NEW LATE PALEOCENE RODENTS (MAMMALIA) FROM BIG MULTI QUARRY, WASHAKIE BASIN, WYOMING

by

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CONTENTS

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ABSTRACT

The earliest North American rodents occur in basal Clarkforkian beds of the Fort Union Formation at Big Multi Quarry near Bitter Creek, northern Washakie Basin, Sweetwater County, Wyoming, and in closely correlative Fort Union beds formerly accessible in the Eagle Coal Mine near Bear Creek, northern Clark's Fork Basin, Carbon County, Montana. Two new species of early Clarkforkian rodents, *Paramys adamus* and *Alagomys russelli*, are described from Big Multi Quarry. *Paramys adamus* is represented by virtually complete upper and lower dentitions, which demonstrate that this species is one of the most primitive North American paramyids yet discovered. These specimens form the basis for a reevaluation of the content and stratigraphic range of *P. atavus*, which is known with certainty only from Bear Creek. *Alagomys russelli* is the first North American record for the enigmatic rodent family Alagomyidae, otherwise known from ?late Paleocene-early Eocene localities in Mongolia and China. Phylogenetic analysis of dental and gnathic traits suggests that Alagomyidae form the sister group of all other undoubted rodents. At least two rodent clades, alagomyids and basal paramyids, seem to have invaded North America from Asia at the beginning of Clarkforkian time, but only the paramyids persisted to undergo a significant evolutionary radiation in North America.

RESUME

Les plus anciens rongeurs d'Amérique du Nord se trouvent dans les couches clarkforkiennes basales de la Formation Fort Union, dans la Big Multi Quarry près de Bitter Creek, au nord du Bassin de Washakie (Sweetwater County, Wyoming), et dans les couches Fort Union d'âge voisin autrefois accessibles dans la Mine Eagle Coal près de Bear Creek, au nord du Bassin de Clark's Fork (Carbon County, Montana). Deux nouvelles espèces de rongeurs clarkforkiens anciens, *Paramys adamus* et *Alagomys russelli*, sont décrits de la Big Multi Quarry. *Paramys adamus* est représenté par ses dentitions supérieure et inférieure quasi complètes, qui montrent que cette espèce est l'un des paramyidés nord-américains les plus primitifs découverts jusqu'ici. Ces spécimens permettent de réévaluer le contenu et l'extension stratigraphique de *P. atavus*, qui n'est connu avec certitude que de Bear Creek. *Alagomys russelli* est la première mention de l'énigmatique famille des Alagomyidae, rongeurs connus par ailleurs dans des localités ?Paléocène supérieur-Eocène inférieur de Mongolie et de Chine. L'analyse phylogénétique des caractères dentaires et mandibulaires suggère que les Alagomyidae sont le groupe-frère de tous les autres rongeurs incontestables. Deux groupes de rongeurs au moins, les alagomyidés et les paramyidés, semblent avoir envahi l'Amérique du Nord depuis l'Asie au début du Clarkforkien, mais seuls les paramyidés ont survécu pour donner une radiation évolutive notoire en Amérique du Nord.

INTRODUCTION

The fossil record of Paleocene rodents is sparse. Middle Paleocene strata in the Qianshan Basin, Anhui Province, southern China, have yielded *Heomys orientalis*, variously considered a very rodent-like eurymylid or a rodent (Li 1977, Meng *et al.* 1994). The oldest universally accepted rodent is North American *Paramys atavus*, known from a right lower molar (probably M_2), a left P^4, and some incisors from Eagle Coal Mine, near Bear Creek in the northern Clark's Fork Basin, Carbon County, Montana (Jepsen 1937, McKenna 1961). The age of the Bear Creek locality has been somewhat controversial. Several workers (e.g., Simpson 1929, Jepsen 1937, McKenna

1961, Korth 1984) have advocated a Tiffanian correlation for its mammalian fauna, whereas most recent workers (e.g., Rose 1981, Archibald *et al.* 1987, Ivy 1990, Gingerich 1994) have viewed the Bear Creek mammalian fauna as correlative with early Clarkforkian zone Cf1. For the purposes of this study, it is sufficient to note that the records of *Paramys atavus* from Bear Creek are older than most, if not all, of the paramyid specimens described from exposures farther south in the Clark's Fork Basin of Wyoming by Ivy (1990). With the exception of the Asian *Tribosphenomys minutus*, all other definite Paleocene rodents are also members of the family Paramyidae and are North American in provenance (Korth 1984, Ivy 1990). *Tribosphenomys*, which is considered here to be an alagomyid rodent, is known only from the Bayan Ulan beds of Inner Mongolia (Meng *et al.* 1994). Correlation of the Bayan Ulan beds with the Paleocene-Eocene boundary and/or the North American sequence of land mammal ages is debatable (Russell & Zhai 1987), but we advocate a pre-Bumbanian (late Paleocene) age for the Bayan Ulan beds that yielded *Tribosphenomys*.

Clarkforkian mammal faunas are scarce in North America outside of the Clark's Fork Basin itself (Rose 1981, Archibald *et al.* 1987). Perhaps the most diverse of these comes from Big Multi Quarry near Bitter Creek, in the northern Washakie Basin, Wyoming. Discovered and initially worked by field crews under the direction of Dr. Donald E. Savage (University of California, Berkeley) in the 1970s, Big Multi Quarry has been profitably worked by field parties from the Carnegie Museum of Natural History each year since 1992. Not only is the Big Multi fauna remarkably diverse given its Clarkforkian age, but it also seems to be closely correlative biostratigraphically with the Bear Creek, Montana, fauna (see below). As such, the rodents of the Big Multi fauna are among the oldest North American members of the order. Here, we describe the rodents of the Big Multi fauna. These include nearly complete dentitions of a new, primitive species of *Paramys* and the first North American records of the Alagomyidae, otherwise known only from Bumbanian localities in the Nemegt Basin, southern Mongolia (Dashzeveg 1990b), Wutu Basin, Shandong Province, eastern China (Tong & Dawson 1995), and the (likely pre-Bumbanian) Bayan Ulan beds of Nei Mongol Autonomous Region, China (Meng *et al.* 1994).

It is appropriate for several reasons to describe the rodents from Big Multi Quarry in a volume of studies dedicated to the distinguished paleontological career of Donald E. Russell. As was noted previously, Big Multi Quarry was first worked by crews under the direction of Dr. Donald E. Savage, who was Donald Russell's intellectual mentor and frequent collaborator. Moreover, the locality adds to the record of mammals from the Paleocene, an interval of time on which Russell published numerous influential studies. The new record of North American alagomyids adds evidence on intercontinental dispersal of early Tertiary Holarctic mammals, which was also a frequent subject of Russell's interest. Finally, these early rodents add to our knowledge of phylogenetic relationships among the Glires, another topic to which he has made important contributions (Dashzeveg & Russell 1988, Dashzeveg *et al.* 1987, Flynn *et al.* 1987).

Abbreviations: AMNH, American Museum of Natural History
CM, Section of Vertebrate Paleontology, Carnegie Museum of Natural History
UCMP, Museum of Paleontology, University of California

UM, Museum of Paleontology, University of Michigan
YPM-PU, Yale Peabody Museum, Princeton Collection

l, anteroposterior length	w, transverse width
wtr, transverse width of trigonid	wta, transverse width of talonid.

BIG MULTI QUARRY

Rose (1981, pp. 131-132) provided an annotated mammalian faunal list for Big Multi Quarry based on collections made by the University of California Museum of Paleontology. Among the taxa Rose reported from this locality is *Plesiadapis cookei*, which is an index fossil for middle Clarkforkian zone Cf2 (Rose 1981, Archibald *et al.* 1987). Our additions to the Big Multi Quarry mammalian fauna lead us to conclude that it is more likely correlative with early Clarkforkian zone Cf1 than with middle Clarkforkian zone Cf2. This new appraisal is based on the occurrence of the tillodont *Azygonyx xenicus* (Gingerich & Gunnell 1979, Gingerich 1989), the plesiadapoid *Carpolestes nigridens*, the plagiomenid *Planetetherium*, and abundant litocherine erinaceomorphs (cf. *Cedrocherus* n. sp.) in the Big Multi Quarry assemblage. Although some of these taxa range as late as the lower part of zone Cf2 in the Clark's Fork Basin (Rose 1981), others are more characteristic of strata no younger than zone Cf1. For example, *Planetetherium* has never been found in rocks younger than Cf1, and the litocherine genus *Cedrocherus* has been reported previously only from the middle-late Tiffanian (Gingerich 1983, Gunnell 1994). Additionally, the new paramyid from Big Multi Quarry is more primitive than any of the paramyids from the Clark's Fork Basin described by Ivy (1990), being comparable in stage of evolution with *Paramys atavus* from Bear Creek, Montana. Given the close morphological correspondence and partial overlap in size described for *Plesiadapis gingerichi* and *P. cookei* by Rose (1981), it seems possible that the Big Multi specimens referred to the latter species by Rose actually represent large individuals of *P. gingerichi*. A larger sample of relatively complete plesiadapid dentitions from Big Multi Quarry will be necessary for a more definitive assessment of the species allocation of this taxon. Pending the recovery of such a diagnostic sample of plesiadapids from Big Multi Quarry, we provisionally attribute its mammalian fauna to early Clarkforkian zone Cf1.

SYSTEMATIC PALEONTOLOGY

Family ALAGOMYIDAE DASHZEVEG, 1990

ALAGOMYS DASHZEVEG, 1990

Two Asian species of the tiny Paleogene rodent *Alagomys* have been described: *A. inopinatus* from Tsagan Khushu, Quarry 1, low in the Bumban Member of the

Naran-bulak Formation, Mongolian People's Republic (Dashzeveg 1990b); and *A. oriensis* from the County Mine Locality of the Wutu Basin, Shandong Province, China (Tong & Dawson 1995). Both of these Asian occurrences of *Alagomys* can be referred with confidence to the Bumbanian land mammal age of Russell & Zhai (1987), which is widely regarded as an early Eocene correlative of the Wasatchian land mammal age of North America and the Sparnacian of Europe (Dashzeveg 1982, 1988, Krause & Maas 1990: 93). However, correlation of the Asian Bumbanian land mammal age with the sequences of land mammal ages on other Holarctic continents is based solely on mammalian biostratigraphy, and remains to be corroborated by other means. Given this situation, it may be significant that the new North American species of *Alagomys* described below is early Clarkforkian in age. Bumbanian carpolestids are also known from the County Mine locality in the Wutu Basin that yielded *Alagomys oriensis* (Beard & Wang 1995), further suggesting that correlation of the basal Bumbanian with the basal Wasatchian/Sparnacian may be premature.

Alagomys russelli nov. sp.

(Plate 1; Table 1)

Holotype: CM 68692, right mandibular ramus with I, P_4–M_2.

Referred specimens: UCMP 138607, fragment of right mandible; CM 68143, lower I; CM 69744, left dP_4; UCMP 138102, CM 69772, left P_4; UCMP 138097, 138101, CM 69747, 69769, left $M_{1\text{ or }2}$; UCMP 138096, 138098-99, 138103-4, CM 69745-46, 69749, right $M_{1\text{ or }2}$; UCMP 138100, left M_3; CM 69748, right M_3; CM 68137, 69742, right $M^{1\text{ or }2}$; CM 69741, 69743, 69770, left $M^{1\text{ or }2}$; CM 69771, right M^3; CM 69346, left M^3; unnumbered incisors.

Horizon and locality: Early Clarkforkian (Cf1), Big Multi Quarry (UCMP locality V76134; CM locality 2433), Washakie Basin, Wyoming.

Diagnosis: Differs from other species of *Alagomys* in having a narrower trigonid on P_4, with protoconid and metaconid more closely spaced. Further differs from *A. inopinatus* in having anteroposteriorly shorter lower molar trigonids and lacking a mesostyle on the upper molars. Further differs from *A. oriensis* in having anteroposteriorly shorter M^3 with much smaller metaconule and shorter M_3. Two layered incisor enamel, with pauciserial portio interna.

Etymology: Named for Donald E. Russell in honor of his many contributions to mammalian paleontology.

Description

The record of this new species is still meager, consisting of two partial mandibular rami, isolated incisors and cheek teeth. Fortunately, all permanent teeth except P^3 and P^4 are known. The mandibular rami (Pl. 1E, I) show that the single rounded mental foramen occurred below P_4. The area for insertion of the masseter muscle is a depression on the lateral surface of the jaw that extends anteriorly to the level of the anterior or middle part of M_2. The anterior, curved margin of the masseteric fossa is slightly ridged in UCMP 138607, but this feature is absent in the holotype (CM 68692), an individual with well worn teeth (Pl. 1H).

The complete lower incisor of the holotype is narrow transversely and slightly tapered in width anteriorly. Enamel covers the anterior surface and about one-quarter of the lateral side. The pulp cavity is a narrow slit. The tooth extends back along the ventral edge of the jaw past M_3, behind which the holotype is broken. The incisor enamel, studied by Dr. Thomas Martin (personal communication, February 1, 1995), "has a pauciserial Schmelzmuster with well developed portio externa with radial enamel (approx. 40% of total enamel thickness). This is a typical two-layered rodent incisor Schmelzmuster. Enamel thickness is about 40 µm (very thin)."

The lower cheek teeth are bunodont and cuspate (Pl. 1A-E). On each, the talonid protrudes farther buccally than the trigonid and the metaconid is the highest cusp. With wear, as in the relatively well worn teeth of the holotype, the metaconid is still the highest cusp, although the occlusal surface is considerably flattened. P_4 has a strongly oblique buccal wall and a relatively narrow anterior margin. The two cusps of the trigonid are closely spaced with a short anteroposterior groove between them. The protoconid is much smaller than the metaconid. An ectolophid extends posterobuccally from the protoconid back to the hypoconid. A cingular shelf occurs low in the notch between trigonid and talonid, buccal to the ectolophid. The posterior wall is thickened

		CM 69771	
M^1	l	0.64	
	w	1.01	
		CM 68137	
M^2	l	0.64	
	w	0.94	
		CM 69346	
M^3	l	0.64	
	w	0.74	
		CM 68692	UCMP 138100
P_4–M_2		2.35	–
P_4	l	0.74	–
	wtr	0.40 (broken)	–
	wta	0.71	–
M_1	l	0.84	–
	wtr	0.74	–
	wta	0.87	–
M_2	l	0.91	–
	wtr	0.74	–
	wta	0.91	–
M_3	l	–	1.01
	wtr	–	0.84
	wta	–	0.87

Table 1.— Measurements (in mm) of *Alagomys russelli*.

into a narrow hypoconulid. Between metaconid and entoconid the talonid valley is well developed.

The lower molars are rhomboidal in shape, related to the anterior protrusion of the metaconid. Each has one trigonid and one talonid root. The small rounded protoconid of each molar is crowded to the anterobuccal side of the trigonid, which is greatly shortened anteroposteriorly. The ectolophid extends posteriorly from the protoconid, expands as a mesoconid, and turns buccally to contact the hypoconid on its anteroexternal side. The hypoconulid is swollen on the posterior cingulum and in unworn teeth is separated from the hypoconid and entoconid by shallow grooves. Following wear the posterior wall of the tooth becomes an even ridge. M_1 has a narrower trigonid than the other molars, M_2 is larger than M_1, and M_3 is easily distinguished from M_{1-2} by its posteriorly expanded hypoconulid lobe. The talonid valley arcs posterobuccally from between the metaconid and entoconid to separate the hypoconid and hypoconulid, indicating some anteroposterior component in chewing motions.

Seven isolated molars constitute the currently known record of the upper dentition (Pl. 1F-G) of this species. M^1 and M^2 are wider transversely than long anteroposteriorly, and have one lingual and two buccal roots. The protocone, which occupies the center of the lingual side, is the highest cusp, followed by the paracone and metacone. The metaconule is slightly larger than the protoconule. The paracone is continued lingually by a loph from which the protoconule protrudes anteriorly. The loph does not extend to the protocone. A cingular shelf anterior to the paracone and loph has its anterior edge formed by a low ridge. The narrow metacone, set on the posterobuccal edge of the tooth, curves posterolingually as a crest along the posterior perimeter of the tooth. This crest contacts the rounded metaconule. A low ridge runs more anterolingually from the metacone. Buccally a cingulum occurs between paracone and metacone; in two of the upper molars the cingulum bends slightly lingually to reach the posterior side of the paracone. There is no trace of a hypocone. The valley between paracone-protoconule and metacone-metaconule branches on both sides of the protocone. The two teeth interpreted as M^1 are larger than M^2, have the paracone set in from the buccal wall and with a short crest running posterobuccally across a narrow buccal shelf. M^3 has a more quadrate shape than the anterior molars, a centrally situated protocone on the lingual side, and smaller metacone and metaconule. Tooth dimensions indicate that the tooth row tapered in width posteriorly from the maximum at M^1.

Of deciduous teeth, only dP_4 is known. A small tooth, relatively longer and narrower than P_4, it has closely set, subequal protoconid and metaconid. The ectolophid is more similar to that on the molars than to that of P_4, extending to the anterobuccal side of the hypoconid. There is a trace of a cuspate hypoconulid, but the tooth is damaged posterolingually so details are unclear.

Comparisons

Whereas specimens of *Alagomys russelli* and the Chinese Early Eocene species *A. oriensis* have been compared directly, only illustrations of the type species, *A. inopinatus* from the Early Eocene of Mongolia, have been available. *Alagomys inopinatus* was described as having non-molariform P^4, with two transverse cusps and roots as in early ctenodactyloid rodents (Dashzeveg 1990b). In *A. oriensis* P_4 is molariform, which would not be expected were its P^4 to resemble that of *A. inopinatus* (Tong & Dawson 1995). P_4 of *A. russelli* is less molarized than in *A. oriensis* but differs considerably from that of early ctenodactyloids (Dawson *et al.* 1984). *A. oriensis* and *A. russelli* differ from *Alagomys inopinatus* in having: lower molars with the protoconid relatively more anterior in position, so that the trigonid is shorter anteroposteriorly; a more nearly continuous buccal cingulum (ectoloph of Dashzeveg 1990b) and absence of a mesostyle on M^{1-2}. *A. oriensis* is, so far as known, very similar to the North American species. The main differences between them are that in the American species: 1) P_4 is more triangular, with a shorter anterior wall, a buccal side that is inclined more distinctly posterobuccally, and a larger buccal cingular shelf; 2) M^3 is anteroposteriorly shorter with a smaller metaconule; and 3) M_3 is shorter and has more crowded cusps. P_4 of *A. oriensis* is intermediate in morphology between the permanent and the deciduous premolar of *A. russelli.* The masseteric fossa in *A. oriensis* extends forward only to the level of the trigonid of M_3, whereas that of *A. russelli* reaches the midline of M_2. Thus, *A. russelli* is arguably primitive relative to *A. oriensis* in having a less molariform P_4, but is derived in its more anteriorly extended masseteric fossa.

Tribosphenomys minutus, from the ?late Paleocene Bayan Ulan beds of Inner Mongolia, has been referred questionably to the family Alagomyidae (Meng *et al.* 1994). In this genus there are a number of very primitive features for a rodent, such as P^4–M^3 with well developed buccal shelf and crests, M_1 and M_2 having a paraconid in one of the two known lower jaws, and a large hypoconulid lobe on M_3. Other differences from *Alagomys* include: upper molars having the protocone anterior to the center of the lingual side, a well developed ridge between metaconule and protocone, and a slightly more cuspate shelf suggesting a hypocone; lower molars having an anterior shelf in front of the protoconid and an anteroposteriorly longer trigonid basin. On the other hand, the many similarities between *Alagomys* and *Tribosphenomys* support reference to a common clade. These include details of the upper molars, including the structure of the paracone, metacone, conules, and associated crests, shape of the lower molars, and the development of the masseteric fossa.

Alagomys has a very strongly developed rhomboidal shape of the lower molars, in relation to the large, projecting metaconid. Somewhat lesser development of this diamond-shape is found in the paramyid *Paramys taurus*, which also resembles *Alagomys* in having a small trigonid. *P. taurus* is now given a stratigraphic range from middle Clarkforkian to middle Graybullian (Ivy 1990). Wood (1962: 57) considered that the small trigonid basin of the molars of *P. taurus* "is surely not primitive, but must represent the results of a forward movement of the metaconid, presumably related also, to the loss of all trace of the paraconid." Current evidence is not adequate to determine whether this character is primitive or developed convergently. Wood also pointed out that this shape of lower molar is "suggestive of sciurid relationships." It could be argued that *Alagomys* is even more squirrel-like in that the upper molars are basically triangular and in the absence of a hypocone. Although one might postulate relationship between alagomyids and sciurids, the cautious, and perhaps realistic path, in view of multiple homoplasies within rodents, is to consider this dental morphology a later convergent development in the sciurids.

Relationships

When first described *Alagomys* was recognized by Dashzeveg (1990b: 42) as a very primitive rodent and considered to be "at the origin of the orders Rodentia and Mixodontia." The very primitive characters of the Mongolian *Alagomys* within the Rodentia, especially in the structure of the incisor enamel, have led others to remove *Alagomys* from the Rodentia entirely. Three possibilities for the relationships of *Alagomys* can be explored.

1) *Alagomys* is a primitive rodent. If *Alagomys* were known only from its lower jaw and dentition, there would be no question of its ordinal affinities. Features characteristic of rodents include dental formula, incisor shape and enamel distribution, masseteric fossa showing that the zygomasseteric complex has moved anteriorly in relation to a shifting forward of the jaw to free up the incisors for gnawing (Turnbull 1970). The lower cheek teeth have the rhomboidal shape found also in some other early rodents, P_4 is molariform, and lower molar morphology is not very distant from that of some paramyids. The upper cheek teeth, on the other hand, do not correspond to those of other earliest rodents in that a hypocone is completely lacking, as are lophs converging on the protocone. In a few features, such as the larger metaconule than protoconule, upper molars of *Alagomys* resemble those of early paramyids in detail. Turnbull (1970: 309), in his landmark study of mammalian mastication, states that in his group that included rodents, "it appears that the masticatory musculature and the dentition made their remarkable evolutionary changes quickly and almost simultaneously. Apparently, the generalized pattern cannot meet adequately the additional requirements imposed by advanced gnawing incisor functions and the accompanying needs to shift the jaws forward to perform these operations. Hence, it is unlikely that the transition stages involving a generalized jaw muscle pattern operating a well-developed 'rodent' dentition will be found." *Alagomys* may be just such a transition stage.

2) *Alagomys* is not a rodent. The incisor enamel of *Alagomys inopinatus* was examined by Martin (1993), who reported that it is thin, the portio interna (PI) has Hunter Schraeger bands (HSB) of the pauciserial type but steeply inclined, and the portio externa (PE) is absent. On the basis of this single character, Martin (1993: 240) has referred *Alagomys* to the order Mixodontia, within which some genera lack a PE. Similarly, Meng and Wyss (1994) are of the opinion that *Tribosphenomys*, which is clearly related to *Alagomys*, is not a rodent, because its incisor enamel, though two-layered, has no HSB. Using this one character does little to explain relationships for animals that are otherwise very rodent-like. The incisor enamel in some early paramyid rodents also lacks a PE (Flynn *et al.* 1987). The character is variable within the Mixodontia, some of which have single layered incisor enamel and some, including *Heomys* and *Eurymylus*, two-layered enamel. Further, *Alagomys russelli* does have a normal rodent type of two-layered incisor enamel with a pauciserial portio interna and radial enamel in the portio externa (see above). The oldest rodent *Paramys atavus* has been described as having an unusual two-layered enamel with the PE not distinct and its prisms oriented perpendicular to the enamel-dentine junction (Martin 1993). Rather than attach greatest weight to this character in early gliriform mammals, it seems more reasonable to regard it as one

that is not yet fully established, as well as one that must be examined very carefully due to the possibility of post-mortem erosion and/or diagenesis of the incisor enamel.

3) *Alagomys* is a derived rodent. Advocates of the eurymylid *Heomys* as the closest sister group to the Rodentia must postulate the presence of a molar hypocone as a plesiomorphous character for that clade. If this is the case, *Alagomys* may be considered to be derived in having lost the hypocone and, in one species, the PE in the incisor enamel. In this case too the allied genus *Tribosphenomys* has reduced but not entirely lost the hypocone and lost the HSB in the inner layer of incisor enamel. This option is weak, for the similarity of the upper molars to various other early mammals, such as zalambdalestids and plagiomenids, weighs heavily in considering the upper dental features of the alagomyids to be truly primitive. *Heomys* may already be too far along the eurymylid path to be a good rodent ancestor (Dashzeveg 1990b).

Option 1 is preferred here. *Alagomys* and its close, but differently derived, relative *Tribosphenomys* are early rodents having developed the zygomasseteric structure, dental formula, and lower molar morphology that characterize all later members of the order. Their primitive state is shown best, based on the incomplete record currently known, in their upper molars and the relatively posterior position of the anterior root of the zygoma. These rodents document an interesting flaw in conventional wisdom in that the paraconid is lost before the hypocone is developed, an indication of mosaic evolution in action.

Family PARAMYIDAE

Paramys atavus JEPSEN, 1937 is among the most frequently cited fossil rodents, although this species remains poorly documented. Its importance stems in part from its basal Clarkforkian (Cf1) stratigraphic position, which for many years made it the geologically oldest rodent in North America, if not in the world. Jepsen (1937) was the first to recognize that rodents were present in the Paleocene of North America, basing this identification on incisors and a lower molar (M_2, holotype of *P. atavus*, YPM-PU 14200) from the Eagle Coal Mine, Bear Creek, Carbon County, Montana. The age of the Bear Creek fauna was considered about equivalent "to the Tiffany of Colorado, the 'Princeton Quarry' of Park County, Wyoming, and the Scarritt Quarry in Sweetgrass County, Montana." Later, McKenna (1961) referred an upper cheek tooth (AMNH 22195) from the Bear Creek locality to *P. atavus*, without specifying whether it was a premolar or a molar. Rose (1981) identified it as P^4. Korth (1984) assigned *P. atavus* to a new genus *Acritoparamys*, along with a variety of other species ranging in age from Clarkforkian to Lostcabinian.

Rose (1981) and Ivy (1990) assigned specimens from the Clarkforkian through late-early Graybullian of the northern Bighorn Basin to *Paramys* or *Acritoparamys atavus*. However, both authors mentioned differences between their referred specimens and the meager type material that made this specific assignment questionable. Korth (1984) reassigned all of Rose's *P. atavus* specimens from the Bighorn Basin to *Apatosciuravus bifax* and pointed out differences from the type material of *P. atavus*, including, in *A. bifax*, the relatively narrower lower molar trigonids. Ivy (1990), in turn, reassigned the same and additional specimens from the Clark's Fork Basin to *Acritoparamys atavus*, noted that P^4 had a mesostyle in his material, absent in the Bear Creek P^4, but considered this to be a variable character. He also mentioned that none of the lower jaws assigned by Korth to *Apatosciuravus bifax* were from the same stratigraphic horizon as its type maxilla, and thus lower dental characters used by Korth for this species were unreliable.

This diversity of opinions is a reflection of a certain homogeneity among these Clarkforkian paramyid rodents. However, precision in taxonomic assignment is desirable, if possible, due to the importance of the morphology exhibited by the oldest known rodent to establish character polarities for the Rodentia. Specimens from the Bighorn Basin assigned by Ivy (1990) to *Acritoparamys atavus* exhibit enough morphological diversity through a long stratigraphic range, early Clarkforkian through middle Graybullian, that they are not reliable in establishing such characters. Taxonomic assignment of Ivy's specimens to *A. atavus*, which have an observed size range below that of the Bear Creek *A. atavus*, may or may not be followed, depending on one's concept of species boundaries. Here the Clark's Fork Basin specimens are considered to be distinct at the species level from the Bear Creek species.

The new species of paramyid rodent from the Big Multi locality has important similarities to the few topotype specimens of *Paramys atavus*, but size and morphological differences support reference to a new species. It is, however, closely allied to *P. atavus*, and its description is followed by a consideration of the generic assignment of these two Clarkforkian rodents.

Paramys adamus nov. sp.

(Plates. 2-3; Table 2)

Holotype: CM 68765, left maxilla with P^4–M^3.

Referred specimens: CM: 68766, right mandible, P_4–M_3; 68767, left mandible, I, M_2; 69347, right mandible with P_4–M_1; 69348, left mandible fragment, M_1; 69761, RP^4; 69762, left $M^{1 \text{ or } 2}$; 69349, M^1; 69350, 69750, M^2; 69354, 69751, M^3; 69763, left ?dP^4; 69752, M_1; unnumbered incisors. UCMP: 138615-16, P^4; 138622, M^2; 138618, M^3; 138619, M_1; 138620, ?M_1; 138621, dP_4; unnumbered incisors.

Horizon and locality: Early Clarkforkian (Cf1), Big Multi Quarry (UCMP locality V76134; CM locality 2433), Washakie Basin, Wyoming.

Diagnosis: Small species of *Paramys* having paracone and metacone of P^4 closely spaced, mesostyle absent; distinct cuspate hypocone on P^4–M^2; lower molar trigonids small, open posteriorly, groove between hypoconulid and entoconid small. Smaller than *Paramys atavus*.

Etymology: From Latin, *ad*, to or toward, and *mus*, mouse, referring to the position of this primitive rodent pointing the way toward later rodents.

Description

Jaws, all permanent teeth except P^3 and dP_4 are represented for this new species, which includes the UCMP specimens that Rose (1981: 132) referred to as "cf. *Paramys atavus.*"

Although the type maxilla, CM 68765, does not preserve the entire anterior zygomatic root, it appears that the posterior side of that root was aligned with the space between P^4 and M^1. In the upper tooth row M^2 is the largest tooth, and M^3 tapers in width posteriorly (Pl. 2F). P^4 has the paracone and metacone closely spaced with no mesostyle between them in any of the four known specimens of this tooth (Pl. 2C). Paracone and metacone are subequal in height but the paracone is the larger cusp. A protoconule is present on P^4–M^3; the metaconule is larger and more persistent than the protoconule on P^4–M^2. A distinct cuspate hypocone also occurs on P^4–M^2. On the upper molars, the anterior cingulum forms a relatively wide shelf, and the posterior cingulum terminates in the hypocone on P^4–M^2. The protocone is slightly anterior to the center of the lingual side on M^1 and central on M^2. A thin ridge connects the metaconule to the protocone. The cusps and conules wear deeply (compare Pl. 2F, a worn specimen, and 2A). M^3 is expanded posterobuccally and has a narrow metacone and a small metaconule on a low loph that does not reach as far as the metacone (Pl. 2B).

		CM 68765		
P^4–M^3		6.30		
P^4	l	1.22		
	w	1.49		
M^1	l	1.56		
	w	1.90		
M^2	l	1.70		
	w	1.70		
M^3	l	1.70		
	w	1.56		
		CM 68766	CM 69347	CM 68767
P_4–M_3		6.70	–	–
P_4	l	1.36	1.08 (unerupted)	–
	wtr	1.08	1.02	–
	wta	1.15	0.88	–
M_1	l	1.49	1.49	–
	wtr	1.22	1.36	–
	wta	1.49	1.49	–
M_2	l	1.70	–	1.63
	wtr	1.49	–	1.49
	wta	1.49	–	1.56
M_3	l	1.97	–	–
	wtr	1.56	–	–
	wta	1.49	–	–

Table 2.— Measurements (in mm) of *Paramys adamus*.

The robust lower jaw (Pl. 3B, 3C) has two mental foramina, the larger below P_4 and the smaller closely posterior to it. The masseteric fossa is well developed and extends forward to below the talonid of M_2. The cheek teeth increase in size posteriorly, M_2 and M_3 are about equally wide but the latter is elongated (Pl. 3A). P_4 has a wide trigonid, only slightly narrower than the talonid. In CM 69347, in which P_4 is unerupted, the trigonid is wider than the talonid due to the lingual protrusion of the metaconid, by far the largest cusp of the tooth. A small trigonid basin is bordered by anterior and posterior protoconid arms. The least worn M_1, CM 69752, has a short anterior cingulum connected to the protoconid, a metaconid crest directed toward the protoconid, and a short posterior arm of the protoconid that does not close the small trigonid basin. There is a rounded mesoconid, and the hypoconulid is a thickening of the posterior cingulum that connects by a crest to the small entoconid. The trigonid of the molars is short anteroposteriorly, narrower than the talonid on M_1 but about equal in width to it on M_2 (Pl. 2E, 3D). The large talonid basin develops a strong wear facet on the posterior slope of the trigonid. The posterior cingulum-hypoconulid of M_3 forms a prominent posterior protrusion.

The only deciduous tooth represented, dP_4 (Pl. 2D), has distinct, rounded cusps. The trigonid is relatively narrower than on P_4 and has an anterocentrally located "anteroconid." The talonid basin is wide, and a hypoconulid swelling is close to the hypoconid on the posterior cingulum.

Martin (1992) found that the pauciserial enamel in an incisor of *P. atavus* from Bear Creek is thin, and that the enamel prisms in the *portio externa* (PE) have a very low inclination, about 0°, making the boundary between the external and internal portions difficult to distinguish. He considered this lack of inclination not primitive because the mid-Paleocene *Heomys* already has inclined prisms in the PE. His examination of the incisor enamel of *P. adamus* showed a two-layered Schmelzmuster with pauciserial HSB in the portio interna and radial enamel in the portio externa.

Comparisons

Appropriate comparisons with upper and lower incisors, P^4, and the type M_2 of *Paramys atavus* from Eagle Coal Mine (Jepsen 1937, McKenna 1961) show that *Paramys adamus* differs from it in characters that may be considered of species level. First, *P. atavus* is slightly larger (P^4, l 1.5, w 1.8 mm; M_2, l 1.88, wtr 1.69, wta 1.72). Second, in *P. atavus* P^4 has a more convex buccal wall, a more lingual position of the buccal end of the anterior cingulum, and a slightly less well developed hypocone. M_2 is similar to that of *P. atavus* except for larger size in the latter.

Ivy (1990) referred to *Acritoparamys atavus* specimens from the Bighorn Basin that differ from the Bear Creek topotype in several ways. For example, P^4 in UM 73784 has more widely spaced paracone and metacone with a mesostyle between them and lacks the small protoconule that protrudes into the valley anterior to the paracone (compare Ivy 1990: figs. 4, 5C, with McKenna 1961: fig. 1). Ivy (1990) considered the presence of a mesostyle on P^4 to be a variable character. There is no variation in this character in *Paramys adamus* from Big Multi Quarry, and its absence appears to be a reliable character that allies the Big Multi species with that from Bear Creek.

1. Incisor Hunter Schraeger bands pauciserial (0), or absent (1).
2. Number of layers in incisor enamel = one (0), or two (1).
3. Cheek teeth brachydont (0), slightly unilaterally hypsodont (1), or unilaterally hypsodont (2).
4. Number of lower premolars = two (0), or one (1).[a]
5. Molar talonids narrower than trigonids (0), or wider than trigonids (1).
6. Single buccal cusp on P^4 (0), paracone and metacone closely spaced (1), or paracone and metacone widely spaced (2).
7. P_4 hypoconid weak (0), or strong (1).
8. Upper molar hypocones absent (0), present (1), or shelf-like (2).
9. Upper molar conules present (0), metaconule enlarged (1), protoconule and metaconule weak to absent (2), or protoconule reduced (3).
10. Lower molar trigonids closed posteriorly (0), or open posteriorly (1).
11. Lower molar paraconids present (0), weak (1), or absent (2).[b]
12. Upper tooth row tapers in width anteriorly and posteriorly (0), or increases in width posteriorly (1).
13. Anterior root of zygoma above M^2 (0), above M^1 (1), or above P^4 (2).[b]
14. Masseteric fossa extends forward to below coronoid (0), below M_3 (1), or below M_2 (2).[b]
15. M_3 hypoconulid forms posteriorly and transversely substantial third lobe (0), third lobe distinct but narrow (1), third lobe reduced and incorporated into posterior cingulum (2).[b]

[a] Character treated as "irreversible" for purposes of parsimony analysis.

[b] Multistate character treated as "ordered" for purposes of parsimony analysis.

Table 3.— Character Descriptions.

The following dental and gnathic characters formed the basis for a parsimony analysis (see Fig. 1). Characters were polarized using "primitive" placental mammals (i.e., condylarths, insectivores) as outgroups. Primitive states for each character are coded as "0", while derived states are coded as positive integers. Multistate characters were treated as "unordered" for purposes of parsimony analysis unless otherwise noted [a,b].

Relationships of *Paramys atavus* and *P. adamus*

The original assignment of the Bear Creek paramyid to the genus *Paramys* had to be based on the few characters shown by isolated incisors and a single M_2. Jepsen (1937: 296-297) recognized that, "There can be little doubt about the reference of the specimens to *Paramys* until the genus undergoes a restudy and revision which it greatly needs because it probably includes several groups that should have generic rank." When a revision of the Paramyidae appeared, the Bear Creek species remained in the genus *Paramys*, and the inadequate material did not "permit determination of the exact position of this species" (Wood 1962: 60). The next reviewer (Korth 1984), however, referred *P. atavus* to a new genus, *Acritoparamys*, along with other species from the North American Clarkforkian through Lostcabinian. Characters diagnostic of the new genus include: P^4 submolariform with protoconule and small hypocone; M^1 nearly square and equal in size to M^2; and large transversely elongate hypoconulid on lower cheek teeth, separated from entoconid by a distinct groove. Some of these characters are not known for *P. atavus*, but referral of it to the new genus was based primarily on the characters of M_2, on which Korth (1984: 30) recognized a groove between entoconid and posterolophid that is, however, narrower than in other species referred to *Acritoparamys*. Ivy (1990) followed this assignment of *P. atavus* to *Acritoparamys*.

The new species now known from Big Multi Quarry leads to a reexamination of this assignment. In *P. adamus* the connection of entoconid to posterolophid is marked by only a shallow groove, not the distinct notch that is a generic character of *Acritoparamys*. In this character, as in others, there are strong similarities between *Paramys adamus* and *P. atavus*. These two species also share characters of P^4 with *Paramys pycnus* (Ivy 1990: 37-39), a Sandcouleean species that is much larger than the Clarkforkian species but which has a similarly compressed P^4 lacking a mesostyle. *P. adamus* shares other characters with *P. taurus* (Wood 1962: 54; Korth 1984: 11-13), especially in proportions of P_4, with a relatively wide trigonid, and the reduced hypoconulid of the lower molars. *Paramys adamus* shares several primitive rodent characters (e.g., well developed conules, hypocone on P^4–M^2, molars with anteroposteriorly compressed trigonid basin) with some of the species assigned to *Acritoparamys*. However, it appears to share no derived features with species of *Acritoparamys*. Accordingly, *Paramys* is here considered to be the correct generic assignment for both the Big Multi species, *Paramys adamus*, and the Bear Creek species, *Paramys atavus*.

PHYLOGENETIC RELATIONSHIPS OF EARLY RODENTS

In order to assess the phylogenetic position of Alagomyidae with respect to other early mixodonts and rodents, we undertook a parsimony analysis of dental and gnathic traits among a variety of these taxa (see Tables 3, 4). Cranial and postcranial data are currently unavailable for the Alagomyidae, because the only fossils now known for this family are teeth and jaws. Hence, our analysis must be considered preliminary in this respect, but it is offered here as a working hypothesis to be tested by future discoveries of more nearly complete alagomyid fossils.

The taxon-character matrix illustrated in Table 4 was subjected to parsimony analysis using the branch and bound algorithm available in PAUP 3.0s (Swofford 1990). Individual characters were polarized on the basis of comparisons with "primitive" placental mammals (i.e., various insectivores and condylarths). Trees were rooted using a hypothetical ancestor (in which all characters exhibit the primitive or "0" state) as an outgroup. Most, but not all, multistate characters were treated as "unordered" for purposes of parsimony analysis (see Table 3). Character 4 (number of lower premolars) was treated as "irreversible", on the assumption that once a dental locus is phylogenetically suppressed it cannot reappear in subsequent members of a clade. Our search yielded 14 most parsimonious trees (MPTs). A strict consensus tree based on these 14 MPTs is illustrated in Figure 1.

Several aspects of the consensus tree topology merit discussion here. First, in all most parsimonious solutions to our data set, alagomyids, paramyids and ctenodactyloids comprise a clade that excludes the taxa that are often considered as mixodonts (i.e., *Rhombomylus*, *Eurymylus*, and *Heomys*). A number of unambiguous dental and gnathic synapomorphies support the monophyly of this clade, including: loss of P_3 (Character 4, 0 →1); posterior opening of the lower molar trigonids (Character 10, 0 →1); forward displacement of the root of the zygoma and masseteric fossa (Character 13, 0 →1, and Character 14, 0 →1, respectively); and reduction in size of the hypoconulid lobe on M_3 to a distinct, but narrow, third lobe (Character 15, 0 →1). We consider the clade including Alagomyidae, Paramyidae and Ctenodactyloidea to be equivalent to the order Rodentia (Figure 1).

Second, *Alagomys* and *Tribosphenomys* are united (as the family Alagomyidae) by a single unambiguous synapomorphy, the development of widely spaced paracone and metacone on P^4 (Character 6, 0 →2).

Finally, three unambiguous dental and gnathic synapomorphies support the monophyly of a clade consisting of Paramyidae and Ctenodactyloidea, exclusive of Alagomyidae. These include: widening of the upper dental row posteriorly (Character 12, 0 →1); further forward displacement of the root of the zygoma (Character 13, 1 →2); and further reduction of the hypoconulid lobe on M_3, such that it becomes incorporated within the posterior cingulum (Character 15, 1 →2). Therefore, available evidence suggests that the Alagomyidae comprise the sister group of all other undoubted rodents, having diverged from the common ancestry of other rodents prior to the phylogenetic split between the ancestors of paramyids and ctenodactyloids.

The stratigraphic distributions currently known for these taxa are surprisingly concordant with their inferred relationships, although the earliest fossil representatives of several rodent clades are demonstrably lacking. In North America, both Alagomyidae and Paramyidae occur in basal Clarkforkian beds at Big Multi Quarry, indicating that the dichotomy between these taxa must antedate the basal Clarkforkian by some unknown interval of time. In Asia, all three of the major rodent clades treated here coexist in (?basal) Bumbanian beds at the Wutu County Mine Locality (Tong &

Ancestor	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0
Heomys	0 1 1 0 1	0 0 1 3 0	2 0 0 0 0
Eurymylus	0 1 2 0 0	0 0 2 2 0	2 0 0 1 0
Rhombomylus	0 0 2 0 0	0 0 2 2 0	2 0 0 0 0
Cocomys	0 1 0 1 1	0 0 1 1 1	2 1 2 1 2
Paramys	0 1 0 1 1	1 1 1 1 1	2 1 2 2 2
Alagomys	0 1 0 1 1	2 1 0 1 1	2 0 1 2 1
Tribosphenomys	1 1 0 1 1	2 1 1 1 1	1 0 1 1 1

Table 4.— Taxon-character matrix used in parsimony analysis.

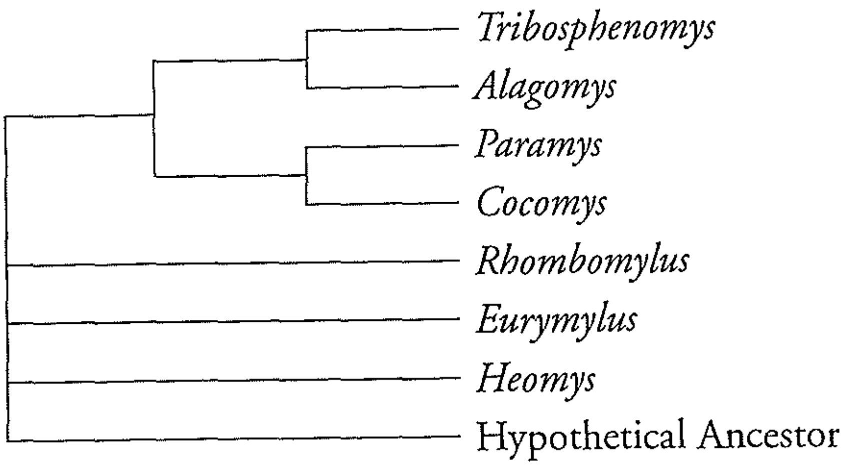

Figure 1.— Strict consensus tree (based on 14 MPTs) depicting phylogenetic relationships among selected early rodents and mixodonts, based on dental and gnathic characters (see Tables 3-4). In 71% of the MPTs *Heomys* forms the sister group of undoubted rodents (i.e., the *Tribosphenomys* + *Alagomys* + *Paramys* + *Cocomys* clade). See text for description of synapomorphies supporting each node.

Dawson 1995), which demonstrates that the dichotomy between Paramyidae and Ctenodactyloidea must antedate the Bumbanian by an unknown interval of time (and that the dichotomy between Alagomyidae and the Paramyidae + Ctenodactyloidea clade is yet more ancient). As we have noted previously, intercontinental correlation of the Asian Bumbanian with the North American and European sequences of land mammal ages remains tenuous; thus, it is impossible to assess precisely how this Asian Bumbanian record of early rodents accords with the basal Clarkforkian record now known from Big Multi Quarry. Nevertheless, we find it interesting that the only pre-Bumbanian definitive rodent currently known from Asia is the primitive alagomyid *Tribosphenomys minutus* from the Bayan Ulan beds of Inner Mongolia (Meng *et al.* 1994). If the tree topology illustrated in Figure 1 is accurate, this early record for Alagomyidae demonstrates that the Paramyidae + Ctenodactyloidea clade must also have been established by the time of deposition of the Bayan Ulan beds. This clade of more typical or "advanced" rodents has yet to be documented in the pre-Bumbanian fossil record of Asia, however.

DISCUSSION

The North American early Clarkforkian record now documents presence of two rodent families, the Paramyidae and the Alagomyidae, here considered to be immigrants into North America from Asia. It may be significant for the preferred habitat of early rodents that several of the oldest rodents in North America and Asia are found in coals (Bear Creek, Wutu) or very carbonaceous deposits (Big Multi).

The Paleocene record of the order Rodentia has several enigmatic aspects. Unless the Asian middle to late Paleocene *Heomys* is a true rodent, not a eurymylid, the oldest record of Paleocene rodents, using currently accepted correlations, stems from the early Clarkforkian of North America. This record must stand until the age of the Bayan Ulan beds that yielded *Tribosphenomys* is more firmly established. The presence of two rodent families at the time of first appearance of the order lends support to the premise that the origin and earliest diversification of the order predates *Heomys*. This interpretation was supported by the early studies of Jepsen (1937: 291-2) on *Paramys atavus*: "Many authors have already suggested that the differentiation of the rodents from other mammals, presumably from insectivores, occurred at least as early as Cretaceous time. The Paleocene teeth herein described support this conjecture because they are as specialized as homologous teeth of some early Eocene paramyids, having no 'more primitive' characteristics that furnish clues to the derivation of the rodents from another order." On the other hand, in his monumental study of the paramyids, Wood (1962) relied heavily on his conviction that paramyids were ancestral to all other rodents and that their rapid diversification in the late Paleocene and early Eocene could be extrapolated back in time to postulate the time of origin for the Rodentia. He was of the opinion that all Paleocene rodents that would be discovered would be members of the Paramyidae and that their differentiation from other mammals took place in the early or early middle Paleocene. The role of paramyids as the most primitive rodents has been strongly challenged by the more recently discovered ctenodactyloids and the alagomyids, modifying Wood's interpretations and warning about relying heavily on absences in the fossil record.

By the Early Eocene some geographic endemism has appeared in the rodent record. In the Early Eocene of Asia there was a diversity of ctenodactyloids (Dawson *et al.* 1984, Dashzeveg 1990a); alagomyids and paramyids are present but less varied (Dashzeveg 1990b, Tong & Dawson 1995). In North America early Wasatchian paramyids are known from the Rocky Mountain region as well as from a recently discovered site in the Gulf Coast of Mississippi. In Lysitean time a greater variety of rodents is known from mid-latitudes of North America. From the Rocky Mountain region, paramyids are joined by sciuravids and cylindrodontids. The Early Eocene record from the North American Arctic and from the Sparnacian of Europe contains only paramyids, mostly of small size.

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LEGENDS OF PLATES

PLATE 1

Alagomys russelli nov. sp.

A-D. Occlusal views of left teeth.
  A. UCMP 138100, M_3.
  B. UCMP 138097, M_2.
  C. UCMP 138101, M_1.
  D. UCMP 138102, P_4.

E. UCMP 138607, Lateral view of right jaw fragment with root of M_1.

F. Occlusal views of CM 68137, left M^2.

G. Occlusal views of CM 69346, left M^3.

H-I. CM 68692, holotype, right jaw with P_4–M_2.
  H. Occlusal view.
  I. Lateral view of two pieces of jaw.

PLATE 2

Paramys adamus nov. sp.

A-E. Occlusal views of right teeth.
  A. UCMP 138622, M^2.
  B. UCMP 138618, M^3.
  C. UCMP 138615, P^4.
  D. UCMP 138621, dP_4.
  E. UCMP 138619, M_1.

F. CM 68765, holotype, occlusal view of left P^4–M^3.

PLATE 3

Paramys adamus nov. sp.

A-B. CM 68766, right jaw with P_4–M_3.
  A. Occlusal view.
  B. Medial view.

C-D. CM 68767, left jaw with M_2.
  C. Lateral view.
  D. Occlusal view.

PLATE 1

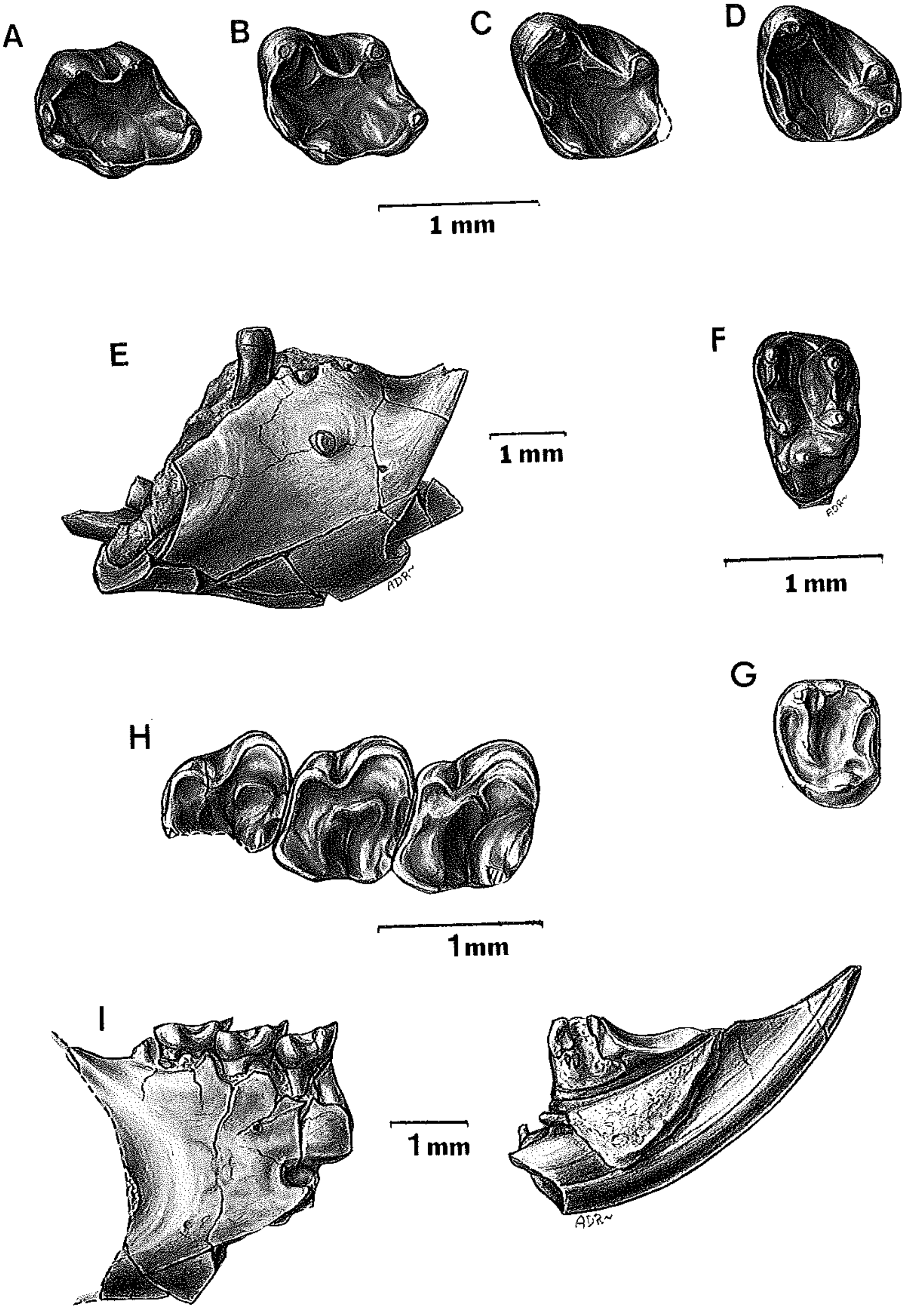
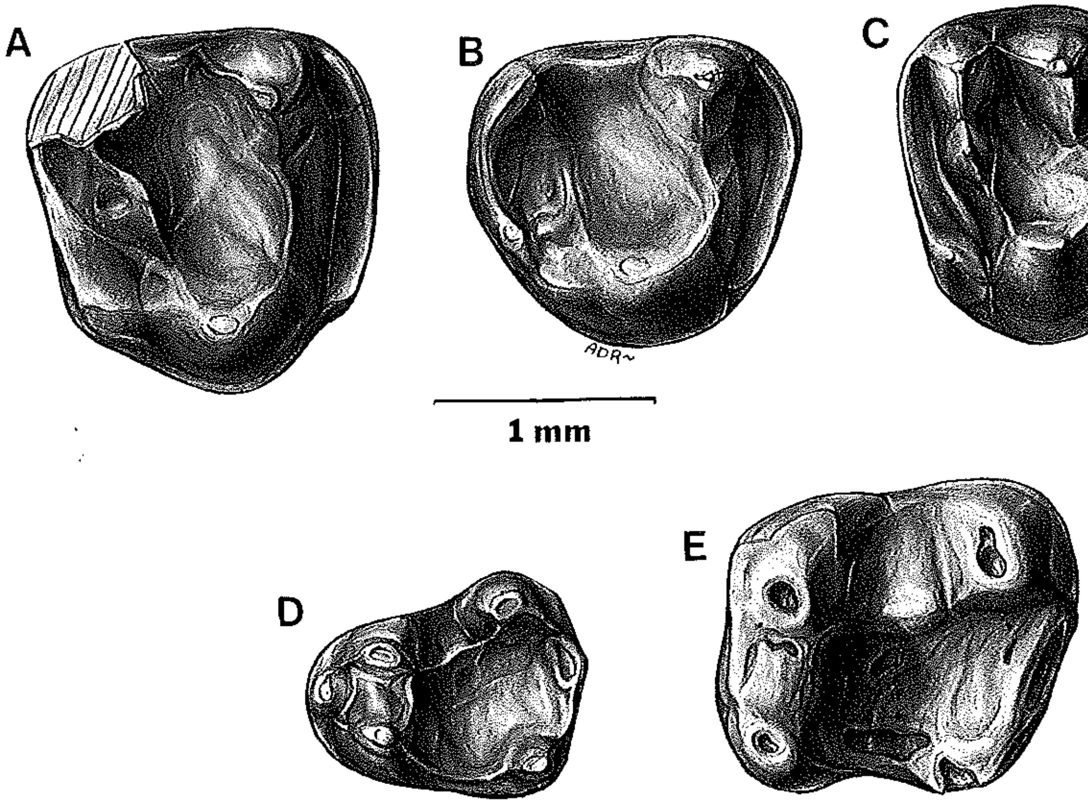


PLATE 2



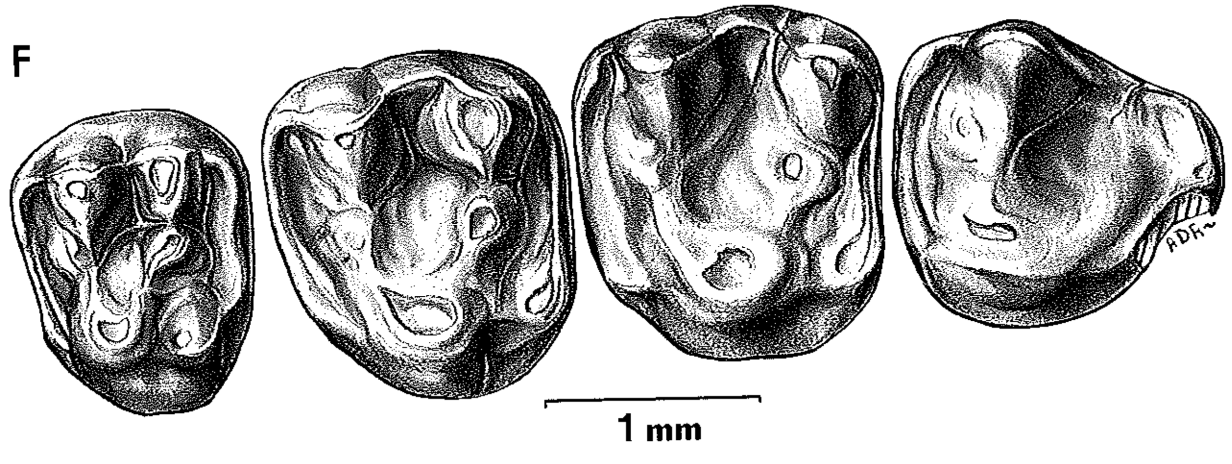


PLATE 3