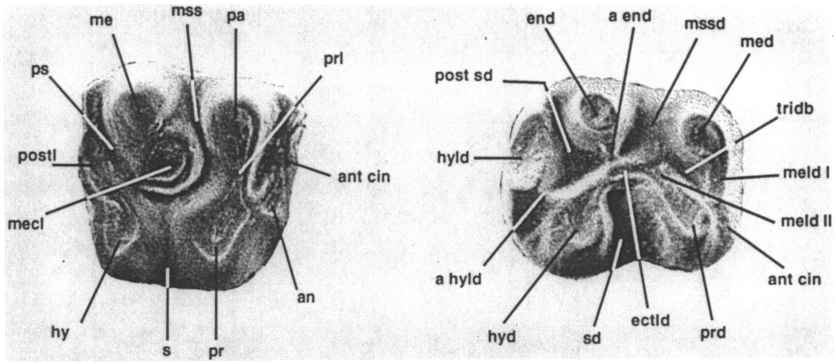


Fig. 2. Terminology of molar structures (following Wang, 1997). Abbreviations: **a end**, arm of entoconid; **a hyld**, arm of hypoconulid; **an**, anterocone; **ant cin**, anterior cingulum; **ectld**, ectolophid; **end**, entoconid; **hy**, hypocone; **hyd**, hypoconid; **hyld**, hypoconulid; **me**, metacone; **mecl**, metaconule; **med**, metaconid; **meld I**, metalophid I; **meld II**, metalophid II; **mss**, mesosinus; **mssd**, mesosinusid; **pa**, paracone; **post sd**, posterosinusid; **postl**, posteroloph; **pr**, protocone; **prd**, protoconid; **prl**, protoloph; **ps**, posterosinus; **s**, sinus; **sd**, sinusid; **tridb**, trigonid basin.

LOCALITY AND AGE: The Mergen locality, Quarry 1, Eastern Gobi Desert of Mongolia; middle Eocene.

DIAGNOSIS: Same as for genus.

DESCRIPTION: The posterior edge of the zygomatic process is anterior to P4. The broken anterior surface of the alveolus for a small, single-rooted dP3 or P3 is represented by a vertical groove in the maxilla. DP4 is light-colored, more heavily worn, and much smaller than the molars. Its crown is molariform and rectangular in outline. Because of wear, the metacone connects with the protocone. The molars are somewhat trapezoidal in outline, being slightly longer labially than lingually. Wear on M1 is more extensive than on M2, but less so than on dP4. The anterior cingulum of M1 is well developed and is at the same height as the protoloph at the junction of the protocone and paracone. Its lingual end is expanded to form a small anterocone, which, after wear, forms a continuous surface posterior to the dP4 hypocone. The protocone is the largest cusp on the crown and is connected with the paracone by a strong protoloph. A protoconule is absent. An entoloph is absent so that the protocone is separated posteriorly from the hypocone by a shallow, transverse groove. The hypocone is large, only slightly smaller than the protocone. From the hypocone the posterior cingulum (posteroloph) extends to the posterior side of the metacone. The paracone is almost equal to the metacone; they are separated by a narrow mesosinus. There is no mesostyle. A large metaconule, confluent at the base with the metacone, occupies most of the mesosinus and is extensively worn, resulting in a circular enamel loop. The metaconule is isolated from the protocone; therefore, the metaloph is incomplete lingually. M2 is similar to M1, except that it is larger, less worn, bears a small mesostyle between paracone and metacone, and has the mesosinus more open due to a proportionally smaller metaconule.

On the mandible the masseteric fossa ends at the level of m1 but a small ridge continues further anteriorly below the middle point of p4. The ventral ridge of the masseteric fossa is strong, whereas the dorsal one is absent on the preserved portion of the mandible. Anterior to the masseteric fossa is a single mental foramen. Judging from the alveolus, the p4 is longer than wide and wider posteriorly than anteriorly; it is probably double-rooted. The m1 metaconid is slightly more anterior than the protoconid; both are connected by a low metalophid I. There is a low and short anterior cingulum in front of the protoconid. The posterior arm of the protoconid (metalophid II) is short, extending posterolingually to join the ectolophid. A short trigonid basin opens posterolingually. The ectolophid is

short and on the longitudinal midline of the tooth; it extends posteriorly to the hypoconid. Because of the lingually placed ectolophid, the sinusid is deep. There is no mesoconid on the ectolophid. The mesostylid is absent. The talonid basin (the mesosinusid and posterosinusid) is small, owing to the large and anteriorly positioned entoconid. The hypoconid and entoconid are conical and equal in size. The entoconid lacks an arm (hypolophid). A weak projection at the posterolingual base of the hypoconid connects with the hypoconulid; the cusps are otherwise separated by a trough. The hypoconulid is large and transversely expanded, with an oval wear facet at its tip. The cusp extends lingually and labially as low ridges. The entoconid and hypoconulid are separated separated by a distinct valley. The m2 differs from m1 in being significantly larger. The entoconid has a short ridge extending to the midpoint of the ectolophid. The connection between the hypoconid and hypoconulid is stronger and the hypoconulid is more transversely elongated than on m1. Comparisons with other ctenodactyloids are provided in the Character Analysis. See table 1 for measurements.

Butomys, new genus

ETYMOLOGY: *But* means "bush" in Mongolian, with the Greek suffix *-mys* for "mouse."

TYPE SPECIES: *Butomys prima* new species

DIAGNOSIS: Small ctenodactyloid; lower molars brachyodont and mainly bunodont, with weak lophs; p4 non-molariform with a heel bearing a conical entoconid and a low transverse ridge; m1-2 ectolophid rudimentary and mesoconid absent; hypoconulid large; masseteric fossa extending below the anterior edge of m1. Differs from Yuomyidae (including *Hohomys* [Hu, 1995]) and Chapattimyidae in having a non-molariform p4. Differs from Cocomyidae and Tamquammyidae in having p4 transversely wider and protoconid larger than metaconid, lower molars with weak ectolophid, absence of mesoconid, and larger and isolated hypoconulid. Differs from Ctenodactylidae in being more cuspate. Differs from *Mergenomys* in being smaller, having less developed metalophid II and ectolophid, and hypolophid extending toward the hypoconid.

Butomys prima, new species

ETYMOLOGY: *Prima*, Latin: "first."

HOLOTYPE: PSS 39/19, a fragment of a right lower jaw with p4-m2 (fig. 4).

LOCALITY AND AGE: The Tsagan Tsav of the Eastern Gobi Desert; middle Eocene.

DIAGNOSIS: Same as for genus.

DESCRIPTION: The masseteric crest extends to the level of the anterior edge of m1. The lower masseteric crest is strong, whereas the upper one is poorly pronounced. The mental foramen is anteroventral to the p4. The lower molar teeth are brachydont and bunodont, with weak lophids. The p4 is non-molariform; it is slightly longer than wide and bears three conical cusps: the protoconid, metaconid and entoconid. Among the three cusps the protoconid is the largest. The metaconid, the smallest, is slightly more anterior than the protoconid and is separated from the latter by a longitudinal groove. The trigonid is higher than the talonid. The talonid is very short, consisting of a conical entoconid on the lingual side and a low ridge labially. The talonid basin is represented by a narrow transverse groove, separating the trigonid from the entoconid. The ectolophid is absent.

The m1 trigonid is narrower than the talonid. The protoconid is larger than the metaconid and bears two wear facets: one on its tip and the other on its anterolabial side. The metalophid I and metalophid II are low, enclosing an oval trigonid basin. The ectolophid is very weak, extending along the midline of the tooth. Because of the weak ectolophid, the mesosinusid and sinusid are confluent, separating the trigonid from the talonid. There is no mesoconid, nor is there a mesostylid. The hypoconid and entoconid are nearly equal in size; they are tear-drop shaped, with their apexes joining slightly posterior to the cusps at the midline of the tooth. The hypoconulid is distinctive, transversely elongate, and nearly isolated from both the hypoconid and entoconid. It projects posteriorly and sends out low ridges lingually and labially to form the posterior edge of the tooth. The m2 is larger than m1. The protoconid and metaconid are farther apart than

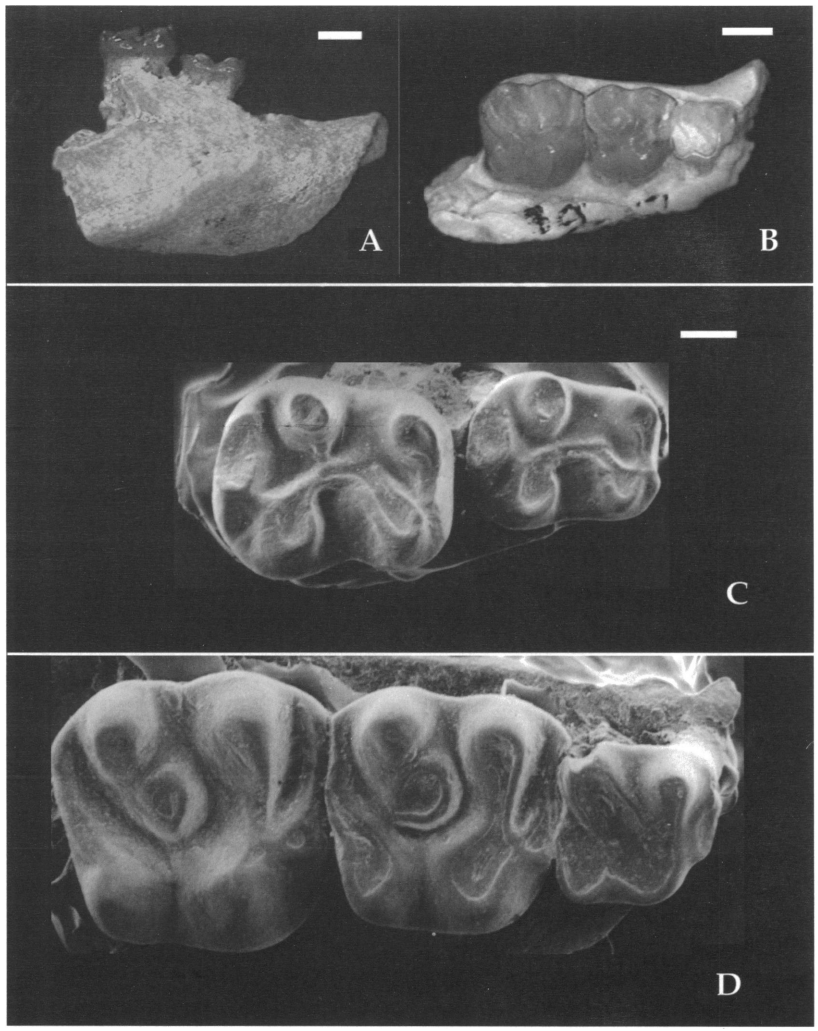


Fig. 3. Material of *Mergenomys orientalis*. A, the labial view of the right lower mandible with m1-m2 (PSS 41/23); B, the crown view of the right upper jaw with dP4-M2 (PSS 41/43, holotype); C, a close-up crown view of m1-m2; and D, a close-up crown view of dP4-M2. Scales = 1 mm in A and B, and 0.5 mm in C and D.

on m1. The m2 metalophid I is as weak as on m1, while the metalophid II is stronger and longer. Although still weak, the short ectolophid on m2 is more distinctive than on m1. It runs along the midline of the tooth and is slightly oblique toward the lingual base of the hypoconid. The shape and relation of the hypoconid and entoconid are similar to those on m1, except that the hypoconulid is more posterior than the entoconid. The hypoconulid is separated from the entoconid, but is connected with the hypoconid by a low ridge. See Character Analysis for comparison and table 1 for measurements.

CHARACTER ANALYSIS

The following is an analysis of characters, primarily from the dentition, that are commonly used in phylogenetic reconstruction of ctenodactyloids. In establishing character polarities, we use *Tribosphenomys* (Meng et al., 1994; Meng and Wyss, 1994) as the outgroup for the ctenodactyloid ingroup. *Tribosphen-*

TABLE 1
Measurements (mm) of Dentitions of *Mergenomys orientalis* and *Butomys prima*

	Length	Width
Mergenomys orientalis		
PSS 41/43		
DP4	1.69	1.15
M1	1.70	1.80
M2	2.00	2.00
PSS 41/23		
m1	1.40	1.10 (tri)/1.30 (tal)
m2	1.76	1.40/1.52
Butomys prima		
PSS 39/19		
p4	0.60	0.60/0.60
m1	1.20	0.80/0.90
m2	1.30	1.00/1.10

omys provides more morphology for comparison than does *Alagomys* (Dashzeveg, 1990b; Tong and Dawson, 1995; Dawson and Beard, 1996). Terminal taxa are genera except the four subfamilies of Ctenodactylidae: Tataromyinae, Karakoromyinae, Distylomyinae and Ctenodactylinae (Wang, 1994, 1997). We do not include some ctenodactyloid taxa in our analysis because of the fragmentary property of specimens and uncertainty in their taxonomy, such as those described by Dashzeveg (1990a) and Shevyreva (1989) from the Bumban fauna of Mongolia. Some of the problems have been discussed by Averianov (1996), but many need further clarification. For the taxa selected, we tentatively accept Averianov's assignment of specimens to established taxa, such as the upper teeth of *Advenimus*; these assignments need to be confirmed because Averianov's criteria of assignment are unclear and the illustrations are difficult to assess. We treat *Saykanomys* as a valid taxon following Averianov (1996) and Tong (1997), although *Saykanomys* has been considered a junior synonymy of *Advenimus* by Dawson et al. (1984). In our analysis, we did not discuss autopomorphies for the terminal taxa. Major sources of data come from the following studies, most of them published recently: Shevyreva (1976, 1989), Dawson et al., (1984), Flynn et al. (1986), Li et al. (1989), Wang (1994, 1997), Hu (1995), Tong and Dawson (1995), Averianov (1996), and Tong (1997).

1. The masseteric fossa: (0) extends below m2 or more posterior, (1) below m1, (2) P4. The masseteric fossa usually extends to the level of m2 in early ctenodactyloids (Hu, 1995) and extends forward during evolution of ctenodactyloids (Tong, 1997). The description by Flynn et al. (1986), "masseteric crest horizontal and extends anteriorly to below p4," was considered a synapomorphy for "Other Ctenodactylidae," which does not include *Tataromys* and *Karakaromys*. Wang (1994) used the description "masseteric fossa shallow and extends to below m1" to diagnose the Ctenodactylidae family. Wang's Ctenodactylidae includes Tataromyinae, Karakoromyinae, Distylomyinae and Ctenodactylinae. The masseteric condition in both *Butomys* and *Mergenomys* is derived.

Wang (1997) also considered "dorsal masseteric crest absent" a synapomorphy for Ctenodactylidae. Because we found this condition difficult to verify in other taxa, we did not include it in our analysis. Nonetheless, this condition is probably present in *Butomys* and *Mergenomys*, more certainly appreciated in the latter because a larger part of the mandible is preserved.

2. The posterior zygomatic root: (0) level with M2, (1) with anterior edge of M1, (2) with anterior edge of P4, (3) significantly anterior to P4. One characteristic of rodents is the forward shift of the anterior root of the zygoma in relation to the cheek teeth. The condition in *Tribosphenomys* (Meng et al., 1994) is considered primitive. The *Mergenomys* condition is similar to that of *Tataromys* but is not so far forward as in other ctenodactylids. We noticed a slight variation of this condition in specimens of *Tataromys*: in some the zygomatic root is slightly more anterior than in others. We follow Averianov (1996) in coding many Eocene taxa, but recognize another condition (state 3) for the ctenodactylids excluding Tataromyinae based on Wang's (1997) observation.

3. P3: (0) small, (1) absent. A small P3 is present in *Tribosphenomys* (Meng et al.,

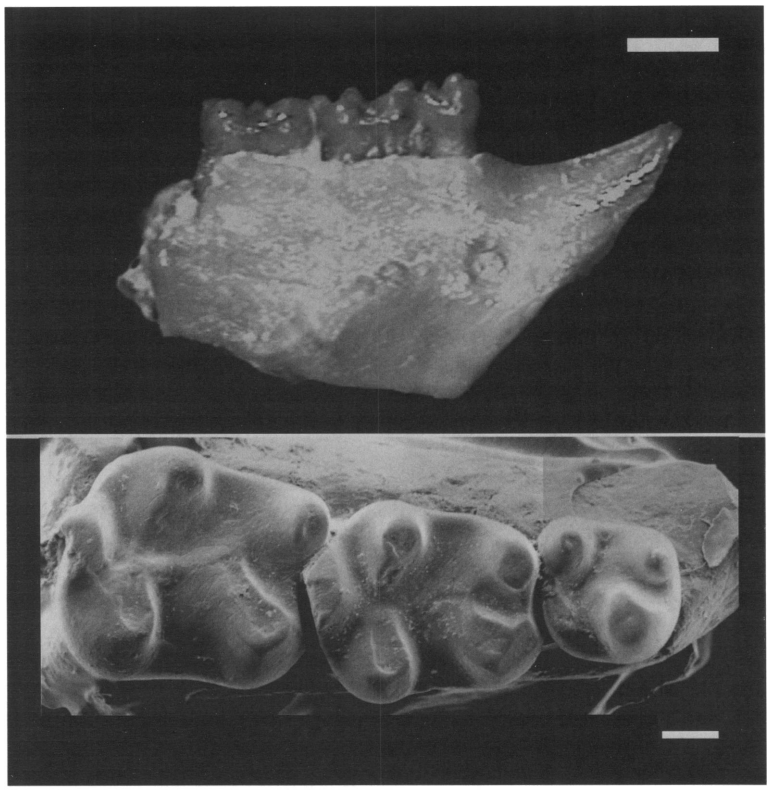


Fig. 4. Material of *Butomys prima*. The labial view of the right mandible with p4-m2 (PSS 39/19, holotype) and the crown views of the lower cheek teeth. Scales = 1 mm above and 0.25 mm below.

1994) and is therefore considered a primitive condition for ctenodactyloids. The loss of P3 is a shared derived feature for Ctenodactylidae (Wang, 1994, 1997). The partial alveolus in the maxilla of *Mergenomys* indicates presence of dP3 or possibly P3. A dP3 is not necessarily followed by a P3 in ctenodactylids. For instance, a dP3 is present in *Karakoromys* but a P3 is absent (Wang, 1997). Therefore, it is uncertain whether a P3 is present in *Mergenomys*. We coded *Mergenomys* and *Butomys* with question marks. P3 occurs universally in other early ctenodactyloids where the tooth or the alveolus is preserved.

4. DP4: (0) triangular, (1) quadrate. The dP4 is molariform in *Cocomys* and *Tamquammys* (Dawson et al., 1984; Li et al., 1989), but it is somewhat triangular due to a narrow lingual portion consisting of a relatively small protocone and hypocone. The dP4 metaloph converges to the protocone as on the molars. In ctenodactylids (*Tataromys*, *Yindirtemys*, *Karakoromys* [=*Terrarboreus*]) the dP4 is also molariform, but with the metaloph instead parallel to the protoloph. The outline of these deciduous teeth is quadrate, except in *Yindirtemys* in which it is anteroposteriorly elongate. The dP4 in *Mergenomys* differs from those of *Cocomys* and *Tamquammys* in being quadrate rather than triangular but is similar to them in having the metaloph extending toward and joining the protocone; the latter feature distinguishes *Mergenomys* from ctenodactylids.

5. P4/p4: (0) molariform, (1) or non-molariform. The last premolars play an important role in establishing relationships among Eocene ctenodactyloids (Dawson et al., 1984). According to Dawson et al., those with non-molariform P4/p4 were grouped into the family Cocomyidae (*Cocomys*, *Tamquammys*, and *Tsinlingomys*) and others with molariform P4/p4 are placed in Yuomyidae

(*Petrokozlovia*, *Yuomys*, *Advenimus*, and *Saykanomys*). More specifically, a molariform P4 has both the metacone and paracone on its labial side, whereas a non-molariform P4 has only the paracone labially. A molariform p4 has the entoconid, hypoconid ,and commonly a small hypoconulid on the talonid, whereas a non-molariform p4 has a conical entoconid and the rest of the talonid is usually a transverse ridge. However, these conditions vary significantly. The molariform premolars of *Yuomys*, for instance, are derived with respect to those of *Advenimus*.

Although a non-molariform last premolar was believed to be primitive (Korth, 1984), this feature has been widely used in ctenodactyloid phylogeny and classification (Flynn et al., 1986; Wang, 1994, 1997; Hu, 1995; Tong and Dawson, 1995). For instance, *Bandaomys* was recently described to share many features with cocomyids, but it was assigned to Yuomyidae with a question mark because of its somewhat molariform premolar (Tong and Dawson, 1995). However, a non-molariform last premolar can be viewed differently. According to Flynn et al. (1986), the family Ctenodactylidae (including *Tamquammys*, *Tsinlingomys*, *Karakaromys*, *Tataromys*, and other Ctenodactylidae) is diagnosed by "Talonid of p4 short and significantly narrower than talonid" and the clade consisting of Yuomyidae and Chapattimyidae is characterized by molariform P4/p4. Apparently, although it is non-molariform, the ctenodactylid p4 can be regarded as a derived condition because it is interpreted to be secondarily reduced (Flynn, pers. comm.). Wang (1994) accepted Shevyreva's (1984) family Tamquammyidae and used the non-molariform p4 as one of three shared derived features (the other two are narrow palate and multiserial incisor enamel) for Tamquammyidae and Ctenodactylidae. *Butomys* has a non-molariform p4 but this condition is unknown in *Mergenomys*. In this study, we choose to divide conditions of the last premolars into molariform and non-molariform, acknowledging that further investigation is needed to accommodate the diverse views exemplified above.

The polarity for this character is uncertain not only because of the different views mentioned above but also because of the uncertainty of the outgroup condition. The molariform last premolars in *Tribosphenomys* were described as permanent teeth, but new material shows that they may be deciduous teeth (Meng et al., 1998). In specimens of *Alagomys* where premolars were preserved (Tong and Dawson, 1995; Dawson and Beard, 1996), the so-called p4 is no less worn than molars, suggesting as well that these premolars are probably dp4. We coded non-molariform as derived in this study, accepting the current interpretation of the last premolars of *Tribosphenomys* and *Alagomys*. Nonetheless, given the same codings for other characters, reversing the polarity of the last premolar generates the same topology of the cladogram.

6. Upper cheek teeth: (0) wider than long, (1) quadrate, (2) longer than wide. The outgroup condition of the cheek teeth outline is transversely wider than it is anteroposteriorly long; within rodents the tooth crown becomes quadrate (Meng et al., 1994). Tong (1997: 223) considered "upper molars changed from transversely wide to elongated" as one of evolutionary tendencies of Eocene ctenodactyloids. Anteroposteriorly elongate upper molars are distinctive in the subfamily Tataromyinae, whereas in other ctenodactylids "cheek teeth proportionally wide" is the case (Wang, 1997: 67); in other words, their upper molars are quadrate.

7. The metaconule on M1-M3: (0) small, (1) absent, (2) inflated. The metaconule is distinctive in *Tribosphenomys* and is a common morphology in ctenodactyloids; it is absent only in Ctenodactylidae (Wang, 1997). According to Flynn et al. (1986) an inflated metaconule was considered a shared derived feature for Chapattimyidae and absence of the metaconule was diagnostic for Ctenodactylidae excluding *Tamquammys* and *Tsinlingomys* (upper dentition of *Tsinlingomys* unknown until recently [Tong, 1997]). The large metaconule in *Mergenomys* resembles those of tamquammyids and chapattimyids. In the tamquammyid *Chuankueimys* described by Tong (1997), the metaconule is little developed, whereas in *Protataromys* (in the family Tataromyidae according to Tong) the metaconule is distinct.

8. The paraconule: (0) present, (1) absent. The paraconule (protoconule) is gen-

erally less developed than the metaconule within ctenodactyloids. Wang (1997) considered "conule absent on M1-3" to be characteristic of the Ctenodactylidae, which implies absence of the paraconule. Averianov (1996) used the paraconule as a separate character and indicated that absence of the paraconule has a wider distribution than does the absence of the metaconule. The paraconule may have greater variation, as well. For instance, *Tamquammys* was coded as having the conule by Averianov (1996), but a new species of the genus, *T. dispinorum* (Tong, 1997), does not have the conule. In the species described by Tong, the protoloph bifurcates to form two small ridges. Because the paraconule is usually weak, its precise identification is difficult, particularly on cheek teeth that are significantly worn.

9. The metaloph on M1-M3: (0) joining protocone, (1) toward but not joining protocone, (2) parallel to the protoloph. The metaloph displays a variety of morphologies. In primitive forms such as the early Eocene *Cocomys* (Li et al., 1989), *Hohomys* (Hu, 1995) and *Bandaomys* (Tong and Dawson, 1995), the metaloph, sometimes weak, connects with the protocone. In advanced species it runs to the entoloph (Tong, 1997). An incomplete metaloph (from metacone, terminating at metaconule) was considered unique for Yuomyidae (Flynn et al., 1986; Wang, 1994). Several new taxa placed in Yuomyidae by Tong (1997) share this condition. In exploring the relationships of ctenodactylids, Wang (1997: 67) further differentiated the metaloph conditions for three groupings: (1) "metaloph complete and joins protocone on M1-M3" for Tataromyinae as one of the family's shared derived features; (2) "metaloph massive, incomplete, and does not join protocone on Ml-M3" for Ctenodactylidae excluding Tataromyinae; and (3) "metaloph connected with posteroloph by distinct short ridge on Ml-M3" for *Euryodontomys*. In *Protataromys* the metaloph extends toward the protocone; it may or may not join the protocone (Tong, 1997). Based on our observation, the metaloph in *Tataromys*, *Yindirtemys* and *Bounomys* does not join the protocone, contra Wangs interpretation; instead, it joins to the entoloph or to the hypocone or even to the posteroloph. In addition, we noticed that an incomplete metaloph that extends toward the protocone is present in *Terrarboreus*, which was considered a synonym of *Karakoromys* by Wang (1994). In other *Karakoromys*, the metaloph is parallel to the protoloph and may have a narrow connection with the hypocone. The metaloph condition in *Terrarboreus* is similar to that of *Protataromys* and *Mergenomys*, suggesting that *Terrarboreus* may remain as a valid taxon because its metaloph condition is more primitive than in other ctenodactylids.

10. The anterior cingulum on Ml-M3: (0) not developed, (1) present but low, (2) low but broad, (3) high and usually joining protoloph. In *Tribosphenomys* (Meng et al., 1994) and *Alagomys* (Dashzeveg, 1990b; Tong and Dawson, 1995; Dawson and Beard, 1996) upper molars are transversely elongate and lack an anterior cingulum. In early ctenodactyloids, an anterior cingulum is developed, butting against the anterior side of upper molars but below the protoloph. As an evolutionary tendency, the anterior and posterior cingula become elevated (Tong, 1997) and eventually the anterior cingulum joins the the protoloph; the latter condition was shared by members of the Ctenodactylidae, including *Protataromys*. The anterior cingulum of *Mergenomys* is high and joins the protoloph so that wear of the cingulum is present, although it is not so advanced as in *Protataromys* and ctenodactylids.

11. The entoloph on M1-M2: (0) weak, (1) well developed, (2) absent. The entoloph (the ridge between the protocone and hypocone) is weak in *Tribosphenomys* and primitive ctenodactyloids such as *Cocomys*. According to Wang (1997) the entoloph is absent on M1-M2 in Tataromyinae but developed on M1-M3 in other ctenodactylids. The Tataromyinae condition is similar to that of *Mergenomys*. However, we believe that some specimens assigned to Tataromyinae by Wang and others we examined in the AMNH collection display a distinct entoloph. Lack of the entoloph is also found in several yuomyids (Tong, 1997) and Baluchimyinae (Flynn et al., 1986). Absence of an entoloph appears variable and may have evolved several times among ctenodactyloids.

12. The sinus: (0) shallow, (1) deep. The sinus is the concave region on

the lingual side between the protocone and hypocone. In primitive forms there is only a shallow, vertical groove. In ctenodactylids the entoloph shifts labially or the protocone and hypocone extend lingually, resulting in a deep sinus. This sinus may be symmetric or oblique (Wang, 1997) and may be broad or narrow, but it is deep compared with other ctenodactyloids. The sinus of *Protataromys* appears to have a transitional condition; we code it as 1 as well.

13. The molar hypocone: (0) small, (1) large, (2) large and more lingual than the protocone. The hypocone is absent or very small in *Tribosphenomys* (Meng et al., 1994) and *Alagomys* (Dashzeveg, 1990b; Tong and Dawson, 1995; Dawson and Beard, 1996). Two derived hypocone conditions are recognized: "hypocone large and equal in size to protocone on M1-M2" in Ctenodactylidae excluding Tataromyinae (Wang, 1997) and "hypocone developed and lingually located" in Chapattimyidae (Wang, 1994). The relatively small hypocone in Tataromyinae may be a result of the anteroposterior elongation of the protocone; therefore, we code the hypocone in all ctenodactylids as "large." The hypocone condition in *Mergenomys* resembles that of *Protataromys*; it is more developed than in other ctenodactyloids except *Yuomys*. Some specimens recently described provide mixed information of the structure. For instance, specimens of *Saykanomys* described by Averianov (1996) show a large hypocone, but others by Tong (1997) have a relatively small hypocone. Because of the poor illustrations provided by Averianov, a precise assessment of these specimens is not possible for this study.

14. The p4 protoconid and metaconid: (0) divided by a longitudinal groove, (1) connected by the metalophid I and II, (2) the posterior arms of the protoconid and metaconid form a Y-shaped connection with the ectolophid. The trigonid in rodents usually consists of the protoconid and metaconid, separated by a longitudinal groove, although a weak metalophid II may exist in some cases. *Yuomys* presents a special case; it has a full molariform p4 and the protoconid and metaconid are connected by the metalophid I and II (Li, 1975). This is probably an apomorphy for *Yuomys*. In ctenodactylids the protoconid and metaconid are connected by strong ridge (the metalophid II); the trigonid is open anteriorly but completely enclosed posteriorly. Furthermore, the ectolophid, running on the longitudinal midline of the tooth, joins the trigonid posteriorly so that the anterior part of the tooth bears a Y-shaped structure of ridges.

15. The lower molars: (0) rectangular or diamond shaped in outline, (1) rounded, (2) anteroposteriorly elongated. Because of the straight anterior edge or anterior extension of the metaconid on lower molars in early ctenodactyloids, the teeth are either rectangular or diamond-shaped, with the metaconid-hypoconid axis longer than the protoconid-entoconid one. In chapattimyids, the oval lower teeth have been recognized as a synapomorphy (Flynn et al., 1986; Wang, 1994). In ctenodactylids, except Karakoromyinae, the lower molars are anteroposteriorly elongated.

16. The paraconid on lower molars: (0) small, (1) absent or confluent with other structures. A small paraconid is present on lower molars that have little wear in *Tribosphenomys* (Meng et al., 1994). This is unquestionably a primitive condition. A rudimentary paraconid on p4 was reported from *Bandaomys* (Tong and Dawson, 1995).

17. The metalophid II: (0) weak, (1) short but distinct, (2) entirely closes the trigonid or extends to the lingual side of the tooth, (3) lost. The metalophid II is a ridge extending from the protoconid, usually toward or joining the metaconid. This ridge is also termed the metalophulid II (Flynn et al., 1986), the posterior protoconid arm (Dawson et al. 1984) or the posterior arm of the protoconid (Wang, 1997). The metalophid II is weak, usually not enclosing the trigonid, in primitive forms. It is short but quite distinct in *Protataromys* (Tong, 1997) and *Karakoromys* (Wang, 1994), leaving the trigonid open posterolingually. We code the Karakoromyinae as 1/2 because the other genus of this subfamily, *Euryodontomys*, has a more developed metalophid II as in other ctenodactylids. In most ctenodactylids, the metalophid II either extends to the lingual side of the tooth or joins the metaconid. In both cases, the trigonid is blocked posteriorly by the metalophid II. Flynn et al. (1986) con-

sidered absence of the metalophid II (their metalophulid II) a synapomorphy in other ctenodactylids (excluding *Karakaromys* and *Tataromys*). It is likely that in more advanced ctenodactylids the metalophid II is either lost or confluent with the metalophid I to form the anterior lobe of the lower molar such as in *Distylomys*.

18. The mesoconid on ml-m3: (0) present, (1) absent. The mesoconid is present in early ctenodactyloids, as pointed out by Wood (1977). Presence of the mesoconid is primitive for ctenodactyloids. In the Eocene forms, absence of the mesoconid is reported in *Tsinlingomys* (Li, 1963), as also noted by several workers (Wood, 1977; Flynn et al., 1986; Hu, 1995) and ctenodactylids. Flynn et al. use this feature to unite *Tsinlingomys* with other members of their Ctenodactylidae. Wang (1994) consider absence of the mesoconid one of several features diagnosing her Ctenodactylidae, which does not include *Tsinlingomys*. New material of *Tsinlingomys* and *Chuankueimys* (Tong, 1997), both in Family Tamquammyidae according to Tong, lacks mesoconids on lower molars. The mesoconid is also absent in *Yuomys* (Li, 1975) and *Stelmomys* (Tong, 1997). Therefore, this feature may not be a good character for diagnosing the Ctenodactylidae. *Mergenomys* and *Butomys* lack mesoconids on lower molars, but their ectolophid morphologies are different from those of *Tsinlingomys* and *Chuankueimys* (see below).

19. The ectolophid: (0) weak and labially positioned, (1) ends posterior to the trigonid, (2) continuous with the protoconid, (3) running on the midline of tooth or more lingually positioned. In *Tribosphenomys* and *Alagomys* the ectolophid is weak and labially positioned; therefore, the talonid basin is wide open. Early ctenodactyloids maintain more or less the same condition except that a mesoconid is developed and in some forms the ectolophid does not reach the protoconid. Tong (1997) considered the ectolophid shifted lingually in his tataromyids, but we believe the lingual shift occurs in ctenodactylids as well (those not included in Tong's Tataromyidae but in Wang's [1997] Ctenodactylidae). The lingual shift of the ectolophid and the anterior migration of the entoconid and hypoconid eventually occupy the original talonid basin. This perhaps represents a transition of tooth function from crushing to grinding mechanics. In this regard, the ectolophid in both *Butomys* and *Mergenomys* is closely similar to that of Ctenodactylidae, although the ectolophid is weak in *Butomys* and that in *Mergenomys* is low. Of the two new genera, the condition of *Mergenomys* is more advanced in that the ectolophid is more pronounced and in the way the hypoconid continues with the ectolophid as in ctenodactylids.

20. The talonid basin: (0) complete, (1) divided into mesosinusid and posterosinusid, (1) the mesosinusid narrow (narrower than the sinusid). Reduction of the trigonid is an evolutionary feature in rodents (Meng et al., 1994). As a result of trigonid reduction the talonid is large and bears a broad basin, such as in *Tribosphenomys* and *Alagomys*. This condition is largely retained in primitive ctenodactyloids such as *Cocomys*. Development of the hypolophid divided the original talonid basin into two parts: the mesosinusid anteriorly and the posterosinusid posteriorly. In advanced forms, the entoconid and hypoconid shift progressively anteriorly and the ectolophid moves lingually; a narrow mesosinusid is thus formed.

21. The hypoconulid on m1-m2: (0) small, (1) enlarged, (2) anteriorly extended. The hypoconulid on m1-m2 is small and transversely oriented in primitive forms. It is enlarged and anteroposteriorly stretched in ctenodactylids (in Tong's [1997] tataromyids). The hypoconulid in *Mergenomys* is enlarged, more so than other ctenodactyloids excluding ctenodactylids, but is still transversely oriented. The hypoconulid in *Butomys* is large but is less developed than in *Mergenomys*.

22. The hypolophid: (0) absent, (1) joins with arms of hypoconid and hypoconulid in front of the hypoconulid, (2) joins only with the hypoconulid, (3) joins the ectolophid in front of the hypoconid. The hypolophid is the ridge extending from the entoconid. Lack of this ridge is a primitive condition, as in *Tribosphenomys*, *Cocomys* and *Bandaomys*. A complete hypolophid is believed to be a derived condition (Averianov, 1996). Where it is present among ctenodactyloids, the hypolophid varies widely. Daw-

son et al. (1984) pointed out the unusual molar pattern in which the arm of the entoconid curves backward to the hypoconulid in *Tsinlingomys*. Wang (1994, 1997) recognized arm of entoconid curves posteriorly and joins hypoconulid on m1 as the only apomorphy for Tamquammyidae, whereas Tong (1997) observed that the hypolophid is developed and directing to hypoconid or ectolophid in tamquammyines, and posteriorly bent in tsinlingomyines. The hypolophid directed to the hypoconid is also seen in other taxa such as *Saykanomys*. We word the hypolophid conditions differently because we believe the hypolophid in *Tsinlingomys* is not particularly bent posteriorly. Instead its morphology is more a result of lacking the arm of the hypoconid. We also believe the hypolophid in *Chuankueimys*, which is placed in Tsinglingomyinae by Tong, is essentially the same as in *Tamquammys*.

23. Cheek teeth: (0) lower crowned, (1) relatively high, (2) hypsodont. Early ctenodactyloids have low tooth crowns. This condition also occurs in *Butomys*, *Mergenomys* and *Protataromys*. In *Tataromys* and more derived species the tooth crown is relatively high. In Distylomyinae and Ctenodactylinae the cheek teeth are hypsodont (Wang, 1994, 1997).

24. Cheek teeth: (0) cusps conical, (1) with strong lophs, (2) tri- or bilobate. Primitively the cheek teeth of ctenodactyloids are bunodont. This condition remains in *Butomys* and *Mergenomys*. In *Protataromys* and other ctenodactylids, the cheek teeth become lophodont. In more advanced forms the tooth crown is trilobate or bilobate (Wood, 1977; Wang, 1997).

25. Infraorbital foramen: (0) protrogomorphous, (1) hystricomorphous. This feature is not preserved in our specimens. We follow Wang (1994) and Averianov (1996) in coding this character.

26. Incisor enamel: (0) pauciserial, (1) multiserial. We follow Wang (1994) and Averianov (1996) in coding this character, except that the enamel condition in *Chapattimys* is changed to pauciserial (Flynn, personal commun.).

PHYLOGENETIC ANALYSIS

Tabulation of the characters is provided in table 2. A total of 22 taxa and 26 characters are involved in the calculation. The data were analyzed using the PAUP program (Swofford, 1993). Many of the characters have multistates (a total of 45 states that are coded as 1, 2, or 3). All characters are unordered and unweighted. The default ACCTRAN optimization was employed. Branch and Bound search yielded two equally most parsimonious trees of 73 steps. The two trees differ in the positions of *Hohomys* and *Saykanomys*; each tree has the following properties: CI = 0.635; HI = 0.365; CI excluding uninformative characters = 0.63; HI excluding uninformative characters = 0.37; RI = 0.789; and RC = 0.501. The strict consensus of the two trees is illustrated in figure 5, which is rooted at the outgroup *Tribosphenomys*. Character diagnostics and apomorphy list for figure 5 are provided in appendix 1.

Figure 6 is the projection of the resulting

TABLE 2
Data Matrix, 26 Characters of 22 Taxa Including the Outgroup *Tribosphenomys*
(Question marks indicate missing data. A = 0/1 and B = 1/2.)

	Character		
	0000000001	1111111112	222222
Taxa	1234567890	1234567890	123456
Tribosphenomys	0000000000	0000000000	000000
Cocomys	0100010001	0000010000	000000
Tsinlingomys	010?010102	1000010111	0200??
Tamquammys	020?010011	0000010011	010011
Yuomys	0200110113	1021010121	030011
Bandaomys	?10?110001	0000010000	0000??
Advenimus	020?110011	1010010001	010011
Hohomys	010?110101	1000010011	01001?
Stelmomys	??0?110111	2000010111	0100??
Saykanomys	010?1100A1	1000010011	010011
Petrokozlovia	?10?110111	1010010011	010011
Birbalomys	?20?112001	2020110021	030011
Chuankueimys	02??011102	1000010121	01001?
Protataromys	????0101B3	1110011132	1301??
Tataromyinae	1B11021123	2111212132	231111
Karakoromyinae	1311011123	111101B132	231111
Distylomyinae	2?????????	???1213132	2322?1
Ctenodactylinae	2311021123	1111213132	232211
Alaymys	020?010101	1000010131	010011
Mergenomys	12?1?12113	201?011132	1300??
Butomys	1????0??00?	???0010131	0100??
Chapattimys	??0?112001	1121110011	0300?0

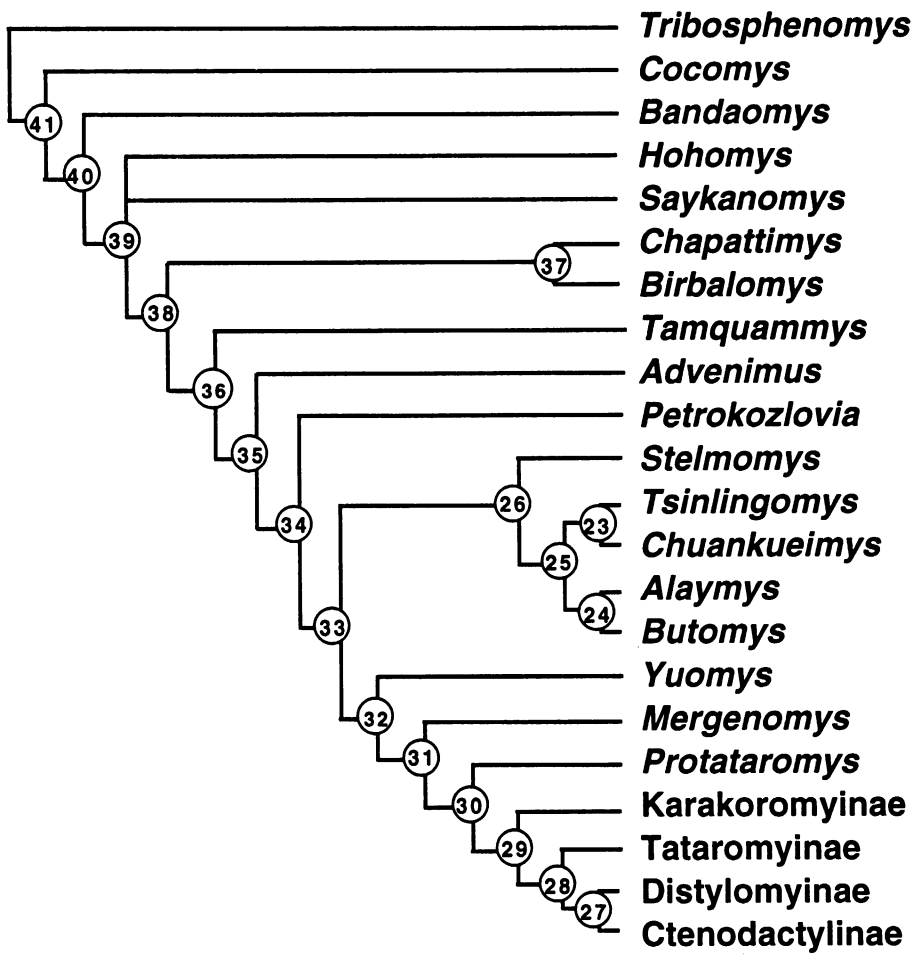


Fig. 5. The strict consensus of two equally most parsimonious trees generated by Branch and Bound search of PAUP. The two trees differ in the postions of *Hohomys* and *Saykanomys*. (CI = 0.644; HI = 0.356; CI excluding uninformative characters = 0.639; HI excluding uninformative characters = 0.361; RI = 0.807; and RC = 0.52). The apomorph lists for the nodes and branches are provided in appendix Ib. See text for more detail.

phylogeny on a geological time scale. The distributions of most selected taxa are based on Wang (1997) for Oligocene taxa and Tong (1997) for Eocene taxa. The temporal data of *Birbalomys* and *Chapattimys* are from McKenna and Bell (1997); correlation of these two taxa with other Eocene ctenodactyloids on the scale furnished by Tong is tentative. The phylogeny appears roughly consistent with the geological distributions of ctenodactyloids; that is, primitive taxa occur earlier than derived ones. Many ctenodactyloids made their first appearances at the beginning of the Eocene; only the Ctenodactylidae survived into the Oligocene and Miocene.

In recent phylogenetic analyses of Ctenodactylidae, Wang (1994, 1997) divided the family into four subfamilies: Tataromyinae, Karakoromyinae, Distylomyinae and Ctenodactylinae. Tataromyinae was considered the sister group of the other three. Our analysis supports Wang's phylogeny and endorses the monophyly of the Ctenodactylidae. However, our analysis places Karakoromyinae as the sister group of the rest Ctenodactylidae. Karakoromyinae, particularly *Karakoromys*,

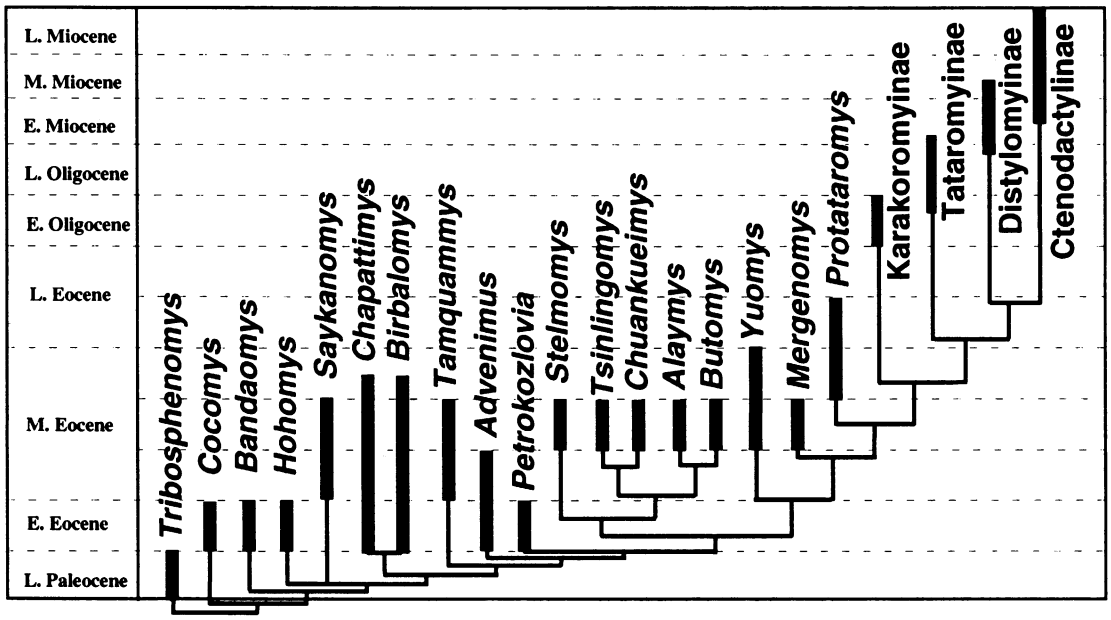


Fig. 6. Projection of the phylogeny on a geological time scale. See text for more detail.

displays some conditions that are to us more primitive than in other ctenodactylids, such as less anteroposteriorly elongated cheek teeth and relatively short metalophid II. If *Terrarboreus* proves to be a synonym of *Karakoromys* (Wang, 1994, 1997), then *Karakoromys* contains specimens that have the metaloph extending toward the protocone, which is another primitive condition for ctenodactylids. Our placement is more consistent with the geological distributions of ctenodactylids, in which *Karakoromys* has the earliest record (Wang, 1997).

Tong (1997) named *Protataromys* and placed it in the family Tataromyidae, which is roughly equivalent to a combination of Tataromyinae and Karakoromyinae of Wang (1997). Our analysis does not support Tongs placement; it instead reveals the sister-group relationship of *Protataromys* to the Ctenodactylidae *sensu* Wang (1997).

Mergenomys is the sister group of Ctenodactylidae (sensu Wang, 1994, 1997) and *Protataromys*. These relationships again raise the issue of how to define taxonomic names, as is discussed by others (Meng and Wyss, 1994; Wyss and Meng, 1996). The name Ctenodactylidae has been used differently by several authors: Wood (1977), Dawson et al. (1984), Flynn et al., (1986), Wang (1994, 1997), and Tong (1997), to name but a few. Wang's concept of Ctenodactylidae, similar to that of Dawson et al., is by far the least inclusive. Both *Mergenomys* and *Protataromys* bear only some of the defining characters for the Ctenodactylidae of Wang. We do not assign the new taxa described here to any established family, nor do we propose any new names.

The grouping of *Tsinlingomys* and *Chuankueimys* supports the subfamily of Tsinlingomyinae (Tong, 1997). We are cautious about the pairing of *Butomys* and *Alaymys* and their link with *Tsinlingomys* and *Chuankueimys*. This is because many characters are missing in *Butomys* and "the morphology of the molars of *Alaymys* was considerably varied" (Averianov, 1996: 653).

The pairing of *Birbalomys* and *Chapattimys* supports the original concept of Chapattimyidae (Hussain et al., 1978; Flynn et al., 1986) but not necessarily the broadly defined one by Averianov (1996); the latter contains many members previously placed in Cocomyidae and is certainly a paraphyletic group.

Relationships among ctenodactyloids are

much more complex. This has been reflected in several recent studies. Tong (1997), for instance, preferred to maintain the family Tataromyidae, which, according to Wang's (1997) analyses, is a paraphyletic taxon. In a cladistic analysis Averianov (1996) concluded that Cylindrodontidae, Ctenodactylidae, and Baluchimyinae form a monophyly, in which Cylindrodontidae and Ctenodactylidae form a sister group, and taxa traditionally included in Chapattimyidae are outgroups to that sister group. We believe that the relationship of the Cylindrodontidae and Ctenodactylidae, represented by *Ardynomys* and *Tataromys* in Averianovs study, is highly questionable. Cylindrodontidae are protrogomorphous rodents found from Asia and North America and their phylogenetic position remains uncertain (Emry and Korth, 1996). Averianov's conclusion, therefore, either implies paraphyly of the ctenodactyloid rodents or suggests that the Cylindrodontidae are a subgroup within ctenodactyloid rodents. Either of the two possibilities requires a reversal of the protrogomorphy of Cylindrodontidae from the hystricomorphy of ctenodactyloids according to Averianov's cladogram. A comprehensive discussion on the Cylindrodontidae is beyond the scope of this study (see Bryant and McKenna, 1995 for a related work disputing relationships of Cylindrodontidae). For the taxa that have been traditionally considered as ctenodactyloids, Averianov's study indicated the paraphyly of several families such as Tamquammyidae, Cocomyidae, Yuomyidae and his broadly defined Chapattimyidae. Our study reveals a similar pattern. The difference between the two studies is that Averianov chose to accept paraphyletic and polyphyletic taxa, whereas we do not. From his cladogram (Averianov, 1996: fig. 9) it is clear that taxa included in Chapattimyidae, such as *Chapattimys*, *Birbalomys*, *Advenimus* and *Saykanomys*, are separated by a clade consisting of *Tamquammys* and *Alaymys*, which belongs to the family of Tamquammyidae. *Tamquammys* and *Alaymys*, on the other hand, are further separated from their family members, such as *Cocomys*, by the family members of Chapattimyidae. This practice encourages not only recognition of unnatural groups, but also promotes a highly unstable taxonomy.

We believe that the Ctenodactylidae, as recognized by Wang (1994, 1997), is monophyletic and that it can be viewed as the "core" taxon of Asian ctenodactyloids. Relationships of other ctenodactyloids to the "core" is the major challenge for the study of the ctenodactyloid phylogeny. The previously recognized families, such as Cocomyidae and Yuomyidae, are paraphyletic and some dental features, such as premolar morphologies, are insufficient to maintain these families. Based on our analysis, and before a better phylogeny based on more anatomic and other evidence becomes available, we suggest that these family names should be used with caution, or simply the use of Ctenodactyloidea without reference to a specific family for the Eocene genera, as we did for *Bumtomys* and *Mergenomys*.

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APPENDIX 1a

Character Diagnostics for Figure 5

(CI, consistency index; HI, homoplasy index; RI, retention index; RC, rescaled consistency index. Character numbers correspond to those in Character Analysis.)

Character	Minimum steps	Tree steps	Maximum steps	CI	HI	RI	RC
1	2	3	6	0.667	0.333	0.750	0.500
2	3	6	9	0.500	0.500	0.500	0.250
3	1	1	3	1.000	0.000	1.000	1.000
4	1	1	3	1.000	0.000	1.000	1.000
5	1	4	9	0.250	0.750	0.625	0.156
6	2	2	3	1.000	0.000	1.000	1.000
7	2	4	7	0.500	0.500	0.600	0.300
8	1	3	9	0.333	0.667	0.750	0.250
9	2	3	10	0.667	0.333	0.875	0.583
10	3	3	9	1.000	0.000	1.000	1.000
11	2	6	8	0.333	0.667	0.333	0.111
12	1	2	5	0.500	0.500	0.750	0.375
13	2	4	10	0.500	0.500	0.750	0.375
14	1	3	6	0.333	0.667	0.600	0.200
15	2	2	5	1.000	0.000	1.000	1.000
16	1	1	1	1.000	0.000	0/0	0/0
17	3	3	6	1.000	0.000	1.000	1.000
18	1	1	10	1.000	0.000	1.000	1.000
19	3	7	14	0.429	0.571	0.636	0.273
20	2	2	9	1.000	0.000	1.000	1.000
21	2	2	6	1.000	0.000	1.000	1.000
22	3	4	13	0.750	0.250	0.900	0.675
23	2	2	4	1.000	0.000	1.000	1.000
24	2	2	5	1.000	0.000	1.000	1.000
25	1	1	2	1.000	0.000	1.000	1.000
26	1	2	3	0.500	0.500	0.500	0.250

APPENDIX 1b

Apomorphy List for Figure 5

(Node numbers correspond to those in Figure 5.)

Branch		Character	Steps	CI	Change
Tribosphenomys ↔ node 41	2	Zygomatic root	1	0.500	0 ↔ 1
	6	Upper teeth L–W	1	1.000	0 ↔ 1
	10	Anterior cingulum	1	1.000	0 ↔ 1
	16	Paraconid	1	1.000	0 ↔ 1
Node 41→ node 40	5	P4/4	1	0.250	1 → 0
	25	Hystricomorphy	1	1.000	0 → 1
	26	Enamel	1	0.500	0 → 1
Node 40 → node 39	11	Entoloph	1	0.333	0 → 1
	19	Ectolophid	1	0.429	0 → 1
	20	Talonid basin	1	1.000	0 → 1
	22	Hypolophid	1	0.750	0 → 1
Node 39 → node 38	2	Zygomatic root	1	0.500	1 → 2
Node 38 → node 36	9	Metaloph	1	0.667	0 → 1
Node 36 → node 35	13	Hypocone	1	0.500	0 → 1
Node 35 → node 34	8	Paraconule	1	0.333	0 → 1
Node 34 → node 33	18	Mesoconid	1	1.000	0 → 1
Node 33 → node 26	13	Hypocone	1	0.500	1 → 0
Node 26 → node 25	5	P4/4	1	0.250	0 → 1
	9	Metaloph	1	0.667	1 → 0
Node 25 → node 23	10	Anterior cingulum	1	1.000	1 → 2
Node 23 → *Tsinlingomys*	2	Zygomatic root	1	0.500	2 → 1
	22	Hypolophid	1	0.750	1 → 2
Node 23 → *Chuankueimys*	7	Metaconule	1	0.500	0 → 1
	19	Ectolophid	1	0.429	1 → 2
Node 25 → node 24	19	Ectolophid	1	0.429	1 → 3
Node 24 → *Butomys*	1	Masseteric fossa	1	0.667	0 → 1
	8	Paraconule	1	0.333	1 → 0
Node 26 → *Stelmomys*	11	Entoloph	1	0.333	1 → 2
Node 33 → node 32	10	Anterior cingulum	1	1.000	1 → 3
	14	p4 trigonid	1	0.333	0 → 1
	19	Ectolophid	1	0.429	1 → 2
	22	Hypolophid	1	0.750	1 → 3
Node 32 → *Yuomys*	13	Hypocone	1	0.500	1 → 2
Node 32 → node 31	1	Masseteric fossa	1	0.667	0 → 1
	3	P3	1	1.000	0 → 1
	4	dP4	1	1.000	0 → 1
	5	P4/4	1	0.250	0 → 1
	17	Metalophid	1	1.000	0 → 1
	19	Ectolophid	1	0.429	2 → 3
	20	Talonid basin	1	1.000	1 → 2
	21	Hypoconulid	1	1.000	0 → 1
Node 31 → node 30	2	Zygomatic root	1	0.500	2 → 3
	9	Metaloph	1	0.667	1 → 2
	12	Sinus	1	0.500	0 → 1
	24	Tooth cusp-lophs	1	1.000	0 → 1
Node 30 → *Protataromys*	14	p4 trigonid	1	0.333	1 → 0
Node 30 → node 29	7	Metaconule	1	0.500	0 → 1
	17	Metalophid	1	1.000	1 → 2
	21	Hypoconulid	1	1.000	1 → 2
	23	Crown height	1	1.000	0 → 1
Node 29 → node 28	6	Upper teeth L-W	1	1.000	1 → 2
	15	Lower molar	1	1.000	0 → 2

APPENDIX 1b
(*Continued*)

Branch		Character	Steps	CI	Change
Node 28 → Tataromyinae	2	Zygomatic root	1	0.500	3 → 12
	11	Entoloph	1	0.333	1 → 2
Node 28 → node 27	1	Masseteric fossa	1	0.667	1 → 2
	17	Metalophid	1	1.000	2 → 3
	23	Crown height	1	1.000	1 → 2
	24	Tooth cusp-lophs	1	1.000	1 → 2
Node 31 → *Mergenomys*	7	Metaconule	1	0.500	0 → 2
	11	Entoloph	1	0.333	1 → 2
Node 34 → *Petrokozlovia*	2	Zygomatic root	1	0.500	2 → 1
Node 35 → *Advenimus*	19	Ectolophid	1	0.429	1 → 0
Node 36 → *Tamquammys*	5	P4/4	1	0.250	0 → 1
	11	Entoloph	1	0.333	1 → 0
Node 38 → node 37	7	Metaconule	1	0.500	0 → 2
	13	Hypocone	1	0.500	0 → 2
	15	Lower molar outl.	1	1.000	0 → 1
	22	Hypolophid	1	0.750	1 → 3
Node 37 → *Birbalomys*	11	Entoloph	1	0.333	1 → 2
	19	Ectolophid	1	0.429	1 → 2
Node 37 → *Chapattimys*	12	Sinus	1	0.500	0 → 1
	14	p4 trigonid	1	0.333	0 → 1
	26	Enamel	1	0.500	1 → 0
Node 39 → *Hohomys*	8	Paraconule	1	0.333	0 → 1

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