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(MAMMALIA) FROM THE CLARKS FORK BASIN, WYOMING**

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Philip D. Gingerich, Director

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SYSTEMATICS OF LATE PALEOCENE AND EARLY EOCENE RODENTIA (MAMMALIA) FROM THE CLARKS FORK BASIN, WYOMING

By

LOGAN D. IVY

Abstract.— Rodents in latest Paleocene and early Eocene age deposits of the Clarks Fork Basin, Wyoming are studied in a stratigraphic framework using new fossil material collected in recent years. Seven genera and 17 species of rodents representing two families, Paramyidae and Sciuravidae, are known from the faunas of the Clarkforkian and early-to-middle Wasatchian land-mammal ages in the Clarks Fork Basin. Four new species, *Paramys pycnus*, *Microparamys cheradius*, *Microparamys hunterae*, and *Knightomys cremneus*, are described here. Discovery of the primitive sciuravid *Knightomys cremneus* places the origin of Sciuravidae in the early Wasatchian and supports the suggestion that sciuravids are descendants of *Microparamys*. *Microparamys hunterae* may have given rise to species of the small sciuravid genus *Pauromys*, *Acritoparamys atwateri* may have given rise to *Acritoparamys francesi*, and *Paramys taurus* may have given rise to *Paramys copei*. *Acritoparamys atavus* is shown to be relatively abundant in the Clarkforkian, corroborating that the Bear Creek, Montana, fauna is Clarkforkian in age. Rodents are not known in North America before the beginning of the Clarkforkian. *Paramys copei*, which appears at the beginning of the Wasatchian, is the only rodent species from the Clarks Fork Basin that is useful as a biostratigraphic indicator. All of the remaining species are either stable evolutionarily or too poorly known to use in biostratigraphic subdivision of the latest Paleocene and early Eocene.

INTRODUCTION

Rodents are a long-lived, diverse, and widespread order of mammals distinguished by reduction of the anterior dentition to a single pair of ever-growing, gliriform, upper and lower incisors. Rodents first appear in the fossil record in North America in the latest Paleocene. They are one of the diagnostic mammalian groups marking the beginning of the transitional Paleocene-Eocene Clarkforkian land-mammal age (Rose, 1981), and rodents are common in collections from the succeeding Wasatchian land-mammal age (early Eocene). Most studies of early rodent systematics and evolution have dealt with specimens from early to middle Eocene and younger beds because, until recently, rodents from older strata were rare and poorly located stratigraphically. For example, in his revision of primitive North American rodents of the family Paramyidae, Wood (1962) had only 10 specimens older than the middle Wasatchian available for study, and these were from widely scattered and poorly correlated localities.

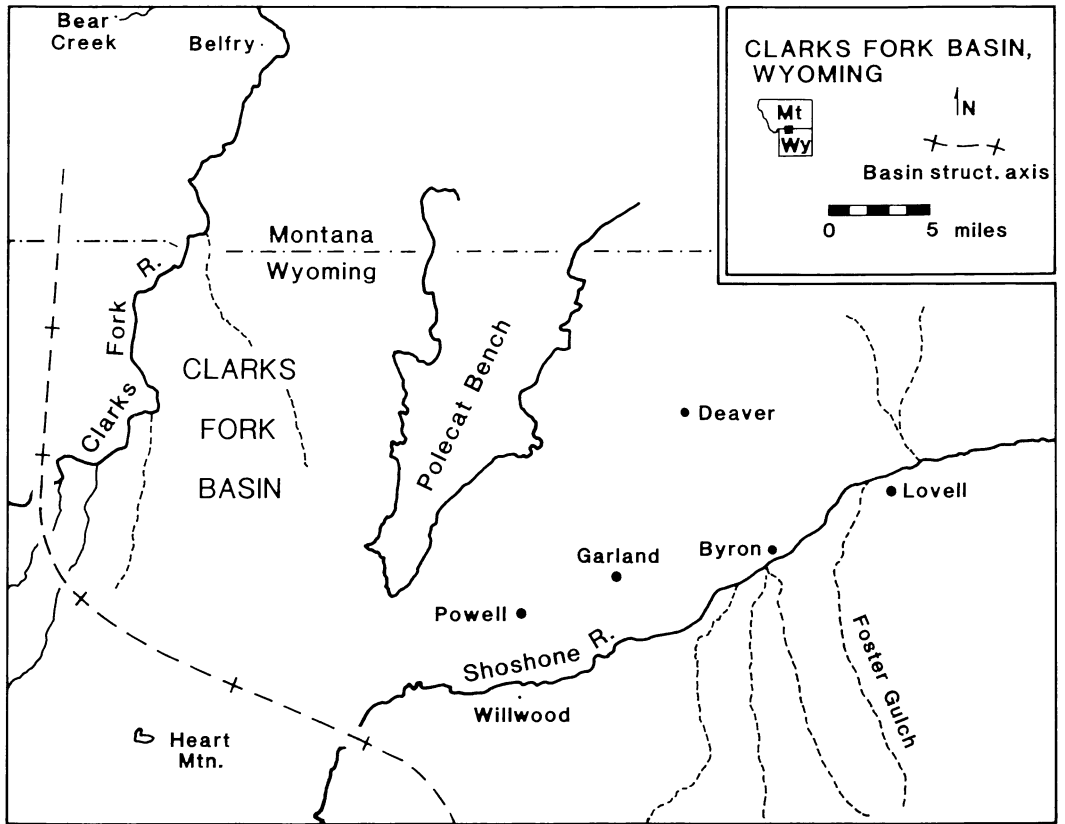


FIG. 1— Map of the study area showing locations of the Clarks Fork Basin and Foster Gulch area of the northern Bighorn Basin, where Paleocene-Eocene transition stratigraphic sections are well exposed in northwestern Wyoming.

A sizable sample of Clarkforkian and early Wasatchian rodents has been collected in recent years from the Clarks Fork Basin northwestern Wyoming. Rose (1981) considered the rodent specimens available in 1979 in his definition of the Clarkforkian land-mammal age, which is defined partly on the first appearance of rodents. His analysis of early rodents was undertaken primarily to characterize the Clarkforkian mammalian fauna and not as a detailed study of evolution of the rodents themselves. Additional specimens collected subsequent to Rose's study justify further, more detailed analysis of Clarkforkian rodents. Rose's study did not deal with rodents from the Wasatchian land-mammal age, for which a large sample is now available in collections at the University of Michigan Museum of Paleontology. Korth (1984) studied some of this material, but his analysis was mostly an investigation and extension of ranges of taxa known from late Wasatchian and younger strata.

Rodent specimens described in this study were collected in the Clarks Fork Basin, Wyoming, by field parties from the University of Michigan. The earliest members of the order known in North America, from the base of the Clarkforkian land-mammal age, are included. These early rodents display all of the diagnostic characteristics of the order, and were probably very similar in life habits to modern ground-living squirrels (Wood, 1962). Since there are no recognizable precursors in underlying Tiffanian beds (late Paleocene) in North America, rodents appear to be immigrants from elsewhere. The problem of the origin of rodents is beyond the scope of this study, although it should be noted that rodents can be plausibly derived from *Heomys*-like eurymyloids in Asia (Li, 1977).

Rodents from the Clarkforkian and early Wasatchian are known from other areas in North America (Rose, 1981; McKenna, 1960), but the largest and best correlated sample is from the Clarks Fork Basin, Wyoming. The Clarks Fork Basin is a structural and topographic basin located in northwestern Wyoming at the northern end of the Big Horn Basin (see Fig. 1). The basin contains a remarkably complete and exceptionally fossiliferous stratigraphic section some 2240 meters thick spanning most of the Paleocene and early Eocene. This section is fluvial in origin, with alternating stream channel sandstones and floodplain fine sandstones and mudstones. The structure of the basin is that of an asymmetrical syncline, with the axis near the southern and western margins of the basin. North and east of the axis the beds dip at 3 to 5 degrees to the southwest, whereas dip angles approach 30 degrees to the northeast on the western and southern side of the axis. Lithologically, Paleocene and early Eocene sediments in the Clarks Fork Basin are divided into two formations, the predominantly Paleocene Fort Union Formation (= "Polecat Bench Formation") and the overlying Willwood Formation. The Willwood Formation is delineated principally by variegated color banding of paleosol origin (Bown, 1979; Rose, 1981), and the boundary between the two formations is time transgressive southward (Rose, 1981).

Paleocene and early Eocene sedimentary rocks in the study area are dissected by drainages of the Clarks Fork and Shoshone rivers into a complex array of badlands. Several Quaternary river terraces can be found in the basin, the most important being Polecat Bench, which was formed by the Shoshone River when it flowed at a higher elevation. The surface of Polecat Bench is protected by a thick bed of Quaternary river gravel and boulders. The sides of Polecat Bench and other minor terraces are dissected into badlands by runoff from highly seasonal rainfall.

Sediments exposed in the Clarks Fork Basin become successively younger as one crosses the basin from northeast to southwest. They range in age from Late Cretaceous on the east side of Polecat Bench to early Eocene (middle Wasatchian) on topographic highs near the axis of the syncline. A stratigraphic section in the Clarks Fork Basin has been measured and subdivided into faunally determined land-mammal ages and biostratigraphic zones (Gingerich and Simons, 1977; Gingerich, 1980; Rose, 1981). The land-mammal ages represented above the Cretaceous are the Puercan, Torrejonian, Tiffanian, Clarkforkian, and early and middle Wasatchian. Rodents appear at the beginning of the Clarkforkian, which has been subdivided by Rose (1981) into three biostratigraphic zones based, respectively, on the presence of *Plesiadapis gingerichi*, *Plesiadapis cookei*, and abundant *Phenacodus-Ectocion*. The early to middle Wasatchian in the Clarks Fork Basin has not received as much attention as the Clarkforkian, and locally derived biostratigraphic zones are not yet available. I will here use the *Cantius* ("*Pelycodus*") zonation of Gingerich (1980), which recognizes *Cantius ralstoni*, *C. mckennai*, and *C. trigonodus* as guide fossils supplementing the Sandcouleean, early Graybullian, and middle Graybullian faunal zones. The latter were reviewed and revised by Schankler (1980; see Fig. 2).

Almost all localities from which rodents of this study were collected can be related to the measured stratigraphic section, either by direct measurement, physical correlation, or, in a few cases, faunal correlation. The vertical stratigraphic range of each locality is about 10 meters, which represents, on average, approximately 27,000 years of geologic time, assuming a constant rate of deposition (Gingerich, 1982). The lowest level from which rodent material has been recovered is UM locality SC-179 (two isolated incisors), which is the lowest locality within the Clarkforkian (Rose, 1981). The highest locality containing rodent specimens is the highest locality in the section, UM locality SC-295 (isolated incisors and an M_2). Rodents are found in virtually all well sampled localities that lie stratigraphically between SC-179 and SC-295.

The majority of the specimens studied here were collected from the surface of the localities. Although a few localities were screen-washed, the abundance of fossil material in most localities was too low to make quarrying and washing worth the considerable time and effort involved. One locality (UM locality SC-188) that was extensively quarried and washed produced an especially abundant rodent fauna. The majority of the smallest rodent specimens

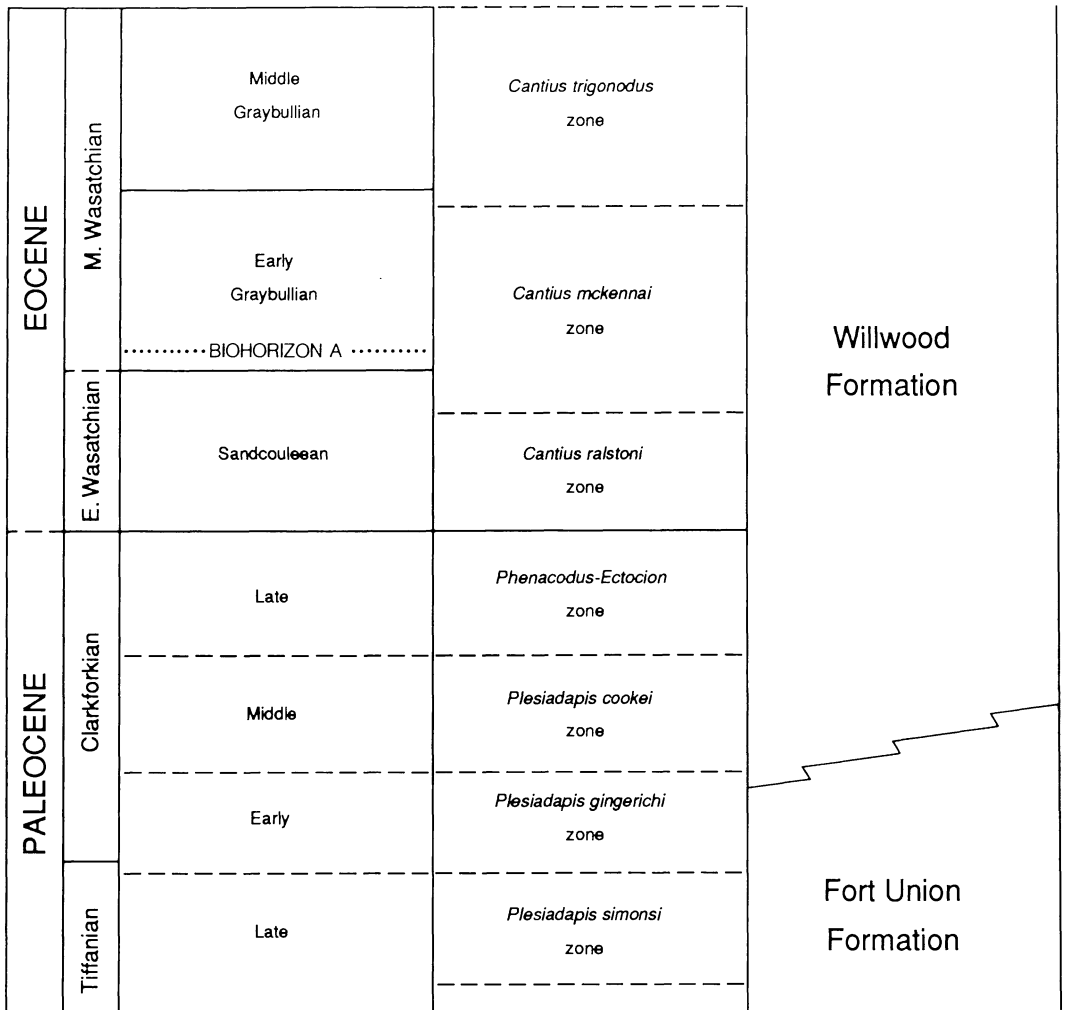


FIG. 2— Faunal zones of the late Paleocene and early Eocene employed in this paper and their correlation with the Tiffanian, Clarkforkian, and Wasatchian land-mammal ages. Dashed lines represent lineage or faunal continuity or other uncertainty. Dotted line indicates possible position of biohorizon A of Schankler (1980).

are known from this locality, supporting Winkler's (1980) conclusion that a sampling bias exists against small fossils in surface-collected samples. Surprisingly, however, the rodents collected from Winkler's study locality by surface collecting, quarrying, and washing do not themselves indicate this bias.

Rodent specimens used in this study consist mostly of isolated, individual teeth; jaws with two or more teeth comprise only about 20% of more than 300 cheek tooth specimens (excluding incisors). Very few cranial or dental specimens have associated postcranial elements. Only four specimens have associated upper and lower cheek teeth, therefore assignment of upper and lower teeth to the same taxon depends upon size associations, occlusal relationships, and descriptions from the literature; this must be done cautiously. Included in the study sample are edentulous mandibles and rostra that are only tentatively assigned to taxa. Several hundred isolated incisors included in the study collection are of

limited taxonomic value, but they do show the stratigraphic range through which rodents are found.

The remainder of this paper will consider first the dental variability of rodents, both in a Recent taxon and in selected taxa from the study collection that are represented in sufficient numbers to allow statistical treatment. The systematics of fossil specimens will be considered next in order to facilitate discussion of the evolution of rodents in the Clarks Fork Basin and to allow a comparison with other rodent bearing faunas reported in the literature. The early evolution of North American rodents will then be discussed in a stratigraphic framework, and some preliminary biostratigraphic implications will be considered.

ABBREVIATIONS AND MEASUREMENTS

Institutional abbreviations used in this paper are as follows:

ACM	— Amherst College Museum, Amherst, Massachusetts.
AMNH	— American Museum of Natural History, New York, New York.
CM	— Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.
FMNH	— Field Museum of Natural History, Chicago, Illinois.
MCZ	— Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
PU	— Princeton University Museum of Natural History (now part of YPM collection, see below).
ROM	— Royal Ontario Museum, Toronto, Ontario.
UM	— University of Michigan Museum of Paleontology, Ann Arbor, Michigan.
USNM	— United States National Museum, Washington, D.C.
YPM	— Yale Peabody Museum, New Haven, Connecticut.

Tooth nomenclature used is that proposed by Wood and Wilson (1936) as revised by Wood (1962).

Statistical abbreviations are: *N*, sample size; *OR*, observed range; *S*, standard deviation; *V*, coefficient of variation. *V* was computed as $100 \times (S/\text{Mean})$ for scalar data and by the method of Lewontin (1966) for ln data. Teeth were measured using either dial calipers (Recent specimens) or a calibrated binocular microscope (fossil specimens). All measurements are in millimeters. Abbreviations of measured dimensions of the teeth are: *l*, length; *w*, width; *aw*, anterior width; *pw*, posterior width; *A*, area, where $A = l \times w$ or $A = l \times [(aw + pw)/2]$.

VARIABILITY

All species exhibit variability in morphology to a greater or lesser degree, depending upon the structure involved. Empirical studies of the dentition of a single Recent species have shown that variation in size of teeth is related to position in the dentary or maxilla, with M1 and M2 being the least variable (Gingerich, 1974; Gingerich and Winkler, 1979). Studies involving closely related species show that variation within a species is often small enough to allow reasonably clear separation of species in morphologic space (Gingerich, 1976). This phenetic clustering provides a basis for the recognition of contemporaneous species.

While there is no *a priori* limit to variability in a single taxon, the amount of variability seen in a single well defined species allows inferences to be made about the amount of variability acceptable in less well defined species. Fossil and living rodents are not necessarily equivalent in terms of variability, but study of Recent rodents can give some idea of the variability expected in Paleocene and Eocene rodents. To minimize uncertainty due to phylo-

TABLE 1— Summary of measurements of *Sciurus niger rufiventer* from Washtenaw Co., Michigan. Descriptive statistics are given for crown length (L), crown width (W), and natural logarithm of crown area (Ln A). N is sample size, OR is observed range of variation, S is standard deviation, and V is normalized coefficient of variation ($100 \times S/\text{Mean}$). S is already normalized for logarithmically transformed data and calculation of V would be meaningless.

Measurement	N	OR	Mean	S	V	
<i>Upper dentition</i>						
P ⁴	L	30	2.5 - 3.2	1.96	0.16	8.2
	W	30	2.5 - 3.3	3.07	0.19	6.1
	Ln A	29	1.8 - 2.3	2.16	0.100	--
M ¹	L	30	2.4 - 2.9	2.64	0.11	4.1
	W	30	3.3 - 3.8	3.53	0.13	3.7
	Ln A	29	2.1 - 2.3	2.23	0.055	--
M ²	L	30	2.6 - 3.1	2.82	0.10	3.5
	W	30	3.5 - 3.8	3.59	0.11	3.1
	Ln A	29	2.2 - 2.4	2.31	0.054	--
M ³	L	29	3.0 - 3.4	3.34	0.11	3.3
	W	29	3.0 - 3.6	3.22	0.13	4.0
	Ln A	28	2.3 - 2.5	2.34	0.056	--
<i>Lower dentition</i>						
P ₄	L	30	2.1 - 2.9	2.60	0.16	6.2
	W	30	1.5 - 2.9	2.53	0.31	12.3
	Ln A	29	1.4 - 2.1	1.87	0.170	--
M ₁	L	30	2.5 - 2.8	2.60	0.08	3.0
	W	30	3.1 - 3.5	3.25	0.10	3.1
	Ln A	29	2.1 - 2.2	2.14	0.041	--
M ₂	L	29	2.6 - 3.0	2.79	0.10	3.6
	W	29	3.1 - 3.6	3.33	0.10	3.0
	Ln A	28	2.2 - 2.3	2.23	0.045	--
M ₃	L	30	3.1 - 3.5	3.30	0.10	3.0
	W	30	2.4 - 3.3	3.10	0.16	5.2
	Ln A	29	2.3 - 2.4	2.33	0.047	--

genetic dissimilarity, the Recent taxa should be closely related, or at least morphologically similar, to the fossil rodents.

In the present study the living fox squirrel, *Sciurus niger rufiventer* from southern Michigan, was studied to ascertain the probable limits of dental variability in primitive rodents. The fox squirrel was chosen because it is considered a generalized member of the Scuriidae, which are in turn closely similar to early Eocene paramyids. The dentition of *Sciurus* is morphologically similar to that of primitive rodents. *Sciurus niger rufiventer* was chosen because a large sample from a restricted geographic area was available and the specimens are reasonably large and easy to measure. Results of the measurements of the teeth of *S. n. rufiventer* are listed in Table 1. Statistical analysis of tooth size in *S. n. rufiventer* shows that M₁ and M² are the least variable of the cheek teeth while the premolars and the incisors are the most variable. Low variability of M₁ and M² in the fox squirrel agrees with reported results from other mammalian taxa (Gingerich, 1974) and may reflect the action of morphogenetic fields as suggested by Butler (1939). Absolute values of the coefficients of variation for the fox squirrel are somewhat lower than reported for most mammalian species (Gingerich, 1974), al-

TABLE 2— Coefficients of variation (V) for lower teeth of *Paramys copei bicuspis*, *Paramys excavatus taurus*, and *Thisbemys plicatus* according to Wood (1962). Wood provides V for samples with N \geq 10. Sample size (N) and coefficient of variation (V) are given for length (L), anterior width (AW), and posterior width (PW).

Measurement	<i>Paramys copei bicuspis</i>		<i>Paramys excavatus taurus</i>		<i>Thisbemys plicatus</i>		
	N	V	N	V	N	V	
P ₄	L	9	--	8	--	13	4.66
	AW	7	--	8	--	10	4.96
	PW	9	--	9	--	12	7.45
M ₁	L	23	5.02	20	4.74	29	5.75
	AW	23	5.78	19	5.53	24	5.21
	PW	22	6.89	19	4.96	26	3.89
M ₂	L	19	4.86	23	4.95	27	4.93
	AW	18	4.66	19	5.88	22	4.71
	PW	18	5.33	20	5.54	26	4.77
M ₃	L	11	5.09	6	--	11	4.47
	AW	10	4.87	5	--	12	4.17
	PW	9	--	5	--	11	5.17

though not greatly so. This lower variability may be due to the restricted geographic range of the measured *Sciurus niger rufiventer*, resulting in a more homogeneous sample than was used for the other species reported. These data suggest that rodents are not unusually variable and that the size of M₁ or M₂ may be considered profitably as taxonomically useful characters.

To determine if the dental variability seen in fossil rodents approximates that of living rodents requires analysis of a reasonably large sample of a fossil rodent species. The sample sizes for *Paramys copei bicuspis*, *Paramys excavatus taurus*, and *Thisbemys plicatus* published by Wood (1962) are sufficiently large for this purpose. *Paramys copei bicuspis* and *Paramys excavatus taurus* have recently been lumped with other paramyid species into *Paramys copei* and *Paramys taurus*, respectively (Korth, 1984). *P. copei bicuspis* and *P. excavatus taurus* probably represent more homogeneous subsets of the species and their dental variability may be less than that for the entire species *P. copei* and *P. taurus*. Coefficients of variation for the lower cheek teeth of *P. copei bicuspis*, *P. excavatus taurus*, and *Thisbemys plicatus*, as published by Wood (1962), are listed in Table 2. Coefficients of variation determined for the three species are no greater than those for other mammals (Gingerich, 1974) but are somewhat greater than for *Sciurus niger rufiventer*. The three fossil species are not from as nearly a restricted time span and area as *S. n. rufiventer*, which may explain the larger variability. Circular reasoning is possible here if size were the main criterion for distinguishing the three fossil species, but Wood delineated these taxa principally on cusp morphology. Other fossil rodent species are known from the early Eocene with nearly the same size range.

In the Clarks Fork Basin material there are no species, as determined by cusp morphology, found in sufficient abundance at any one level for statistical analysis. When tooth size is plotted against stratigraphic level for *Acritoparamys atwateri*, however, the size of the species does not appear to change greatly with time. An analysis of *A. atwateri* should give an estimate of variability, comprised of normal variability of the species and temporal variability. The variability determined should be at least as large, if not larger than that encountered in fossil species from any one time in the Clarks Fork Basin. Table 6 shows that the coefficients of variation for linear measurements are about the same value as those reported by Wood (1962) for *Paramys copei bicuspis*, *Paramys excavatus taurus*, and *Thisbemys plicatus*.

The coefficients of variability for all fossil species described here are greater than those of *S. n. rufiventer* and some are greater than those reported for *P. c. copei*, *P. e. taurus*, and

T. plicatus. In some cases this is a result of the inhomogeneity and small size of the sample measured. The reasonably large samples, such as that for *A. atwateri*, are from differing localities and levels and the larger coefficients show the effects of temporal and geographic variation.

Gingerich (1980) has determined that on a natural logarithmic (ln) scale the tooth area for the least variable tooth in mammalian species will be distributed within ± 0.2 ln units of the mean area, which corresponds to a range of 2-3 standard deviations on each side of the mean. Since the variability of *A. atwateri* is similar to that of other mammals, the expected spread of ln (area) should be about 0.4 units. Analysis of the ln (area) of M_1 of *A. atwateri* (Table 6) shows that one standard deviation equals 0.10 ln units so that a spread of two standard deviations will be 0.20 ln units on each side of the mean, indicating that only 5% of any new specimens of *A. atwateri* should lie outside of a range from 1.38 to 1.70 on a ln scale.

Analyses presented above show that fossil rodents are not unusually variable in size, and tend to cluster about a mean size. If one knows the taxon, one can predict the size of the teeth, but the converse is not necessarily true. Tooth size alone is not always a sufficient parameter for assigning unknown rodents to taxonomic groups. For example, when all the specimens available from the Clarks Fork Basin in the size range of *Acritoparamys atavus* are considered, one finds specimens that fall in the middle of the expected range that are not *A. atavus* (Fig. 3). These specimens show a separation of the anterior cingulum from the protoconid and a more complete posterior lophid than seen in *A. atavus* and belong to the genus *Microparamys*. Study of larger species from the Clarks Fork Basin further emphasizes this problem because as many as three taxa may have overlapping or congruent size ranges. Separating rodents into phenetic clusters based on tooth size is a useful way to begin analyzing them, but tooth size alone will not distinguish all taxa. The definitive phenetic cluster must be based on cusp morphology in addition to size.

Cusp morphology in rodent cheek teeth also varies. The extent of this variability is indicated by a study of the lower cheek tooth morphology of 60 specimens of *Sciurus niger rufiventer*. The general morphology of *S. niger rufiventer* lower cheek teeth is similar to that of primitive rodents of the Clarks Fork Basin. The cheek teeth consist of a large talonid and anteroposteriorly short trigonid. The four principal cusps are the protoconid, metaconid, hypoconid, and entoconid, and these are situated in the corners of the quadrate tooth. Anterior to the protoconid and metaconid is an anterior cingulum that is separated from the protoconid by a groove. Between the protoconid and hypoconid is a mesoconid. The hypoconid and entoconid are connected by a posterior lophid or cingulum.

The amount of separation of the anterior cingulum from the protoconid varies with the crowdedness of the teeth in the jaw, i.e., more crowded molars have anterior cingula closely appressed to the protoconid and less crowded molars have well separated cingula. Lophids of the trigonid vary in length and height and the mesoconids vary markedly in size and complexity. The posterior lophid in *S. n. rufiventer* varies very little except in rugosity. Expression of all morphologies of the cusps varies greatly with wear; for example, the anterior cingulum can appear to be attached to the protoconid in a moderately worn tooth.

These dental morphological variations have a bearing on distinguishing other species of *Sciurus*. Discounting size, *S. niger* and *S. vulgaris* differ in dental morphology only in the height and length of the trigonid lophids. Differences of this magnitude can be seen within *S. niger rufiventer* as a result of normal variation and/or wear.

While there is no way to prove that the same pattern of variability seen in *Sciurus* exists in primitive rodents, the above study suggests that cusp positions are sufficiently variable to require caution when assigning specimens to fossil taxa on the basis of cusp morphology. Without the independent means of determining taxonomic assignment available in Recent species it is difficult to determine if a given dental variant in a fossil is only one of intraspecific variation or one of taxonomic difference. The best approach is to use a complex of several characters.

The importance of using a complex of two or more characters is accentuated by the stereotypic nature of the teeth and jaws of primitive rodents. All primitive rodents studied here

FOSSIL RODENTS OF CLARK'S FORK BASIN

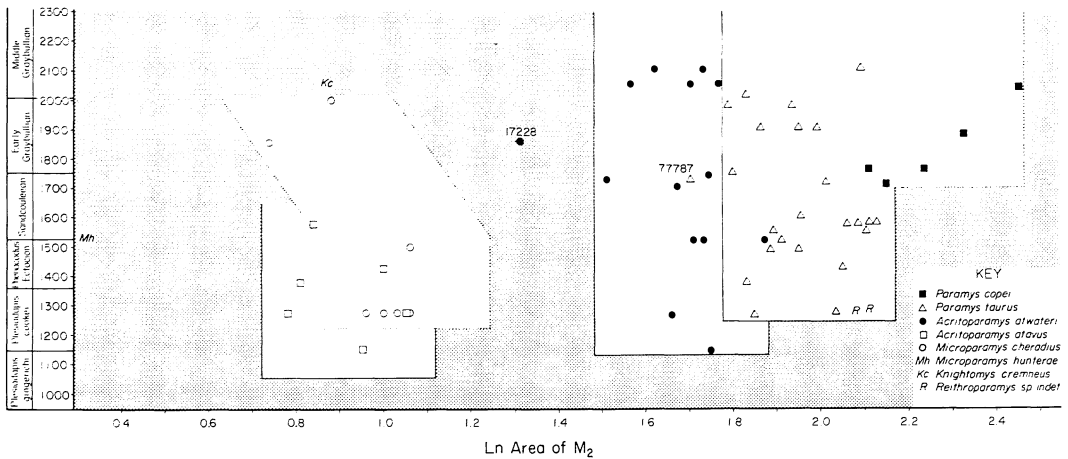


FIG. 3.— Plot of Ln A of M_2 against stratigraphic level for several rodent species from the Clarks Fork Basin. Rodents first appeared in the Clarks Fork Basin at the beginning of the Clarkforkian land-mammal age, at or near the beginning of the *Plesiadapis gingerichi* zone shown here (full range of rodent species documented by incisors is not shown here).

have quadritubercular teeth, with four well defined main cusps plus anterior and posterior cingula. Characters of the teeth available for differentiating taxa include the relative size and positioning of cusps, characteristics that tend to be widely and continuously variable. Previous workers on primitive rodents have used an unfortunate number of comparative descriptors to differentiate taxa, without stating to what the comparisons are being made. For example, the meaning of "large hypocone" in reithroparamyines is not immediately clear without comparative information on the hypocones of paramyines, the taxon to which this comparison refers. Confusion produced by this practice is somewhat mitigated if the dental characters are associated with other characters of the skull and mandible in a complex that defines the taxon, but proper identification of an unknown fossil specimen then requires the presence of the skull and/or mandible. Since most early fossil rodents are known exclusively from isolated teeth and jaw fragments, identifications cannot always be based on all characters used in the original definition. Identification of isolated teeth and jaw fragments must often be based upon the comparative descriptions of variable tooth structures. Resulting identifications consequently are provisional, except possibly when a unique character or set of characters is present; for example, *Lophioparamys* is identifiable even in heavily worn specimens because it is the only known early Eocene rodent taxon in its size range with complex crenulations of the talonid basin.

Tooth wear contributes to the problem of taxonomic assignment of rodent dental material. Heavy wear can result in a featureless tooth surface, while lesser amounts of wear can remove or diminish diagnostic characters. For example, excessive wear might cause a "large hypocone" to be mistaken for a "small hypocone", resulting in misidentification. A serious problem in this regard is removal of the hypoconulid during normal dental occlusion early in the life of the rodent. Several genera and species are distinguished by small differences in the size and connectedness of the hypoconulid.

Three difficulties are encountered in trying to separate Paleocene and Eocene rodent specimens into taxa based on the dentition: 1) at any given taxonomic level there is no guarantee that the taxa are unique in their size ranges, 2) the complex of characteristics used to delineate taxa include variable tooth characters, which are often the only ones available for analysis of less complete specimens, and 3) the expression of dental characteristics can be significantly altered by tooth wear. There are no good answers to questions posed by these

difficulties. Experience with as many specimens as possible is of value in determining the limits of variability and the value of comparative descriptors. Critical literature review is a must. However, the association of rodent fossils into taxonomic groups below the level of subfamily or tribe depends in large part on the interpretive abilities of the researcher. While these interpretations can be brought into some agreement through published analyses of rodent morphology and taxonomic affinities, the stereotypic nature of rodent teeth and the contiguity in size of different species means that opinions will differ on the taxonomy, phylogeny, and evolution of early fossil rodents. A careful worker must be aware of these caveats, and it does not pay to be dogmatic about conclusions in rodent taxonomy, especially those based on small samples.

SYSTEMATIC PALEONTOLOGY

Ideally the systematic assignments in this section should result from an unbiased study of the patterns shown by the morphology of the fossils within a stratigraphic framework. Species names and supraspecific designations should be attached to specimens and lineages in this pattern after comparison of published species types with the observed lineages. Due to the minute character differences involved in some specific determinations and the variability of these characteristics, this ideal approach could not be followed completely. A literature review was necessary to determine which variations previous workers thought significant and worth considering in identifying rodents. A bias toward previous interpretations of evolutionary patterns is unavoidable, although critical evaluation of these interpretations is always appropriate, especially when considering patterns based on small samples.

Restudy and redefinition of all of the genera of primitive rodents is beyond the scope of this study, so the unamended diagnoses that follow are taken from Wood (1962), Korth (1984), and other authors. I have revised generic and specific diagnoses where necessary, and have rewritten the rest in the more useful differential form suggested by Mayr (1969). When comparative descriptors must be used in diagnoses, I have stated to what taxon or feature the character is being compared. This practice is followed where necessary in the descriptive sections. Diagnoses of characters linking genera into higher taxa are discussed in detail by Wood (1962), Black (1971), and Korth (1984).

Order RODENTIA Bowditch, 1821 Suborder SCIUROMORPHA Brandt, 1855

Protrogomorpha Zittel, 1893. Wood, 1962.

Sciurognathi (in part), Wood, 1975.

Hystriognathi (in part), Wood, 1975.

Discussion.— Brandt (1855) originally subdivided the order Rodentia into three suborders, based on the differences in the masseteric musculature. Subsequent workers felt that this three-part subdivision of the order forced some extinct groups into unnatural associations (Wood, 1937; see Wood, 1962 for discussion) and proposed separating early rodents with a primitive, protrogomorphic jaw structure into a suborder of extinct forms that Zittel (1893) termed the Protrogomorpha (see also Wood, 1937, 1955, 1962). Several other subordinal divisions of the Rodentia have been proposed and discarded over the years, and these are discussed in detail by Wood (1962). The suborder Protrogomorpha seems to have gone the way of the others and its use has not been widely accepted. Wood recently abandoned Protrogomorpha for a two-part subdivision of the order reminiscent of Tullberg's (1899) classification based on the presence or absence of the hystriognathous angle on the jaw (Wood, 1975). Evidence Wood advanced for this subdivision of the order is not particularly convincing, and his classification has not widely been accepted. Korth (1984) presents a detail discussion of the evidence against Wood's new suborders, showing that the hystriognathous

jaw angle is not present in some primitive taxa where Wood claimed it was. Recent authors have returned to Brandt's three-fold subdivision, usually without comment or justification, and such convention will be followed here.

Family PARAMYIDAE Miller and Gidley, 1918

Paramyidae Miller and Gidley, 1918. Wood, 1962.
 Ischyromyidae (in part), Simpson, 1945. Stehlin and Schaub, 1951.
 Paramyinae, Black, 1971.

Discussion.— The composition of the Paramyidae, the oldest family of rodents in North America, is a subject of considerable debate among researchers. Wood (1962), in his revision of the family, separated the ischyromyids from paramyids and raised the two groups to family rank. His criteria involved differences in the attachment of the superficial masseter to the zygomatic arch and to the snout, and an arbitrary division at a point when crests on the molars became predominant over cusps. Black (1968) considered these differences between ischyromyids and paramyids to be as small as differences within the family Paramyidae, and he included the two groups in one family, for which the name Ischyromyidae has priority. Wood (1977) disagreed with Black, pointing out that the inclusion of the two groups in one family depends too much on dental characteristics and ignores those of the skull. Wahlert (1974) showed that the skull of *Ischyromys* differs significantly from the skull of *Paramys* in the position and number of the cranial foramina. Differences in cranial foramina, attachment of the masseteric muscles, and in the crestedness of the molars seem sufficient to justify retention of ischyromyids and paramyids as distinct families Ischyromyidae and Paramyidae.

Paramyids are usually divided into two or more subfamilies. Wood (1962) recognized five subfamilies: Paramyinae, Reithroparamyinae, Manitshinae, Microparamyinae, and Prosciurinae. Hartenberger (1975) also recognized five: Ischyromyinae, Paramyinae, Reithroparamyinae, Prosciurinae, and Ailuravinae. Korth (1984) redefined the subfamilies more rigorously, using many more specimens than were available to Wood, and, following Hartenberger, placed Microparamyinae in Reithroparamyinae. Korth also reduced Manitshinae to tribe rank while moving some manitshine species to other subfamilies, and left the predominantly Oligocene Prosciurinae intact. Korth recognized the subfamilies Ailuravinae and Pseudoparamyinae. Paramyinae, Reithroparamyinae, and possibly Pseudoparamyinae are represented among the paramyid rodents studied here.

Subfamily Paramyinae Miller and Gidley, 1918

Paramyidae (in part), Miller and Gidley, 1918.
 Paramyinae Simpson, 1945, p. 77. Wood, 1962, p. 11. Black, 1971, p. 181. Korth, 1984, p. 7.

Included genera.— *Ischyrotomus* Matthew, 1910; *Leptotomus* Matthew, 1910; *Manitshina* Simpson, 1941; *Notoparamys* Korth, 1984; *Paramys*, Leidy, 1871; *Pseudotomus* Cope, 1872; *Quadrotomus*, Korth, 1984; *Thisbemys*, Wood, 1962.

Discussion.— The first literature on this subfamily is somewhat confused. Simpson (1941) lists Paramyinae in his taxonomy of the new tribe Manitshini and discusses the subfamily in an offhand manner without really defining it. In his classification of mammals Simpson (1945) lists the subfamily as "new rank?" and lists the included genera. The majority of these genera are still recognized as members of the subfamily Paramyinae so the subfamily can be considered to have been accepted in Simpson, 1945.

Wood (1962) removed the tribe Manitshini from the Paramyinae, raising the tribe to subfamily rank with included genera of *Ischyrotomus*, *Manitshina*, *Pseudotomus*, and *Plesiarctomys*. Korth (1984) included his new genus *Quadrotomus* in the Manitshini which he reduced back to tribe rank after following Michaux (1968) and removing *Plesiarctomys* to the

Pseudoparamyinae Michaux, 1964. Korth placed those paramyine genera not included in Manitshini in the tribe Paramyini.

As presently constituted, Paramyinae contains large primitive rodents which can be distinguished from members of the Reithroparamyinae by the lack of hypocones on P⁴, smaller hypocones on the upper molars, posteriorly positioned anterior root of the zygoma, connected entoconid and posterior lophid, robust rostrum, lack of interparietals, non-coossified auditory bulla, and nasals extending posterior to the premaxillae. Paramyines are distinguished from pseudoparamyines only by the posterior extension of the nasals and the shape of P⁴.

Paramys Leidy, 1871

Paramys Leidy, 1871, p. 231. Loomis, 1907, p. 123. Mathew, 1910, p. 45. Wood, 1962, p. 12.

Type.— *Paramys delicatus* Leidy, 1871.

Included species.— Type; *Paramys copei* Loomis, 1907; *P. delicatior* Leidy, 1871; *P. excavatus* Loomis, 1907; *P. taurus* (Wood, 1962); and *P. pycnus* new species.

Diagnosis.— Medium to large paramyids with small to absent mesoconid, and smaller hypocone than in other genera of the subfamily; protoloph complete, metaloph not; coarse enamel crenulations of *Thisbemys* lacking; lacks crest from entoconid into talonid, lower incisors are not distinctive, and talonid and trigonid basins are wider than in *Leptotomus*; lack the double connection of the entoconid and posterior lophid and inset hypocone of *Notoparamys*; lack the multiple metaconules, entoconid crest to hypoconid, and separation of entoconid and posterior lophid of *Rapamys*.

Discussion.— A complete description of *Paramys* is presented by Wood (1962). This genus has long been the "waste basket" genus of the Paramyidae because in the past primitive rodents of general paramyid morphology have been automatically assigned to the genus. In recent years, study of better and more abundant material has resulted in the removal of some species to other genera and synonymy of some species within the genus (see Korth, 1984, for a discussion). As a result, the genus is no longer as predominant in terms of diversity in the early Cenozoic as was previously thought. However, specimens of *Paramys* are still the most abundant rodents in early Tertiary collections and the genus is known from North America, Europe, and possibly Asia.

Paramys copei Loomis, 1907

Fig. 4c,d. Table 3

Paramys delicatissimus (in part), Leidy, 1871, p. 231.

Plesiarctomys delicatissimus (in part), Cope, 1877, p. 172, Pl. xlv, fig. 9, 12.

Paramys copei Loomis, 1907, p. 128.

Paramys primaevus Loomis, 1907, p. 124, fig. 1.

Paramys quadratus Loomis, 1907, p. 126, fig. 2.

Paramys bicuspis Loomis, 1907, p. 128, fig. 4.

Paramys major Loomis, 1907, p. 128, fig. 5.

Paramys copei, Wood, 1962, p. 44, fig. 13-15.

Paramys copei bicuspis, Wood, 1962, p. 46, fig. 16.

Paramys copei major, Wood, 1962, p. 48, fig. 17A-H.

Type.— AMNH 4755, skull, mandibles, and fragmentary postcranials from the Lost Cabin of the Wind River Formation, Wyoming.

Referred specimens.— Mandible: UM 65378. Isolated lowers: UM 76535, 77790, 77827, 77829, 77831, 77832, 77835, 77849, 77850, 77852, 77854, 77855. Maxillae: UM 65378, 73433, 76004. Isolated uppers: UM 77870, 77885, 77888, 77893.

Stratigraphic range of referred material.— Early to middle Wasatchian, Sandcouleean (latest *C. ralstoni* zone) to middle Graybullian (*C. trigonodus* zone).

TABLE 3— Descriptive statistics for measurements of *Paramys copei* from the Clarks Fork Basin, Wyoming. Abbreviations as in Tables 1 and 2.

Measurement	N	OR	Mean	S	V
<i>Upper dentition</i>					
P ⁴	L	1	3.3	--	--
	W	1	3.7	--	--
	Ln A	1	2.49	--	--
M ¹	L	4	2.8 - 3.5	2.98	0.29
	W	4	3.0 - 3.6	3.43	0.25
	Ln A	4	2.1 - 2.5	2.32	0.16
M ²	L	5	2.7 - 3.5	3.10	0.32
	W	5	3.2 - 3.7	3.42	0.20
	Ln A	5	2.1 - 2.6	2.35	0.17
M ³	L	2	3.1 - 3.3	3.20	--
	W	2	3.0 - 3.2	3.10	--
	Ln A	2	2.2 - 2.3	2.30	--
<i>Lower dentition</i>					
P ₄	L	2	2.8 - 2.9	2.85	--
	AW	2	2.3 - 2.2	2.25	--
	PW	2	2.7 - 2.8	2.75	--
	Ln A	2	2.0 - 2.0	1.99	--
M ₁	L	3	3.0 - 3.2	3.10	0.08
	AW	3	2.5 - 3.0	2.73	0.21
	PW	3	2.7 - 3.2	2.93	0.21
	Ln A	3	2.1 - 2.2	2.17	0.08
M ₂	L	6	3.0 - 3.5	3.16	0.19
	AW	6	2.7 - 3.2	2.96	0.20
	PW	6	2.8 - 3.4	3.15	0.22
	Ln A	6	2.1 - 2.5	2.26	0.12
M ₃	L	3	3.6 - 3.9	3.73	0.13
	AW	3	2.7 - 2.9	2.80	0.08
	PW	3	2.7 - 2.8	2.73	0.05
	Ln A	3	2.3 - 2.4	2.33	0.05

Diagnosis.— Intermediate sized paramyine; 30-35% larger than *P. taurus* and *P. excavatus*; 20-30% smaller than *P. delicatus*; slightly smaller than *P. delicatior* but has smaller hypoconulid, less complete ectolophid, more posterior masseteric fossa under posterior margin of M₂ or anterior margin of M₃, and lacks isolated entoconid on M₃.

Discussion.— *Paramys copei* has undergone considerable taxonomic revision in recent years, which is summarized by Korth (1984). In the Clarks Fork Basin the earliest definitive record of this species based on cheek teeth is in the Sandcouleean of the early Wasatchian. Rose (1981) listed five large upper incisors from the Clarkforkian as *Paramys* cf. *excavatus*, but Korth (1984) referred these to *Paramys copei* based on size and on the lateral extent of the enamel. Since Rose's study, six additional large upper incisors that are similar in size and enamel distribution to the five previously described incisors have been recovered from Clarkforkian beds. These incisors not only agree in size and extent of enamel with *Paramys copei* but they also resemble incisors of *Franimys amherstensis* Wood, 1962, as noted by Korth (1984). The distribution of enamel on the upper incisors of *F. amherstensis* is variable; the

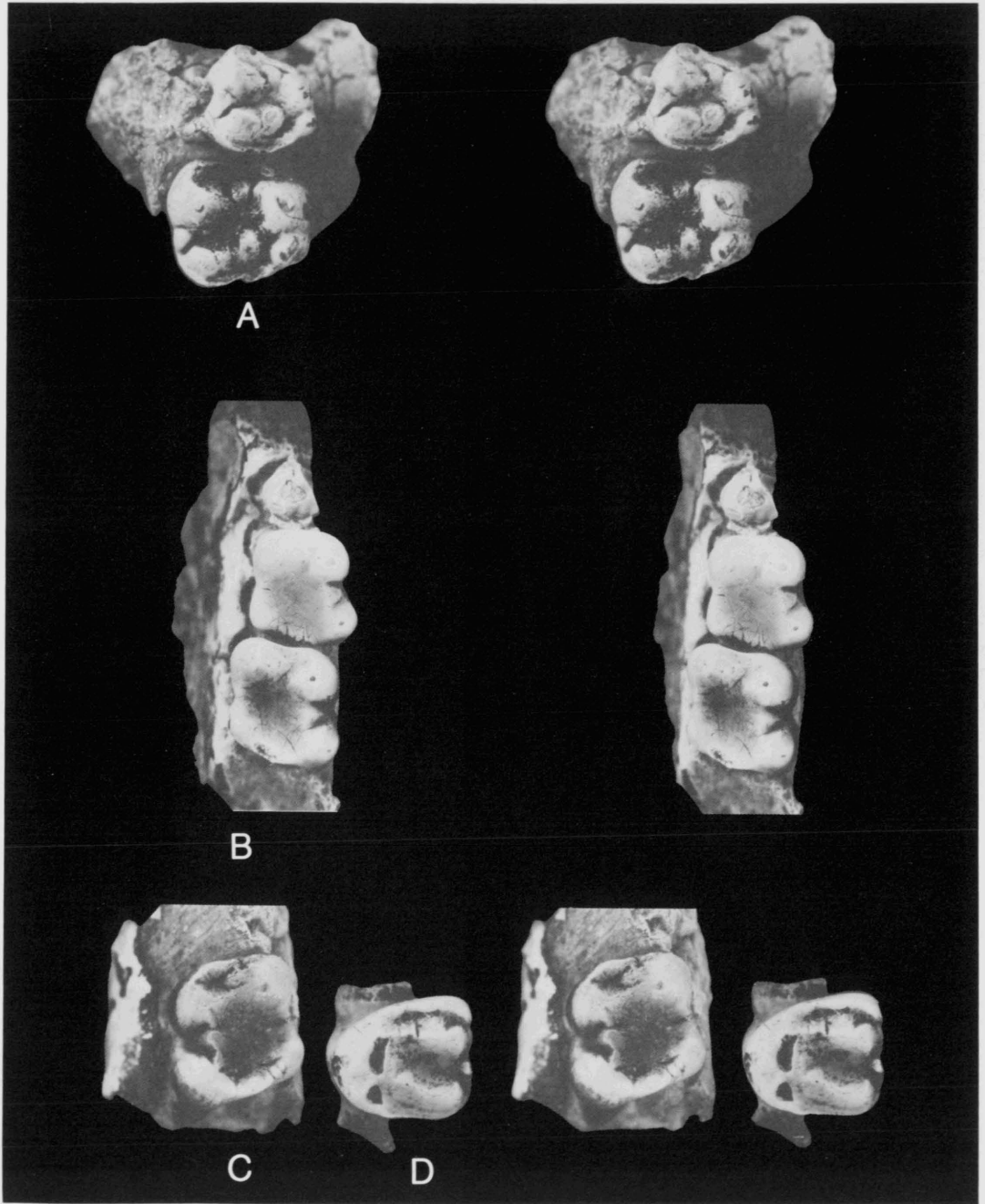


FIG. 4—Dentition of *Paramys taurus* and *Paramys copei*. A, *Paramys taurus*, UM 69665, right maxilla with dP^4 and M^1 . B, *Paramys taurus*, UM 76575, right mandible with $M_{1,2}$. C, *Paramys copei*, UM 77849, left M_2 . D, *Paramys copei*, UM 76004, left M^1 . All specimens in occlusal view, approximately 6 \times natural size, anterior toward top of page.

lateral extent of the enamel on the right incisor is greater than on the left incisor in the type specimen. The distribution of the enamel on incisors of *P. copei* is also variable, and it partly overlaps the range of *F. amherstensis* (Wood, 1962, p. 43). Unequivocal assignment of the 11 large upper incisors from the Clarkforkian to either species is not possible considering the variability in enamel extent and the similar incisor size of the two species. Therefore, the incisors are left unassigned pending discovery of better material in which incisors and molars are associated. It should be noted, however, that *F. amherstensis* is represented in the Clarkforkian by molars while *P. copei* is not. Until molars of *P. copei* are found in the Clarkforkian, the basal extent of this species must remain the Sandcouleean of the early Wasatchian.

Paramys taurus (Wood, 1962

Fig. 4a,b. Table 4

Paramys delicatissimus (in part), Leidy, 1871, p. 231.

Plesiarctomys delicatissimus (in part), Cope 1877, p. 170, Pl. xlv, fig. 9, 12.

Paramys excavatus taurus Wood, 1962, p. 56, fig. 17G-N.

Paramys excavatus obliquidens Wood, 1962, p. 58, fig. 18O-P. *Paramys* cf. *excavatus* (in part), Rose, 1981, p. 117, fig. 63.

Paramys taurus, Korth, 1984, p. 11, fig. 2.

Type.— MCZ 4463, right and left mandibles with LP₄-M₃ and RM₁-M₃, from east of Tatman Mt, Bighorn Basin, Wyoming, Wasatchian, earliest upper Graybullian.

Referred specimens.— Dentaries: UM 64651, 64974, 65117, 65120, 65203, 65275, 69419, 69554, 69615, 71385, 71731, 72861, 72873, 73021, 73405, 73804, 73915, 75044, 75443, 76228, 76229, 76371, 76478, 76575, 77117, 77823, 77907. Isolated lowers: UM 66185, 73020, 76559, 77727, 77786, 77787, 77788, 77794, 77795, 77796, 77798, 77801, 77802, 77811, 77814, 77819, 77824, 77825, 77826, 77828, 77830, 77834, 77836, 77838, 77840, 77841, 77842, 77843, 77848, 77851. Maxillae: UM 69661, 72886, 76665, 76839. Isolated uppers: UM 77723, 77724, 77735, 77748, 77756, 77857, 77865, 77866, 77873, 77876, 77878, 77883, 77886, 77890, 77891, 77920.

Stratigraphic range of referred material.— Clarkforkian to middle Wasatchian, *Plesiadapis cookei* zone to middle Graybullian (*C. trigonodus* zone).

Diagnosis.— Small paramyine about the size of *P. excavatus* but lower molars more rhomboidal in occlusal outline ("diamond-shaped" of Wood, 1962); has larger mesoconid and hypoconulid on lower molars, and hypocone variably present on P⁴; 25-30% smaller than *P. copei*; 20-25% smaller and lacks enlarged P⁴ and hypocone on P⁴ of *P. nini*; 10-15% larger than *P. pycnus*.

Discussion.— Paramyine rodents in the size range of *Paramys taurus* were first extensively revised by Wood (1962) who subdivided the specimens into a number of subspecies of *P. excavatus* based upon relatively minor differences of molar and incisor shape. Wood considered the subspecies to be temporal subspecies, an uncommon usage since the term subspecies usually refers to geographic subdivisions of a species.

Designation of subspecies of *P. excavatus* is not useful. Korth (1984) considers Wood's subspecies *P. excavatus* sufficiently distinct from the other subspecies to warrant specific designation as *P. excavatus*. Korth also places *P. excavatus gardneri* in *Thisbemys plicatus*. Characters used by Wood to distinguish *P. e. taurus* and *P. e. obliquidens* are variably present in specimens assigned to both subspecies and the two subspecies are rarely distinguishable.

Rose (1981) assigned several specimens from Clarkforkian beds to *Paramys* cf. *excavatus*, some of which are referred here to *P. taurus*. The specimens (UM 65117, 65120, and 66185) have the characteristics of *P. taurus*: rhomboidal lower molar occlusal outline and distinct mesoconids and hypoconulids. The size of the specimens and the continuity of the entoconid and posterior lophid preclude the assignment of these lower teeth to *Acritoparamys*.

TABLE 4— Descriptive statistics for measurements of *Paramys taurus* from the Clarks Fork Basin, Wyoming. Abbreviations as in Tables 1 and 2.

Measurement	N	OR	Mean	S	V	
<i>Upper dentition</i>						
P ⁴	L	3	2.3 - 2.4	2.33	0.05	2.1
	W	3	2.7 - 2.8	2.78	0.02	0.8
	Ln A	3	1.8 - 1.9	1.87	0.03	--
M ¹	L	10	2.4 - 2.9	2.61	0.19	7.3
	W	10	2.5 - 3.6	2.97	0.29	9.8
	Ln A	10	1.8 - 2.3	2.04	0.17	--
M ²	L	2	2.6 - 2.7	2.60	--	--
	W	2	2.7 - 3.0	2.85	--	--
	Ln A	2	1.9 - 2.1	2.00	--	--
M ³	L	5	2.7 - 3.2	2.98	0.17	5.7
	W	5	2.7 - 2.9	2.85	0.09	3.1
	Ln A	5	2.0 - 2.2	2.14	0.08	--
<i>Lower dentition</i>						
P ₄	L	10	2.2 - 2.7	2.41	0.19	7.8
	AW	10	1.4 - 1.9	1.76	0.15	8.5
	PW	10	1.8 - 2.3	2.16	0.20	9.3
	Ln A	10	1.3 - 1.7	1.54	0.16	--
M ₁	L	22	2.4 - 3.0	2.71	0.16	6.1
	AW	22	2.0 - 2.6	2.25	0.14	6.2
	PW	22	2.3 - 2.8	2.57	0.15	5.8
	Ln A	22	1.6 - 2.1	1.87	0.11	--
M ₂	L	28	2.5 - 3.1	2.76	0.18	6.6
	AW	28	2.2 - 2.9	2.54	0.19	7.5
	PW	28	2.2 - 3.0	2.72	0.17	6.3
	Ln A	28	1.8 - 2.2	1.97	0.12	--
M ₃	L	21	2.7 - 3.6	3.30	0.20	6.2
	AW	19	2.3 - 2.9	2.60	0.16	6.0
	PW	19	2.2 - 2.7	2.52	0.14	5.6
	Ln A	19	1.8 - 2.3	2.11	0.12	--

The specimens of lower molars here identified as *P. taurus* have a mean size that is somewhat smaller than the subspecies described by Wood (1962, tables 16-18). The mean and range of measurements are within the lower portion of the published size range of *P. e. taurus*, however, and these specimens are considered smaller members of *P. taurus*. Four specimens have molars which are significantly smaller than the remainder of the species and are designated *Paramys* cf. *taurus*. Specimens UM 69615, 73804, and 75044 have a more rounded posterior occlusal outline than is typical of *P. taurus* and the entoconid is set far forward. These specimens may be members of *P. pycnus*, but without associated uppers, this cannot be proven. UM 77787 differs from *P. taurus* morphologically as well as in size. It has a small mesoconid and no hypoconulid as in *P. excavatus*, but it is too small and rhomboidal to be referred to *Paramys excavatus*.

Within *P. taurus* the bulbousness of the cusps, position of the ectolophid, size of the hypoconulid, and anterior-posterior length of the teeth vary. In some specimens the size of the hypoconulid is reduced to near that characteristic of *P. excavatus*, as defined by Korth (1984).

In these specimens other characteristics indicative of *P. excavatus* are not present, and consequently they are placed in *P. taurus*. Some specimens have a somewhat larger hypoconulid, approaching that seen in reithroparamyines, but without the requisite isolated entoconid. In others the talonid basin is slightly reduced by bulbous cusps and an inset ectolophid resembling *Leptotomus*, but not to a sufficient degree to be included in that genus as a new, smallest species. Specimens included in *P. taurus* are sufficiently varied that taxonomic splitting is possible based on single characters, but no set of characters varies as a group within the available sample, requiring that the specimens be placed in one species.

***Paramys pycnus* new species**

Fig. 5a. Table 8

Type.— UM 76249, right maxilla with P⁴-M², from UM locality FG-25, east of Coon Creek in S₂ of Section 26, T54N, R97W, Gilmore Hill NE quadrangle, Wyoming, early Wasatchian, latest Sandcouleean (earliest *C. mckennai* zone).

Referred specimens.— UM 77881, LM¹ from UM locality SC-64, early Wasatchian, late-early Graybullian (late *C. mckennai* zone).

Etymology.— *pyknos*, Gr., dense, compact; in reference to the compact aspect of the molars.

Diagnosis.— Smallest species of the genus; 10-15% smaller and with relatively larger hypocones than *P. taurus*; anteroposteriorly compressed P⁴.

Description.— The posterior margin of the anterior root of the zygoma is level with the anterior margin of M¹. The elongate anterior cingulum of P⁴ is expanded in the parastylar region to form a square anterolabial corner which is labial to the large paracone. The protoloph contains a small protoconule and swings anteriorly to near the elongate anterior cingulum. The metacone is marginal, transversely elongate, and separated from the metaconule. A short ridge runs labially from the protocone forming the lingual portion of the metaloph but ends in a small conule before reaching the metaconule. The posterior cingulum runs from the labial margin and swings slightly anteriorly near the smaller metaconule to meet the protocone level with its apex. There is no hypocone or mesostyle.

M¹ and M² are nearly the same size and they are similar in morphology. The anterior cingulum is long, reaching from the level of the apex of the protocone to a point labial to the paracone. The cingulum is expanded into a small parastylar cusp that is separated from the paracone by a narrow groove. The protoloph contains a distinct protoconule slightly anterior to the protoloph. The metaloph contains a rounded metaconule connected to the protocone only by a low ridge. The metacone is in the posterolabial corner of the tooth and is the same size as the paracone. The two cones are separated by a small mesostyle which is separated from each cone by a groove that extends slightly into the trigon. The posterior cingulum extends lingually from even with the apex of the metacone and it is expanded into a relatively large hypocone, about one-third the size of the protocone, set nearly as far lingually as the protocone. The hypocone is separated from the protocone by a groove that extends down the lingual margin of the tooth and it is separated from the metaconule by a wide valley that extends labially to separate the posterior cingulum from the metaloph. The protocone is broad and extends a swelling into the trigon. The lophs are parallel.

M² differs from M¹ only in a having less isolated metaconule that is broadly connected to the metacone, a less inflated parastylar region, and wider separation of the paracone and metacone.

Discussion.— The specimens described here show features characteristic of both *Acritoparamys* and *Paramys*. A large metaconule and separation of the hypocone from the protocone are features of *Acritoparamys*, and the lack of hypocone on P⁴, posterior position of the zygoma root, and parallel lophs are characteristic of *Paramys*. The size of the specimen is in the range of *Franimys ambos* Korth, 1984 as well as *A. atwateri*, but the presence of a protoconule and the position of the anterior zygoma root is not characteristic of *F. ambos*. The size of the metaconule and hypocone in upper molars is a variable character in both

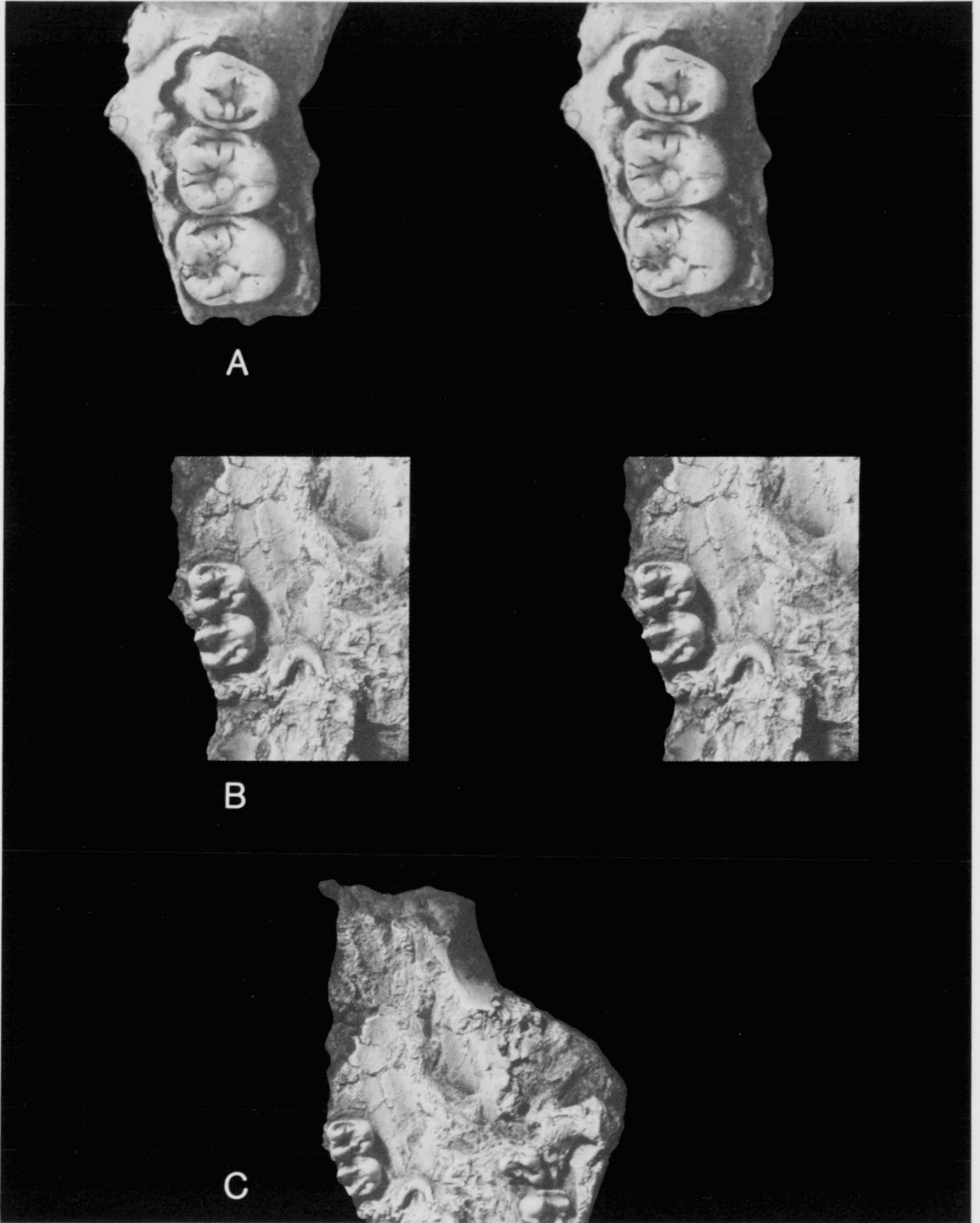


FIG. 5— Dentition of *Paramys pycnus* and *Cf. Notoparamys* sp. A, *Paramys pycnus*, UM 76249 (holotype), right maxilla with P¹-M¹, approximately 6× natural size. B, *cf. Notoparamys* sp., UM 67282, left M¹ and M² in maxilla, approximately 3× natural size. C, *cf. Notoparamys* sp., UM 67282, maxilla with LM¹⁻² and RM¹⁻², approximately 1.5× natural size. All specimens in occlusal view, anterior toward top of page.

Acritoparamys and *Paramys*, requiring a subjective opinion as to when they are "large". Other characters should be used in conjunction with the size of the cusps and in this case the position of the anterior zygoma and morphology of P⁴ dictate referral to *Paramys*.

Notoparamys Korth, 1984

Notoparamys Korth, 1984, p. 20

Cf. *Notoparamys* sp.

Fig. 5b,c. Table 8

Referred specimen.— UM 67282, crushed skull with RM¹⁻² and LM¹⁻², from UM locality SC-145, middle Wasatchian, middle Graybullian (*C. trigonodus* zone).

Description.— The skull is crushed and nothing can be determined about the nasals, interparietals, or auditory bullae. The posterior margin of the anterior root of the zygoma is even with the posterior margin of the P⁴ alveolus. An alveolus for P³ is present. The alveolus indicates that P⁴ was nearly the same size as M¹.

M¹ and M² are nearly the same size although M² is slightly wider. The anterior cingulum of M¹ is long, reaching from the labial margin of the protocone to the labial margin of the tooth. The cingulum widens anteriorly in the parastylar region and turns labially and posteriorly to meet the paracone labial to its apex. The paracone is large, one-third the size of the protocone, and inset from the labial margin. The protoloph is short, containing a protoconule isolated from the paracone and connected to the protocone by a short ridge. The metaconule is double, with the two conules subequal in size; the lingual metaconule is connected to the protocone by a low ridge that trends somewhat anteriorly. The lophs are subparallel. The protocone is high, lingually placed, and, in addition to the two main lophs, has a short low ridge running from its apex into the trigon.

The hypocone is separated from the protocone by a deep groove that runs down the lingual margin of the tooth to the base of the crown. The hypocone is a large swelling on the posterior cingulum, approximately one-fifth the size of the protocone, well separated from the lingual metaconule, and almost as lingually placed as the protocone. The posterior cingulum is broad, cusped, and ends even with the apex of the metacone. The metacone is as large as the paracone and it is inset from the labial margin, although not as much as the paracone. The mesostyle is double and the cusps are rounded.

The M² is similar to M¹ in outline and shape. The hypocone is smaller than it is on M¹ and it is inset from the lingual margin to near the lingual metaconule. The metaconules are not as large as on M¹ and the parastylar region of the anterior cingulum is not as inflated. The protoloph has a small protoconule that is broadly connected to the paracone through the loph and is separated from the protocone. The mesostyle is single, the metacone is on the labial margin, and the posterior cingulum is shorter than in M¹. In all other features M² is the same as M¹.

An upper incisor is present with a rounded anterior face and flat medial and lateral sides. The enamel is restricted, just reaching the lateral side and not reaching the medial side. The anterior face lacks a sulcus.

Discussion.— This specimen is distinguished from *Paramys copei* by its larger size and larger, more separated hypocones on the molars. The distinctness of the hypocones, the rectangular shape of the molars, and the double metaconules also distinguish this specimen from *Paramys delicatus*, while these characteristics plus the expansion of the parastylar region of M¹, and the position of the hypocone near the metaconule on M² resemble characteristics of *Notoparamys* Korth, 1984. The specimen is slightly smaller than *Notoparamys costilloi* (Wood, 1962), and the specimen differs further by the more lingual position of the hypocone on M¹, the unexpanded parastylar region and single mesostyle of M², and the more labial position of

the cones on M^2 . These differences rule out assignment of UM 67282 to *N. costilloi*, but the assignment to *Notoparamys*, while not certain, is probably correct.

Thisbemys Wood, 1959

Thisbemys Wood, 1959a, p. 163.

Cf. *Thisbemys* sp.

Referred specimen.— UM 67425, left mandible with P_4 , early Wasatchian, Sandcouleean (latest *C. ralstoni* zone).

Description and discussion.— This specimen has a P_4 much smaller than the alveoli of M_1 or M_2 . The tooth is without a hypoconulid, has a widely separated protoconid and metaconid and a large, round mesoconid. Mental foramina are high in the mandible and close together under the posterior and anterior margins of P_4 . The incisor has a flat anterior face, parallel sides and enamel extending half way along the lateral margin. There are no obvious crenulations in the talonid of the P_4 , but the small size of the tooth and the position of the mental foramina suggest affinities to *Thisbemys*.

Paramyinae gen. and sp. indet.

Referred specimens.— UM 76251 (RM_2), 77818 (LM_3), 77837 (RM_3), 77884 (RP^4) from the Clarkforkian, *Phenacodus-Ectocion* zone (P^4) and the early Wasatchian, Sandcouleean (*C. ralstoni* zone) (M_3s), and latest Sandcouleean (*C. mckennai* zone) (M_2).

Description and discussion.— These four specimens are from different localities and stratigraphic levels. The M_3s are the size of *Paramys copei* but both have enlarged, isolated hypoconulid lobes over that species. UM 77837 has a ridge descending the posterior face of the trigonid from the protoconid and a long, cusped ectolophid. UM 77818 has a very large, anteriorly located entoconid, low, isolated mesoconid and small metastylid. P^4 is anteroposteriorly compressed and is near the size of P^4 of *Franimys amherstensis* but it is slightly crenulated, eroded on the posterior margins, and has two labial roots, while P^4 in *F. amherstensis* has a single labial root.

The M_2 , UM 76251, has a low crest from the entoconid to the hypoconulid anterior to the posterior lophid. Both the posterior lophid and this crest are interrupted by grooves. Whether this crest is an extension of the entoconid or is bifurcation of the posterior lophid is obscured by wear and breakage where the crests meet the entoconid. The size of the tooth is near that of *Notoparamys arctios*, but the features could as easily be that of a *Reithroparamys* species.

Subfamily Reithroparamyinae Wood, 1962

Reithroparamyinae Wood, 1962, p. 117. Black, 1971, p. 181. Korth, 1981, p. 25.

Included genera.— *Reithroparamys* Matthew, 1920; *Microparamys* Wood, 1959; *Lophoparamys* Wood, 1962; *Acritoparamys* Korth, 1984; *Apatosciuravus* Korth, 1984.

Discussion.— Wood (1962) originally erected this subfamily to contain medium sized paramyids with "incipiently hystricognathous" jaw angles, which he thought were precursors of the South American caviomorphs. Dawson (1977) and Korth (1984) have shown that most rodents in the early Eocene had jaw angles that can be considered incipiently hystricognathous but are actually sciurognathous, invalidating Wood's distinguishing characteristic for the subfamily. Black (1971) discussed the Reithroparamyinae, broadening the definition of the subfamily to include all small rodents of the Paramyidae. He included the Microparamyinae in

the subfamily and removed *Rapamys* Wilson, 1940 to the Paramyinae. Korth (1984) redefined the Reithroparamyinae in a more rigorous manner, including in the definition such characters as the relationship of the nasals and premaxillae, the presence of a hypocone on all upper cheek teeth, and the isolation of the entoconid from the enlarged hypoconulid on the lower molars. These characters distinguish this subfamily from Paramyinae, necessitating the removal of part of *Franimys* Wood, 1962 from the Reithroparamyinae into a new subfamily and the inclusion of material from the Paramyinae under a new genus, *Acritoparamys*. Korth's readjustment of the Reithroparamyinae and Paramyinae appears justified from the material studied here and his subfamilial designations will be followed.

Acritoparamys Korth, 1984

Paramys (in part), Leidy, 1871, p. 231.

Reithroparamys (in part), Mathew, 1920, p. 168.

Acritoparamys Korth, 1984, p. 28.

Type.— *Paramys francesi* Wood, 1962.

Included species.— *Type*; *Acritoparamys atavus* (Jepsen, 1937); *A. atwateri* (Loomis, 1907); *A. pattersoni* (Wood, 1962); and *A. wyomingensis* (Wood, 1959).

Discussion.— This genus is diagnosed and described by Korth (1984). Korth erected *Acritoparamys* to contain species that could no longer be included in Paramyinae under his more rigorous definitions of the subfamily and included genera. Included in *Acritoparamys* are species removed from Paramyinae that would not fit into any previously described reithroparamyine genus and species that were excluded from established reithroparamyine genera as a result of emended definitions of those genera; such as *A. atwateri*, which was previously assigned to *Reithroparamys*.

Acritoparamys is easily distinguished from *Lophioparamys* and *Reithroparamys* in all but heavily worn specimens, but differentiation of small species of *Acritoparamys* from *Microparamys* is more difficult. Separation of the anterior cingulum, the smaller hypoconulid, and the less isolated entoconid characteristic of *Microparamys* are features that are obscured by moderate wear. Separation of the anterior cingulum in primitive *Microparamys* is especially small and difficult to distinguish in worn specimens. For this reason the assignment of small specimens from the early Clarkforkian to either genus is more provisional than the assignment of other later or larger specimens.

Acritoparamys atavus (Jepsen, 1937)

Figs. 6, 7, 8a-e. Table 5

Paramys atavus Jepsen, 1937, p. 297, Pl. 1. Mckenna, 1961, p. 3, fig. 1. Wood, 1962, p. 60, fig. 21. Rose, 1981, p. 117, fig. 62.

Acritoparamys atavus, Korth, 1984, p. 29, fig. 12a,b.

Apatosciuravus bifax (in part), Korth, 1984, p. 42.

Type.— PU 14200, RM₂ from the Eagle Coal Mine, Bear Creek, Montana.

Referred specimens.— Dentaries: UM 65244, 65765, 69871, 71173. Isolated lowers: UM 69219, 72865, 77705, 77712, 77716, 77737, 77740, 77745, 77752, 77757, 77762, 77783, 78872, 78881, 78882. Maxillae: UM 73614, 73784. Isolated uppers: UM 69219, 75471, 77703, 77708, 77709, 77715, 77717, 77729, 77730, 77734, 77751, 77760, 77761, 77763, 77768, 77773, 77805, 77844, 77921, 78873, 78886.

Stratigraphic range.— Cheek teeth (including the type) are known from the *Plesiadapis gingerichi* zone of the Clarkforkian to the late-early Graybullian (*C. mckennai* zone).

Diagnosis.— Smallest species of the genus; 30-35% smaller than *A. atwateri* and *A. francesi* and has less isolated entoconid; differs further from *A. francesi* by presence of high, nearly enclosed trigonid.

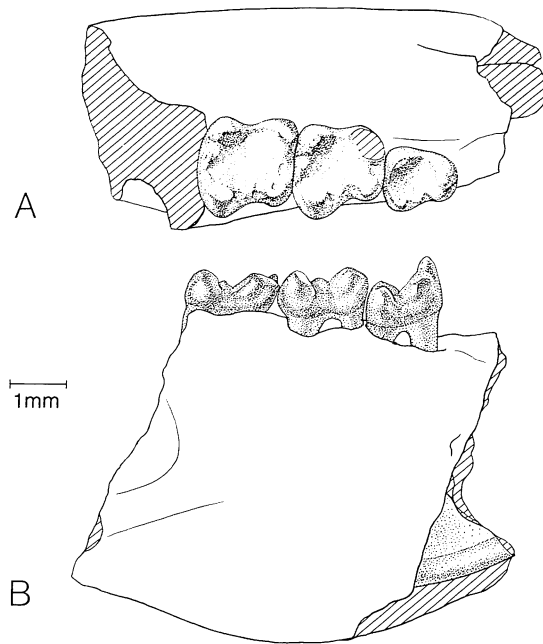


FIG. 6— *Acritoparamys atavus*, UM 69871, right dentary with P_4 - M_2 . A, occlusal view. B, lateral view.

Description.— All of the dentition of *Acritoparamys atavus* is now known, although the only M_3 associated with other cheek teeth is from UM 65244, which is heavily worn. P_4 is submolariform with the protoconid closely appressed to the large metaconid but separated by a shallow groove. There is no anterior cingulum. The talonid basin is fully molariform with a large hypoconid, equal in size to the entoconid, indistinct hypoconulid, and weakly isolated entoconid. The entoconid is separated from the metaconid by a deep notch. The mesoconid exists as a swelling on the inset ectolophid and it is separated from the hypoconid and protoconid by shallow valleys.

M_1 and M_2 are nearly the same size, though the trigonid of M_1 is somewhat narrower labiolingually. The metaconid of M_1 is located far forward and near the lingual corner of the tooth. The anterior cingulum connecting the metaconid with the protoconid is low, leaving the trigonid nearly open anteriorly. The anterior cingulum meets the protoconid near the lingual margin of the cusp and it is not separated from the protoconid. The metalophid extends across the back of trigonid onto the lower slope of the metaconid and nearly closes the trigonid posteriorly in unworn specimens. An arm of the metalophid extends nearly to the center of the trigonid basin. The mesoconid is a distinct swelling on the ectolophid, inset from the labial margin of the tooth and separated from the hypoconid and protoconid by shallow valleys. The hypoconid is low, large, and somewhat rounded with a flat anterior face. It is connected to the hypoconulid by a low ridge which may carry a very shallow valley in unworn specimens. The hypoconulid is low, elongate, and convexly curved in a posterior direction. The entoconid is located in the posterolabial corner of the tooth, separated from the hypoconulid by a narrow, shallow notch that disappears with moderately heavy wear. The entoconid is separated from the metaconid by a wide valley, slightly raised above the level of the broad talonid.

M_2 is very similar to M_1 although the trigonid is slightly wider, making the tooth more square. The only M_3 known in a dentary is the badly worn and broken specimen UM 65244. This specimen suggests that the posterior margin of M_3 is formed by an enlargement of the hypoconid and posterior lophid, and that the entoconid is isolated by a groove. Several isolat-

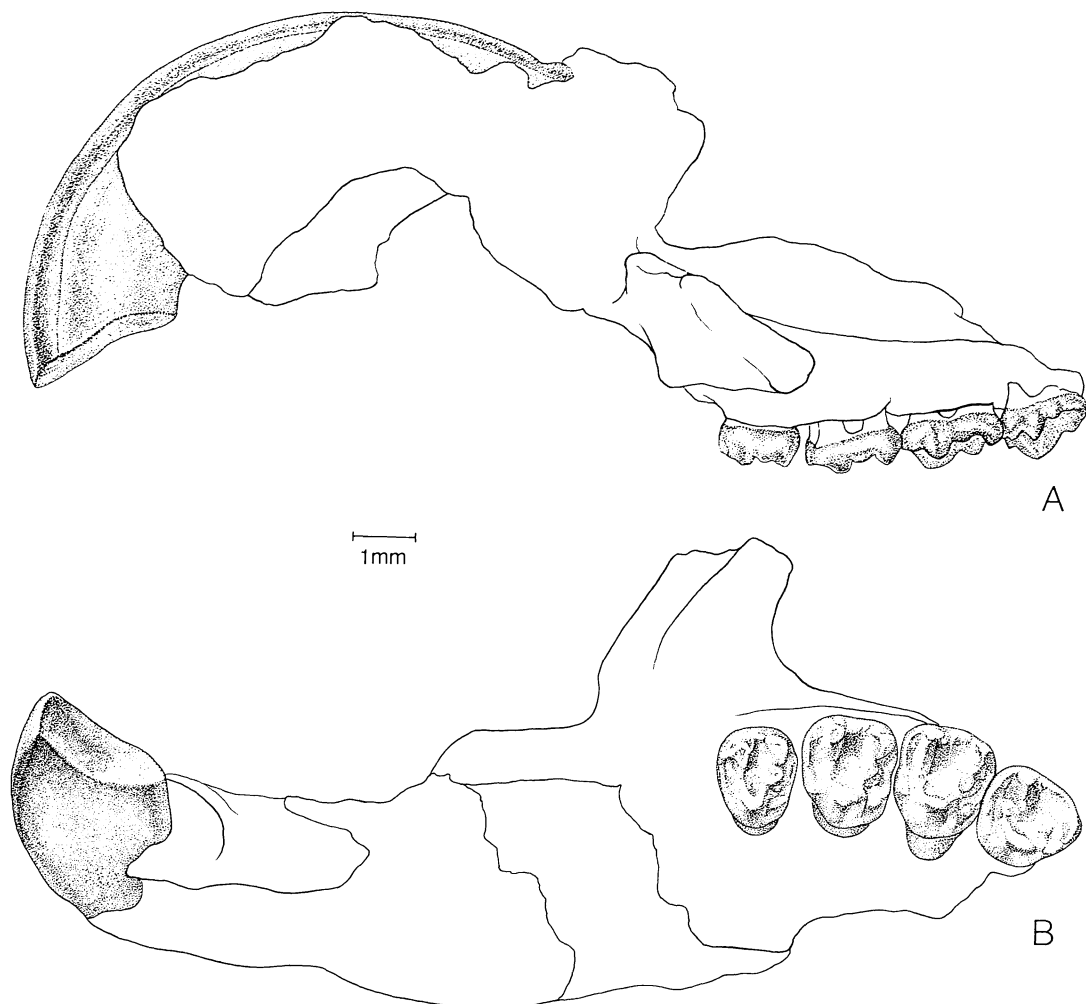


FIG. 7.—*Acritoparamys atavus*, composite of UM 73784, left maxilla with I¹, P⁴-M², and UM 73614, left M³. A, lateral view. B, occlusal view.

ed M₃s have been tentatively assigned to *A. atavus* based on size and the similarity of the trigonids to the trigonids of M₂ of the type and referred specimens. These specimens show a larger labiolingually elongated mesoconid than on M₁ and M₂, connected to the hypoconid by a low ectolophid, the enlarged hypoconulid separated from the enlarged hypoconid by a shallow groove, and a metastylid between the anteriorly positioned entoconid and the metaconid.

The mandible is relatively deep for rodents in this size range, with a masseteric fossa ending beneath the anterior half of M₂. The anterior mental foramen is under the posterior end of the diastema, and a second, minute foramen lies beneath the posterior margin of P₄ at the same level as the anterior foramen. Incisors have been adequately described elsewhere (Jepsen, 1937) and they differ little from other small paramyid incisors.

The maxillary dentition is known from a combination of two specimens, UM 73784 (LP⁴-M²) and UM 73614 (LdP⁴, M²-M³). The posterior margin of the anterior root of the zygoma is even with the center of P⁴ and the anterior root has a crest, marking the anterior attachment of the masseter, even with the anterior half of the alveolus of P³.

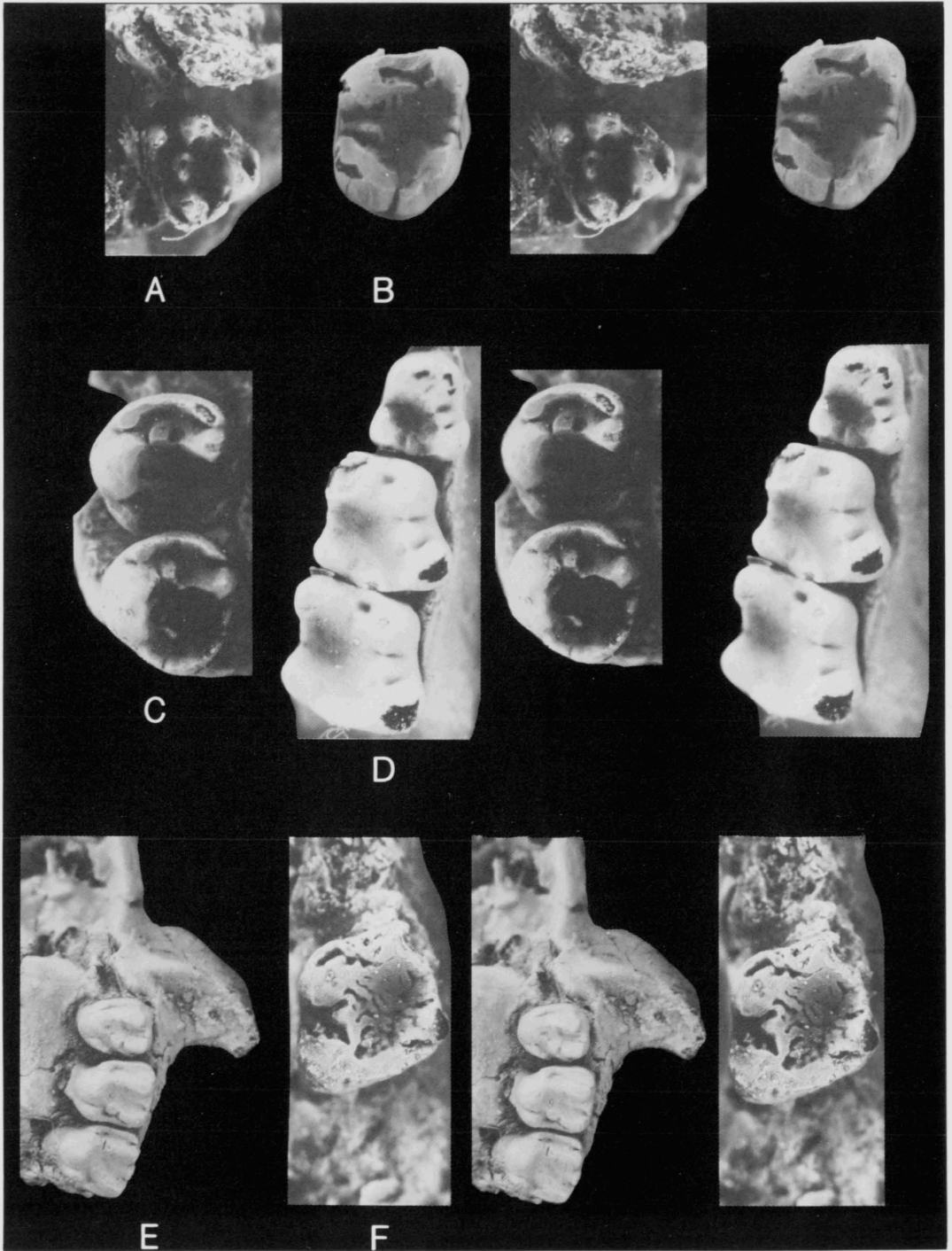


FIG. 8.— Dentition of *Acritoparamys atavus* and *Lophioparamys murinus*. A, *Acritoparamys atavus*, UM 73614, LdP⁴. B, *Acritoparamys atavus*, UM 78872, LM₃. C, *Acritoparamys atavus*, UM 73614, LM²⁻³. D, *Acritoparamys atavus*, UM 69871, right mandible with P₄-M₂. E, *Acritoparamys atavus*, UM 73784, right maxilla with P⁴-M². F, *Lophioparamys murinus*, UM 75094, left mandible with M₂. All specimens in occlusal view, figures A - D and F approximately 12× natural size, figure E approximately 6× natural size, anterior toward top of page except A where anterior is toward the right.

TABLE 5— Descriptive statistics for measurements of *Acritoparamys atavus* from the Clarks Fork Basin, Wyoming. Abbreviations as in Tables 1 and 2.

Measurement	N	OR	Mean	S	V	
<i>Upper dentition</i>						
P ⁴	L	3	1.2 - 1.4	1.33	0.09	6.8
	W	3	1.6 - 1.7	1.67	0.05	2.8
	Ln A	3	0.7 - 0.9	0.80	0.10	--
M ¹	L	7	1.6 - 1.7	1.62	0.05	3.1
	W	7	1.8 - 1.9	1.86	0.05	2.7
	Ln A	7	1.0 - 1.2	1.10	0.04	--
M ²	L	6	1.5 - 1.8	1.60	0.10	6.3
	W	6	1.7 - 1.9	1.77	0.07	4.2
	Ln A	6	0.9 - 1.2	1.04	0.10	--
M ³	L	8	1.5 - 1.9	1.72	0.10	5.8
	W	8	1.5 - 1.8	1.60	0.09	5.5
	Ln A	8	0.8 - 1.2	1.01	0.11	--
<i>Lower dentition</i>						
P ₄	L	4	1.1 - 1.4	1.23	0.11	8.9
	AW	4	0.8 - 1.0	0.90	0.07	7.9
	PW	4	1.0 - 1.3	1.15	0.11	9.6
	Ln A	4	0.0 - 0.5	0.22	0.17	--
M ₁	L	8	1.4 - 1.7	1.56	0.09	5.5
	AW	9	1.1 - 1.4	1.31	0.09	7.5
	PW	9	1.4 - 1.8	1.55	0.15	9.8
	Ln A	8	0.5 - 0.9	0.79	0.12	--
M ₂	L	5	1.5 - 1.9	1.68	0.13	7.9
	AW	5	1.4 - 1.5	1.42	0.04	2.8
	PW	5	1.4 - 1.7	1.57	0.11	7.0
	Ln A	5	0.8 - 1.1	0.92	0.11	--
M ₃	L	5	1.6 - 2.0	1.90	0.15	8.2
	AW	4	1.4 - 1.6	1.50	0.07	4.7
	PW	5	1.3 - 1.6	1.48	0.11	7.4
	Ln A	4	0.8 - 1.2	1.05	0.13	--

Only the alveolus of P³ remains, indicating that the tooth was single rooted and much smaller than P⁴. P⁴ of *A. atavus* has been adequately described by McKenna (1961) and the P⁴ of UM 73784 agrees with his description and illustration in all features except the presence of a minute mesostyle. The presence of a mesostyle may be a variable character.

M¹ is nearly square in occlusal outline. The anterior cingulum begins low on the anterior margin of the protocone and it is separated from the protoloph by a valley. A small thickening is variably present at the lingual end of the anterior cingulum, and the cingulum is enlarged in the parastylar region before turning posterobuccally to contact the paracone just slightly labial to the apex. The protoloph is complete with a protoconule swelling that variably invades the valley between the protoloph and the anterior cingulum. The paracone is large, pyramidal, and merges with the protoloph. A large mesostyle is closely appressed to the paracone and separated from the metacone by a groove. The metacone is in the posterolabial corner of the tooth and is connected to the rounded metaconule by a low, anteriorly placed ridge. The single metaconule is connected to the protocone by a low ridge. The hypocone is

a swelling on the posterior cingulum separated from the protocone by a shallow valley that continues as a groove down the lingual margin of the tooth. The hypocone is inset from the lingual margin and it is separated from the metaconule by a deep valley that extends labially to separate the posterior cingulum from the metaloph. The posterior cingulum is short and merges with the metacone lingual to the labial margin of the tooth. The protoloph and metaloph converge on the anterior and posterior ends of the protocone, respectively, and both are straight.

M² is only slightly longer than M¹ and differs in having a longer mesostyle, more divergent lophs, and a shorter posterior cingulum. The protoconule is more distinct, the parastylar region is less inflated, and the hypocone is smaller, although more widely separated from the protocone. The metaconule is less distinct with a broader connection to the metacone.

The anterior cingulum, paracone, and protoloph of M³ resemble those of M². The expanded posterior basin contains a small isolated cusp that may be the metaconule. The posterior and labial margins of the tooth are raised and contain inflated areas that correspond to the mesostyle in the central labial margin and the metacone in the posterolabial corner. No hypocone is discernible and the posterior cingulum is represented by a short loph posterior to and separated from the protocone.

Specimen UM 73614 retains the dP⁴ in place (see Fig. 8a). The tooth is molariform with a well separated hypocone positioned lingual to the protocone. Both cingula are wide and curve around labial to the paracone and metacone, forming, with the mesostyle, a nearly complete labial shelf. The metaloph is made up of multiple metaconule cusps while the protoloph is interrupted by a valley in the position of the protoconule. The protocone and metacone are rounded, isolated cusps while the paracone is a somewhat elongated pyramid forming part of the protoloph. DP⁴ has three roots widely spread.

Discussion.— *Acritoparamys atavus* was originally described by Jepsen (1937) as *Paramys atavus*, based on an isolated M₂ and unassociated incisors found at the Eagle Coal Mine, Bear Creek, Montana. Van Houten (1944) attributed a single incisor from the Bighorn Basin to *P. atavus* and McKenna (1961) described what is clearly a P⁴ from the Bear Creek locality, attributing it to *P. atavus*. Wood (1962) designated an isolated lower molar from UM locality SC-119 (locality number subsequently assigned) to *Microparamys sp. A*, which Rose (1981) placed within *P. atavus*. Korth (1984) also grouped Wood's specimens with the specimens Rose referred to *P. atavus* and here referred to *Acritoparamys atavus*.

Since 1975, field crews from the University of Michigan have collected several dentaries and teeth from the Clarks Fork Basin that are clearly referable to *Acritoparamys atavus*. Rose (1981) described and figured some of these specimens and referred them to *Paramys atavus*. He did not have sufficient material to assign any upper molars to *Paramys atavus*, although he suggested that some small upper molars in the collection at that time could be referred to the species.

Material collected since Rose completed his study includes two maxillae with cheek teeth and isolated upper molars that can be assigned to *A. atavus* and not to species of *Microparamys* or *Apatosciuravus*. Reasons for this assignment are: 1) the teeth are in the size range expected for uppers of *A. atavus*; 2) the position of the posterior margin of the anterior root of the zygoma is even with the center of P⁴, which agrees with the position for *Acritoparamys* but is posterior to the position seen in *Microparamys* or *Apatosciuravus*; 3) the morphology of P⁴ on UM 73784 agrees with that of the P⁴ described by McKenna (1961), except for the presence of a minute mesostyle; 4) the hypocones on M¹ and M² are smaller than the hypocones on molars of *Microparamys* and they are much smaller and further inset than those of *Apatosciuravus*; 5) the molars are more cuspsate than in *Apatosciuravus* molars; 6) the material was collected from the same locality that yielded lowers of *A. atavus*.

The presence of the minute mesostyle on P⁴ of the referred specimens is in disagreement with the Bear Creek P⁴ (McKenna, 1961). An alternative to considering the presence of a mesostyle on P⁴ a variable character is to erect a new species of *Acritoparamys*, based only on uppers, which differs from *A. atavus* in this character. Such action would seem to be a clear case of oversplitting. The conservative approach will be followed here, and the upper dental

material is assigned to *A. atavus* with the presence of a mesostyle on P⁴ considered a variable character.

Korth (1984) maintained that *A. atavus* is unique to the Bear Creek locality and that the lower molars described by Rose (1981) and referred to *A. atavus* belong to a separate taxon (*Apatosciuravus bifax*). His reasons are that the posterior lophid on the Clarks Fork Basin specimens is more continuous with the entoconid than on *A. atavus* and that the greater size and more square shape of the Bear Creek rodent separates it from the Clarks Fork Basin material. Korth's interpretation of the connection of the entoconid with the posterior lophid is in error in that the UM specimens show the same entoconid isolation as the type of *A. atavus*. The type specimen is larger than the range of variation seen in the Clarks Fork Basin specimens, but only slightly. To say that the type is in a different size category based on the few available specimens is to presume more than the data allow. Further, Rose (1981) suggested that the Bear Creek locality is in the *Plesiadapis gingerichi* zone, earlier than the *P. cookei* zone where most of the specimens here described are from. Specimens of *A. atavus* that are known from later horizons than the bulk of the sample suggest that *A. atavus* is decreasing in size with time. If such is the case then the type is within this secular trend.

The other objection, that the type has a wider trigonid, is true by only a few percent of the talonid width, well within normal variability seen in other species, such as *Acritoparamys atwateri* and *Paramys taurus*.

Some of the specimens here placed in *A. atavus* were referred by Korth (1984) to his new genus and species, *Apatosciuravus bifax*. *Apatosciuravus bifax* is based on a maxilla with distinctive characters from Dorsey Creek, in the Bighorn Basin, which is probably upper Graybullian in age. Upper molars with the large hypocones distinctive of *Apatosciuravus bifax* are not known from the well sampled locality from which the majority of the *A. atavus* material has been recovered (SC-188). One specimen (UM 69219) that Korth states is an upper of *Apatosciuravus bifax* from SC-188 has a smaller hypocone, less complete crests, and is similar in morphology to the upper molars in maxillae referred to *A. atavus*. The type of *Apatosciuravus bifax* has no associated lower teeth. Lower dentitions that Korth assigns to *Apatosciuravus bifax* are from different localities and different stratigraphic levels than the type, and he gives no reasons for assigning these lowers to *A. bifax*. Similarity of these lower molars to those of *A. atavus* and an absence of specimens of *Apatosciuravus bifax* in the Clarkforkian suggests that it is wiser to refer these lowers to *A. atavus*.

Acritoparamys atwateri (Loomis, 1907)

Fig. 9. Table 6

Paramys atwateri Loomis, 1907, p. 127, fig. 3.

Reithroparamys atwateri, Wood, 1962, p. 133, fig. 45A-C.

Paramys annectens Rose, 1981, p. 119, fig. 65.

Acritoparamys atwateri, Korth, 1984, p. 31, fig. 13, 14.

Type.— ACM 180, left mandible with M_{1,2}, from Tatman Mt., Bighorn Basin, Wyoming, Wasatchian, earliest upper Graybullian.

Referred specimens.— Dentaries: UM 66887, 66888, 69352, 71177, 71228, 72087, 73037, 73074, 73077, 73451, 76140, 76399, 76626, 76756, 77242, 77383. Isolated lowers: UM 66757, 72597, 77398, 77515, 77706, 77741, 77747, 77749, 77755, 77789, 77791, 77792, 77793, 77807, 77808, 77809, 77810, 77813, 77815, 77816, 77817, 77821, 77833, 78880. Maxillae: UM 64808, 68448, 69335, 69779, 69950, 73239, 73840, 77864. Isolated uppers: UM 72080, 77100, 77704, 77710, 77774, 77820, 77858, 77859, 77860, 77861, 77862, 77863, 77867, 77871, 77872, 78887.

Stratigraphic range of referred material.—Clarkforkian to Wasatchian, *Plesiadapis cookei* zone to middle Graybullian (*C. trigonodus* zone).

Diagnosis.— Intermediate sized member of the genus about the same size as *A. francesi*; 30-35% larger than *A. atavus*; 25-30% smaller than *A. pattersoni*; differs from *A. francesi* by

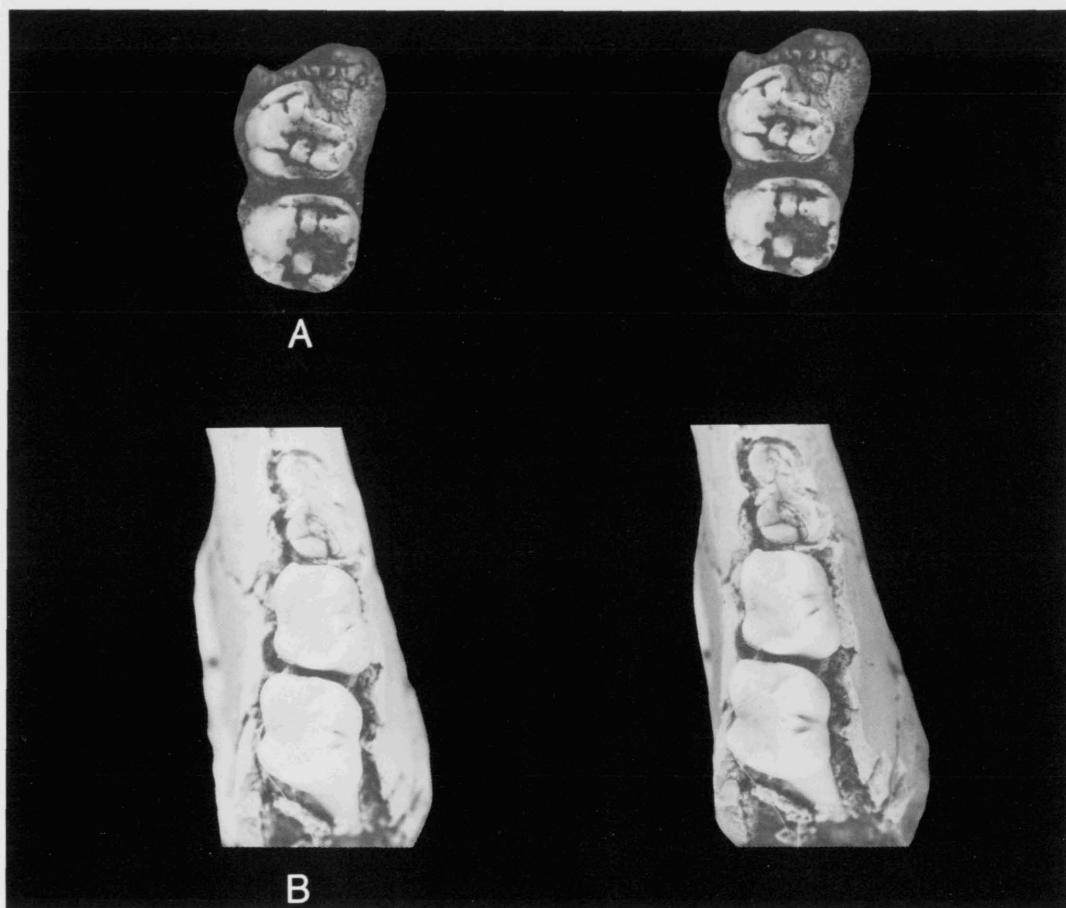


FIG. 9.— Dentition of *Acritoparamys atwateri*. A, UM 64808, left maxilla with M^{1-2} . B, UM 73037, right mandible with M^{1-2} . All specimens in occlusal view, approximately $6\times$ natural size, anterior toward top of page.

smaller hypoconulid, longer metalophid, shorter P^4 , less pronounced metaconule on M^1 , and lack of minor connection of metaconule and hypocone on M^1 and M^2 ; lacks inflated parastyle on P^4 and large metaconule on M^1 and M^2 of *A. wyomingensis*.

Discussion.—Loomis (1907) described the type of *Acritoparamys atwateri* from "the foot of Tatman Mt., near Otto, Wyo." which is probably earliest upper Graybullian in age (Schankler, pers. comm.). The oldest specimen included in the species (UM 71177 from UM locality SC-74) is from the base of the *Plesiadapis cookei* zone of the Clarkforkian, which corresponds to the base of the Eocene (see fig. 2 and Rose, 1981). Specimens described here and elsewhere (Wood, 1962; Korth, 1984) indicate a continuous record of *A. atwateri* from the base of the Eocene to the upper Graybullian and possibly the Lysitean.

Rose (1981) erected a new species, *Paramys annectens*, with PU 19256 from the lower *Plesiadapis cookei* zone of the Clarkforkian as the type, and UM 71177 from the *Plesiadapis cookei* zone as a referred specimen. These two specimens show the isolated entoconid and larger mesoconid of reithroparamyines as compared to paramyines. The shape of the trigonid, amount of isolation of the entoconid, position of the masseteric fossa, and size places these specimens in *Acritoparamys atwateri*, making *P. annectens* a junior synonym.

TABLE 6— Descriptive statistics for measurements of *Acritoparamys atwateri* from the Clarks Fork Basin, Wyoming. Abbreviations as in Tables 1 and 2.

Measurement	N	OR	Mean	S	V	
<i>Upper dentition</i>						
P ⁴	L	2	1.8 - 2.1	1.95	--	--
	W	2	1.9 - 3.0	2.45	--	--
	Ln A	2	1.2 - 1.9	1.54	-	--
M ¹	L	6	2.2 - 2.5	2.35	0.10	4.3
	AW	7	2.4 - 3.1	2.61	0.22	8.4
	Ln A	6	1.7 - 2.1	1.82	0.13	--
M ²	L	8	2.0 - 2.5	2.28	0.13	5.7
	W	7	2.2 - 2.8	2.53	0.22	8.4
	Ln A	7	1.5 - 2.0	1.74	0.14	--
M ³	L	10	2.1 - 2.8	2.45	0.19	7.8
	W	10	2.0 - 2.6	2.36	0.20	8.5
	Ln A	10	1.4 - 1.9	1.74	0.12	--
<i>Lower dentition</i>						
P ₄	L	3	1.7 - 2.3	1.97	0.25	12.7
	AW	3	1.3 - 1.4	1.40	0.08	5.7
	PW	3	1.5 - 2.0	1.83	0.12	6.6
	Ln A	3	1.0 - 1.4	1.15	0.15	--
M ₁	L	17	2.1 - 2.5	2.34	0.13	5.7
	AW	17	1.7 - 2.4	1.95	0.16	8.2
	PW	17	2.0 - 2.5	2.23	0.13	5.8
	Ln A	17	1.4 - 1.7	1.58	0.10	--
M ₂	L	17	2.2 - 2.7	2.38	0.13	5.5
	AW	14	2.0 - 2.5	2.21	0.14	6.3
	PW	16	2.1 - 2.5	2.33	0.13	5.4
	Ln A	14	1.5 - 1.9	1.68	0.10	--
M ₃	L	11	2.6 - 3.1	2.79	0.18	6.6
	AW	11	1.9 - 2.5	2.21	0.17	8.0
	PW	11	1.9 - 2.5	2.10	0.18	8.6
	Ln A	11	1.6 - 2.0	1.79	0.14	--

The two maxillae which Rose (1981) referred to *Paramys* cf. *excavatus*, UM 69335 and UM 69950, show the enlarged molar hypocones, molar size, and anteriorly placed posterior margin of the anterior root of the zygoma characteristic of *A. atwateri* and are so assigned here. Lower dentitions that Rose placed in *P.* cf. *excavatus* are referred above to *P. taurus* and the incisors are discussed under *P. copei*.

The lineage remains in the same size range throughout the stratigraphic section exposed in the Clarks Fork Basin. The morphology changes through the section as the hypoconulid becomes slightly more bulbous and the metalophid and the posterior arm of the protoconid become shorter, resulting in a more posteriorly open trigonid. These changes in morphology approach the characters of *A. francesi* but are not sufficiently great to place the younger specimens in *A. francesi*. Differences between uppers of *A. atwateri* and *A. francesi* are matters of size of cusps (metaconule and hypocone), but the sample of upper teeth is too small to determine if the later members of *A. atwateri* are also trending toward *A. francesi*.

One specimen of *A. atwateri*, UM 71228, is problematic in that the heavily worn teeth are distinctly smaller than those of other specimens designated *A. atwateri*. The size of this specimen is as follows— P_4 : $l = 1.7$, $aw = 1.3$, $pw = 1.5$; M_1 : $l = 1.9$, $aw = 1.6$, $pw = 1.8$; M_2 : $l = 2.0$, $aw = 1.7$, $pw = 2.0$. The discernable morphology of the teeth and jaws is identical with that of other *A. atwateri* specimens so this specimen only differs by smaller size. In the absence of other unworn, small specimens the difference is not considered sufficient to warrant specific designation, and UM 71228 is referred to *Acritoparamys* cf. *atwateri*.

Acritoparamys atwateri resembles the contemporaneous species, *Paramys taurus* and is differentiated by its smaller size, a larger hypoconulid, and an isolated entoconid. These characters vary, and isolated molars of each species at mutual extremes of variation can resemble each other closely. Further ambiguity is introduced by moderate wear of the posterior margin of the tooth, which can remove or reduce the distinguishing characters of the hypoconulid and entoconid. Size becomes the main distinguishing feature with worn specimens, the smaller ones assigned to *A. atwateri* and larger to *P. taurus*.

The intermediate sized species *Paramys pycnus* complicates this distinction. Lower teeth of *P. pycnus* are probably misidentified as larger *A. atwateri* and/or smaller *P. taurus* specimens. From the similarity of *P. pycnus* upper molars to those of *A. atwateri*, the lowers should resemble *A. atwateri*. Without associated uppers and lowers of *P. pycnus* there is at present no way to distinguish these lowers in the material at hand.

Acritoparamys cf. *A. francesi*

Referred specimens.— UM 77803 (RM₁) and 77868 (RM²), from the Clarkforkian, *Phenacodus-Ectocion* zone and the early Wasatchian, Sandcouleean (latest *C. ralstoni* zone), respectively.

Description and discussion.— These specimens are the size of *A. francesi* and *A. atwateri*. The metalophid on M_1 is short and posteriorly directed, leaving the trigonid widely open posteriorly, as in *A. francesi*, but the hypoconulid is smaller than is characteristic for that species. M^2 has a metaconule nearly the size of the metacone which is rounded as in *A. francesi*, but lacks the close association of the metaconule and hypocone. Both specimens are from levels considerably older than the oldest reliably identified *A. francesi* specimens and the scarcity of specimens makes this identification very tentative.

Acritoparamys cf. *A. pattersoni*

Referred specimens.— UM 72177 (LM₁, RM₂), 77839 (LM₁), 77845 (LM₁), from the early Wasatchian, Sandcouleean (*C. ralstoni* zone) (UM 72177, 77845) and early Graybullian (*C. mckennai* zone) (UM 77839).

Description and discussion.— These *Acritoparamys* molars are in the size range of *A. pattersoni* but lack either the posteriorly open trigonid (UM 77845) or the bulbous cusps (UM 72177) of the species. M_1 , UM 77839, is similar to Wood's description and figure of the type of this species. All the specimens predate the earliest previously known specimens of the species from the Lost Cabin equivalent of the Debeque Formation. The scarcity of material, particularly P_4 , requires only a tentative referral of these specimens to *A. pattersoni*.

Acritoparamys sp. indet.

Referred specimens.— UM 75881 (L mand. with $M_{1,2}$), 77722 (RM₁), 77736 (RdP₄), 77738 (LP₄), 77797 (RM₁), 77800 (LM₂), 77847 (LM₂), 77879 (RM₂), and 78891 (RdP₄) from the Clarkforkian, *Plesiadapis cookei* zone to the early Wasatchian, early Graybullian (*C. ralstoni* zone).

Description and discussion.— These unassociated specimens fall into two groups, the first group (UM 75881, 77736, 77880, 77847, 77879, 78891) is near the size of *A. atwateri* and the second group (UM 77722, 77738) is near the size of *A. atavus*. The mandible UM 75881 from the Sandcouleean contains molars that are very worn and broken so that only size, shape, position of the masseteric fossa, and position of the mental foramina place this specimen in *Acritoparamys*. The dP_4 s (UM 77736 from the *Plesiadapis cookei* zone and UM 78891 from the early Graybullian) are the correct size for *A. atwateri* but there is no referred dP_4 in this species to compare them to. M_1 , UM 77797, from the *Phenacodus-Ectocion* zone is elongate with an anteroposteriorly expanded trigonid and double connection of metaconid and protoconid like *Reithroparamys debequensis* but without the requisite entoconid crest. M_2 , UM 77800, from the Sandcouleean is rhomboidal with an enclosed trigonid basin, elongate hypoconid, high metaconid, and small mesoconid. The protoconid is worn but the course of the anterior cingulum suggests that the cingulum and protoconid are separated. M_2 , UM 77847, from the Sandcouleean resembles M_2 of *Paramys excavatus* in square shape, small mesoconid, and trigonid, but the hypoconulid is larger than characteristic for that species and the entoconid is isolated by a narrow groove as in reithroparamyines. The upper molar, UM 77879, from the *Phenacodus-Ectocion* zone resembles *A. francesi* uppers in the close association of the metaconule and hypocone and the anterior cingulum expanded in the parastylar region, but the metaconule is much smaller than the metacone, contrary to the diagnosis of *A. francesi*.

Of the small members of this group the M_1 , UM 77722, from the *Plesiadapis cookei* zone has a deep trigonid basin set off by a narrow anterior cingulum and metalophid. An arm from the metaconid enters the center of the basin, but no corresponding arm of the protoconid is present. The anterior cingulum is not separated from the protoconid as is the case in *Microparamys*, and the hypoconulid is small and in the center of the posterior lophid. The lower premolar, UM 77738, from the *Phenacodus-Ectocion* zone resembles the premolar of *A. atavus* but is too large.

Lophioparamys Wood, 1962

Paramys (in part), Leidy, 1871, p. 231.
Lophioparamys Wood, 1962, p. 167.

Type species.— *Paramys murinus* Matthew, 1918.

Included species.— Type; *Lophioparamys debequensis* Wood, 1962; and *L. woodi* Guthrie, 1971.

Diagnosis.— Differs from other reithroparamyine genera by the presence of a highly complex pattern of ridges and crests in basins. Except for these crenulations, it resembles *Microparamys* closely; about 20% smaller than *Reithroparamys*; differs from *Thisbemyis*, the other paramyid with crenulated enamel, by more prominent ridges and smaller size (app. 50%).

Lophioparamys murinus (Matthew, 1918)

Fig. 8f

Paramys murinus Matthew, 1918, p. 617, fig. 37.
Lophioparamys murinus, Wood, 1962, p. 168, fig. 56A-C.

Type.— AMNH 15131, right and left mandibles with all teeth but RP_4 , from "Gray Bull beds of the Wasatch (Willwood) formation, Bighorn Basin, Wyoming."

Referred specimens.— UM 75094, left mandible with M_2 ; UM 75650, right mandible with heavily worn M_2 .

Occurrence of referred material.— Sandcouleean of the early Wasatchian (*C. ralstoni* zone) for UM 75094, middle Graybullian of the middle Wasatchian (*C. trigonodus* zone) for UM 75650.

Diagnosis.— Very complex crenulations in basins; metalophid larger than other species with posteriorly convex bend; 20-25% larger than *L. debequensis*, which has a straight metalophid; 10-20% smaller than *L. woodi*.

Discussion.— *Lophioparamys murinus* is known in the Clarks Fork Basin only by two M_2 s, one of which is so heavily worn that only the crenulations remain to permit generic distinction. Both specimens are slightly smaller than the type specimen with $l = 1.8$, $aw = 1.8$, and $pw = 1.9$ for UM 75094; width = 1.7 for the broken and worn UM 75650. The specimens are 15-20% larger than the only known M_2 of *L. debequensis*, the next smaller species (Wood, 1965). The relationship of the entoconid and hypoconulid, what can be seen of the metalophid, the patterns of the crenulations in the talonid, and the manner of separation of the anterior cingulum all agree with *L. murinus*. Previously the only known specimen of *L. murinus* was the type from "Gray Bull beds of the Wasatch formation, Bighorn Basin, Wyoming" (Mathew, 1918). The unworn specimen (UM 75094) described here is slightly older than the type, extending the range of the species to near the base of the Wasatchian. This specimen indicates that the prominence of the metalophid can be quickly reduced by wear, suggesting that metalophid shape may not be a useful character in distinguishing worn specimens of *Lophioparamys*. Available specimens suggest that there are clusters representing distinct size groups, so that size may be the most useful character to distinguish species in this genus.

Microparamys Wood, 1959a

Paramys (in part), Leidy, 1871, p. 231.

Microparamys Wood, 1959a, p. 162. Wood, 1962, p. 158.

Type.— *Paramys minutus* Wilson, 1937.

Included species.— Type; *Microparamys cheradius* new species; *M. dubius* (Wood, 1949); *M. hunterae*, new species; *M. perfossus* Wood, 1974; *M. reginensis* Korth, 1984; *M. scopaiodon* Korth, 1984; *M. tricus* (Wilson, 1940); and *M. sp D* Wood, 1962.

Diagnosis.— Small paramyids; anterior cingulum on lowers separated from protoconid; hypocone separated from protocone on uppers; posterior margin of anterior root of zygoma even with anterior margin of P^4 ; differs from *Lophioparamys* by lack of crenulations in basins of molars; differs from all other reithroparamyine genera by separation of the anterior cingulum from the protoconid; has less isolated entoconid and larger hypocone than *Acritoparamys*; 40-60% smaller than *Reithroparamys* and lacks entoconid crest into talonid; has smaller hypocone and more posterior anterior root of zygoma than *Apatosciuravus*.

Discussion.— When erecting this genus, Wood (1962) thought that the specimens he described were too varied to long remain in one genus. Subsequent work has proven this correct as several species have been removed to other genera (see Korth, 1984 for a discussion). Guthrie (1971) maintained that the genus did not extend into the lower Eocene after he removed *M. lysitensis* and *M. cathedralis* to *Knightomys*, but the two species named by Korth and the species described here indicate that *Microparamys* extends nearly to the base of the Clarkforkian and at least to the base of the Eocene.

Microparamys cheradius new species

Figs. 10, 11. Table 7

Type.— UM 73609, left mandible with dP_4 - M_2 , from UM locality SC-188, *Plesiadapis cookei* zone of the Clarkforkian.

Referred specimens.— Isolated lowers: UM 77719, 77720, 77753, 77775, 77781, 77782, 77784, 77919, 78876. Isolated uppers: UM 72057, 77713, 77726, 77728, 77733, 77739, 77744, 77758, 77767, 77769, 78875, 78878, 78883, 78884, 78885.



FIG. 10—*Microparamys cheradius*, UM 73609 (holotype), left dentary with dP_4 - M_2 . A, occlusal view. B, lateral view.

Stratigraphic range.— Clarkforkian to middle Wasatchian, referred specimens are from UM locality SC-188, *Plesiadapis cookei* zone of the Clarkforkian, and from the *Phenacodus-Ectocion* zone; two questionably referred specimens are from the early and middle Graybullian of the Wasatchian (*C. mckennai* and *C. trigonodus* zones).

Etymology.— *cheras*, Gr., silt or mud; in reference to the depositional material of the type locality.

Diagnosis.— About the same size as *M. minutus* but has higher trigonid, more complete metalophid, less separated anterior cingulum, an arm from the metaconid entering the trigonid basin, and a less isolated entoconid; differs from *M. scopaiodon* by larger, higher trigonid, complete transverse metalophid, swelling of metaconid into trigonid, more rounded mesoconid, less isolated and smaller entoconid; 25% larger than *M. reginensis* and *M. hunterae*.

Description.— The molars of *Microparamys cheradius* are rhomboidal in occlusal outline and M_1 is smaller than M_2 . dP_4 is elongate with widely separated, subequal protoconid and metaconid in an elevated trigonid. An anterior cingulum closes the trigonid basin anteriorly and is expanded into a small cusp anterior to the metaconid. There is a minute mesoconid on the high ectolophid. The posterior margin of dP_4 is rounded and covered by the anterior margin of M_1 in the type. The entoconid is set forward of the posterior margin of the tooth which curves anterolingually to meet the entoconid. There are no other P_4 s that can be reliably referred to this species.

The M_1 is nearly rectilinear in occlusal outline with a wide trigonid area nearly the width of the posterior margin of the tooth. The anterior cingulum extends labially to just beyond the middle of the protoconid, from which it is separated by a shallow valley that is eliminated by wear. The lingual extent of the anterior cingulum is to near the lingual edge of the metaconid and the anterior cingulum forms a narrow shelf along the anterior metaconid face. The metalophid is complete, going from the protoconid up onto the posterior face of the metaconid and closing the trigonid basin posteriorly. The trigonid basin is half filled by a wide labial expansion of the metaconid. The mesoconid is large, rounded, and connected to the protoconid and hypoconid by a low, narrow ectolophid. The rounded hypoconid is connected to the hypoconulid by a ridge which makes an oblique angle with the hypoconulid. The hypoconulid is longer than half the posterior lophid and is separated from the high, rounded entoconid by a shallow, pinching groove. The entoconid is set slightly forward of the posterior margin and is separated from the metaconid by a deep valley without a metastylid.

M_2 is very similar to M_1 except for a wider trigonid and the entoconid more separated from the hypoconulid.



FIG. 11— Dentition of *Microparamys cheradius*. A, UM 77758, RP^4 , anterior to right. B, UM 72057, $RM^{1\alpha 2}$, anterior to right. C, UM 78875, RM^3 , anterior to right. D, UM 77720, RM_3 , anterior toward top of page. E, UM 73609 (holotype), left mandible with dP_4-M_2 , anterior toward top of page. All specimens in occlusal view, approximately 12 \times natural size.

TABLE 7— Descriptive statistics for measurements of *Microparamys cheradius* from the Clarks Fork Basin, Wyoming. M¹ and M² here cannot be distinguished. Abbreviations as in Tables 1 and 2.

Measurement	N	OR	Mean	S	V	
<i>Upper dentition</i>						
P ⁴	L	2	1.4 - 1.4	1.38	--	--
	W	2	1.6 - 1.7	1.65	--	--
	Ln A	2	0.8 - 0.9	0.82	--	--
M ^{1,2}	L	8	1.5 - 1.7	1.58	0.07	4.4
	W	8	1.7 - 1.9	1.83	0.07	3.6
	Ln A	8	0.9 - 1.2	1.05	0.07	--
M ³	L	4	1.8 - 1.9	1.88	0.04	2.7
	W	4	1.7 - 1.7	1.70	--	--
	Ln A	4	1.1 - 1.2	1.16	0.02	--
<i>Lower dentition</i>						
M ₁	L	1	1.6	--	--	--
	AW	1	1.4	--	--	--
	PW	1	1.5	--	--	--
	Ln A	1	0.8	--	--	--
M ₂	L	8	1.5 - 1.8	1.68	0.11	6.5
	AW	7	1.3 - 1.6	1.46	0.09	6.2
	PW	7	1.5 - 1.7	1.60	0.08	5.0
	Ln A	7	0.7 - 1.1	0.96	0.10	--
M ₃	L	1	2.0	--	--	--
	AW	1	1.7	--	--	--
	PW	1	1.6	--	--	--
	Ln A	1	1.2	--	--	--

M₃ has an anterior cingulum and metalophid similar to M₁ and M₂, but the labial extension of the metaconid into the trigonid basin is absent and the trigonid is anteroposteriorly compressed. The posterior margin is formed by the enlarged hypoconid and smaller hypoconulid. The entoconid is separated from the hypoconulid by a notch, is anteroposteriorly elongated, and is forward along the lingual margin, level with the posterior half of the mesoconid. Anterior to the entoconid is a large, rounded metastylid separated from the entoconid by a deep notch and the metaconid by a shallower notch.

The mandible is slender with a sharp, dorsal keel in the diastema. There are two mental foramina. The large, anterior foramen is under the posterior end of the diastema and the smaller, posterior foramen is under the anterior margin of M₁ at the same level as the anterior foramen. The masseteric fossa ends under the anterior margin of M₂. The type does not retain an incisor and since small paramyid incisors are all closely similar, assignment of any isolated incisor to this species was not considered justifiable.

The upper dentition is represented by isolated teeth which can be only tentatively assigned to this species. On P⁴ the anterior cingulum originates low on the protocone and extends labially to end low on the paracone even with the apex of the paracone. The paracone and metacone are subequal size pyramids which are separated by a valley containing a small mesostyle. The protoloph is thin with a small protoconule. The metaloph contains a large metaconule separated from the metacone and connected to the protocone. The hypocone is a large swelling of the posterior cingulum separated from the protocone by a deep groove and from the metaconule by a wide valley. The wide posterior cingulum extends to the labial

margin of the tooth as far as the apex of the metacone, from which it is separated by a shallow groove.

M¹ and M² are equal in morphology and squarish in occlusal outline with elongate anterior and posterior cingula, complete protoloph with protoconule, and a large, isolated metaconule. The paracone and metacone are subequal in size and the intervening mesostyle is anteroposteriorly elongated and labial to the apexes of the cones. The hypocone is separated from the protocone by a wide valley that extends labially between the metaloph and the wide, cusped posterior cingulum. The lophs converge on the protocone, which is set lingual to the hypocone. There is variation in the connection of the metaconule to the protocone, ranging from a thin ridge to a wide loph. The protoloph often has a protoconular swelling between the loph and the anterior cingulum. The separation of M¹ from M² is difficult in isolated uppers without a maxilla for reference and such a delineation was not thought justified in the material at hand.

M³ has a wide anterior cingulum which is separated from the paracone and protocone by a groove. The anterior portion of M³ is otherwise like M¹⁻². The posterior extension of the tooth is formed by a swelling which may correspond to the metacone. An elongate swelling connected to the protocone by a ridge is present in the basin in the area of the metaconule. The labial margin contains an elongate mesostyle separated from the metacone by a deep groove. A swelling on the posterolingual corner of the tooth, adjacent to the protocone and isolated by a shallow groove, corresponds to the posterior cingulum.

Discussion.— *Microparamys cheradius* is in the same size range as *Acritoparamys atavus* but has a less isolated entoconid and the separated anterior cingulum of *Microparamys*. The high trigonid, less separated anterior cingulum, and older occurrence distinguish this species from *M. minutus* and *M. scopaiodon*. Two specimens UM 77781 and 77784 are questionably referred to this species because the trigonid on these specimens is anteroposteriorly compressed, the labial extension of the metaconid into the trigonid basin is reduced and the hypoconulid is labially situated resulting in a more isolated entoconid than is characteristic for *M. cheradius*. These specimens approach *M. minutus* in morphology but the height of the trigonid and the small separation of the anterior cingulum are not characteristic of *M. minutus*. These may be transitional forms between *M. cheradius* and *M. minutus* in that they are from localities higher in the section than the rest of the species.

The association of upper cheek teeth with the lowers described above is somewhat arbitrary since there is as yet no known natural association. Uppers assigned to this species are in the size range expected, have an enlarged hypocone over similar sized *Acritoparamys atavus* specimens, as expected in *Microparamys*, and are from the same locality as the lowers (SC-188). The uppers are relatively cusped and resemble *A. atavus* in features other than the hypocone such that they appear "primitive", as would be expected in such early members of *Microparamys*. Other small upper molars from the Clarks Fork Basin have the large hypocones of *Microparamys* but are less like *A. atavus* than the uppers described here. While these other uppers may be truly associated with the lowers of *M. cheradius* there is presently no way to decide. Assignment of the described upper cheek teeth to this specimen is only tentative, therefore, and may be invalidated by the discovery of better material.

***Microparamys hunterae* new species**

Figs. 12, 13a. Table 8

Type.— UM 66968, left mandible with M₁ talonid, M₂, and labial half of M₃, from UM locality SC-123, early Wasatchian, Sandcouleean (*C. ralstoni* zone).

Referred specimens.— Type only.

Etymology.— Named for Elizabeth Hunter who found the type specimen in July of 1976.

Diagnosis.— Approximately same size as *M. reginensis* but differs by having only one mental foramen, a shorter, less well separated anterior cingulum, and larger, less elongate mesoconids; similar to *M. scopaiodon* but has less elongate mesoconid and is 20% smaller;

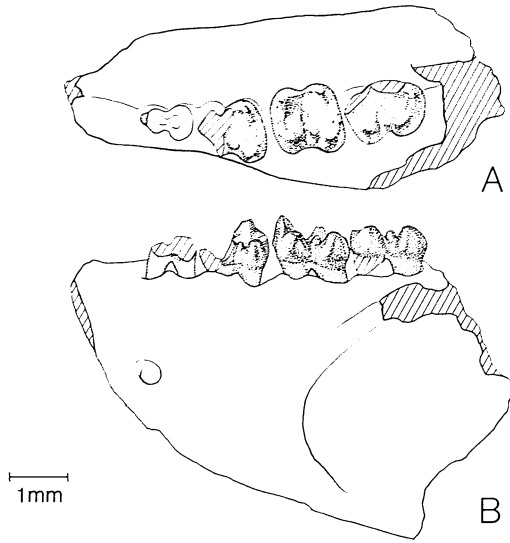


FIG. 12—*Microparamys hunterae*, UM 66968 (holotype), left dentary with $M_{1,3}$. A, occlusal view. B, lateral view.

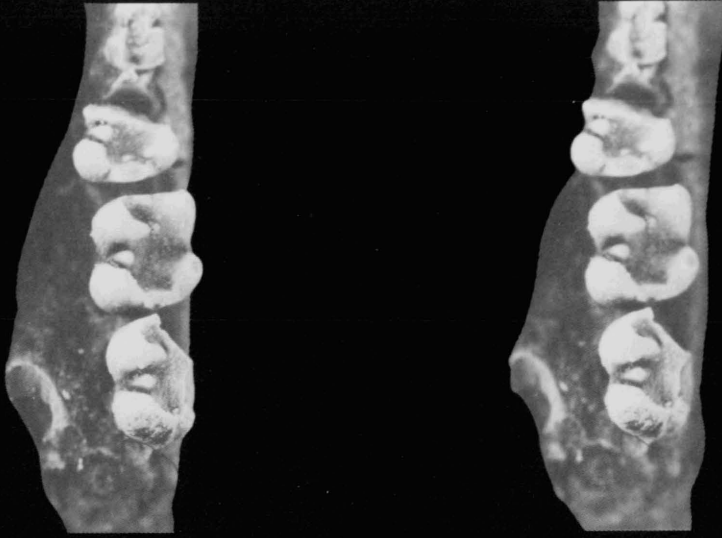
20% smaller than *M. minutus* and *M. cheradius*, has less complete, more oblique metalophid, and less well separated anterior cingulum.

Description.— The type of *Microparamys hunterae* retains the talonid of M_1 , all of M_2 , and the labial half of M_3 . From the size of the roots P_4 was approximately 70% the length of M_1 or M_2 . The talonid of M_1 shows a large, separated, round mesoconid inset from the labial margin. There is no ectolophid. The hypoconulid is distinct, separated from the hypoconid by a shallow groove and the entoconid by a deep valley. The posterior margin curves anterolingually to meet the isolated entoconid. The entoconid has a short crest running out from the labial face into the talonid basin, similar to the crest seen in *Reithroparamys*.

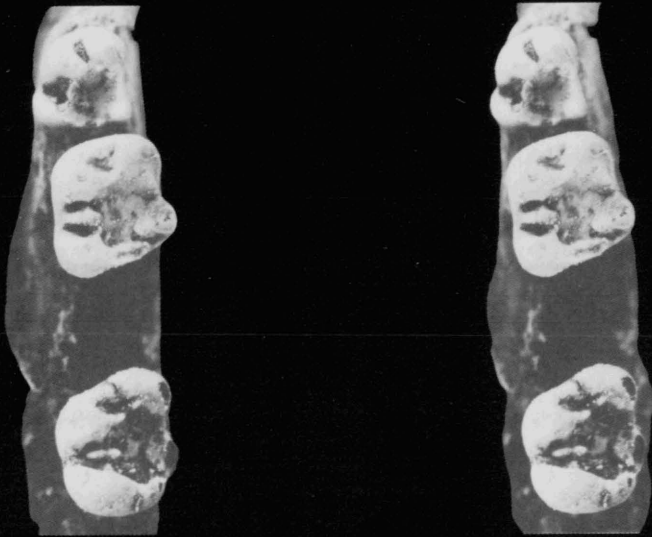
The M_2 is complete and has a low anterior cingulum that is only slightly separated from the protoconid. The anterior cingulum closes off the trigonid anteriorly and extends lingually to midway along the anterior margin of the labiolingually narrow metaconid. The metaconid is situated in the anterior-lingual corner of the tooth. The trigonid is open anteriorly since the high metalophid that extends from the protoconid does not reach the base of the metaconid. The mesoconid is as in M_1 . The hypoconid extends a short arm anteriorly to the labial side of the mesoconid. The posterior lophid is widely connected to the hypoconid and contains a hypoconulid that is one-third the tooth width long and separated from the entoconid by a narrower and shallower groove than the same feature in M_1 . The entoconid is similar to that of the M_1 but lacks the short ridge into the talonid basin. There is no metastylid present and the entoconid is separated from the metaconid by a deep valley nearly to the level of the talonid.

The labial half of M_3 reveals a high anterior cingulum which apparently is set more anterior than in M_2 . Separation of the anterior cingulum and protoconid is not as great as in M_2 . The remainder of the anterior of M_3 is closely similar to M_2 . The posterior margin is formed by a backward extension of the hypoconid with a strongly connected posterior lophid, and the apparent posterolingual corner is formed by the hypoconulid which is separated from the hypoconid by a shallow groove.

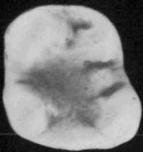
The mandible is deep for the size of the teeth when compared with other small forms of *Microparamys*, and it has only one mental foramen low under the anterior margin of P_4 . The masseteric fossa is delineated by a heavy ridge and ends under the anterior margin of M_2 . The anterior margin of the lower incisor is rounded, the medial side is flat, the lateral side is



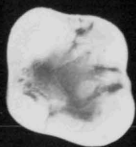
A



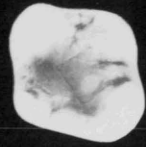
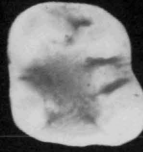
B



C



D



rounded, and the widest part of the lower incisor is about half way back from the anterior face. The enamel just reaches the medial margin and the lateral extent of the enamel is covered.

Discussion.— In form if not in size *Microparamys hunterae* most resembles *M. scopaiodon* from the middle Wasatchian, middle Graybullian locality Hackberry Hollow in the northern Bighorn Basin (UM locality SC-192). *M. hunterae* and *M. scopaiodon* may be ancestor-descendant, although there is some indication that *M. scopaiodon* is present in the middle Clarkforkian (see below). The most probable relationship is that the two species share a common ancestor, perhaps in the earliest Clarkforkian.

M. hunterae resembles *Pauromys* Troxell, 1923 in such features as the single mental foramen, the size and oblique direction of the metalophid, the posteriorly open trigonid, and the large separation of the entoconid from the posterior lophid on M_1 . Separation of the anterior cingulum from the protoconid in *M. hunterae* is not as great as in *Pauromys*, nor is the lingual end of the cingulum separated from the metaconid as in the latter genus. *M. hunterae* lacks the hypolophid characteristic of sciuravids, the masseteric fossa ends more posteriorly than is characteristic of *Pauromys*, and the mesoconid is not anteroposteriorly compressed and labiolingually elongate as in *Pauromys*. *Microparamys hunterae* displays a mosaic of characters intermediate between later microparamyines and sciuravids. The lack of the sciuravid lophate characteristics and the presence of the diagnostic separation of the anterior cingulum places *M. hunterae* in *Microparamys*.

Microparamys cf. *M. minutus*

Referred specimens.— UM 77731 (RM₂), 77785 (LM₂), 78892 (RM³), from the Clarkforkian, *Plesiadapis cookei* zone and the early Wasatchian, Sandcouleean (*C. ralstoni* zone) and early Graybullian (*C. mckennai* zone), respectively.

Description and discussion.— The specimens are near the size of *M. minutus*, fall within the morphological variation of the species (Dawson, 1967), and do not exhibit the distinguishing characteristics of *M. scopaiodon* or *M. cheradius*. The age of the specimens is older than the oldest previously reported occurrence of this species and the worn nature of the specimens makes this identification tentative.

Microparamys cf. *M. scopaiodon*

Referred specimen.— UM 77711 (RM₂), from the Clarkforkian, *Plesiadapis cookei* zone.

Description and discussion.— This specimen is missing the anterolingual corner to near the protoconid so that positive identification is impossible. The size, shape of the mesoconid, configuration of the posterior lophid and entoconid, and what can be seen of the anterior cingulum and its relation to the protoconid agree with *M. scopaiodon*.

←

FIG. 13— Dentition of *Microparamys hunterae*, *Knighthomys cremneus*, *Reithroparamys* cf. *debequensis*, and *Reithroparamys* sp. indet. A, *Microparamys hunterae*, UM 69968 (holotype), left mandible with M_1 - M_3 , approximately 12× natural size. B, *Knighthomys cremneus*, UM 73257 (holotype), left mandible with P_4 - $M_{1,3}$, approximately 12× natural size. C, *Reithroparamys* cf. *debequensis*, UM 77853, RM₁, approximately 6× natural size. D, *Reithroparamys* sp. indet., UM 77771, RM₂, approximately 6× natural size. All specimens in occlusal view, anterior toward top of page.

TABLE 8— Measurements of teeth of *Microparamys hunterae*, *Reithroparamys* sp. indet., Cf. *Notoparamys* sp., *Paramys pycnus* from the Clarks Fork Basin. Abbreviations as in Tables 1 and 2.

Species	Specimen	Tooth	L	AW	PW	Ln A
<i>Microparamys hunterae</i>	UM 66968	M ₁	--	--	1.1	--
	"	M ₂	1.2	1.1	1.2	0.32
	"	M ₃	1.4	--	--	--
<i>Reithroparamys</i> sp. indet.	UM 77700	M ₂	2.8	2.8	2.9	2.08
	UM 77742	M ₂	2.7	2.3	2.5	1.87
	UM 77771	M ₂	3.0	2.7	2.8	2.11
Cf. <i>Notoparamys</i> sp.	UM 67282	M ¹ (L)	4.1	4.4	--	2.89
	"	M ¹ (R)	3.8	4.5	--	2.84
	"	M ² (L)	3.9	4.7	--	2.91
	"	M ² (R)	3.8	4.5	--	2.84
<i>Paramys pycnus</i>	UM 76249	P ⁴	1.8	2.1	--	1.33
	"	M ¹	2.1	2.3	--	1.60
	"	M ²	2.2	2.6	--	1.74
	UM 77881	M ¹	2.3	2.8	--	1.86

Microparamys sp. indet.

Referred specimens.— UM 76460 (L mandible with P₄ and M₂), 77707 (RP⁴), 77732 (RM¹), 77766 (RP⁴), 77770 (LM₃), 77777 (RM₃), 77778 (LP⁴), 78874 (RM²). All but one specimen are from UM locality SC-188, *Plesiadapis cookei* zone of the Clarkforkian, UM 76460 is from the early Wasatchian, Sandcouleean (*C. ralstoni* zone).

Description and discussion.— The mandible, UM 76460, is referable to *Microparamys* by the lingual margin of the broken M₂ which shows the anterior cingulum separated from the protoconid by a narrow groove. The masseteric fossa ends below the anterior margin of M₂ and a small mental foramen is preserved under the talonid of P₄. The hypoconulid on M₂ was apparently well separated from the entoconid since the large, lingual slope of the hypoconulid is preserved. The specimen is larger than any known *Microparamys* species from this level, making the assignment tentative.

The specimens of P⁴, UM 77707 and 77778, are small, have larger hypocones, and are not as anteroposteriorly compressed as premolars of *A. atavus*, the other possible assignation. Lower premolars assigned to *Microparamys* can be separated into two groups. The group listed here was arbitrarily assigned to *Microparamys* sp. indet. whereas the other group of premolars was arbitrarily assigned to *M. cheradius*. Specimens of M₃, UM 77770 and 77777, have the separated anterior cingulum of this genus, an isolated entoconid, and an accessory cusp posterior and labial to the mesoconid. These M₃s are the same size as in *M. cheradius* but were not included due to the metalophids not reaching the metaconid. They have a less separated anterior cingulum than *M. minutus*.

The group of small specimens, UM 77732, 77766, and 78874, are all uppers with wide cingula, thin lochs, and small conules. The hypocone is of a size typical of *Microparamys* and linguallly placed on the molars, and the metacone is separated from the posterior margin of the tooth by the elongate posterior cingulum.

Reithroparamys Matthew, 1920

Paramys (in part), Leidy, 1871, p. 231.

Reithroparamys Matthew, 1920, p. 168. Wood, 1962, p. 118.

Type.— *Paramys delicatissimus* Leidy, 1871 .

Included species.— *Type*; *Reithroparamys debequensis* Wood, 1962; *R. huerfanensis* Wood, 1962; *R. matthewi* Wood, 1962; and *R. gidleyi* (Peterson, 1919).

Diagnosis.— Medium size paramyids; crest from entoconid into talonid toward ectolophid; single mental foramen; differ from other reithroparamyine genera by presence of entoconid crest; lack second mental foramen of *Acritoparamys*; 40-60% larger than *Microparamys* and lack separation of anterior cingulum; 40-50% larger than *Lophioparamys* and lack crenulations of the enamel.

Reithroparamys cf. *R. debequensis* Wood, 1962

Fig. 13c

Reithroparamys debequensis Wood, 1962, p. 134, fig. 45D-G. Korth, 1984, p. 28, fig. 11.

Type.— FMNH P-26726, left mandible with P₄-M₃, from Lysite Horizon of Debeque Fm., near Rifle, Colorado.

Referred specimens.— UM 77804, LM₁; 77853, RM₁

Stratigraphic range of referred material.— Middle Wasatchian, middle Graybullian (*C. trigonodus* zone).

Diagnosis.— About the same size as *R. huerfanensis* but has shorter entoconid crest, double connection of metaconid with protoconid, more elongate M₁, and anterior cingulum distinct from metaconid. Differs from *R. delicatissimus*, *R. matthewi*, and *R. gidleyi* by shorter entoconid crest and less complete metalophid.

Discussion.— Wood (1962) has adequately described the lower cheek teeth of *Reithroparamys debequensis*. Specimens referred here are widely different in size, but they resemble *R. debequensis* more than other species of the genus and do not differ sufficiently to justify a new species on such scanty material. UM 77853 with measurements of $l = 3.2$, $aw = 2.7$, and $pw = 3.0$ is closer to the size of *R. gidleyi*, but lacks the long entoconid crest of that species. Further, UM 77853 has the double metaconid to protoconid connection and enlarged mesoconid of *R. debequensis*. UM 77804 is smaller with measurements of $l = 2.5$, $aw = 1.9$, and $pw = 2.3$, and similarly resembles *R. debequensis*.

Reithroparamys sp. indet.

Fig. 13d. Table 8

Referred specimens.— UM 77700, LM₂; 77742, LM₂; 77771, RM₂.

Occurrence.— The three specimens are from UM locality SC-188 in the *Plesiadapis cookei* zone of the Clarkforkian.

Description.— These isolated molars have a rhomboidal occlusal outline and prominent metaconids. The anterior cingulum is short, connected to the metaconid, and separated from the protoconid by a shallow groove that disappears with wear. The metalophid is short and connects the metaconid to the protoconid, posteriorly enclosing the minute, high trigonid basin. Two posterior arms of the protoconid descend the posterior face of the trigonid, one directed toward the entoconid and the other directed toward the lingual end of the hypoconulid. The large mesoconid is connected to the protoconid and hypoconid by a very low ectolophid. The mesoconid extends into the talonid toward the entoconid. The hypoconid is rounded, has only a minor anterior extension labial to the mesoconid, and is connected to the enlarged

hypoconulid by a short ridge. The hypoconulid is separated from the entoconid by a notch which persists through much wear. The entoconid is the smallest main cusp on the tooth, situated in the posterolingual corner. A crest extends from the entoconid into the talonid basin parallel to the hypoconulid, reaching the level of the middle of the hypoconulid. The entoconid is separated from the metaconid by a lingual notch raised slightly above the floor of the talonid. A short ridge enters the anterior part of the notch from low on the posterolingual edge of the metaconid and may correspond to a metastylid.

Discussion.— The specimens described here resemble members of *Reithroparamys* in size, presence of an entoconid crest, separation of the hypoconulid from the entoconid, and shape of the trigonid. In no complex of features are the specimens referable to any described species of *Reithroparamys*, however. The specimens most resemble *R. mathewi* in the shape of trigonid, length of entoconid crest, and size, but the shape of the mesoconid and hypoconid disagree with those of *R. mathewi*. Separation of the anterior cingulum from the protoconid also distinguishes these specimens from other *Reithroparamys* species. The anterior cingulum does not extend labially but ends at the lingual margin of the protoconid, differing from the style of anterior cingulum separation seen in *Microparamys*. The material at hand consists of two slightly worn molars and one very worn molar. This material is not considered sufficient to erect a new species.

Reithroparamyinae gen. and sp. indet.

Referred specimens.— UM 73927 (LdP₄), 77702 (RM²), 77714 (RM¹), 77725 (LdP⁴), 77746 (RM¹), 77776 (LM¹), 77779 (LP⁴), 77780 (RdP⁴), 77869 (RM¹), 77880 (LM²), 77882 (RP⁴), 77892 (RdP⁴), 78879 (LM²), from the Clarkforkian, *Plesiadapis cookei* zone to the middle Wasatchian, middle Graybullian (*C. trigonodus* zone).

Description and discussion.— The dP₄, UM 73927, from the lower Graybullian is elongate with a distinct cusp anterior to the metaconid, a widely separated protoconid and metaconid, and an isolated entoconid. Due to a lack of referred dP₄s from known species, this specimen could not be identified beyond the subfamily. The three specimens of dP⁴, UM 77725, 77780, and 77892, from the *Plesiadapis cookei* zone, middle Graybullian, and early Graybullian, respectively, are similarly unassignable. P⁴ UM 77882 from the *P. cookei* zone is a relatively large tooth near the size of *A. atwateri* with a distinct hypoconulid swelling on the posterior cingulum, but the tooth is anteroposteriorly compressed and has a more lingually placed paracone than *A. atwateri*. P⁴ UM 77779 from the *Phenacodus-Ectocion* zone is the same size as P⁴ of *Acritoparamys atavus*, but it has a larger hypocone and an elongate mesostyle. The tooth is too anteroposteriorly compressed to belong to *Microparamys*.

The two upper molars, UM 77776 and 77869, from the *P. cookei* zone and the Sandcouleean, respectively, have long cingula which extend to a point labial to the paracone and metacone, connecting with a shelf along the labial margin of the tooth. The paracone and metacone are small and subequal in size, the posterior cingulum contains small cusps, and the hypocone is lingually positioned. The two molars differ in that UM 77869 has a double metaconule, less expanded parastylar region, and a smaller mesostyle invading the trigon than UM 77776.

Two upper molars, UM 78879 and 77880, from the Sandcouleean and middle Graybullian, respectively, are almost circular in occlusal outline with high cingula, thin lophs with elongate conules, small hypocones for the genus, and low, elongate mesostyles. The lophs converge as in other reithroparamyines.

Three small upper molars, UM 77702, 77714, and 77746, from the *P. cookei* zone have a large hypocone typical of *Microparamys*, a wide anterior cingulum, complete lophs, and are near the size of *M. cheradius*. The lophs are parallel as opposed to converging. These may be variants of *M. cheradius*.

Subfamily Pseudoparamyinae Michaux, 1964

Franimys Wood, 1962Cf. *Franimys amherstensis*, Wood, 1962

Referred specimens.— UM 77856 (LM²), 77875 (RM²), from the Wasatchian, early and middle Graybullian (*C. mckennai* and *C. trigonodus* zones), respectively.

Description and discussion.— These two specimens resemble M² of *F. amherstensis* in position of the hypocone, length of the posterior cingulum, size, and shape. The type and only specimen of *F. amherstensis* is quite worn so that little other information is available for identification. These specimens are from considerably later than the type and may be assignable to other species.

Family SCIURAVIDAE Miller and Gidley, 1918

Knightomys Gazin, 1961

Tillomys (in part), Marsh, 1872, p. 219.

Sciuravus (in part), Marsh, 1871, p. 122.

Microparamys (in part), Wood, 1959, p. 162.

Dawsonomys (in part), Gazin, 1961, p. 94.

Knightomys Gazin, 1961, p. 193.

Type species.— *Tillomys senior* Gazin, 1952

Included species.— Type; *Knightomys cremneus* new species; *K. depressus* (Loomis, 1907); *K. huerfanensis* (Wood, 1962); and *K. minor* (Wood, 1965).

Emended diagnosis.— Small sciuravids with cusped cheek teeth; isolated entoconid with incomplete hypolophid entering talonid; mesoconid distinct and extends into talonid; second minute mental foramen variably present on mandible posterior to larger foramen; less lophate than *Dawsonomys* with incomplete hypolophid and lack high, enclosed, trigonid; lack separation of the anterior cingulum from metaconid, are 30-40% larger, and have a relatively larger P₄ than *Pauromys*; less lophate than *Sciuravus*.

Discussion.— Gazin (1961) erected *Knightomys* after the discovery of more complete material of *Tillomys senior* Gazin, 1952 from the Knight member of the Wasatch Formation indicated that *T. senior* was sufficiently distinct from other members of *Tillomys* to warrant generic status. Wood (1965) added *Sciuravus depressus* Loomis, 1907 to the genus and included the degree of loph importance vs. cusp importance as a defining character. Guthrie (1971) synonymized *Microparamys lysitensis* Wood, 1962 and *M. cathedralis* Wood, 1962 with *K. depressus*, stating that the observed differences were due to heavy wear reducing the molar crest height of the "*Microparamys*" species. Korth (1984) placed *Dawsonomys minor* Wood, 1965 in *Knightomys* based on new material. The assignment allowed Korth to consider the presence of a second mental foramen as a character distinguishing *Knightomys* from *Dawsonomys* and *Pauromys*.

***Knightomys cremneus* new species**

Figs. 13b, 14. Table 9

Type.— UM 73257, right mandible with I₁, P₄-M₁, and M₃, part of snout with left and right I₁, from UM locality SC-255, middle Wasatchian, middle Graybullian (*C. trigonodus* zone).

Referred specimens.— UM 72967, left mandible with worn M₁; UM 77245, left mandible with M₁ and broken M₂; right mandible with incomplete M₁; UM 78888, RM₃; UM 78889, LM₁; UM 78890, RM₃.

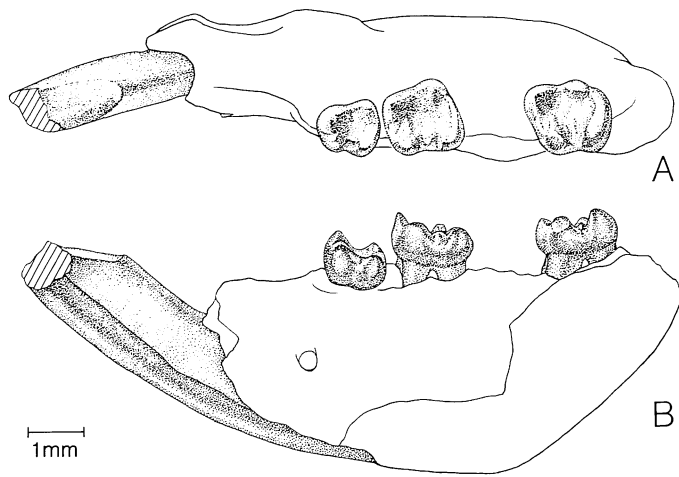


FIG. 14—*Knightomys cremneus*, UM 73257 (holotype), left dentary with I_1 , P_4 , M_1 , and M_3 . A, occlusal view. B, lateral view.

Stratigraphic range.— Early to middle Wasatchian, Sandcouleean (latest *C. ralstoni* zone) to middle Graybullian (*C. trigonodus* zone).

Etymology.— *kremnos*, Gr., overhanging wall or bank; in reference to the cliffs above the type locality.

Diagnosis.— Small species approximately the same size as *K. minor* but has a more complete metalophid, higher trigonid; smaller, less isolated metaconid, shorter, less distinct hypolophid, and second mental foramen only variably present.

Description.— P_4 is rhomboidal in occlusal outline with the metaconid the largest cusp. The protoconid is widely separated from the metaconid by a valley that terminates anteriorly in a low cingulum. The ectolophid is low, inset about $1/3$ the tooth width, and without a mesoconid. The hypoconid is anteroposteriorly compressed and is mostly labial to the ectolophid, extending an arm labially and slightly anteriorly toward the labial margin. The posterior lophid has a small hypoconulid, is broadly connected to the hypoconid, and is separated from the entoconid by a groove. The entoconid is in the posterolingual corner of the tooth and is separated from the metaconid by a wide valley. There is no hypolophid on P_4 .

The occlusal outline of M_1 is nearly rectangular with the anterior width nearly the same as the posterior width. The anterior cingulum is widely connected to the protoconid, separated from the metaconid by a shallow groove, and contains a central cusplule which extends slightly into the trigonid. The metalophid extends medially to the base of the metaconid, closing off the trigonid posteriorly with a low wall. The trigonid is elevated above the level of the talonid to half the height of protoconid. The metaconid projects a short arm laterally into the trigonid and is slightly anteroposteriorly compressed with a slight concavity on the posterior face. The mesoconid is large, labiolingually elongated from the labial margin to slightly into the talonid, and separated from the protoconid and hypoconid by shallow valleys. A very low ectolophid is present, inset from the apexes of the hypoconid and protoconid.

The hypoconid of M_1 is lateral to the ectolophid and the medial end of the mesoconid and is without the short, anterolabially directed crest of *K. minor*. The hypoconid is widely connected to the hypoconulid by the posterior lophid. The posterior lophid and hypoconulid run posterior to the entoconid and are separated from the entoconid by a obliquely, medially directed valley. The entoconid is forward of the posterior margin and extends a short hypolophid into the talonid to level with the center of the hypoconulid. The metaconid and entoconid are separated by a wide notch as deep as the talonid basin.

TABLE 9— Measurements of teeth of *Knightomys cremneus*. Abbreviations as in Tables 1 and 2.

Measurement	UM 72967	UM 73257	UM 77245	UM 78888	UM 78889	UM 78890
<i>Lower dentition</i>						
P ₄	L	--	1.1	--	--	--
	AW	--	0.9	--	--	--
	PW	--	1.1	--	--	--
	Ln A	--	0.07	--	--	--
M ₁	L	1.4	1.4	1.4	--	1.3
	AW	1.1	1.2	1.4	--	1.2
	PW	1.3	1.4	1.5	--	1.3
	Ln A	0.48	0.58	0.69	--	0.47
M ₂	L	--	--	1.6	--	--
	AW	--	--	1.6	--	--
	PW	--	--	--	--	--
	Ln A	--	--	0.91	--	--
M ₃	L	--	1.4	1.3	1.3	--
	AW	--	1.3	--	1.1	--
	PW	--	1.3	1.3	1.1	--
	Ln A	--	0.60	0.52	0.36	--

The M₂ is known from the broken specimen UM 77245 which shows only that M₂ is similar in morphology to M₁. M₂ appears to be more rectangular, and to have a larger entoconid, larger hypoconid, and higher trigonid than M₁; but the broken nature of the tooth makes these observations uncertain.

The trigonid of M₃ is similar to that of M₁, although the metaconid is set farther forward and is turned more labially on the posterior face. The metalophid is thinner than in M₁ and the trigonid is lower. The mesoconid is greatly anteroposteriorly compressed, doubled, and extends into the talonid basin medial to the low ectolophid. The posterior margin of M₃ is formed by a swelling of the hypoconid and posterior lophid, resulting in a rounded profile. The entoconid is separate, rounded, and set forward even with the mesoconid.

The mandible of the type has only one mental foramen located below the anterior margin of P₄ and the posterior end of the diastema. Mandibles of the referred specimens have a minute mental foramen variably placed posterior to the larger one. In all three mandibles the masseteric fossa ends under the posterior margin of M₁ and is delineated by a ridge. The lower incisor has a slightly rounded anterior face with a flattened medial face and gently curving lateral face. The widest part of the lower incisor is just back of the anterior face and the enamel extends 1/3 the tooth length along the lateral face while just reaching the medial face.

Discussion.— *Knightomys cremneus* shows a mosaic of features from three different genera. The occlusal outline of M₁, the transverse orientation of the metalophid, and the shape of I₁ are features of *Microparamys*. The high trigonid and the single foramen are features reminiscent of *Dawsonomys* as well as *Microparamys*. The short hypolophid, isolated entoconid, anterior position of the masseteric fossa, and shape of the mesoconid are features found in *Knightomys*. *K. cremneus* is placed in *Knightomys* as a result of the differences between it and *Microparamys* and *Dawsonomys*. *K. cremneus* differs from species of *Microparamys* by the lack of a separated anterior cingulum, the greater isolation of the entoconid and the presence of a stronger hypolophid. *K. cremneus* differs from species of *Dawsonomys* by the less developed lophes on the molars, the shortness of the hypolophid, and the lesser separation of the entoconid from the posterior lophid.

While *K. cremneus* cannot be placed in *Microparamys* or *Dawsonomys* it does not completely fit the definition of *Knightomys* due to the lack of a consistent second mental foramen. A possible solution would be to erect a new genus for this primitive rodent, but, aside from the mental foramen, differences between *K. cremneus* and other species of *Knightomys* are not sufficient to warrant such distinction. Therefore, I include *K. cremneus* in *Knightomys* after emending the definition to account for this early sciuravid.

CONCLUSIONS

The rodent fauna from the Clarks Fork Basin is diverse at the earliest well sampled Clarkforkian locality (SC-188, *Plesiadapis cookei* zone), indicating that the rodents had originated and undergone initial radiation elsewhere. Nonetheless, the rodents in the early Clarkforkian are close to the base of the radiation. Teeth of the rodent taxa represented in SC-188 are quite similar, suggesting that morphological differentiation had not progressed very far. Defining characters are present, but not as definitely expressed as in later members of these rodent groups. For example, the separation of the anterior cingulum of *Microparamys cheradius* is much less than is seen in later species of *Microparamys*. The isolation of the entoconid in early members of *Acritoparamys atwateri* and in *M. cheradius* is less than is seen in later members of *A. atwateri* or in later *Microparamys* species.

The diversification of rodents that occurred during the Clarkforkian and early and middle Wasatchian included the appearance of one and possibly two lines of sciuravids. The appearance of *Knightomys cremneus* in the late Sandcouleean extends the range of that genus, and sciuravids, into the early Wasatchian. Characters of *K. cremneus* are intermediate between *Microparamys* and *Knightomys*, suggesting that *Knightomys* and *Microparamys* are closely related. Korth (1984) has stated that the lack of a separated anterior cingulum on early species of *Knightomys* precludes an ancestor-descendant relationship between *Microparamys* and *Knightomys*. Separation of the anterior cingulum in the early species *Microparamys cheradius* is very small, suggesting that the appearance of this separation was relatively recent. If the separation of the anterior cingulum is considered a unitary advanced character, as suggested by Korth, then the relation of *Knightomys* and *Microparamys* might be through a recent common ancestor of probable Clarkforkian age.

Microparamys hunterae resembles species of *Pauromys* in characters of the molar trigonid and mandible and may be ancestral to *Pauromys*. *M. hunterae* also resembles *M. scopaiodon*, which species could also be ancestral to *Pauromys*. The relationship of *M. hunterae* and *M. scopaiodon* is unclear but may be one of common ancestry. If *Pauromys* is descended from either species, and if *Knightomys* and *Microparamys* share a most recent common ancestor then there is a possibility that *Knightomys* and *Pauromys* have different points of origin in the *Microparamys* lineage, resulting in a paraphyletic origin for Sciuravidae. Unfortunately, the small size of species of *Pauromys* results in a scarcity of specimens and there is insufficient material known of these rodents to fully understand the affinities of *Pauromys* to *Microparamys* and *Knightomys*.

Other evolutionary diversifications in rodents are the possible derivation of *Microparamys minutus* from *M. cheradius* and *Acritoparamys francesi* from *A. atwateri*. Unequivocal specimens of *M. minutus* and *A. francesi* are not known from the Clarks Fork Basin, but later specimens of *M. cheradius* and *A. atwateri* resemble *M. minutus* and *A. francesi*, respectively. *Paramys copei* and *Lophioparamys murinus* appear in the Wasatchian, as do probable members of *Reithroparamys debequensis* and *Notoparamys*. *P. copei* can plausibly be derived from *P. taurus* by an increase in size. Other species have no known precursors in the Clarkforkian of the Clarks Fork Basin. Either precursors of these somewhat rare species have yet to be found in the basin or the species evolved elsewhere and migrated into the basin at a time near the beginning of the Wasatchian.

The uncertainty about the appearance of these rarer species is a result of the general scarcity of rodent fossils in the record from the Clarks Fork Basin. Of the more than 6000

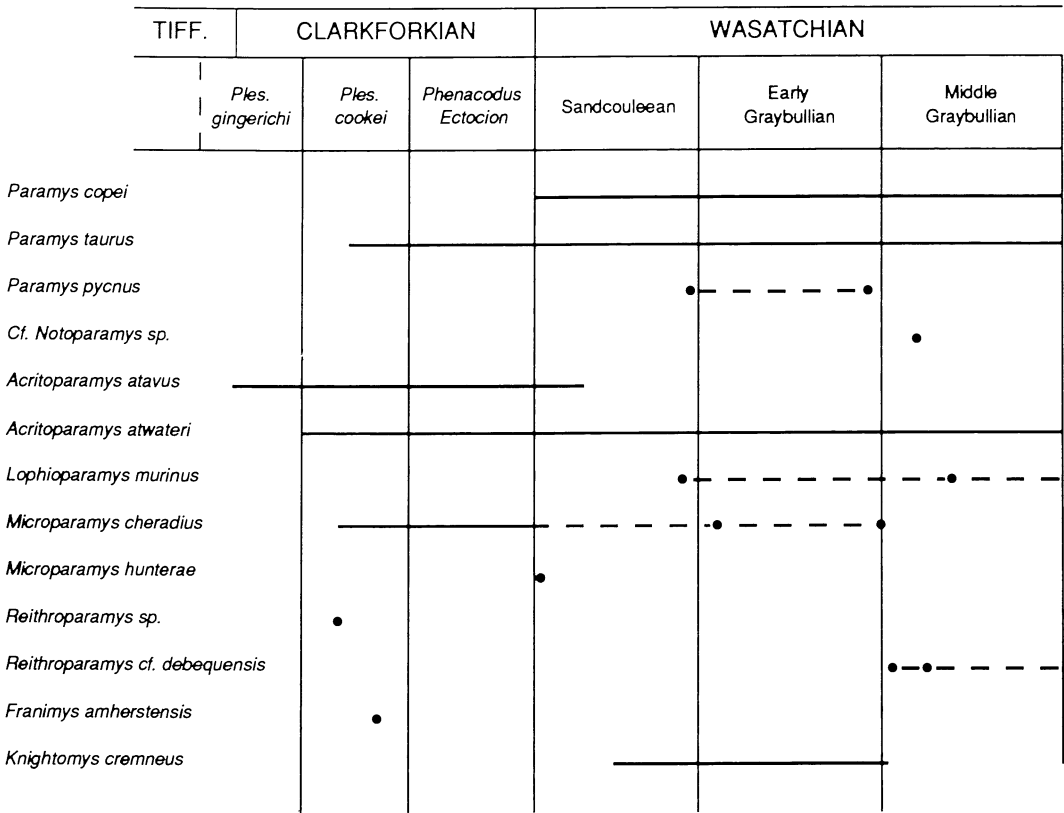


FIG. 15— Stratigraphic ranges of early Tertiary rodent species in the Clarks Fork Basin and Foster Gulch area. Solid circles represent rare single occurrences for a given species and dashed ranges are poorly known.

specimens collected from the Clarks Fork Basin by University of Michigan field crews between 1975 and 1981, only about 300 specimens are rodent cheek teeth, mostly isolated molars. One reason for the scarcity of rodent molars in this collection is their small size. In surface collecting small fossils tend to be overlooked, as has been shown by Winkler (1980) and by the greater abundance of rodent teeth from localities that have been screen washed such as SC-188. The incisors are larger and several hundred have been found, but these are not very useful taxonomically, except for unique forms. Incisors can be used to indicate a possible range for a species, but, as the incisor information for *P. copei* shows, caution is necessary.

The uncertainty resulting from the small sample size does not permit any definitive biostratigraphic subdivision of the Clarkforkian and early and middle Wasatchian based on rodents. The base of a biostratigraphic zone is indicated by the first appearance of the defining taxon or taxa. In the present rodent fossil record from the Clarkforkian and early to middle Wasatchian there is no way to determine if the first appearance of a rodent species corresponds with its evolution or immigration, or if earlier specimens of the species have been overlooked.

Some general remarks on the biostratigraphic extent of the rodent species are possible, with the caveat that new discoveries may invalidate these observations (Fig. 15). Six species appear in the Clarkforkian: *Acritoparamys atavus* first appears in the *Plesiadapis gingerichi* zone and *A. atwateri*, *Paramys taurus*, *Microparamys cheradius*, *Franimys amherstensis*, and *Reithroparamys sp. indet.* appear in the *Plesiadapis cookei* zone. *A. atwateri* and *P. taurus* are abundant throughout the entire section in the Clarks Fork Basin after they appear, while

A. atavus and *M. cheradius* are only rarely present in Wasatchian strata. *F. amherstensis* has not been positively identified in any other specimens except the type so it may be an exclusively Clarkforkian rodent. *Reithroparamys* sp. indet. is only known from the well sampled locality SC-188 and may also be a purely Clarkforkian rodent, but the material is too scanty to be sure of this.

During the Wasatchian seven new species appear: *Paramys copei*, *P. pycnus*, *Lophioparamys murinus*, *Microparamys hunterae*, and *Knightomys cremneus* appear in the Sandcouleean while cf. *Notoparamys* sp. and *Reithroparamys* cf. *debequensis* appear in the middle Graybullian. All of these species except *P. copei* are known from only a few, or one, specimen so the true ranges of the species are not yet certain. Specimens of *Paramys copei* are more abundant since, as a large rodent, it is more likely to be collected. If the large upper incisors found in Clarkforkian localities belong to *Franimys amherstensis* then *P. copei* may be restricted to the Wasatchian and could serve as a guide fossil. Cf. *Notoparamys* sp. is likewise a large rodent from a level that is well sampled so *Notoparamys* may tentatively be considered to make its first appearance in the middle Graybullian.

The first appearance of rodents in North America at the beginning of the Clarkforkian has been questioned by Korth (1984). Korth maintains that the type of *Acritoparamys atavus* from the Bear Creek, Montana locality is unique to that locality and is not found in the Clarkforkian. He further states that the mammalian fauna at Bear Creek places the locality in the Tiffanian, which puts the first appearance of rodents in North America in the Tiffanian. As mentioned above, *A. atavus* is not unique to Bear Creek, but is found in relative abundance in the *Plesiadapis cookei* zone of the Clarkforkian. Korth's reasoning about the stratigraphic positioning of the mammalian fauna at Bear Creek is not convincing, and the age of the locality is most probably early *Plesiadapis gingerichi* zone, as stated by Rose (1981). The first appearance of rodents in North America is at the base of the Clarkforkian. The first species for which cheek teeth are known is *Acritoparamys atavus* from the *Plesiadapis gingerichi* zone.

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