AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3253, 18 pp., 6 figures, 1 table December 21, 1998

A New Eocene Cylindrodont Rodent (Mammalia, Rodentia) from the Eastern Gobi of Mongolia

DEMBERELYIN DASHZEVEG[1] AND JIN MENG[2]

ABSTRACT

A new genus and species of cylindrodont rodents, *Proardynomys borkhoii*, from the middle Eocene Mergen locality of the Eastern Gobi, Mongolia, is among the earliest cylindrodontids of Asia. Comparisons with cylindrodontids, sciurids, aplodontids, ischyromyids, and ctenodactyloids show that *P. borkhoii* is most similar to *Ardynomys olseni* of the Cylindrodontidae in having the p4 trigonid basin open anteriorly; the lower molars with two anterior and one posterior root; the metalophid II extending from the protoconid toward the metaconid and enclosing a small trigonid basin; a short ectolophid bearing no mesoconid; the hypoconid projecting anterolabially; the entoconid separated from the posterolophid but connected with the ectolophid in front of the hypoconid by a complete hypolophid; the metastylid crest and entoconid separated by a narrow gap at the lingual edge of the tooth; a strong posterolophid bearing no hypoconulid; and the lower incisor with uniserial enamel ultrastructure. It differs from *A. olseni* in having a rounded ventral surface on the lower incisor; the molar teeth lower crowned and the trigonid higher than the talonid; the lophs and lophids narrower and less well developed; the hypoconid not unicuspal hypsodont; the anterior part of the talonid basin wide open; and a lower metastylid crest bordering the lingual margin of molars. A recent proposal of a sister group relationship between Cylindrodontidae and Ctenodactylidae is reviewed and is rejected because of insufficient evidence. The possibility that the Cylindrodontidae are related to sciuromorphs, particularly Sciuridae and Aplodontidae, is speculated; these taxa may have been derived from an ischyromyid stock.

[1] Geological Institute of the Mongolian Academy of Science, Ulaanbaatar, Mongolia.
[2] Research Associate, American Museum of Natural History; Department of Biology and Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts, Amherst, MA 01003.

 ISSN 0003-0082 / Price $2.20

INTRODUCTION

As part of a Mongolian–American paleontological project that was organized by the Mongolian Academy of Sciences and American Museum of Natural History, in 1991 and 1992 the senior author screenwashed bone-bearing deposits at the middle Eocene Mergen locality of the Eastern Gobi. Numerous remains of small mammals were collected from the light-gray sandy clay of the Mergen sections. The Mergen sediments are biostratigraphically correlative to the Tsagan Tsav assemblage and are estimated as middle Eocene. Fossils known from Mergen include two rodents (a new ctenodactyloid species [Dashzeveg and Meng, 1998] and *Yuomys* sp.); a tupaiodontine insectivore (*Zaraalestes*); a lagomorph (*Gobilagus* sp.); and two tapiroids (*Lophialetes expeditus* and *Breviodon minutus*). Here we describe a new cylindrodont from the Mergen locality. If the age determination of the Mergen sediments is correct, this new taxon is among the earliest cylindrodonts of Asia, and its morphology sheds new light on the relationships of Cylindrodontidae.

Cylindrodontidae are protrogomorphous rodents found in Asia and North America (Emry and Korth, 1996a). This family contains about 10 genera, most of which are from the Eocene and Oligocene of North America and some of which are from Asia (Emry and Korth, 1996a; McKenna and Bell, 1997). The new taxon described here is most similar to, but more primitive than, *Ardynomys*. The latter occurs in late Eocene of Asia and North America. Based on our analysis, we agree with other workers that the Cylindrodontidae does not belong to Hystricognathi or Hystricognathiformes (Bryant and McKenna, 1995). We disagree with Averianov (1996) that Cylindrodontidae and Ctenodactylidae form a sister-group relationship. The new data support the assessment that cylindrodontids are a primitive group of rodents, not far derived from the protrogomorphous–sciurognathous rodent stock (Emry and Korth, 1996a) and are probably related to Sciuridae and Aplodontidae.

Because little is known about the upper molars of the new taxon, we found it premature to conduct a phylogenetic analysis for the Cylindrodontidae. We therefore focus our comparisons and discussion primarily on morphologies and taxonomy. The anatomical terminology for tooth structures is illustrated in figure 1.

SYSTEMATICS

ORDER RODENTIA BOWDICH, 1821
FAMILY CYLINDRODONTIDAE MILLER AND GIDLEY, 1918

Proardynomys, new genus

ETYMOLOGY: *Pro-* (Latin) means "before" and implies a cylindrodont rodent that is more primitive than *Ardynomys*.

TYPE SPECIES: *Proardynomys borkhoii*, new species.

DIAGNOSIS: *Proardynomys* differs from other cylindrodonts in having lower crowned molars, less-developed lophids, higher trigonid, lower and narrower hypoconid, broader and more open mesosinusid, and oval-shaped cross section of the lower incisor. It differs from other Eocene rodents in having complete protoloph, no conules on M1, short but strong ectolophid bearing no mesoconid, hypoconid extending anterolabially, metastylid crest and entoconid separated by a narrow gap at the lingual edge of the tooth, strong posterolophid bearing no hypoconulid, and slim but complete hypolophid extending from a distinct entoconid to the ectolophid in front of the hypoconid.

Proardynomys borkhoii, new species

Figures 2–3

HOLOTYPE: PSS 41-30 (Paleotology and Stratigraphy Section of Geological Institute, Mongolian Academy of Sciences), a fragmentary left mandible with p4–m3.

REFERRED SPECIMENS: PSS 41-29, a fragmentary left mandible with m1 and m2; PSS 41-39, an isolated right M1.

LOCALITY AND AGE: Quarry 2 of the Mergen locality, Eastern Gobi Desert, middle Eocene.

DIAGNOSIS: As for the genus.

ETYMOLOGY: The species is named for the steppe Borkhoi of the Eastern Gobi.

DESCRIPTION: The anterior edge of the

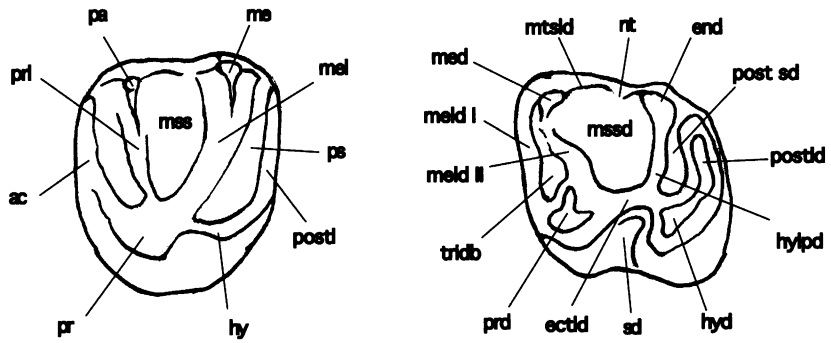

Fig. 1. Terminology of molar structures (following Wang, 1997a, except for msc, nt, and postld). Abbreviations: **ac**, anterior cingulum; **ectld**, ectolophid; **end**, entoconid; **hy**, hypocone; **hyd**, hypoconid; **hylpd**, hypolophid; **me**, metacone; **med**, metaconid; **meld I**, metalophid I; **meld II**, metalophid II; **mtsld**, metastylid crest; **mss**, mesosinus; **mssd**, mesosinusid; **nt**, notch; **pa**, paracone; **postld**, posterolophid; **post sd**, posterosinusid; **postl**, posteroloph; **pr**, protocone; **prd**, protoconid; **prl**, protoloph; **ps**, posterosinus; **sd**, sinusid; and **tridb**, trigonid basin.

masseteric fossa is below the posterior half of m2 on PSS 41-29. What has been preserved of the ascending ramus suggests sciurognathy. A single mental foramen is anteroventral to the p4 on the lateral side of the mandible. The incisor is located beneath the tooth row and ends in the ascending ramus posterolateral to the m3. The ventral surface of the incisor is rounded, its cross section is oval (3.6 mm maximum depth and 2.3 mm maximum width), and the ventral and most of the lateral surfaces are covered with enamel. The diastema measures 11 mm. The tooth row is slightly arched labially. The p4 has two roots and is narrower anteriorly than posteriorly. Its protoconid and metaconid are well developed and are separated by a longitudinal groove anteriorly; the two cusps are equal in diameter, but the metaconid is much higher than the protoconid. The metalophid I is absent, and the metalophid II is low, connecting the two trigonid cusps posteriorly. The posterior surfaces of the protoconid and metaconid form a gentle slope that continues into a broad talonid. The hypoconid is large and anterolabially extended. The ectolophid runs posterolabially from the protoconid to the anteromedial side of the hypoconid. There is no mesoconid on the ectolophid. The sinusid is deep and opens anterolabially. The hypoconid extends lingually to form the posterolophid, on which no hypoconulid is distinguishable. The entoconid is at the lingual edge of the tooth, from which a weak hypolophid extends to the ectolophid. Between the hypolophid and posterolophid is a transverse valley, the posterosinusid, which opens lingually. Dentition measurements are given in table 1.

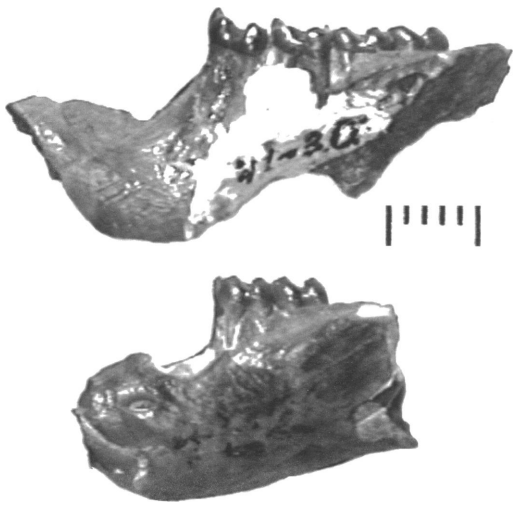

Fig. 2. Left partial mandibles of *Proardynomys borkhoii* (above, the holotype [PSS 41-30], and below, referred material [PSS 41-29]) from the middle Eocene Mergen locality, Eastern Gobi Desert, Mongolia. Scale bar = 5 mm.

The lower molars are low crowned and have two anterior and one posterior root. The m1 and m2 are similar to each other except that the m2 is larger and has a wider trigonid.

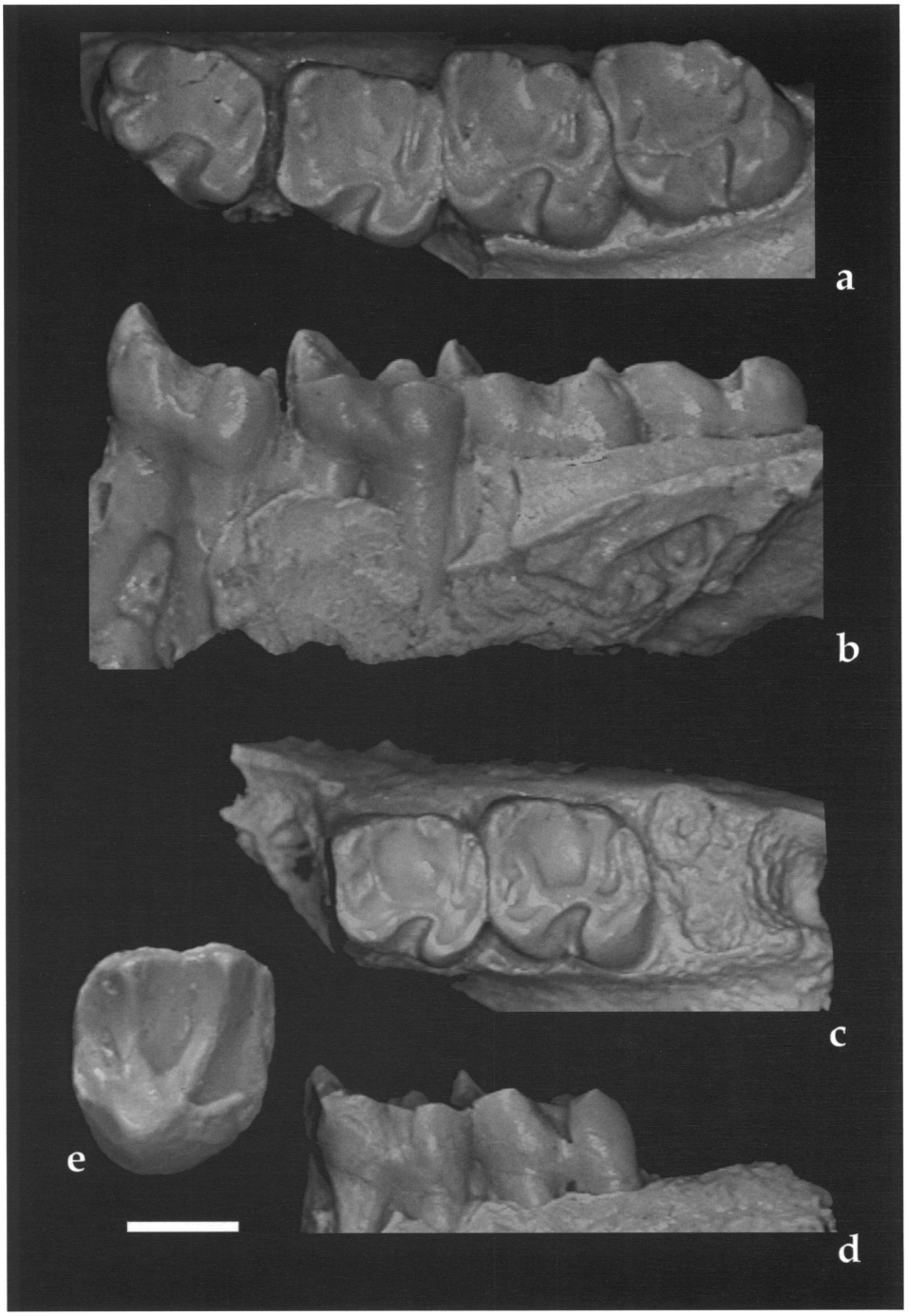

Fig. 3. *Proardynomys borkhoii*: **a** and **b,** the crown and lateral views of left p4-m3 of holotype (PSS 41-30); **c** and **d,** the crown and lateral views of left m1 and m2 of PSS 41-29; and **e,** the crown view of the right M1 of PSS 41-39. Scale bar = 2 mm.

TABLE 1
Measurements (in mm) of *Proardynomys borkhoii*

Specimens and dentition	Length	Width (tri/tal)[a]
(PSS 41-30)		
p4	4.10	2.32/3.00
m1	3.82	2.90/3.44
m2	4.10	3.46/3.38
m3	4.36	3.45/3.26
PSS 41-29		
m1	3.54	2.70/3.00
m2	3.70	3.06/3.14
PSS 41-39		
M1	3.70	4.24

[a] Trigonis/talonid.

Owing to wear of the labial side of the tooth, the protoconid is much lower than the metaconid. The straight metalophid I connects the two trigonid cusps and forms the anterior edge of the tooth. The metalophid II extends anterolingually to the labial side of the metaconid and encloses the trigonid posteriorly. With wear, the trigonid becomes a small, isolated basin in an oval or diamond shape. A low metastylid crest extends posteriorly from the metaconid, defining the lingual edge of the tooth. The ectolophid is short but strong and, with wear, becomes confluent with the protoconid anteriorly and the hypoconid posteriorly. The mesoconid is absent. As in p4, the sinusid is deep and the hypoconid projects anterolabially. The hypoconid and protoconid are at the same height after wear. The entoconid is more prominent than on p4 and is positioned on the lingual edge of the molars. The hypolophid is complete, extending from the entoconid to the ectolophid anterior to the hypoconid. Because of its posterior position, the hypolophid divides the talonid basin into a narrow posterosinusid posteriorly and a broad mesosinusid anteriorly. A narrow notch separates the metastylid crest and the entoconid. The posterosinusid separates the entoconid from the posterolophid on the lingual side of the tooth. The posterolophid is strong but a hypoconulid is not developed.

The m3 is slightly longer than the m2. Its metaconid leans more anteriorly than does its protoconid. The hypolophid is less well developed than those of m1 and m2. The posterior end of the tooth is rounded.

The protocone of the M1 is aligned with the paracone. The hypocone, if any, is weak. The paracone and metacone are marginal, anteroposteriorly compressed. The protoloph and metaloph are strong and converge on the protocone, making a V-shaped structure. Conules are absent. Anterior and posterior cingula are present but are lower than the protolophid and metalophid. There is no mesostyle.

Because of the limitations of the specimen, only the longitudinal section of the lower incisor enamel from the referred specimen (PSS 41-29) was studied. An SEM photograph (fig. 4a) shows that the enamel ultrastructure of *P. borkhoii* is most comparable with, but not typical of, the uniserial enamel (Korvenkontio, 1934; Koenigswald, 1985; Wahlert, 1989; Martin, 1992). The enamel is thinner than that of *Ardynomys olseni* (figs. 3, 4) but is similar in that the two layers of the enamel are roughly equal in thickness. The Hunter-Schreger bands (HSB) in the inner layer (*portio interna*) are inclined toward the tip of the incisor in the longitudinal section. Although the bands are one prism wide, the boundaries between decussating bands are not as well defined as in the enamel of *A. olseni*. The orientations of prisms in the outer layer (*portio externa*) are not clearly revealed from the longitudinal section, but it appears that they do not bend sharply apically as in *A. olseni*. The crystallites of interprismatic matrix (IPM) are roughly perpendicular to the enamel–dentine junction and have a small angle to the direction of the prisms.

COMPARISONS WITH RELATED TAXA

ARDYNOMYS: *Proardynomys* is comparable with *Ardynomys* in general morphology and is most similar to *A. olseni* in tooth morphology and enamel microstructures (figs. 4–6). *Ardynomys olseni* was originally described by Matthew and Granger (1925) from the "early Oligocene" Ardyn Obo (= Ergilin Dzo; see Dashzeveg, 1996) Formation of Mongolia; the formation is now considered late Eocene because of the new

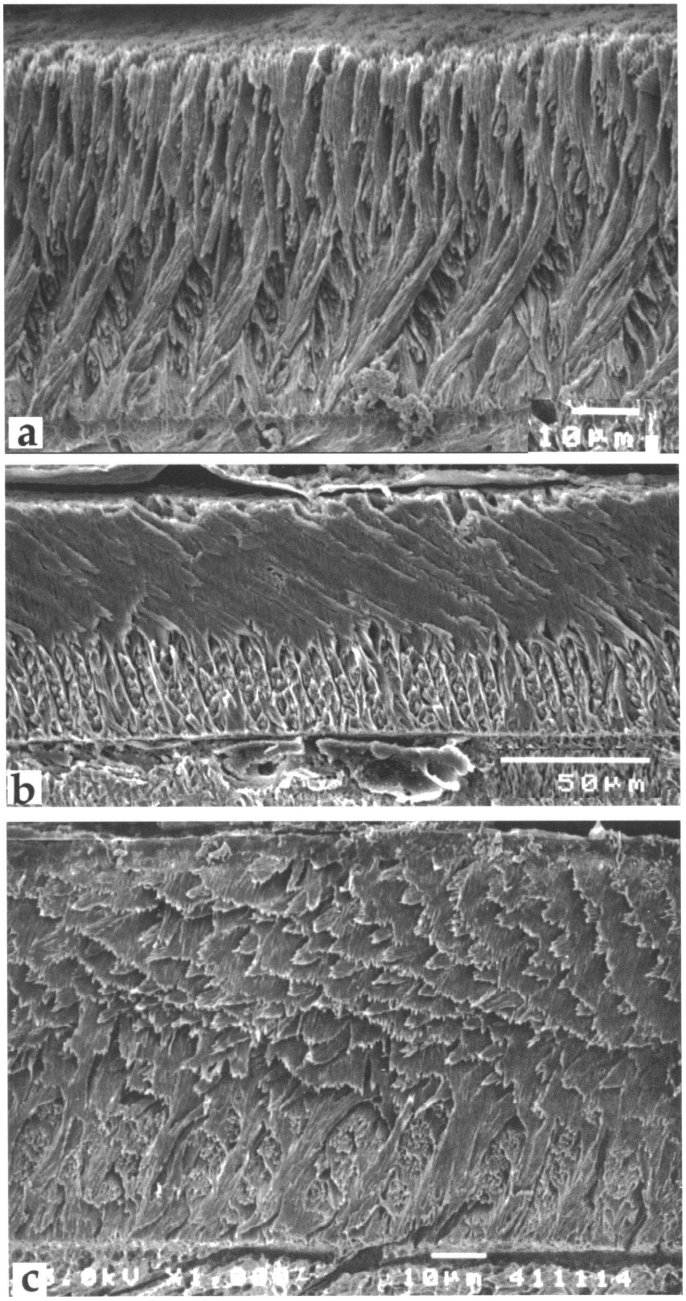

Fig. 4. **a,** Longitudinal section of the lower incisor of *Proardynomys borkhoii* (PSS 41-29); **b,** longitudinal section of the lower incisor of *Ardynomys olseni* (AMNH 20371); and **c,** longitudinal section of the lower incisor of *Ardynomys occidentalis* (no AMNH catalog number; specimen label: Mont. 14-145, McCarrthys Mt.). The tip of the tooth is to the right in a and c and to the left in b.

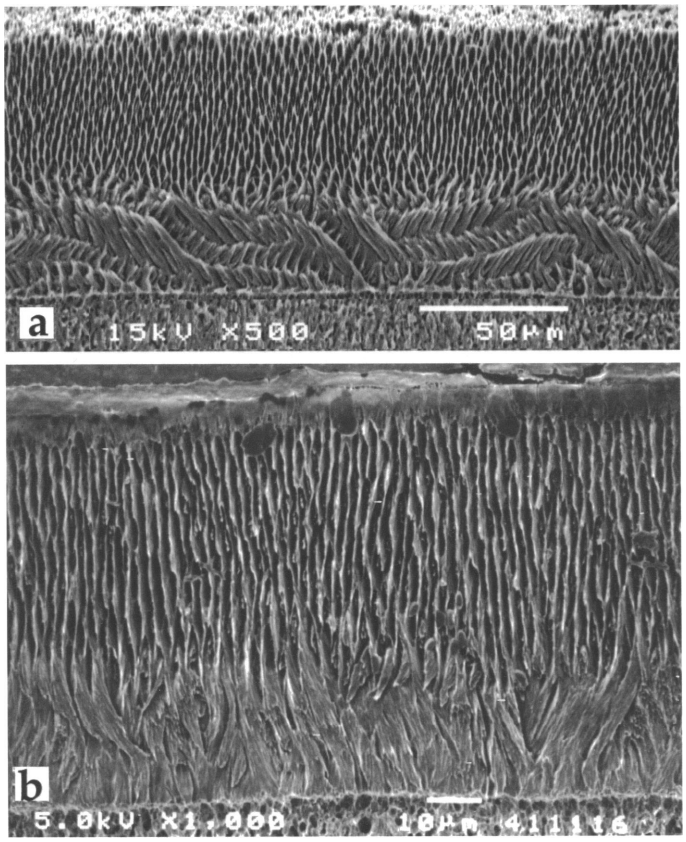

Fig. 5. **a** and **b,** Cross-sectional views of the lower incisors from *Ardynomys olseni* (AMNH 20371) and *A. occidentalis* (no AMNH catalog number; specimen label: Mont. 14-145, McCarrthys Mt.).

placement of the Eocene–Oligocene boundary for the Mongolian Paleogene (Meng and McKenna, 1996, 1998; Wang, 1997a; but see Dashzeveg, 1993, 1996). Four additional species of *Ardynomys* have been reported: *A. vinogradovi* from the late Eocene Ergilin Dzo Formation (Shevyreva, 1976; fig. 4c); *A. kazachstanicus* from middle Oligocene beds in Kazakhstan (the beds may well be early Oligocene by our age determination) (Vinogradov and Gambarian, 1952: fig. 4d); *A. occidentalis* from the Chadronian of North America (Burke, 1936; Wood, 1970, 1974; Korth, 1992); and *A. russelli* from the late Eocene Alag Tsab locality of Mongolia (Dashzeveg, 1996).

Ardynomys olseni is more primitive than are other species of the genus except possibly *A. russelli*, in which molar morphology is unclear because of deep wear of the teeth. *Ardynomys kazachstanicus*, *A. vinogradovi*, and *A. occidentalis* share some more derived features, such as having more rounded tooth crowns, stronger lophids, more anteriorly positioned hypolophids, more reduced trigonids, and more prominent hypoconids (fig. 6). Based on *A. olseni* as the representative of *Ardynomys*, *Proardynomys* and *Ardynomys* are comparable in the following features. The p4 trigonid basin opens anteriorly. Lower molars have two anterior and one posterior root. The metalophid II extends from the protoconid toward the metaconid and encloses a small trigonid basin. The ectolophid is short but strong, bearing no mesoconid. With wear the ectolophid connects the protoconid and hypoconid. The hypoconid projects anterolabially so that the sinusid is deep and opens anterolabially. The entoconid is distinct and separated from the posterolophid. The hypolophid is long and complete (weaker on p4 and m3) and joins the ectolophid in front of

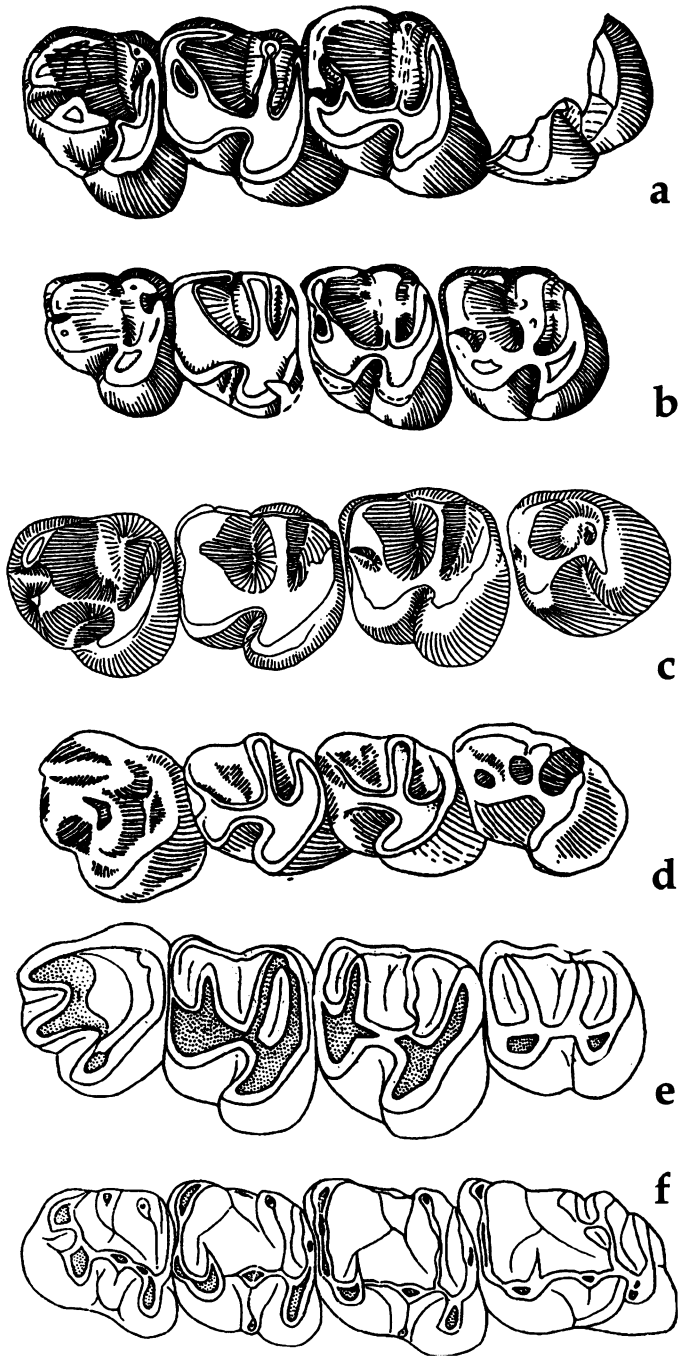

Fig. 6. A comparison of lower cheek teeth of **a** and **b,** *Ardynomys olseni* (based on Wood, 1970); **c,** *A. vinogradovi* (based on Shevyreva, 1976); **d,** *A. kazachstanicus* (based on Shevyreva, 1976); **e,** *Pseudocylindrodon* (based on Wang, 1986); and **f,** *Prosciurus relictus* (based on Wang, 1986). Some illustrations have been photographically reversed to facilitate comparison with figure 2. Figures are not to scale.

the hypoconid. The hypolophid does not migrate anteriorly, and a narrow posterosinusid is formed between the posterolophid and hypolophid. The metastylid crest and the entoconid are separated by a narrow gap at the lingual edge of the tooth. The posterolophid is strong, but the hypoconulid is not present. The wear pattern of the protoconid–hypoconid is similar. The lower incisor has uniserial enamel ultrastructure.

We take this opportunity to clarify an uncertainty about the ultrastructure of the incisor enamel in Cylindrodontidae. Observations of this structure in early cylindrodonts were inconsistent and confusing. Emry and Korth (1996a), citing Wahlert (1968), considered uniserial enamels as a general condition for cylindrodonts, although Wahlert (1968) observed the enamel of only *Cylindrodon fontis*. Citing Martin (1992), Bryant and McKenna (1995) believed that *Dawsonomys*, *Mysops*, and *Ardynomys* have pauciserial enamel. The pauciserial condition in *Ardynomys* is also implied by Averianov (1996). In fact, however, Martin (1992: plate 4, figs. 1 and 2) described the enamel of *Ardynomys* as uniserial and that of *Dawsonomys* and *Mysops* as pauciserial. Because the specimen Martin used is from "*Ardynomys* sp. indet." and because the images he illustrated appear incomplete, we here provide additional evidence of enamel ultrastructure from *A. olseni* and *A. occidentalis* (figs. 4, 5). Our study shows that the enamel of *A. olseni* is uniserial and is consistent with the observation by Martin (1992). Therefore, within the family Cylindrodontidae, the uniserial condition is confirmed in *Ardynomys* and more derived taxa, whereas the pauciserial enamel occurs in only *Dawsonomys* and *Mysops*. However, although incisor enamels of *A. olseni* and *A. occidentalis* are similar in having a thick portio externa, they differ in some details. In *A. olseni* the HSB of the portio interna is well defined and the IPM of the portio externa forms narrow laminae. In *A. occidentalis* the HSB of the portio interna is less defined, the number of prisms in each band is fewer than in *A. olseni*, and the IPM of the portio externa forms broader laminae. These structures show that certain variation of enamel microstructure is present among congeneric species. Although we consider the enamel microstructure in *Proardynomys* as uniserial, it is less typical than that of *A. olseni* and *A. occidentalis* and is certainly more derived than that of *Mysops* (Martin, 1992: plate 6, figs. 4, 5). The *Proardynomys* condition may represent a transitional stage between the pauciserial and uniserial conditions within the lineage of cylindrodontids.

Although *Proardynomys* has the basic tooth morphology of *Ardynomys*, it differs from *Ardynomys* in having the following primitive conditions. The ventral surface of the incisor is rounded and the enamel structure is less typical of the uniserial condition. The molar teeth are lower crowned, and the crown surface is not flat. The trigonid, particularly the metaconid, is significantly higher than the talonid. The lophs and lophids are narrower and less well developed. The hypoconid is less expanded and is not unicuspal hypsodont. The width to length ratio of cheek teeth is smaller than that in *Ardynomys*. The m3 is less reduced and is not oval shaped. The talonid basin is more open. The metastylid crests bordering the lingual margin of molars are lower.

OTHER CYLINDRODONTS: The earliest record of a possible cylindrodont rodent is *Dawsonomys woodi* (Gazin, 1961) from the Wasatchian (early Eocene) of North America, but placement of this species in the Cylindrodontidae is questionable (Korth, 1984; Emry and Korth, 1996). *Dawsonomys woodi* lacks several features that we consider typical of cylindrodontids. Its tooth cusps are more bulbous than lophate. The protoconid and hypoconid are far apart from each other and, unlike the condition in cylindrodonts, the hypoconid does not project anterolabially. A mesoconid exists on m1 (which is the only known molar), whereas in cylindrodontids the mesoconid is absent. The sinusid is shallow and broad, in contrast to a deep and narrow sinusid in cylindrodontids. Although the hypolophid is present, it extends posterolabially to join the hypoconid, as in the case of some early ctenodactyloids such as *Tamquammys* (Dawson et al., 1984); in cylindrodonts, the hypolophid extends labially to join the ectolophid anterior to the hypoconid. Korth (1984) also noticed similarities between *Dawsonomys* and early Asian ctenodactyloids, such as the trigonid structure of

p4 and m1; however, the fragmentary material prevents any conclusive relationship.

The Bridgerian (middle Eocene) *Mysops* from North America is probably an unquestionable cylindrodont (Wilson, 1938, 1949; Korth, 1984; Emry and Korth, 1996a). Tong (1997) recently reported comparable *Mysops* material from the middle Eocene Irdinmanhan of Henan, China, and pointed out that the material is younger but less specialized than the North American *Mysops*. Because Tong's new materials are a few isolated teeth, taxonomic assessment is difficult. Compared with the North American *Mysops*, *Proardynomys* is more primitive in having lower-crowned teeth, a higher metaconid on the trigonid, and a less expanded and elevated hypoconid. The p4 and molars are less lophate, the talonid basin of molars is broader, the posterosinusid is less developed, and the cheek teeth are less rounded in outline. However, the uniserial enamel microstructure of *Proardynomys* is more derived than the pauciserial condition of *Mysops* (Martin, 1992).

The genera *Morosomys* and *Sepulkomys* were described as cylindrodonts by Shevyreva (1976). Emry and Korth (1996a) considered *Morosomys* a synonym of *Tsaganomys*. In a thorough study of *Tsaganomys*, Bryant and McKenna (1995) suggested *Sepulkomys* a synonym of *Tsaganomys* but did not mention *Morosomys*. Other workers still consider *Morosomys* a cylindrodont (Dashzeveg, 1996; Tong, 1997; Tyutkova, 1997). *Morosomys* was regarded as a junior synonym of *Tsaganomys* in the new mammal classification (McKenna and Bell, 1997). Judging from the illustration of *Morosomys* (Shevyreva, 1976), it is clear that the relatively low-crowned cheek teeth of *Morosomys* differ significantly from those of *Tsaganomys*. In general, worn and unworn cheek teeth of *Tsaganomys* (Bryant and McKenna, 1995: fig. 11) are much more derived than those of *Morosomys*. *Morosomys* is probably a valid taxon, although its taxonomic relationship is debatable. The lower teeth of *Morosomys* are similar to those of *Proardynomys* in general shape, development of the hypolophid, and a weak or absent mesoconid. It differs from *Proardynomys* and other cylindrodonts in having a longer trigonid and the metalophid II (the posterior arm of the protoconid) short or absent; when the metalophid II is present, it extends posterolingually. In addition, the m3 of *Morosomys* bears a distinctive mesostylid. Upper teeth of *Morosomys* are unknown, preventing further comparison. *Morosomys* also shows some similarities to the aplodontid *Prosciurus*. The most significant difference between the two is a well-developed mesoconid on the lower cheek teeth of *Prosciurus*. Discovery of upper teeth and study of the enamel ultrastructure may clarify the taxonomic position of *Morosomys*.

The cylindrodont genus *Orientocylindrodon* (Tong, 1997) from Henan, China, is based on only upper teeth, which makes its comparison with other taxa difficult because most Asian cylindrodonts are represented by lower dentition. Tong noted, however, that these teeth have distinct hypocones and that their lingual surfaces are square shaped, in contrast to the rounded outline in other cylindrodonts.

Polinaomys was described recently from the early Oligocene Chlkarnura Formation of Kazakhstan (Tyutkova, 1997). Tyutkova considered this new taxon "a more archaic form [than, e.g., *Pseudocylindrodon*] lacking in well-pronounced features denoting specializations for digging." Unfortunately, the description of the new material was apparently erroneous in several aspects, such as "P4 is conical" and "P3 is rectangular," to give a few examples. The identifications of the teeth are also highly questionable. For instance, the "p4" is probably a dp4 because of its elongated shape and its deeper wear than on molars. The same is true for the "P3 and P4" of *Polinaomys*; that is, the "P3" is possibly a dP3. (Our considerations have been confirmed by personal communication with Emry, National Museum of Natural History, who made personal observations of the specimens.) Thus, the presence of P3 in *Polinaomys* has yet to be confirmed. In *Cylindrodon*, P3 is usually lost but a conical dP3 is present (Black, 1965; Emry and Korth, 1996a), which is also shown in a specimen of *Cylindrodon frontis* that we examined (uncataloged AMNH specimen: Mont. Box 121, West Exposure, Pipestone Springs, Montana). Judging from the illustrations (Tyutkova, 1997: fig. 1), the teeth of *Polinaomys*

are more rounded in crown view and more lophodont than those of *Proardynomys*, and the entolophid is anteriorly positioned, as in later cylindrodonts.

Other cylindrodonts include *Anomoemys* (Wang, 1986), *Pseudocylindrodon* (Burke, 1935, 1938), *Cylindrodon* (Douglass, 1901; Emry and Korth, 1996a), *Pareumys* (Black, 1970, 1974), *Jaywilsonomys* (Ferrusquía and Wood, 1969), possibly *Sespemys* (Wilson, 1934; Wood, 1980; McKenna and Bell, 1997; but see below), and *Downsimys* (Flynn et al., 1986; McKenna and Bell, 1997). These taxa are more derived than *Proardynomys* in having cheek teeth with higher crowns and additional lophodonty, as illustrated by *Pseudocylindrodon* (fig. 6e). In their brief review of the Cylindrodontidae, Emry and Korth (1996a) considered that *Ardynomys* and *Anomoemys* are the only cylindrodonts known from Asia, without commenting on the status of *Pseudocylindrodon mongolicus* reported from Mongolia (Kowalski, 1974; Shevyreva, 1976). Occurrence of *Pseudocylindrodon* in Asian Oligocene is regarded as possible in the classification by McKenna and Bell (1997). *Anomoemys* is from the "middle Oligocene" Hsanda Gol Formation of Mongolia (Matthew and Granger, 1923); that formation is now considered to be early Oligocene (Bryant and McKenna, 1995; Meng and McKenna, 1998; McKenna et al., in prep.). *Pseudocylindrodon* is also known from North America (Burke, 1935; Korth, 1992; Emry and Korth, 1996a), whereas *Anomoemys* remains monotypic, containing only *A. lohiculus* (= *Prosciurus lohiculus*; Wang, 1986) from Asia. Some taxa that have been previously placed in Cylindrodontidae, such as *Tsaganomys*, have been removed from the family (Bryant and McKenna, 1995; Emry and Korth, 1996a).

SCIURIDS: The earliest known sciurids are from the latest Eocene of North America and Oligocene of Europe. The North American forms are represented by *Douglassia jeffersoni* (Black, 1963; Emry and Thorington, 1982; Korth and Emry, 1991; Emry and Korth, 1996b), although the placement of *Douglassia jeffersoni* in the family Sciuridae has been questioned by others because of its protrogomorphous zygomatic morphology (Vianey-Liaud, 1974, 1985; Wood, 1980). Vianey-Liaud considered the European *Palaeosciurus goti* the earliest true sciurid. Fossil sciurids are rare in Asia, and unquestionable species are known only in the Neogene (Korth, 1994).

Detailed comparison shows that sciurids differ from *Proardynomys* in several aspects. The metaconid of sciurids is significantly anterior to the protoconid. The molar cusps are bulbous and marginally placed. The entoconid connects the posterolophid to form a ridge on the posterolingual margin of molars. The hypolophid is generally absent or weakly developed, as in *Douglassia jeffersoni* (Emry and Korth, 1996b). The talonid basin is broad because of the absence of the hypolophid and the marginally positioned cusps. The ectolophid is relatively long and labial, bearing a distinct mesoconid. The protoconid and hypoconid are distantly separated. The sinusid is shallow and broad. The lower cheek teeth are wider than long and have two roots in early forms and four roots in later ones. In addition, the anterior edge of the masseteric fossa on the mandible of *Proardynomys* is more posteriorly positioned below posterior m2, whereas in sciurids the anterior limit of the masseteric fossa is below the posterior root of m1 or farther anteriorly (Emry and Korth, 1996b). Owing to the anterior extension of the metaconid and the fusion of the entoconid and posterolophid, the crown outline of sciurid molar is somewhat rhomboid, with the long axis passing through the metaconid and hypoconid and the short axis through the protoconid and entoconid. The upper molar of *Proardynomys* lacks conules and is more lophate than early sciurids, such as *Douglassia*, *Palaeosciurus*, and other forms (Black, 1963). Additional characters of sciurids are summarized by Korth (1994).

APLODONTIDS: A comparison between cylindrodonts and aplodontids is warranted for the reason that at least two taxa, *Anomoemys lohiculus* and *Sespemys*, have been placed once in either of the Cylindrodontidae or Aplodontidae. A review of studies about the taxonomic position of *A. lohiculus* has been provided by Wang (1986), who concluded that *A. lohiculus* is a cylindrodont, not an aplodontid. When *Sespemys* was described (Wilson, 1934), its taxonomic position was unclear, although it was assigned to Ischy-

romyidae and was believed to be intermediate between *Ischyromys* and *Sciurus*. *Sespemys* was then considered a cylindrodont by several workers (Burke, 1936; Wood, 1937, 1980; Simpson, 1945). Alternatively, Korth (1994) considered *Sespemys* a primitive aplodontid. The study histories of *Sespemys* and *A. lohiculus* reflect morphological similarities between taxa from the Cylindrodontidae and Aplodontidae. The most prominent similarity between these two groups is probably development of the hypolophid. However, the hypolophid has a variety of shapes and is distributed in several taxa (Dashzeveg and Meng, 1998). The development of the hypolophid varies within aplodontids (Rensberger, 1975; 1982). In primitive forms, such as *Prosciurus*, the hypolophid is either long and extends to the ectolophid, such as in *Prosciurus relictus* (Wood, 1937: fig. 6f), or short and joins the hypoconulid, such as in *Prosciurus vetustus* (Black, 1965). On the other hand, *Prosciurus* has a short metalophid II that points medially or posteromedially, a distinct mesostylid, a mesoconid, a long ectolophid, a broad sinusid, and a more posteriorly restricted hypoconid. These features distinguish aplodontids from cylindrodonts. By these features, except the mesoconid, *Sespemys* appears more similar to aplodontids than to sciurids.

ASIAN ISCHYROMYIDS: Among species in the Ischyromyidae, Flynn et al. (1986) suggested *Hulgana* should be placed in Cylindrodontidae. *Hulgana* was originally thought an early Oligocene rodent (Dawson, 1968), but the traditional early Oligocene of Asia is now considered to be late Eocene (Meng and McKenna, 1996, 1998; Wang, 1997a, b). Emry and Korth (1996a), however, believed the dentition of *Hulgana* to be that of a simplified ischyromyid rather than that of a cylindrodontid. The lower teeth of *Hulgana* are more sciurid-like in having the posterolophid–entoconid connection, a lack of a hypolophid, the ectolophid more labially positioned, and a broader talonid basin. *Hulgana* shows its primitiveness in having the anterior limit of the masseteric fossa between m2 and m3. Lack of the mesoconid and hypoconulid on the lower molars of *Hulgana* is similar to the condition in *Proardynomys*, but the most distinctive feature between the two genera is the lack of the hypolophid in *Hulgana*. The M1 assigned to *Proardynomys* shows some similarities to that of *Hulgana*. Both have an anteriorly positioned protocone, which connects to the labial cusps by protoloph and metaloph. Conules are not distinct and there is no sign of a discrete hypocone (Dawson, 1968). If the assignment of the M1 to the new genus were correct, it suggests a certain affinity of *Proardynomys* to ischyromyid-like forms. Other Eocene ischyromyids, such as *Taishanomys* and *Acritoparamys*? from Wutu, China (Tong and Dawson, 1995), are primitive and cast little light on the relationships of Cylindrodontidae.

CTENODACTYLOIDS: Most Asian rodents of the early Tertiary are ctenodactyloids (Dawson et al., 1984; Flynn et al., 1986; Li et al., 1989; Dashzeveg, 1990; Wang, 1994; Averianov, 1996; Emry et al., 1998). However, the phylogeny and taxonomy of this group have been controversial. Although placed in the Ctenodactyloidea, these rodents were further subdivided into three families: Cocomyidae, Yuomyidae (Dawson et al., 1984; but see Dashzeveg, 1990 and Averianov, 1996), and Chapattimyidae (Hussain et al., 1978; Flynn et al., 1986). These families are probably paraphyletic (Dashzeveg and Meng, 1998). McKenna and Bell (1997) did not use the superfamily Ctenodactyloidea in their classification of mammals; instead, they considered the three families as subfamilies and placed them, with the fourth subfamily Baluchimyinae, in the family Chapattimyidae. Despite the taxonomic problems, similarities have been noticed between primitive cylindrodonts and ctenodactyloids such as *Yuomys* and *Petrokzlovia* (Li, 1975; Shevyreva, 1976; Hussain et al., 1978; Averianov, 1996). For instance, Li (1975) proposed three possibilities for the taxonomic placement of *Yuomys*: (1) as a new family or subfamily; (2) as a member of Cylindrodontidae; or (3) as a member of Ischyromyidae. Li chose the last assignment.

Yuomys resembles cylindrodonts in having a complete hypolophid that joins the ectolophid in front of the hypoconid, the lack of the mesoconid, and the development of crests on molars. It differs from cylindrodonts in several aspects: the P4 and p4 are molariform and larger than the M1 and m1 respectively;

the metalophid II is short and incomplete on lower molars; the hypoconulid is distinct; the posterolophid does not extend to the lingual side of the molars; the hypocone is well developed and lingual to the protocone on M1 and M2; the metaloph does not reach the protocone; and the skull is hystricomorphous.

The cheek teeth assigned to *Petrokozlovia* show considerable variation (Averianov, 1996). The holotype *Petrokozlovia notos* (Shevyreva, 1976: fig. 6V, pl. II, 4v) is actually not significantly similar to early cylindrodonts in that, for instance, the hypolophid is incomplete and the expanded hypoconid does not project anterolabially. Other specimens of *Petrokozlovia* (Shevyreva, 1976; Averianov, 1996) show that upper molars have low anterior cingula, incomplete metalophs, and distinct conules and hypocones.

DISCUSSION

The phylogenetic position of the Cylindrodontidae has been controversial. Wood (1980, 1981, 1984) included this family in his infraorder Franimorpha based on the subhystricognathous mandible. According to Wood, Franimorpha plays a central role in the origin of Caviomorpha and Hystricognathi. Several workers (Korth, 1984; Luckett and Hartenberger, 1985; Wilson, 1986; Meng, 1990; Emry and Korth, 1996a), who consider that the subhystricognathous mandible is not significant and that other features demonstrate the paraphyly of Franimorpha, disagree with Wood's hypothesis. Furthermore, Emry and Korth found no dental and cranial features to support the inclusion of Cylindrodontidae in the Hystricomorpha and considered the phylogenetic position of Cylindrodontidae undetermined.

A new proposal regarding the relationships of Cylindrodontidae was made by Averianov (1996) in his review of Eocene ctenodactyloid rodents from Asia. Averianov (1996: 657) stated:

> The monophyly of the three rodent groups, Cylindrodontidae, Ctenodactylidae, and Baluchimyinae (not used here), seems to be indisputable. As the Chapattimyidae do not include all the taxa that have been nested within it (Cylindrodontidae, Ctenodactylidae, and three genera of tamquammyids), it is not a monophyletic taxon, but paraphyletic. It is considered here, following Wood (1977) and Hartenberger (1982), as a lower grade within ctenodactyloid rodents, but requires family status. The protrogomorphy of cylindrodonts may be secondar[il]y derived, as in the case of the Bathyergidae (Maier and Schrenk, 1987).

As we pointed out in a separate study (Dashzeveg and Meng, 1998), Averianovs conclusion either implies paraphyly of the ctenodactyloid rodents or suggests the Cylindrodontidae a subgroup within ctenodactyloid rodents. Each of the two possibilities requires a reversal of the protrogomorphy of Cylindrodontidae from the histricomorphy of ctenodactyloids according to Averianovs phylogeny.

Several aspects of Averianov's proposal are questionable. First, because the Miocene Baluchimyiinae (Flynn et al., 1986) was not included in Averianov's cladistic analysis, it is not clear how the indisputable monophyly of Cylindrodontidae, Ctenodactylidae, and Baluchimyinae was obtained. Second, Averianov applied 17 characters to a group consisting of 20 taxa. This insufficient data set casts doubt on the resolution of calculated relationships. Third, although he did not specify the condition of the enamel ultrastructure in *Ardynomys*, Averianov coded it as primitive, the same as in several primitive forms such as *Tribosphenomys*, *Cocomys*, and *Paramys*. The enamel ultrastructure of these latter taxa is pauciserial (Wahlert, 1989; Martin, 1992; Meng and Wyss, 1994). Given that the multiserial condition (as in *Tataromys)* and uniserial condition (as in *Ardynomys*) are probably derived independently from the pauciserial condition (Martin, 1992), the *Ardynomys–Tataromys* sister group appears highly unlikely. Therefore, a generalization that Cylindrodontidae and Ctenodactylidae form a sister group is contradicted by this character. Fourth, it is unclear what Averianov uses as the taxonomic content of the family Cylindrodontidae. Averianov included only *Ardynomys* as representative of Cylindrodontidae and *Tataromys* as representative of Ctenodactylidae in his analysis but stated (1996: 643), "In cheek tooth morphology (especially lower teeth) *Petrokozlovia* is basically similar to early cylindrodonts (e.g., *Ardynomys* and *Hulgana*)." Apparently, *Hulgana* (Dawson, 1968) was a member of the Cylindrodontidae according to Averianov. As we mentioned above, *Hul-*

gana has not been established as a cylindrodont. Nonetheless, if *Hulgana* was a cylindrodontid, then the character states scored for cylindrodonts should be reconsidered. For instance, P3 absent, metaconule absent, and hypolophid complete were scored by Averianov as derived conditions in *Ardynomys*, and the first two were the only synapomorphies that diagnose the *Ardynomys–Tataromys* pairing. However, P3 is present and the hypolophid is absent in *Hulgana* (Dawson, 1968), which creates inconsistency for characters applied to Cylindrodontidae as a whole. Finally, although absence of P3 is a derived feature for Ctenodactylidae (Wang, 1994, 1997a), P3 is present in all cylindrodonts, with the possible exception of *Cylindrodon* (Burke, 1936, 1938; Wood, 1970; Dashzeveg, 1996) for Emry and Korth (1996a) have noted P3 or possibly dP3 in *Cylindrodon*. Therefore, absence of P3 is certainly not a synapomorphy for *Ardynomys* and *Tataromys*. Cylindrodontidae may have evolved from Asian ctenodactyloids, but if this is the case, the departure of these two families is unlikely at the level at which *Ardynomys* and *Tataromys* form a sister group. From the above discussion, we believe that the Cylindrodontidae–Ctenodactylidae sister group is not supported by sufficient evidence. The new material described here and ctenodactylid-like forms reported elsewhere (Tong, 1997; Dashzeveg and Meng, 1998) suggest that Cylindrodontidae and Ctenodactylidae are distantly separated lineages.

Although Emry and Korth (1996a) considered the systematic position of the Cylindrodontidae uncertain, they pointed out that cylindrodonts have been regarded as a primitive group of rodents, not far derived from the protrogomorphous–sciurognathous rodent stock. Based on evidence of cranial foramina, Wahlert (1974) suggested that cylindrodonts were related to ischyromyids; he considered cylindrodonts as a subfamily of the Ischyromyidae. The new taxon supports those authors assessments because it further demonstrates several similarities between cylindrodonts and primitive forms such as North American paramyids. These similarities include a molariform p4, the p4 trigonid basin longitudinally oriented and open anteriorly, the hypoconid labially or anterolabially or both extended in some taxa, a protoconid–hypoconid wear pattern, and a poorly developed hypocone on upper molars. Although a clear picture of the relationship is yet to emerge, we speculate that cylindrodontids are probably related to Sciuridae and Aplodontidae.

In considering that Oligocene cylindrodonts were all derived independently from the Eocene *Mysops*, Wilson (1949: 95) stated:

> The cheek teeth of *Ardynomys* are less specialized than those of *Cylindrodon*, and also on the whole than those of *Pseudocylindrodon*. At least, *Pseudocylindrodon neglectus* resembles *Cylindrodon* more closely that does *Ardynomys*. The dentition of *P. medius*, however, is closer to that of *Mysops* than is that of any other Oligocene member of the group. *Cylindrodon* and *Pseudocylindrodon* appears to be more related to each other than either is to *Ardynomys*.

However, Wood (1970) believed that *Ardynomys* and *Pseudocylindrodon* are more closely related than either is to the more hypsodont *Cylindrodon*. The new material demonstrates that on the one hand *Ardynomys* is more readily derivable from *Proardynomys* and on the other hand *Proardynomys* is not a descendant of *Mysops* because *Proardynomys* is more primitive than *Mysops* in several aspects, as mentioned above. This suggests that *Proardynomys* and *Mysops* may represent two evolutionary lineages within the Cylindrodontidae. These lineages may have evolved from a morphotype that had a *Mysops* type of enamel microstructure and molar patterns similar to that of *Proardynomys*.

ACKNOWLEDGMENTS

We thank Drs. M. C. McKenna, R. H. Tedford, and M. Norell for access to the collection of rodents at the American Museum of Natural History. We thank Drs. R. J. Emry, W. W. Korth, and J. H. Wahlert for instructive comments. Meng's research was supported by the University of Massachusetts and a National Science Foundation grant (DEB-9508685).

REFERENCES

Averianov, A.
1996. Early Eocene Rodentia of Kyrgyzstan. Bull. Mus. Natl. Hist. Nat. Paris 4e sér., 18C: 629–662.

Black, C. C.
1963. Miocene rodents from the Thomas Farm Local Fauna, Florida. Bull. Mus. Comp. Zool. 128: 483–501.
1965. Fossil mammals from Montana. Rodents from the Early Oligocene Pipestone Springs Local Fauna. Ann. Carnegie Mus. 38: 1–48.
1970. A new *Pareumys* (Rod. *Cylindrodon*) from the Duchesne River formation, Utah. Fieldiana Geol. 16: 453–459.
1974. Paleontology and geology of the Badwater Creek Area, central Wyoming, Part. 9. Additions to the Cylindrodont rodents from the late Eocene. Ann. Carnegie Mus. 45: 151–160.

Bryant, J. D., and M. C. Mckenna
1995. Cranial anatomy and phylogenetic position of *Tsaganomys altaicus* (Mammalia: Rodentia) from the Hsanda Gol Formation (Oligocene), Mongolia. Am. Mus. Novitates 3156: 42 pp.

Burke, J. J.
1935. *Pseudocylindrodon*, a new rodent genus from the Pipestone Springs Oligocene of Montana. Ann. Carnegie Mus. 25: 1–4.
1936. *Ardynomys* and *Desmatolagus* in the North American Oligocene. Ibid.: 135–154.
1938. A new Cylindrodont rodent from the Oligocene of Montana. Ibid. 27: 255–275.

Dashzeveg, D.
1990. The earliest rodents (Rodentia, Ctenodactyloidea) of Central Asia. Acta. Zool. Cracoviensia 33: 11–35.
1993. Asynchronism of the main mammalian faunal events near the Eocene-Oligocene boundary. Tertiary Res., 14: 141–149.
1996. A new *Ardynomys* (Rodentia, Cylindrodontidae) from the Eocene of the Eastern Gobi Desert, Mongolia. Palaeovertebrata 25: 339–348.

Dashzeveg, D., and J. Meng
1998. New Eocene Ctenodactyloid rodents from Eastern Gobi Desert of Mongolia and a phylogenetic analysis of ctenodactyloids based on dental features. Am. Mus. Novitates. 3246: 20 pp.

Dawson, M. R.
1968. Oligocene Rodents (Mammalia) from East Mesa, Inner Mongolia. Am. Mus. Novitates 2324: 11 pp.

Dawson, M. R., C. Li, and T. Qi
1984. Eocene ctenodactyloid rodents (Mammalia) of eastern and Central Asia. *In* R. M. Mengel (ed.), Papers in vertebrate paleontology honoring Robert Warren Wilson. Carnegie Mus. Nat. Hist. Spec. Publ. 9: 138–150.

Douglass, E.
1901. Fossil Mammalia of the White River Beds of Montana. Trans. Am. Philos. Soc. Philadelphia 20: 237–279.

Emry, R. J., and W. W. Korth
1996a. Cylindrodontidae. *In* D. R. Prothero and R. J. Emry (eds.), The terrestrial Eocene-Oligocene transition in North America: 399–416. New York: Cambridge Univ. Press.
1996b. The Chadronian squirrel "*Sciurus*" *jeffersoni* Dauglass, 1901: a new generic name, new material, and its bearing on the early evolution of Sciuridae (Rodentia). J. Vertebr. Paleontol. 16: 775–780.

Emry, R. J., and R. W. Thorington, Jr.
1982. Descriptive and comparative osteology of the oldest fossil squirrel, *Protosciurus* (Rodentia: Sciuridae.). Smithson. Contrib. Paleobiol. 47: 1–35.

Emry, R. J., L. A. Tyutkova, S. G. Lucas, and B. Wang
1998. Rodents of the Middle Eocene Shinzhaly fauna of eastern Kazakstan. J. Vertebr. Paleontol. 18: 218–227.

Ferrusquia-Villafranca, I., and A. E. Wood
1969. New fossil rodents from the Early Oligocene Rancho Gaitan Local Fauna, North Eastern Chihuahua, Mexico. Pearce Sellards Ser., Texas Mem. Mus. 16: 1–13.

Flynn, L. J., L. L. Jacobs, and E. H. Lindsay
1985. Problems in muroid phylogeny: relationship to other rodents and origin of major groups. *In* P. Luckett and J.-J. Hartenberger (eds.), Evolutionary relationships among rodents—A multidisciplinary analysis: 589–616. New York: Plenum Press.

Flynn, L. J., L. L. Jacobs, and I. U. Cheema
1986. Baluchimynae, a new ctenodactyloid rodent subfamily from the Miocene of Baluchistan. Am. Mus. Novitates 2841: 50 pp.

Gazin, C. L.
1961. New sciuravid rodents from the lower Eocene Knight formation of western Wyoming. Proc. Biol. Soc. Washington 73: 193–194.
Hartenberger, J.-L.
1982. A review of the Eocene rodents of Pakistan. Contrib. Mus. Paleontol. University of Michigan 26: 19–35.
Hussain, S. T., H. de Bruijn, and J. M. Leinders
1978. Middle Eocene rodents from the Kala Chitta Range (Punjab, Pakistan). Proc. K. Ned. Akad. Wet. 81: 74–112.
Koenigswald, W. Von
1985. Evolutionary trends in the enamel of rodent incisors *In* P. Luckett and J.-J. Hartenberger (eds.), Evolutionary relationships among rodents—A multidisciplinary analysis: 403–422. New York: Plenum Press.
Korth, W. W.
1984. Earliest Tertiary evolution and radiation of rodents in North America. Bull. Carnegie Mus. Nat. Hist. 24: 1–71.
1992. Cylindrodonts (Cylindrodontidae, Rodentia) and a new genus of eomyid, Paranamatomys, (Eomyidae, Rodentia) from the Chadronian of Sioux County, Nebraska. Trans. Nebraska Acad. Sci. 19: 75–82.
1994. The Tertiary records of rodents in North America. New York: Plenum Press, 324 pp.
Korth, W. W., and R. J. Emry
1991. The skull of Cedromus and a review of the Cedromurinae (Rodentia, Sciuridae). J. Paleontol. 65: 984–994.
Korvenkontio, V. A.
1934. Mikroskopische Untersuchungen an Nagerincisiven unter Hinweis auf die Schmelzstructur der Backenzähne. Histologisch-Phyletische Studie. Ann. Soc. R. Zool. Vanamo 2: 1–274.
Kowalski, K.
1974. Middle Oligocene rodents from Mongolia. Results of the Polish-Mogolian Paleontological expeditions Part. V. Paleontol. Pol. 78: 197–202.
Li, C.
1975. *Yuomys*, a new ischyromyid rodent genus from the upper Eocene of North China. Vertebr. PalAsiat. 13: 58–70.
Li, C., J. Zheng, and S. Ting
1989. The skull of Cocomys lingchaensis, an Early Eocene Ctenodactyloid rodent of Asia. *In* C. C. Black and M. R. Dawson (eds.), Papers on fossil rodents—In honor of Albert Elmer Wood. Nat. Hist. Mus. Los Angeles C. Sci. Ser. 33: 179–192.
Luckett, W. P., and J.-L. Hartenberger
1985. Evolutionary relationships among rodents: comments and conclusions. *In* P. Luckett and J.-J. Hartenberger (eds.), Evolutionary relationships among rodents—A multidisciplinary analysis: 685–712. New York: Plenum Press.
Maier, W., and F. Schrenk
1987. The Hystricomorphy of the Bathyergidae, as determined from ontogenetic evidence. Z. Säugetierk. 52: 156–164.
Martin, T.
1992. Schmelzmikrostructur in den incisiven alt-und neuweltlicher hystricognather Nagetiere. Palaeovertebrata, Mém. Extraordinaire 1–168.
Matthew, W. D., and W. Granger
1923. New Bathyergidae from the Oligocene of Mongolia. Am. Mus. Novitates 101: 5 pp.
1925. New creodonts and rodents from the Ardyn Obo formation of Mongolia. Ibid. 197: 7 pp.
McKenna, M. C., and S. K. Bell
1997. Classification of mammals above the species level. New York: Columbia Univ. Press.
Meng, J.
1990. The auditory region of *Reithroparamys delicatissimus* (Mammalia, Rodentia) and its systematic implications. Am. Mus. Novitates 2972: 35 pp.
Meng, J., and M. C. McKenna
1996. The Mongolian remodeling in the global frame-Paleogene faunal turnovers and biostratigraphy. J. Vertebr. Paleontol. Suppl. 16: 52A–53A.
1998. Faunal turnovers of Palaeogene mammals from the Mongolian plateau. Nature 394: 364–367.
Meng, J., and A. R. Wyss
1994. The enamel microstructure of *Tribosphenomys* (Mammalia, Glires): functional and phylogenetic implications. J. Mamm. Evol. 2: 185–203.
Rensberger, J. M.
1975. Haplomys and its bearing on the origin of Aplodontoid rodents. J. Mammal. 56: 1–14.
1982. Patterns of dental change in two locally persistent successions of fossil Aplodontid Rodents. *In* B. Kurten (ed.), Teeth: form, function and evolution: 233–249. New York: Columbia Univ. Press.

Shevyreva, N. S.
1976. Paleogene rodents of Asia (Families Paramyidae, Sciuravidae, Ischyromyidae, Cylindrodontidae). Trans. Paleontol. Inst. Acad. Nauk. SSSR. 158: 1–116.
Simpson, G. G.
1945. The principles of classification and a classification of mammals. Bull. Am. Mus. Nat. Hist. 85: 1–350.
Tong, Y.
1997. Middle Eocene small mammals from Liguanqiao Basin of Henan Province and Yuanqu Basin of Shanxi Province, Central China. Palaeontol. Sinica 18 C26: 1–256.
Tong, Y., and M. R. Dawson
1995. Early Eocene rodents (Mammalia) from Shangdong Province, China. Ann. Carnegie Mus. 64: 51–63.
Tyutkova, L. A.
1997. A new cylindrodontid (Rodentia, Mammalia) from the *Indricotherium* fauna. J. Paleontol. 31: 662–666.
Vianey-Liaud, M.
1974. *Palaeosciurus goti* nov. sp., écureuil terrestre de l'Oligocène moyen du Quercy. Données nouvelles sur l'apparition des Sciuridés en Europe. Ann. Paléontol. Vertébr. 60: 103–122.
1985. Possible evolutionary relationships among Eocene and Lower Oligocene rodents of Asia, Europe and North America. *In* P. Luckett and J.-J. Hartenberger (eds.), Evolutionary relationships among rodents—a multidisciplinary analysis: 277–309. New York: Plenum Press.
Vinogradov, B. C., and P. P. Gambarian.
1952. Oligocene cylindrodonts of Mongolia and Kazakhstan (Cylindrodontidae, Glires, Mammalia). Trans. Paleontol. Inst., Akad. Nauk SSSR. 41: 13–42. [in Russian]
Wahlert, J. H.
1968. Variability of the rodent incisor enamel as viewed in thin section, and the microstructure of the enamel in fossil and recent rodent groups. Breviora 309: 1–18.
1974. The cranial foramina of protrogomorphous rodents, an anatomical and phylogenetic study. Bull. Mus. Comp. Zool. 146: 363–410.
1989. The three types of incisor enamel in rodents. Nat. Hist. Mus. Los Angeles Cty. Sci. Ser. 33: 7–16.
Wang, B.
1985. Zapodidae (Rodentia, Mammalia) from the Lower Oligocene of Qujing, Yunnan, China. Mainz. Geowiss. Mitt./ Geol. Landesamt Rheinland- Pfalz 14: 245–267.
1986. On the systematic position of *Prosciurus lohiculus*. Vertebr. PalAsiat. 24: 285–294.
1994. The Ctenodactyloidea of Asia. *In* Y. Tomida, C. K. Li, and T. Setoguchi (eds.), Rodent and lagomorph families of Asian origin and diversification. Tokyo Nat. Sci. Mus. Monogr. 8: 35–47.
1997a. The mid-Tertiary Ctenodactylidae (Rodentia, Mammalia) of eastern and central Asia. Bull. Am. Mus. Nat. Hist. 234: 1–88.
1997b. Problems and recent advances in the division of the continental Oligocene. J. Stratigraphy 21: 81–90.
Wilson, R. W.
1934. Two rodents and a lagomorph from the Sespe of the Las Posas Hills, California. Carnegie Inst. Washington Publ. 453: 11–17.
1938. Review of some rodent genera from the Bridger Eocene. Pts. I–III. Am. J. Sci. 5: 123–137, 207–222, 297–304.
1949. Early Tertiary rodents for North America. Carnegie Inst. Washington Publ. 584: 59–83.
1986. The Paleogene record of the rodents; fact and interpretation Vertebrate phylogeny and philosophy. A tribute to George Gaylord Simpson. Univ. Wyoming Contrib. Geol. 3: 163–175.
Wood, A. E.
1937. The Mammalian fauna of the White River Oligocene. Trans. Am. Philos. Soc. Philadelphia 28: 155–269.
1970. The Early Oligocene rodent *Ardynomys* (Family Cylindrodontidae) from Mongolia and Montana. Am. Mus. Novitates, 2418: 18 pp.
1974. Early Tertiary vertebrate faunas Vieja group Trans-Pecos, Texas: Rodentia. Texas Mem. Mus. Bull. 21: 1–112.
1977. The evolution of the rodent family Ctenodactylidae. J. Palaeontol. Soc. India 20: 120–137.
1980. The Oligocene Rodents of North America. Trans. Am. Philos. Soc. Philadelphia 70: 1–68.
1981. The origin of the Caviomorph rodents from a source in Middle America. A clue to the area of origin of the platyrrhine primates. *In* R. L. Ciochon and

A. B. Chiarelli (eds.), Evolutionary biology of the New World Monkeys and Continental Drift: 79–91. New York: Plenum Press.

1984. Hystricognathy in the North American Oligocene rodent *Cylindrodon* and the origin of the caviomorpha, *In* R. M. Mengel (ed.), Papers in paleontology honoring R. W. Wilson. Carnegie Mus. Nat. Hist. Spec. Publ. 9: 151–160.

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates* and *Bulletin* published during the last five years are available at World Wide Web site http://nimidi.amnh.org. Or address mail orders to: American Museum of Natural History Library, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: scipubs@amnh.org

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).