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Review of the North American Eocene and Oligocene Apatemyidae (Mammalia: Insectivora)

Robert M. West

The insectivoran family Apatemyidae has long been an enigma to paleomammalogists. The paucity of large samples has contributed to uncertainty in the systematics of the family, as most authors have based their conclusions on small samples. Recently McKenna (1963) affirmed the assignment of the apatemyids to the Insectivora, and Szalay (1968) suggested their origin from the Paleocene Palaeoryctidae.

This paper is the result of a collation of all available North American Eocene apatemyid material. I encountered many specimens that had not been recognized or reported, so the number of known specimens is far greater than that assumed by previous investigators. In addition, some useful material has been collected recently from a number of North American localities, some long known, others newly discovered.

I have revised the taxonomy of the Eocene Apatemyidae on the basis of these larger, although still imperfect, samples. The occurrence, morphology and evolutionary trends of the Apatemyidae are also considered. Unfortunately, despite the amount of material now present in the various collections, the problem of small samples that plagued earlier investigators has not been alleviated.

The following abbreviations identify the source of specimens referred to beyond:

AMNH—American Museum of Natural History, New York, Department of Vertebrate Paleontology
FAM—American Museum of Natural History, New York, Frick Collection of American Mammals
AC—Amherst College, Amherst, Mass.
UCR—University of California, Riverside
UCMP—University of California, Berkeley, Museum of Paleontology
CM—Carnegie Museum, Pittsburgh, Pa.
UCM—University of Colorado Museum, Boulder
KU—University of Kansas, Lawrence
MCZ—Harvard University, Cambridge, Mass., Museum of Comparative Zoology
LACM-CIT—Los Angeles County Museum of Natural History, California Institute of Technology Collection
PU—Princeton University, Princeton
RAM—Ray Alf Museum, Webb School, Claremont, Calif.
ROM—Department of Vertebrate Paleontology, Royal Ontario Museum, Toronto
SDSM—South Dakota School of Mines and Technology, Rapid City
USNM—Department of Vertebrate Paleontology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.
YPM—Yale University, New Haven, Peabody Museum of Natural History

TAXONOMIC HISTORY

The first North American apatemyids (*Apatemys bellus* and *A. bellulus*) were described (1872) from the upper part of the middle Eocene Bridger Formation of southwestern Wyoming by Marsh, who referred *Apatemys* to the Insectivora, *sensu* Marsh (an extremely inclusive group). Matthew (1899) reclassified this genus as an ischyromyid rodent.

Matthew (1909) proposed the family Apatemyidae to include *Uintasorex* and *Trogolemur* along with *Apatemys* and tentatively placed them in the Insectivora. Subsequently, Matthew (1915) extended the Apatemyidae, still considered insectivorans, to include the Eocene genera *Phenacolemur* and *Nothodectes* (= *Plesiadapis*). This began a period of association of the apatemyids and plesiadapid primates. The Apatemyidae were formally synonymized with the Plesiadapidae, as primates, by Matthew in 1918.

A late Paleocene apatemyid, *Labidolemur soricoides* from the Tiffany beds of southern Colorado, was recognized by Matthew and Granger (1921). Matthew (1921) extended the apatemyids (as Plesiadapidae) into the late Eocene by describing *Stehlinius uintensis* from the Uinta Formation of northern Utah. The preoccupied name, *Stehlinius*, was replaced with *Stehlinella* (Matthew 1929).

The list of middle Eocene apatemyids was lengthened by Troxell's (1923) descriptions of the Bridgerian *A. rodens.* Simpson (1929) named another species of *Labidolemur*, *L. kayi*, from Bear Creek, Montana (late Paleocene), and Jepsen (1930) described *Teilhardella chardini* from the early Eocene Gray Bull beds of the Bighorn Basin, Wyoming.

Jepsen (1934) published a comprehensive review of the apatemyids in conjunction with the description of the first early Oligocene representative, *Sinclairella dakotensis*, based on a superb skull and jaws from the White River Badlands of South Dakota. He separated the Plesiadapidae and Apatemyidae, and provided the essence of our modern interpretation of both families. Following Matthew (1909) Jepsen (1934:305) placed the Apatemyidae in the Insectivora "for the sake of convenience in keeping the Primates more compact, and because the fossil Insectivora are already a reservoir of groups with undefinitive characters."

Additional apatemyids were described in the 1950's and 1960's: *Teilhardella whitakeri* Simpson (1954) from the early Eocene San Jose Formation of the San Juan Basin of New Mexico; *Apatemys downsi* Gazin (1958) from the Sespe late Eocene of California; *Apatemys hurzeleri* Gazin (1962) from the La Barge beds (Lost Cabin equivalent), early Eocene of the northern Green River Basin; and *A. hendryi* Robinson (1966*b*) on material from the late Eocene of the Badwater Creek area of central Wyoming.

Several recent workers have given careful attention to apatemyid systematics. McKenna (1960) referred *Labidolemur kayi* to *Apatemys*, extending *Apatemys* back to the late Paleocene, and questioned the generic validity of *Teilhardella.* He also suggested consideration of the Eocene apatemyids as two parallel lineages differentiated by the development of p4, the fossa beneath p4, and the size and arrangement of the mental foramina.

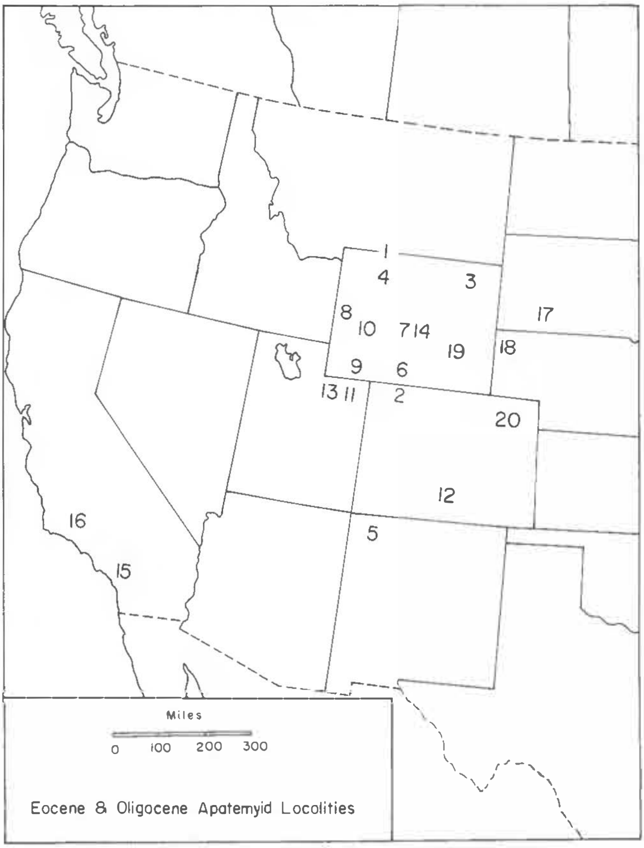

FIG. 1.—Distribution of apatemyid-producing localities: 1, northern Bighorn Basin and Bear Creek areas, Ft. Union Formation, late Tiffanian; 2, Four Mile area, Wasatch Formation, early Wasatchian; 3, Powder River Basin, early Wasatchian; 4, Bighorn Basin, Willwood Formation, early Wasatchian; 5, San Juan Basin, San Jose Formation, early Wasatchian; 6, Bitter Creek area, Wasatch Formation, ?early Wasatchian; 7, Wind River Basin, Wind River Formation, middle and late Wasatchian; 8, northwestern Green River Basin, Wasatch Formation, late Wasatchian; 9, southern Green River Basin, Bridger Formation, Bridgerian; 10, northeastern Green River Basin, Bridger Formation, Bridgerian; 11, Powder Wash, Green River Formation, early Bridgerian; 12, Huerfano Basin, Huerfano Formation, ?early Bridgerian; 13, Uinta Basin, Uinta Formation, Uintan; 14, Wind River Basin, "Tepee Trail" Formation, Uintan; 15, Laguna Riviera, Santiago Formation, Uintan; 16, Tapo Ranch, Sespe Formation, Uintan; 17, Big Badlands, White River Formation, Chadronian; 18, Sioux County area, White River Formation, Chadronian; 19, Bates Hole, White River Formation, Chadronian; 20, Weld and Logan Counties, White River Formation, Orellan.

McKenna's (1963) review of the Paleocene Apatemyidae included an updated familial diagnosis as well as detailed descriptions of *Jepsenella praepropera*, *Labidolemur soricoides*, *Apatemys kayi*, and the possible Tiffanian apatemyid *Unuchinia*. Aside from two illustrations, Eocene apatemyids were not considered.

TABLE 1.—*Eocene and Oligocene North American occurrences of apatemyids.*

	Simpson (1953:127)		This survey	
Time	Known specimens	Localities	Known specimens	Localities
Oligocene	1	1	13	13
Late Eocene	1	1	17	6
Middle Eocene	7	2	50	37
Early Eocene	1	1	49	28
Late Paleocene	1	1	2	2
Total	11	6	129	84

Robinson (1966*a*) noted the presence of two species of *Apatemys* in the Huerfano Formation, and suggested that *A. rodens* and *A. bellulus* might be conspecific, based on the number of p4 roots. Guthrie (1967) followed McKenna (1960) and synonymized *Teilhardella* and *Apatemys*. He retained all the existing species with one exception: *A. hurzeleri* was considered a synonym of *A. whitakeri*.

In his classification of the Insectivora, Van Valen (1967) followed McKenna (1963) in assigning *Unuchinia* to the Apatemyidae and recognized the distinct nature of that genus by placing it in a monogeneric subfamily, Unuchiniinae, while allocating all the other recognized apatemyids, including all Eocene forms, to the subfamily Apatemyinae.

Recent faunal studies have indicated the presence of *Apatemys* in additional areas: West (1973*a*) reported *A. bellus* from the lower Bridger Formation of the northern Green River Basin; West, in West and Atkins (1970), discussed a specimen of *Apatemys* sp. from the upper Bridger Formation at Tabernacle Butte, also in the northern Green River Basin; Delson (1971) reported *A. chardini* in an early Eocene fauna from the Powder River Basin of northeastern Wyoming; and Savage, in the course of 1971 field work, found *Apatemys* in early Wasatchian beds near Bitter Creek, Wyoming (personal communication).

NATURE OF THE APATEMYID SAMPLE

Apatemyids are uncommon elements of the various Eocene faunas, although they are not so rare as presumed by Simpson (1944, 1953). Specimens are known from most of the major Eocene and Oligocene areas (Fig. 1); their abundance is generally proportional to both the size of the collection and the techniques employed in amassing it. Due to the small size of apatemyids, they are better represented in washed collections than in those picked up from the surface. As shown in Table 1, the increased number of known specimens has not affected the specimen/locality ratio, which remains low.

It is difficult to quantify the relative abundance of apatemyids in percentages of individuals in faunas, as adequate data on collection size are seldom available. Several instances in which such numbers are known are tabulated in Table 2. This information suggests that at least one per cent of the individuals in

TABLE 2.—*Proportions of apatemyids in various Eocene localities.*

Reference	Localities	Age	Collecting technique	% Minimum no. of individuals	% Total no. of specimens
McKenna (1960)	8 at four Mile area, NW Colorado combined	Early Greybull	Prospecting and Washing	5.3	1.0
Guthrie (1967)	Lysite area, central Wyoming	Lysitian	Prospecting only	0.3	—
West (1973*a*)	Fault, New Fork-Big Sandy area, N Green River Basin, Wyoming	Bridger B	Prospecting and Washing	1.8	0.3
West, unpublished	East Hill, S Green River Basin, Wyoming	Bridger B	Prospecting and Washing	—	1.0
West, unpublished	Sage Creek, S Green River Basin, Wyoming	Bridger B	Prospecting and Washing	—	0.8

early or middle Eocene faunas are apatemyids, but the abundance is readily apparent only in washed collections.

Wasatchian apatemyids are known from northern New Mexico to northern Wyoming, although they have not yet been reported from several areas within this range, including the Hoback Basin, the Red Desert area and the Laramie Basin in Wyoming, and the Big Bend area of Texas. The Bridgerian range is more restricted, southern Colorado[1] to southwestern Wyoming; middle Eocene continental beds that have not yet produced *Apatemys* include the lower Washakie Formation of south-central Wyoming, and a complex series of poorly known beds at the northwest end of the Wind River Basin, central Wyoming. Uintan apatemyids are known from northeastern Utah, central Wyoming and southern California. Apatemyids are not known from the upper Washakie Formation of Wyoming, or the Climbing Arrow Formation of southwestern Montana. Oli-

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[1] This is dependent upon the interpretation of the upper beds (B) of the Huerfano Formation. Robinson (1966*a*) suggested the possibility of their being equivalent to the Bridger A, a unit recently carefully examined by McGrew and Sullivan (1970), who pointed out the similarity of the Bridger A fauna to that of the Bridger B. This suggests that the Huerfano B is indeed latest early Eocene, rather than earliest middle Eocene as its fauna is quite distinct from the Bridger B fauna. Conceptually the argument is trivial as it is apparent that discrete lines cannot be drawn; it does, however, affect accounts of temporal distribution to a disproportionate degree.

TABLE 3.—*Correlation of presumed taxonomic criteria*

Size	p4 root	Mental foramina	Fossa	No. of individuals		
				Wasatchian	Bridgerian	Uintan
large	1	2	present	4	5	—
large	2	2	present	2	—	—
large	2	1	present	1	4	—
large	1	1	absent	1	—	—
large	1	1	present	—	7	2
small	1	1	present	3	6	—
small	2	1	absent	1	—	—
small	1	2	present	—	1	—
Total				12	23	2
Percentage with one p4 root				67%	83%	100%

gocene apatemyids are known from the White River Group in northeastern Colorado, northwestern Nebraska, southwestern South Dakota, and east-central Wyoming; they have not yet been reported from early Oligocene beds at Pipestone Springs in southwestern Montana, or from the Cypress Hills, southwestern Saskatchewan.

Apatemyid specimens seldom provide much morphologic information. Most specimens are either isolated teeth or fragments of dentaries; upper teeth are far less common than lower teeth. There are only four instances of definite association between upper and lower teeth, one each from the Wasatchian, Bridgerian, Uintan, and Chadronian. Two complete skulls are known, of which only PU 13585, the holotype of *Sinclairella dakotensis*, is anatomically useful. Three cranial fragments are available; one was considered by West and Atkins (1970), and the other two are discussed below. No postcranial material has been associated even tentatively with any apatemyid. The nature of the specimens thus severely hinders biological analysis and interpretation of the family.

TAXONOMIC CRITERIA

Apatemyid taxonomy has been based on four criteria: number of roots (and correspondingly, size and development of the crown) of the fourth lower premolar; individual size; development of a fossa on the labial side of the mandible, lateral to the root(s) of p4; and the number and placement of mental foramina. Because the value of these criteria, both singly and in various combinations, is questionable, each will be discussed.

Roots of p4.—The number of roots (Figs. 7, 10, 11, 12, 13, 17, 18) has been a primary apatemyid taxonomic criterion since *Apatemys* was established by Marsh. Matthew (1909) illustrated *A. bellus* and *A. bellulus*, with one and two roots respectively, in his discussion of Bridgerian apatemyids. Jepsen (1934:302) noted the extremes shown by Matthew, but questioned the significance of this distinction, "however, other specimens of *Apatemys* bridge these structural gaps, and most surface features of the two species are very similar." Simpson (1954:3)

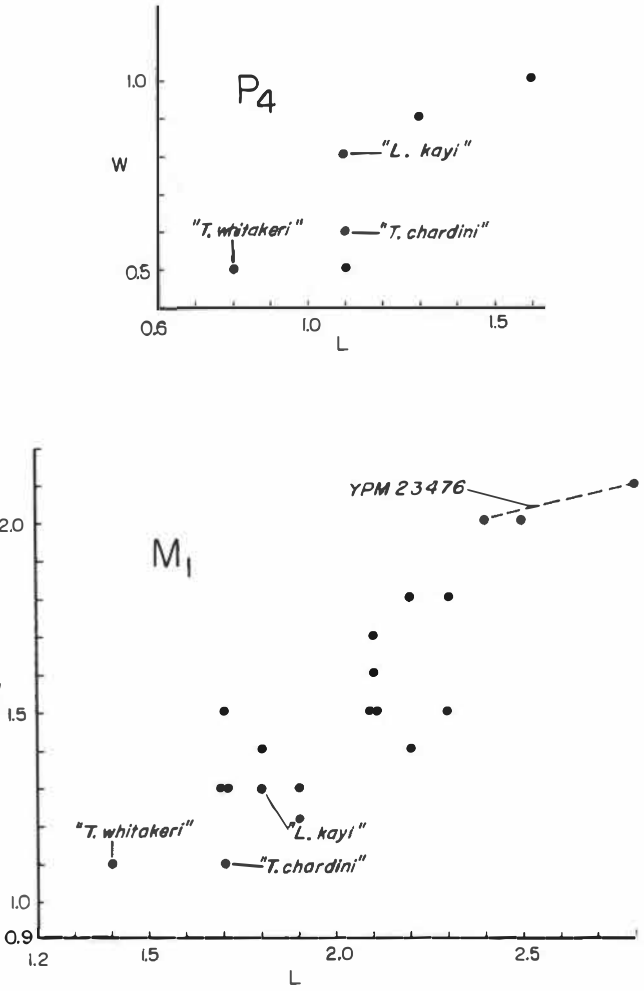

FIG. 2—Size-frequency graph of late Tiffanian and Wasatchian *Apatemys bellus* p4 and m1. Various holotypes and the large Yale specimen are indicated.

continued this line of thought, "It is possible that it [number of p4 roots] has no systematic value but only represents great variation of an almost vestigal tooth in unispecific populations. . . . The question cannot be settled until samples sufficiently large to demonstrate intraspecific variation are obtained, which is likely to be a long time if past collecting history is repeated."

Many additional specimens are now available, but the situation is no clearer. Attempts to relate roots of p4 to other presumed taxonomic criteria have been fruitless. Correlation with both individual size and number of mental foramina is poor in the Wasatchian sample (Table 3). It is better in the Bridgerian sample, where the relationship was first proposed, but the value of that correlation

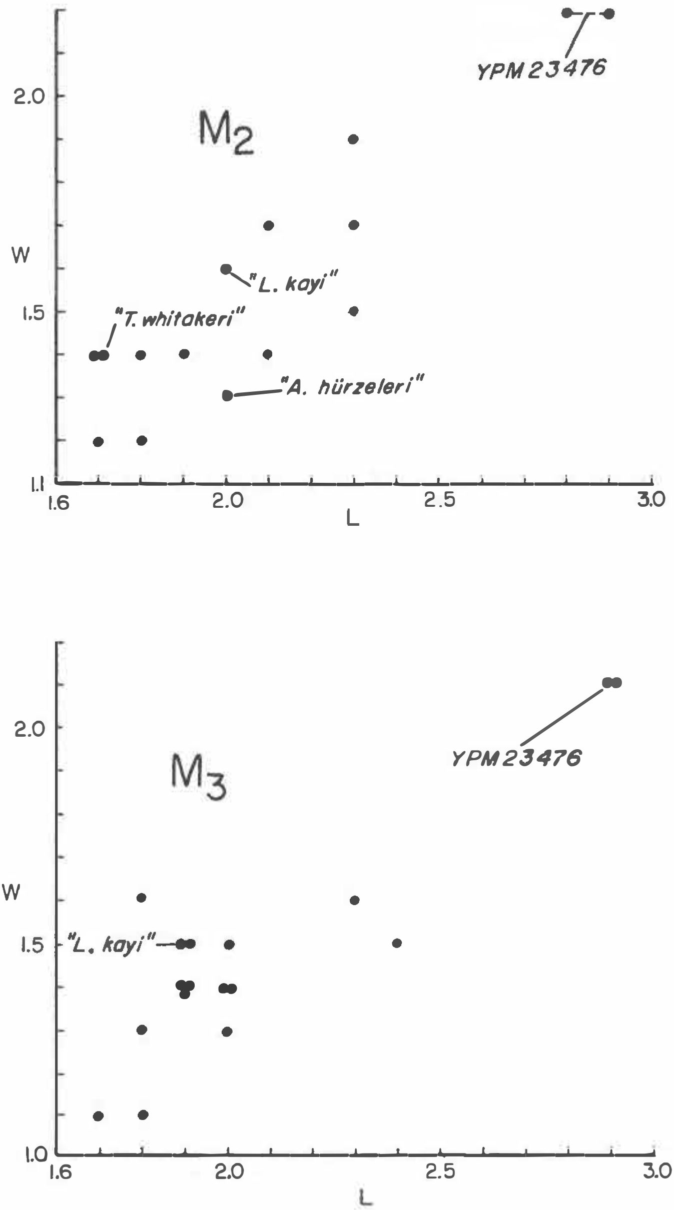

FIG. 3—Size-frequency graph of late Tiffanian and Wasatchian *Apatemys bellus* m2 and m3. Various holotypes and the large Yale specimen are indicated.

is impaired by the large proportion of specimens lacking p4. The Uintan and oligocene samples are inadequate for the investigation of possible correlations.

Specimens possessing either one or two roots, as well as some having one large root with a central constriction, are known from throughout the early and middle

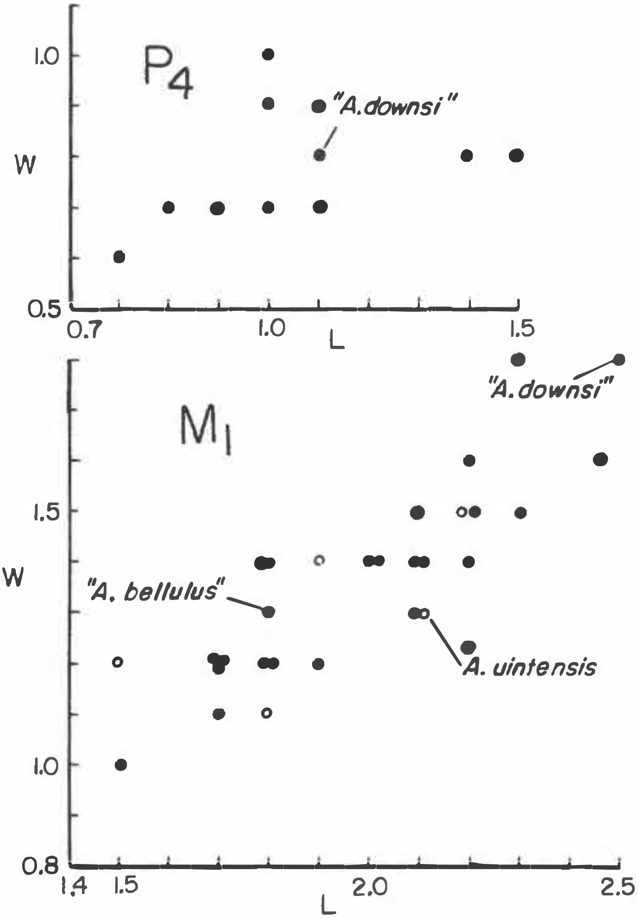

FIG. 4.—Size-frequency graphs of middle and late Eocene *Apatemys* p4 and m1. *A. bellus* (all middle Eocene and one late Eocene) indicated by solid circles; *A. uintensis* indicated by open circles. Various holotypes are indicated.

Eocene. The increase in the proportion of single-rooted p4's through the Eocene suggests variation with a tendency toward simplification of p4, rather than the presence of two continuous parallel lineages separated primarily on this basis. The significance of the varying degrees of development of p4 during the Wasatchian and Bridgerian is unclear. Perhaps this matter would be clarified by examination of the correlative upper teeth; unfortunately the material for such a study is not known.

Size.—There is little change in size within the Apatemyidae throughout the Eocene. Attempts were made to divide the sample from each geographic area and each age into size-determined groups (Figs. 2, 3, 4, 5). These analyses were not, in most cases, suggestive of differentiation into discrete groups. In only three cases are there possible distinctions. YPM 23476 (*A. bellus*) from the early Wa-

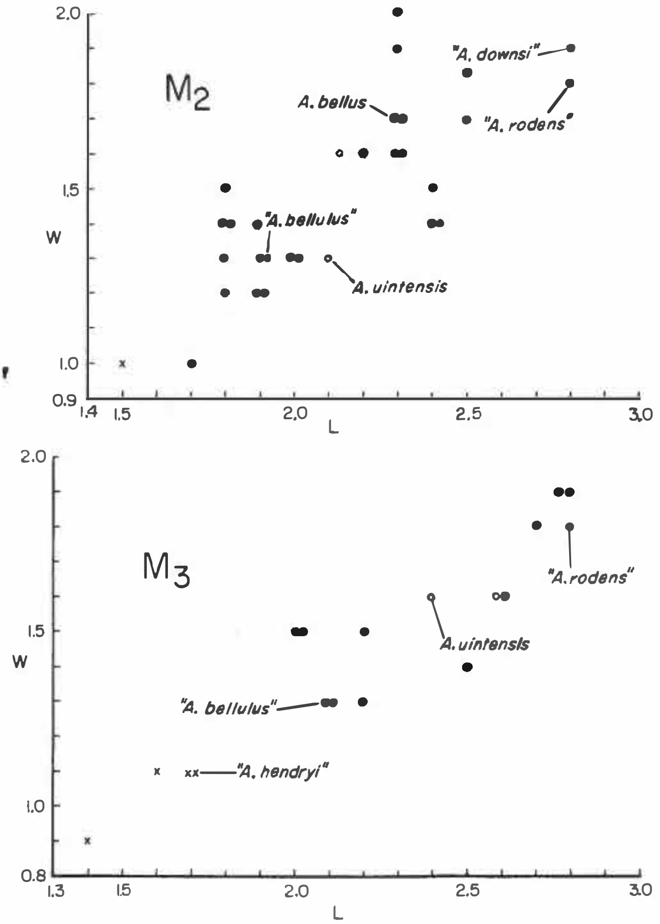

FIG. 5.—Size-frequency graphs of middle and late Eocene *Apatemys* m2 and m3. *A. bellus* indicated by open circles; *A. uintensis* indicated by open circles; material included in Robinson's *A. hendryi* indicated by x's. Various holotypes indicated.

satchian of the Bighorn Basin is larger than all other known Wasatchian specimens. A scatter diagram of Bridgerian m1 size (Fig. 4) shows division into three groups, weakly correlated with the number of p4 roots. However, the proportion of individuals with p4 retained is not great, and this correlation is not so clear when the other molars are considered. Finally, specimens referred by Robinson (1966*b*) to *A. hendryi* from the late Eocene are at the small end of the Uintan size range (Fig. 5); their p4 is unknown.

Determininations of the amount of variation in measurements of lower teeth in both the Wasatchian and Bridgerian samples of *Apatemys* confirm the conclusion that all may be assigned to a single species. Over 95 per cent of the measurements fall within one standard deviation of the population mean, and comparison of the distribution of the measurements shows only a small increase in size in the middle Eocene sample. *T*-tests were run on these samples, with the conclusion that at 95 per cent or higher levels of confidence both early and middle Eocene samples could be drawn from the same statistical population. However, statistically based conclusions must be accepted with some caution, as the samples upon which they are based are inadequate for this purpose. The specimens were drawn from many localities and from different levels within the early and middle Eocene of North America and then rather arbitrarily grouped for the purposes of analysis. Thus indiscriminate use of them as biologically realistic samples is dangerous.

Although *t*-tests indicate the probability of all specimens being drawn from a single population, coefficients of variation calculated on this same suite of measurements are high, frequently more than 10. This is suggestive of a heterogeneous sample and is a logical result of the nature of this particular population with its great range of temporal and geographic sources. Coefficient of variation is therefore not considered as significant in the statistical interpretation of *Apatemys* as are the comparisons of sample means.

Sinclairella of the Oligocene is much larger than any of its known Eocene predecessors, but there is no basis at present for relating it to any particular part of the Eocene apatemyid spectrum.

Fossa.—The taxonomic utility of the labial fossa on the dentary (Figs. 7, 10, 11, 12, 13, 14, 18) was first proposed by McKenna (1960:47). He believed that the best-developed fossae were associated with single-rooted lower fourth premolars and multiple mental foramina. Conversely, those individuals having double-rooted lower fourth premolars and single mental foramina were presumed to have smaller fossae or fossae lacking altogether. I am unable to make this association; it appears that the fossa is almost universally present in Eocene apatemyids (Table 3), and occurs with both extremes of p4 root development.

Such a fossa may have been the site of a lymph or secretory gland, which opened into the mouth labial to the toothrow. It may also have been the seat of a sensory structure. Uncertainty as to the function(s) of the fossa further reduces its utility as a taxonomic criterion.

Number of mental foramina.—This feature (Figs. 7, 10, 11, 12, 13, 14, 17, 18) was also used by McKenna (1960) in his suite of apatemyid taxonomic criteria. He believed that a single mental foramen was correlated with a single-rooted p4. Guthrie (1967:11) and Delson (1971:326-327) both attempted to use this criterion and found it unsatisfactory, as I have. As shown in Table 3, both single and multiple foramina are common. The actual number of nerve exits has little if any functional significance and varies without apparent pattern.

In summary, the criteria discussed above occur in a considerable variety of combinations, especially apparent in the middle Eocene sample. Thus, the taxonomy presented below is not based primarily on any of these four criteria. Rather, it is constructed upon the general development (or reduction) of p4, with the single and double-rooted conditions of p4 combined into a single variable Eocene species. It essentially divides Eocene apatemyids into two grades of evolution, differentiated by well-developed or reduced lower fourth premolars.

REVISED TAXONOMY

Order INSECTIVORA Illiger, 1811

Family APATEMYIDAE Matthew, 1909

(Provisional diagnosis in McKenna, 1963:12-13

Apatemys Marsh, 1872

1872. *Apatemys* Marsh, Amer. J. Sci., Ser. 3, 4:30.
1921. *Stehlinius* Matthew, Amer. Mus. Novit., 14:2.
1929. *Stehlinella* Matthew, J. Mamm., 10:171.
1930. *Teilhardella* Jepsen, Proc. Amer. Phil. Soc., 69:126.

Type species.—Apatemys bellus Marsh, 1872, Bridger Formation, middle Eocene, southwestern Wyoming.

Included species.—Type species and *A. uintensis.*

Range.—Late Paleocene to late Eocene.

Distribution.—Western North America.

Diagnosis.—Size small to moderate (length of m1, 1.4-2.5); large procumbent lower canine; bladelike p1 or p2; m1 usually more elongate than m2, with the addition of a small antero-lateral cusp alongside the paraconid; m3 longer than either ml or m2; molar row about twice the length of premolar row; molar talonid cusps fused into an encircling crest, open internally; mental foramen single or multiple, exits beneath anterior molars; frequently a small depression on the labial side of the dentary beneath p4; upper diastema before the single-rooted premolars; upper molars initially triangular, becoming more rectangular with the progressive reduction of the ectoflexus and enlargement of the hypocone.

Apatemys bellus Marsh, 1872

(Figs. 2-5, 7-14, Table 4)

1872. *Apatemys bellus* Marsh, Amer. J. Sci., Ser. 3, 4:30.
1872. *Apatemys bellulus* Marsh, Amer. J. Sci., Ser. 3, 4:31.
1923. *Apatemys rodens* Troxell, Amer. J. Sci., 5:504
1929. *Labidolemur kayi* Simpson, Ann. Carnegie Mus., 19:120.
1930. *Teilhardella chardini* Jepsen, Proc. Amer. Phil. Soc., 69:126.
1954. *Apatemys whitakeri* Simpson, Amer. Mus. Novit., 1654:1.
1958. *Apatemys downsi* Gazin, Smithsonian Misc. Coll., 136(1):89.
1962. *Apatemys hurzeleri* Gazin, Smithsonian Misc. Coll., 144(1):26.
1966. *Apatemys hendryi* Robinson, Ann. Carnegie Mus., 38:318.

Holotype.—YPM 13512, Bridger C or D, late middle Eocene, southern Green River Basin, Wyoming.

Range.—Late Paleocene to late Eocene.

Distribution.—Western North America.

Diagnosis.—Size small to moderate; p4 with one or two roots, well-developed crown; p3 missing; p1 or 2 developed into a prominent procumbent blade; lower molar paraconid reduced; upper premolars single-rooted; upper molars with prominent ectoflexus and small hypocone.

Remarks.—A. bellus has the longest temporal range of the two species recognized here and displays considerable variation. However, attempts to divide this sample into coherent morphospecies were not successful.

TABLE 4.—*Statistical data for* Apatemys bellus.

Teeth	Variate	N	OR	$\bar{X}$	SD
p1-2	length	0			
	width	1	1.1		
p4	length	12	0.8-1.6	1.13	.24
	width	12	0.5-1.0	.75	.18
m4	length	44	1.4-2.8	1.93	.27
	width (trigonid)	37	1.0-2.1	1.32	.26
	width (talonid)	40	1.0-1.9	1.36	.19
m2	length	45	1.5-2.9	2.06	.31
	width (trigonid)	35	1.0-2.0	1.49	.26
	width (talonid)	36	1.0-2.0	1.44	.21
m3	length	37	1.4-2.9	2.08	.37
	width (trigonid)	29	0.7-2.1	1.42	.28
	width (talonid)	29	0.8-1.7	1.21	.22
P3	length	1	2.5		
	width	1	1.4		
P4	length	2	1.7-2.2	1.95	
	width	2	1.7-2.1	1.90	
M1	length	5	1.4-2.7	2.26	.58
	width	5	1.5-2.6	2.14	.59
M2	length	14	1.2-2.5	1.94	.42
	width	15	1.3-2.9	2.30	.53
M3	length	4	1.6-2.3	1.90	
	width	4	2.5-3.3	3.00	

There is much diversity in size among Wasatchian *A. bellus*, ranging from PU 13236 (holotype of *Teilhardella whitakeri*) with an m1 length of 1.4 to YPM 23476 with an m1 length of 2.4 (Fig. 8). Size, plotted on a scatter diagram (Figs. 2, 3), shows both small and large groups, but the bimodality is not strong enough to confirm the existence of two (or more) species; this conclusion is supported statistically by *t*-tests.

Bridgerian *A. bellus* shows less diversity than the Wasatchian sample, but there is less geographic range, and the time involved in the Bridgerian is probably much less than that in the Wasatchian. Size-frequency diagrams (Figs. 4, 5) do not show discrete groups; the holotypes of Marsh (1872) and Troxell (1923) are, rather, extremes within a continuous sample. When those specimens previously assigned to *A. bellus* and *A. bellulus* are considered independently there are some correlations between size and number of roots on p4; however, I do not believe that this warrants specific designation.

Few Uintan specimens have been referred to *A. bellus*. If the small individuals referred by Robinson to *A. hendryi* (the p4 is unknown) are referrable either to a separate species or to *A. uintensis*, only a single specimen (LACM-CIT 5202, holotype of *A. downsi*) represents late Eocene *A. bellus*. This particular specimen has a smaller p4 than do middle Eocene representatives of *A. bellus* and follows the trend toward reduction of that tooth.

TABLE 5.—*Statistical data for* Apatemys uintensis.

Teeth	Variate	N	OR	$\bar{X}$
p1-2	length	1	3.9	
	width	1	1.6	
p4	length			
	width			
m1	length	2	1.9-2.1	2.00
	width (trigonid)	2	1.1-1.3	1.20
	width (talonid)	2	1.3-1.4	1.35
m2	length	2	2.1	
	width (trigonid)	2	1.4-1.7	1.55
	width (talonid)	1	1.5	
m3	length	2	2.4-2.6	2.50
	width (trigonid)	2	1.6	
	width (talonid)	2	1.3-1.4	1.35
P4	length	1	1.4	
	width	1	0.9	
M1	length	1	2.5	
	width	1	1.7	

Apatemys uintensis (Matthew 1921)

(Figs. 5, 15-18, Table 5)

1921. *Stehlinius uintensis* Matthew, Amer. Mus. Novit., 14:2.
1929. *Stehlinella uintensis* Matthew, J. Mamm., 10:171.

Holotype.—AMNH 1903, Uinta Formation (possibly early Uintan White River pocket), late Eocene, Uinta Basin, Utah.

Range.—Late Eocene.

Distribution.—Western North America.

Diagnosis.—Size as in larger individuals of *A. bellus*; p4 tiny, commonly indicated by empty alveolus; upper molars with smaller ectoflexus and larger hypocone than those of *A. bellus*.

Remarks.—Specimens from Utah and southern California are assigned to *A. uintensis.* There is little size variation in this suite, at least partially a result of the small sample size. The Uinta Basin specimen (AMNH 1903) has a markedly curved lower canine, whereas the Californian individuals (UCMP 86295 and 86296 and UCR 12832) show less curvature (Figs. 15, 17). An additional differentiation is the more stout coronoid process of the Californian specimens.

Sinclairella Jepsen, 1934

1934. *Sinclairella* Jepsen, Proc. Amer. Phil. Soc., 74:291.

Type species.—Sinclairella dakotensis Jepsen 1934.

Included species.—Type species only.

Range.—Early and middle Oligocene; provisionally referred specimens from the late Eocene of France (Sudre, 1969).

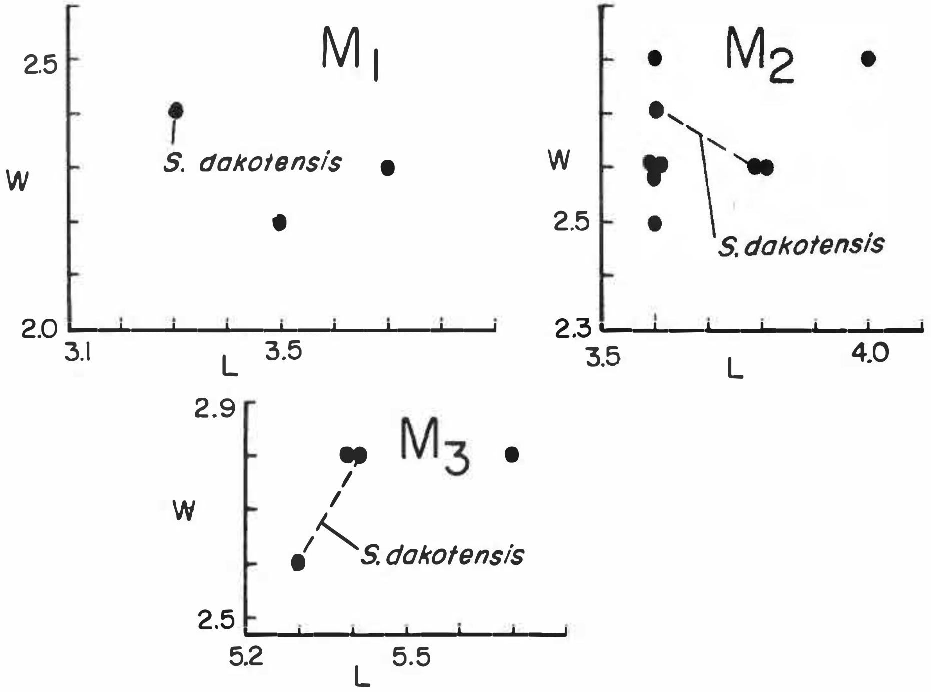

FIG. 6.—Size frequency graphs of m1, m2 and m3 of Oligocene *Sinclairella dakotensis*. Holotype, PU 13585, is indicated.

Distribution.—Western North America; provisionally referred specimens from the late Eocene of southern France at Aix (Sudre, 1969).

Diagnosis.—As for the single species.

Sinclairella dakotensis Jepsen, 1934
(Figs. 6, 19, 20, Table 6)

1934. *Sinclairella dakotensis* Jepsen, Proc. Amer. Phil. Soc., 74:291.

Holotype.—PU 13585, early Oligocene, White River group, southwestern South Dakota.

Range.—early and middle Oligocene.

Distribution.—Western North America.

Diagnosis.—Size large (length of m1, 3.3-3.7); p4 tiny (only alveolus available); paraconid on lower molars greatly reduced; m3 elongate, with expanded hypoconulid; molar row about four times the length of the premolar row; upper molars squared through virtual elimination of ectoflexus and enlargement of hypocone; single mental foramen opens beneath posterior root of m1; small fossa on labial side of dentary beneath p4.

Remarks.—A morphologic study of this species, based on PU 13585, is necessary but is not attempted here. Additional preparation of that specimen has exposed much area not available to Jepsen, and it is now possible to study the

TABLE 6.—*Statistical data for* Sinclairella dakotensis.

Teeth	Variate	N	OR	*X*	SD
p1-2	length				
	width	1	1.8		
m1	length	3	3.3-3.7	3.50	
	width (maximum)	3	2.2-2.4	2.30	
m2	length	8	3.6-4.0	3.70	.15
	width (maximum)	8	2.0-2.8	2.60	.24
m3	length	3	5.4-5.7	5.50	
	width (maximum)	3	2.8	2.80	
P2	length	1	3.2		
	width	1	1.6		
P3	length	1	2.4		
	width	1	1.2		
P4	length	2	2.1-2.4	2.25	
	width	2	1.1-1.6	1.35	
M1	length	3	3.9-4.1	4.00	
	width	3	3.3-3.7	3.50	
M2	length	4	3.4-3.8	3.55	
	width	4	4.1-4.6	4.25	
M3	length	1	3.2		
	width	1	4.4		

basicranium. If apatemyids are indeed derivatives of the Palaeoryctidae (Szalay, 1968), intensive study of the *Sinclairella* skull should produce some insight into the Paleocene members of that important family, albeit by a rather circuitous route (M. C. McKenna, personal communication).

Sinclairella is the climax of known North American apatemyid evolution and shows the most advanced condition of the trends carried through the Eocene. Therefore, upper and lower dentitions of *Sinclairella dakotensis* are illustrated in Figs. 18 to 20 to facilitate direct comparisons with the illustrations of the various Eocene apatemyids, and Fig. 6 allows size comparisons.

MORPHOLOGIC TRENDS

Consideration of morphologic trends is perhaps a more realistic approach to Eocene apatemyids than is taxonomic revision. The five trends that are the most apparent include: 1) reduction and specialization of the premolar series (obviously closely related to root condition and development of p4 discussed above); 2) elongation of the lower molars; 3) reduction of the amount of enamel on the lower canine; 4) reduction of the molar paraconid; and 5) progressive squaring of the upper molars.

Reduction and specialization of premolars.—This trend is a major aspect of apatemyid evolution, as it is indicative of the shortening of the jaws during the entire history of the family.

In the process of ongoing work, McKenna (personal communication) has determined the probable sequence of development of the typical apatemyid dental formula (that of the Eocene forms upon which the family is based). He has revised also the homologies of the specialized anterior teeth so prominent in Eocene individuals. The lower teeth, according to McKenna's interpretation, are c, pl (or p2), p4, ml, m2, and m3, a numbering system that is adopted here. The upper dentition with which these occlude is poorly known, as there are no Eocene individuals with associated upper and lower premolar series, and no Paleocene upper premolars are known.

AMNH 48999 (*A. bellus* from the early Wasatchian) shows the presence in the upper dentition of two enlarged incisors and two premolars (Fig. 9). This is identical to the dental pattern already known in the skulls of *A. uintensis* and *Sinclairella*, as well as the maxillary fragments from the middle Eocene described by West and Atkins (1970). The upper anterior teeth had been reduced to the optimum number by early Wasatchian and, other than simplification and decrease in size, underwent no further material change or reduction in number. Comparison of *A. bellus*, *A. uintensis*, and *Sinclairella* shows this progressive p3 and p4 simplification (Figs. 9, 16, 19). The first (or second) lower premolar became enlarged into a bladelike structure, whereas p4, a prominent tooth in the latest Paleocene and earliest Eocene individuals, was reduced to a peg by the late Eocene (*A. uintensis*). There was an increase in the proportion of single-rooted lower fourth premolars in the middle Eocene, although both conditions were present throughout. The latest individual of *A. bellus* (LACM-CIT 502) also has the smallest p4.

The blade is badly represented in preserved dentaries, and a single isolated specimen of pl(2) has been found in the Huerfano Formation of Colorado (Fig. 13). The holotype of *A. uintensis* (AMNH 1903) retains the blade, as does that of *Sinclairella.* While the anterior premolar was becoming increasingly bladelike, its root was displaced labially by the enlargement of the lower canine root. This attribute was developed early in apatemyid evolution, as it is clearly present in the early Tiffanian apatemyid, *Labidolemur* (West, 1973*b*).

There is no upper slicing tooth obviously coordinate to the lower blade, and the basic function of the blade is not clear. It may have acted to hold materials against the upper incisors.

The upper premolars are not so specialized as the lowers, as they are small, single-rooted teeth. It is difficult to interpret any direct occlusion of the blade with these.

Elongation of the lower molars.—Progressive lengthening of the lower molars, especially m3, has been noted by several authors. Jepsen (1934:303) called attention in particular to m3, "the heel to m3 is seen to lengthen progressively in comparison with the trigonid of this tooth." The elongation is strikingly apparent when *Sinclairella* is contrasted with Eocene apatemyids (Figs. 7, 8, 12, 15, 18, 20). Table 7 indicates length-width ratios on all available lower teeth and points out the elongation of m3 in the *Apatemys-Sinclairella* transition, of the lower molars during the Wasatchian-Bridgerian interval, and the reduction of p4 through the Eocene.

TABLE 7.—*Length-width proportions of lower teeth of Apatemyidae.*

	p4	m1	m2	m3
Oligocene *Sinclairella*	—	1.5 (3)	1.4 (8)	2.0 (4)
Uintan *Apatemys uintensis*	—	1.5 (3)	1.4 (2)	1.6 (5)
Bridgerian *Apatemys bellus*	1.4 (6)	1.6 (18)	1.4 (16)	1.6 (9)
Wasatchian *Apatemys bellus*	1.7 (6)	1.4 (18)	1.3 (11)	1.4 (14)

Number of specimens measured indicated in parentheses.

Enamel distribution on the lower canine.—It is well established (Jepsen, 1934; McKenna, 1960, 1963) that the amount of enamel on the lower canine decreased through the history of the Apatemyidae. McKenna (1963) described and illustrated the completely enamel-covered crown of the canine of *Labidolemur soricoides*, with the enamel sheath stopping short of entry into the alveolus. Latest Paleocene *A. bellus* from Bear Creek (late Tiffanian) has a thin coating of dorsal enamel that is worn through on the occlusal surface. This pattern follows into the early and middle Eocene, and the unworn canine of MCZ 17942 (late Bridgerian *A. bellus*) has a thin enamel covering on the occlusal surface. By late Eocene (*A. uintensis*), the enamel is reduced further, and Matthew (1921) suggested that if there was dorsal enamel in this individual (AMNH 1903), it was only on the tip of the canine. Jepsen (1934) pointed out the absence of enamel from the dorsal side of the canine of *Sinclairella.*

Two changes in the shape of the canine parallel the reduction of enamel. Through the Eocene, the lower canine became more curved (most noticeable in *A. uintensis*), and the occlusal surfaces more narrowed. Paleocene and earlier Eocene apatemyids had flat dorsal canine surfaces, with small marginal irregularities giving the tooth a somewhat palmate appearance. By late Eocene the canine was a laterally compressed tooth with a small dorsal surface.

Paraconid reduction.—The Paleocene apatemyids (McKenna, 1963; Szalay, 1968) had generalized lower molars, with well-developed paraconids on the leading edges of the trigonids. Through the Eocene, and especially late in the Eocene, this anterior cusp was reduced, and by the Oligocene, the lower molars were essentially a pair of transverse lophs, the anterior of which was based on the protoconid and metaconid, and the posterior one was based on the posterior talonid crest (primarily the hypoconulid). The paraconid is always strongest on the anterior molars and remains visible on the m1 of *Sinclairella.* The lower first molar of Eocene apatemyids also has a fourth, accessory trigonid cusp, lying anterolabially to the paraconid. In many individuals, this cusp extends farther forward than does the paraconid, giving the trigonid a parallelogram shape.

Squaring of the upper molars.—Thanks to the recognition of upper molars of *Jepsenella* (Szalay, 1968), progressive alterations in upper molar configuration can be documented from the Torrejonian to the Orellan. Several changes contribute to the squaring of the molars, giving them larger occlusal surfaces. The hypocone, accessory to the posterior part of the tooth in early forms, became increasingly incorporated into the main part of the tooth. Simultaneously it was

TABLE 8.—*Measurements, in millimeters, of apatemyid specimens containing upper and lower teeth in association.*

	Upper			Lower		
	Length	Width		Length	Trigonid width	Talonid width
YPM 23476—*A. bellus*, Wasatchian						
P4	2.3	1.8				
			rm1	2.4	2.0	1.8
			lm1	2.8	2.1	1.9
			rm2	2.8	2.2	2.0
			lm2	2.9	2.2	2.0
			rm3	2.9	2.1	1.7
			lm3	2.9	2.1	1.6
MCZ 17942—*A. bellus*, late Bridgerian						
			m1	2.2	1.4	1.5
M2	1.8	2.5				
			m3	2.7	1.8	1.5
AMNH 1903—*A. uintensis*, Uintan						
			p1 or 2	3.9	1.6	
P4	1.4	0.9				
M1	2.5	1.7	m1	2.1	1.3	1.3
			m2	2.1	1.4	—
			m3	2.4	1.6	1.4
PU 13585—*S. dakotensis*, Chadronian						
I2	3.2	1.6				
P3	2.4	1.2				
M1	4.0	3.7	m1	3.3	2.1	2.4
M2	3.4	4.6	lm2	3.6	2.6	2.7
			rm2	3.8	2.4	2.6
RM3	3.2	4.4	lm3	5.4	2.8	2.4
LM3	3.3	4.5	rm3	5.3	2.6	2.3

raised to the level of the primary cusps so that it had a greater participation in occlusion. The parastyle was reduced in size as the ectoflexus became less prominent. This resulted in a smoother external face to the molar. The ultimate result was a four-cusped tooth, which shows functional parallels with multituberculates, rodents, and primates.

CRANIAL MORPHOLOGY

Mandible.—New specimens from the middle Eocene at Tabernacle Butte (*A. bellus*: MCZ 17942) and the late Eocene at Laguna Riviera (*A. uintensis*: UCMP 86295, 86296; UCR 12832) permit comparisons of a sequence of dentaries from the middle Eocene to the Oligocene (Figs. 14, 17). This new material is added to the previously known dentaries of *A. uintensis* (AMNH 1903) (Fig. 15) and *S.*

dakotensis (PU 13585) (Fig. 18). Unfortunately no complete Wasatchian dentaries are known; the best specimen (YPM 23476), which contributes little morphologic information, is badly fractured and distorted. Measurements of AMNH 1903 and MCZ 17942 and others having associated upper and lower teeth are given in Table 8.

MCZ 17942 and UCR 12832 have smoothly convex ventral sides, whereas AMNH 1903 has a concave lower side beneath the posterior part of the canine root. All three specimens have a deep masseteric fossa on the labial side, extending anteriorly to a position beneath the posterior part of m3.

The articular condyle is rounded. This is especially apparent in MCZ 17942 and to a lesser extent in *A. uintensis*. The condyle is at the posterior terminus of a heavy bony ridge along the base of the masseteric fossa. The articular surface of the condyle in MCZ 17942 is directed somewhat internal to the fore-aft lineation of the entire jaw. It is situated on the same level as the toothrow, an important consideration in the analysis of masticatory mechanics.

There is a stout uninflected angular process on the dentary. It is a ventral flange in *A. uintensis*, where it extends posteriorly almost as far as the condyle. It is much smaller in *A. bellus* and not as markedly flangelike. It is small also in *Sinclairella*, in which the reentrant between the condyle and the angular process is reduced from the condition found in *Apatemys*.

The coronoid process is large; its base is about one-half the length of the dentary in MCZ 17942 and UCR 12832 and a little less than half in *Sinclairella* and in the holotype of *A. uintensis*. As shown in the accompanying illustrations, the coronoid is relatively larger and rises at a steeper angle behind the molars in the Californian specimens than in the others. The leading edge of the coronoid process on all apatemyids is a broad bony bar, whereas the posterior part of the coronoid is much thinner, as it is recessed into the masseteric fossa. The coronoid flares dorsally, thus permitting relatively narrow jaws to articulate with a skull that broadens markedly behind the orbital region.

Immediately anterior to the condyle, on the lingual surface, is the mandibular foramen, the persumed entrance for branches of the mandibular nerve into the mandible. Ends of this nerve emerged anteriorly from the mental foramen on the labial side of the jaw. This nerve was presumably accompanied by a branch of the internal maxillary artery.

Skull.—Apatemyid skulls are more poorly known than their dentaries. Only three have been reported, of which only one, *Sinclairella* (PU 13585), contributes much detail to our knowledge of the apatemyid skull. *Heterohyus quercyi* from the Eocene Quercy Phosphorites, described in detail by Chardin (1921), has been lost, and the holotype of *A. uintensis* is so badly distorted that little information can be extracted from it. However, several recently collected cranial fragments of early and middle Eocene age add to our concept of earlier North American apatemyids.

AMNH 48999 (Fig. 9), a distorted rostrum of *A. bellus*, was recovered from the early Eocene Willwood Formation, Bighorn Basin, Wyoming. In addition to showing the upper tooth formula of early Eocene *Apatemys* (2-0-2-3), it displays a great deal of structural similarity to *Sinclairella* and *Heterohyus.* Rotational distortion has obscured the true dimensions of the specimen, but the remaining structures clearly show the constricted anterior end of the palate. Preparation of the anterior part of the left orbit has revealed the lacrimal duct (inside the orbital rim), the infraorbital foramen, and the sphenopalatine duct, in dorso-ventral sequence. This pattern compares favorably with the late Bridgerian maxillary fragment described by West and Atkins (1970). A deep pit is present on the maxilla above m2 on the front of the zygomatic process. This pit is smaller in the new Bridgerian specimen (MCZ 17942); AMNH 1903, due to its poor preservation, does not show such a pit. It is likely that this pit contained a secretory gland.

The maxillary-premaxillary suture is visible in AMNH 48999, confirming the identification of the enlarged anterior teeth as incisors but fracturing of the cranial bones obscures other sutures. This specimen has a substantial supraorbital crest, as in *Sinclairella.* This feature is not so apparent in AMNH 1903, probably due to crushing, and the supraorbital area is not preserved in any Bridgerian specimen.

A second maxillary fragment is included in MCZ 17942, the dentary of which was described above, but no premolars are present (Fig. 14). Excavation of the opening of the internal nares reveals a single passageway. A median flange extends upward from the palatines, but there is no reciprocal projection from the vomer. The internal nares open at the level of m3, as in *Sinclairella* and apparently as in AMNH 48999 in which a portion of the right margin of the internal nares is all that is present. The region of the lacrimal duct and infraorbital foramen is absent in MCZ 17942.

ECOLOGY

The absence of recognized apatemyid postcranial material seriously inhibits investigation of the likely habits of the group. However, the extant New Guinean phalangerid, *Dactylopsila trivirgata,* has a markedly similar dentition and cranial structure (McKenna, 1963). This species is a nocturnal, arboreal marsupial with a dietary preference for insects. Rand (1937) described the dual function of the enlarged anterior teeth as: 1) tearing open rotten logs and removing loose bark while searching for insects and 2) puncturing the exoskeletons of beetle larvae. Apatemyid teeth conceivably could have functioned in a similar fashion, and the blade (p1 or 2) could have been quite effective at slicing through insect exoskeletons. The similarities between the wear and structure of the anterior teeth of these two genera likewise suggest parallels in the mechanics of holding food in the mouth.

The articular condyle of *Apatemys* (MCZ 17942) is spherical whereas that of *Dactylopsila* is laterally extended into a rounded bar. This suggests that apatemyids may have been capable of more lateral jaw movement than *Dactylopsila.* There seems to be considerable fore-aft movement in both genera, as the enlarged lower tooth in each occludes and abrades with two upper incisors. Both I2 and

I3 of *Dactylopsila* are substantially worn as a result of contact with the lower canine.

Dactylopsila has no premolar blade, and its upper anterior premolars are relatively larger than those of the apatemyids. The tiny p3 in *Dactylopsila* is in the same position as the diastema in *Apatemys.*

The general molar pattern in *Dactylopsila* is strikingly similar to the terminal apatemyid pattern of *Sinclairella.* This, combined with the possible functional similarities in the anterior teeth, somewhat overcomes the absence of apatemyid skeletal material. A possible modern equivalent does exist. At the very least, comparison between apatemyids and *Dactylopsila* is not unreasonable at our present state of knowledge.

REFERRED SPECIMENS

An asterisk indicates a specimen recorded in the literature but not examined in the course of this study.

Apatemys bellus.—LATE PALEOCENE: CM 11703, p4-m3; 11534, c; Eagle Coal Mine, Bear Creek, Montana, Fort Union Group, late Tiffanian. PU 20848, ml-m3; Polecat Bench area, Wyoming, Fort Union Group, late Tiffanian.

EARLY EOCENE: UCM 28408, m3; 28409, m3; 28410, m2; UCMP 59308, ml; Despair Quarry, Four Mile area, northwestern Colorado, Wasatch Fm., early Greybullian. UCMP 44784, ml-m3; 47157, m2; 59310, ml; Timberlake Quarry, Four Mile area, northwestern Colorado, Wasatch Formation, early Greybullian. UCMP 44096, m3; Kent Quarry, Four Mile area, northwestern Colorado, Wasatch Fm., early Greybullian. UCMP 59309, ml; Alheit Pocket Four Mile area, northwestern Colorado, Wasatch Fm., early Greybullian. UCMP 46167, m2 m3; West Alheit Pocket, Four Mile area, northwestern Colorado, Wasatch Fm., early Greybullian. AMNH 59603, edentulous dentary; 59637, M2; 59647, ml; 80936, m2; 80937, ml; 80938, ml; 80939, M1; 80941, M2; 80942, M1; 80943, m3; 80944, m3; 80945, m3; 80946, m2; 80947, m2; East Alheit Pocket, Four Mile area, northwestern Colorado, Wasatch Fm., early Greybullian. UCMP 46976, m3; Univ. California loc. V5423, Four Mile area, northwestern Colorado, Wasatch Fm., early Greybullian. UCMP 46645, m3; 47156, M2; Sand Quarry Four Mile area, northwestern Colorado, Wasatch Fm., early Greybullian. AMNH 48999, partial skull; Bighorn Basin, Wyoming, Willwood Fm., Greybullian. ROM acc. no. 382, C; Sternberg loc. 382, near Elk Creek, Bighorn Basin, Wyoming, Willwood Fm., Greybullian. ROM A00410, p4-m2; Bighorn Basin, Wyoming, Willwood Fm., Greybullian. ROM A289, edentulous dentary; Sternberg loc. 289, Bighorn Basin, Wyoming, Willwood Fm., Greybullian. PU 17884, ml-m3; Hackberry Hollow, Bighorn Basin, Wyoming, Willwood Fm., Greybullian. YPM 23476, fragments of skull and jaws; Yale loc. 134, Bighorn Basin, Wyoming, Willwood Fm., Greybullian. UCR 12203, p4-ml; north of Emblem, Bighorn Basin, Wyoming, Willwood Fm., Greybullian. PU 13236, p4-ml; Elk Creek, Bighorn Basin, Wyoming, Willwood Fm., Greybullian. ROM acc. no. 271, ml-m3; Sternberg loc. 271, Bighorn Basin, Wyoming, Willwood Fm., Greybullian. ROM 4249, p4-m3; Southwest of Basin, Bighorn Basin, Wyoming, Willwood Fm., Greybullian. KU 8664, edentulous dentary; KU Wyoming, loc. 34, south fork of Elk Creek, Bighorn Basin, Wyoming, Willwood Fm., Greybullian. AMNH 48004, p4-m2; San Juan Basin, New Mexico, San Jose Fm., Greybullian. UCMP unnumbered, level S, Quarry 5, Bitter Creek Area, southern Wyoming. Wasatch Formation, Greybullian. CM 22634, ml-m2; 22635, edentulous dentary, 20884, edentulous dentary; central Wind River Basin, Wyoming, Lysite member of Wind River Fm., Lysitean. AC 2502*, ml-m3; 2956*, ml-m3; 4300*, m2-m3; central Wind River Basin, Wyoming, Lysite member of Wind River Fm., Lysitean. CM 22010, ml-m2; 22011, m3; Loc. 2, central Wind River Basin, Wyoming, Lost Cabin member of Wind River Fm., Lost Cabin age. CM 22013, edentulous dentary; Loc. 1, central Wind River Basin, Wyoming, Lost Cabin mem. of Wind River Fm., Lost Cabin age. USNM 18438, m1-m3; Boysen Reservoir area, central Wind River Basin, Lost Cabin mem. of Wind River Fm., Lost Cabin age. USNM 22386, m2; LaBarge area, northwestern Green River Basin, Wyoming, New Fork Tongue of Wasatch Fm., Lost Cabin age.

Middle Eocene: YPM 11759, edentulous dentary; 11766, m2; 13520, m1-m2; 13524, p4-m2; 15267, P3-M1; 15284, M2-M3; 16215, edentulous dentary; 16216, m1-m2; 16217, m2; uncertain localities in the southern Green River Basin, Wyoming, Bridger Fm., Bridgerian. UW 1321, p4-m2; Big Sandy loc., northeastern Green River Basin, Wyoming, lower Bridger Fm., early Bridgerian. RAM 6911-1 (field no.), m2; near camp on Leavitt Creek, southern Green River Basin, Wyoming, Blacks Fork mem. of Bridger Fm., early Bridgerian. AMNH 91779, M2-M3; Reservior loc., southern Green River Basin, Wyoming, Blacks Fork Mem. of Bridger Fm., early Bridgerian. AMNH 91381, m 3; 91382, m2; 91777, m2; 91778, m3; 91780, m2; 91781, m2; 91782, m1; Sage Creek loc., southern Green River Basin, Wyoming, Blacks Fork Mem. of Bridger Fm., early Bridgerian. AMNH 91776, m2; East Hill loc., southern Green River Basin, Wyoming, Blacks Fork Mem. of Bridger Fm., early Bridgerian. PU 13843 (=AMNH 18994), m1-m3; Grizzly Buttes West, southern Green River Basin, Wyoming, Blacks Fork Mem. of Bridger Fm., early Bridgerian. YPM 16214, P3; Leavitt's Ranch, southern Green River Basin, Wyoming, Blacks Fork Mem. of Bridger Fm., early Bridgerian. YPM 14938, m3; Grizzly Buttes, southern Green River Basin, Wyoming, Blacks Fork Mem. of Bridger Fm., early Bridgerian. USNM 54-67 (field no.), m1-m3; 10 miles east of Lyman, southern Green River Basin, Wyoming, Blacks Fork Mem. of Bridger Fm., early Bridgerian. USNM 77-65 (field no.), p4-m3; Millersville, southern Green River Basin, Wyoming, Blacks Fork Mem. of Bridger Fm., early Bridgerian. USNM 4-57 (field no.), edentulous dentary; southern Green River Basin, Wyoming, Blacks Fork Mem. of Bridger Fm., early Bridgerian. USNM 17765, M1-M3; North of Cedar Mt., southern Green River Basin, Wyoming, Blacks Fork Mem. of Bridger Fm., early Bridgerian. AMNH 17484, edentulous dentary; Loc. II, Huerfano Basin, Colo., upper Huerfano Fm., ?early Bridgerian. YPM 16444, p3-m1; 16477, m1-m2; Loc. II, Huerfano Basin, Colorado, upper Huerfano Fm., ?early Bridgerian. CM 6413, edentulous dentary; 13313, m3; 13413, m1; 13429, m1; 13860, m1; 25000, m1; Powder Wash, Uinta Basin, Utah, Green River Fm., early Bridgerian. YPM 12973, m2-m3; southern Green River Basin. ?Twin Buttes Mem. of Bridger Fm., late Bridgerian. YPM 13512, m2; 13513, m1-m3; 14955, M2; 14966, m3; 16219, m1-m2; 16221, edentulous dentary; various localities in vicinity of Lonetree, southern Green River Basin, Wyoming, Twin Buttes Mem. of Bridger Fm., late Bridgerian. AMNH 11425, p4, m2; 12046, m1-m3; 12048, p4-m2; Henry's Fork area (several levels), southern Green River Basin, Wyoming, Twin Buttes Mem. of Bridger Fm., late Bridgerian. USNM 13276, m1-m3; 13277, p3; five miles north of Lonetree, southern Green River Basin, Wyoming, Twin Buttes Mem. of Bridger Fm., late Bridgerian. YPM 13521, edentulous dentary; near Phil Mass Ranch, southern Green River Basin, Wyoming, Twin Buttes Mem. of Bridger Fm., late Bridgerian. UW 1609, M2; Tabernacle Butte loc. 7, northern Green River Basin, Wyoming, upper Bridger Fm., late Bridgerian. MCZ 17942, partial skull and jaws; Tabernacle Butte Misery Quarry, northern Green River Basin, Wyoming, upper Bridger Fm., late Bridgerian. FMNH PM 15060, p4-m1; Fault loc., northern Green River Basin, lower Bridger Formation, early Bridgerian.

Late Eocene: LACM-CIT 5202*, p4-m2; Tapo Ranch, Ventura Co., California Sespe Fm., Uintan. CM 15021, m3; 15679, m1; 15680, M1; 16802, M2; Loc. 5, Hendry Ranch Mem., "Tepee Trail" Fm., Wind River Basin, Wyoming, Uintan. CM 15638, m3; 15737, m3; 15740, M2; 15744, m3; 23156, m2; 26026, m1; 26458, m1; 28354, M2; Loc. 5A, Hendry Ranch Mem. of "Tepee Trail" Fm., Wind River Basin, Wyoming, Uintan.

Apatemys uintensis.—Late Eocene: AMNH 1903, skull and jaw; Uinta Fm. (White River Pocket?), Uinta Basin, Utah, Uintan. UCMP 86296, edentulous dentary with canine; Laguna Riviera, California, (V6839), Santiago Fm., Uintan. UCR 12832, dentary with c, m1; Laguna Rivera, California, (RV6830), Santiago Fm., Uintan. UCMP 86295, dentary with m1; Half

Day Pocket, Santiago Fm., San Diego Co., California, Uintan.

Sinclairella dakotensis.—Early Oligocene: AMNH (FAM) 79400, m2-m3; 79401, m2; Bates Hole, Wyoming, Brule Fm., White River Gp., Chadronian. RAM 381*, M1; 598*, m2; 1000*, m1; 1001*, m2; 1079*, m2; 3013*, m2; Sioux Co., Nebraska, Chadron Fm., White River Gp., Chadronian. PU 13585, skull and jaws; Corral Draw, South Dakota, Chadron Fm., White River Gp., Chadronian.

Middle Oligocene: SDSM 230-4308, m1-m3; Shannon Co., South Dakota, Brule Fm. White River Gp., Orellan. UCM 21073*, M2; Mellinger Loc., Weld Co. Colorado, Cedar Creek Fm, White River Gp., Orellan. KU 11210, P4-M2; Logan Co., Colorado, White River Gp., Orellan. RAM 1674*, M2; Weld Co., Colorado, White River Gp., Orellan.

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FIG. 7.—Stereophotographs of late Paleocene *Apatemys bellus*, CM 11703, holotype of *Labidolemur kayi* Simpson, 1929. Scale units equal 5 millimeters.

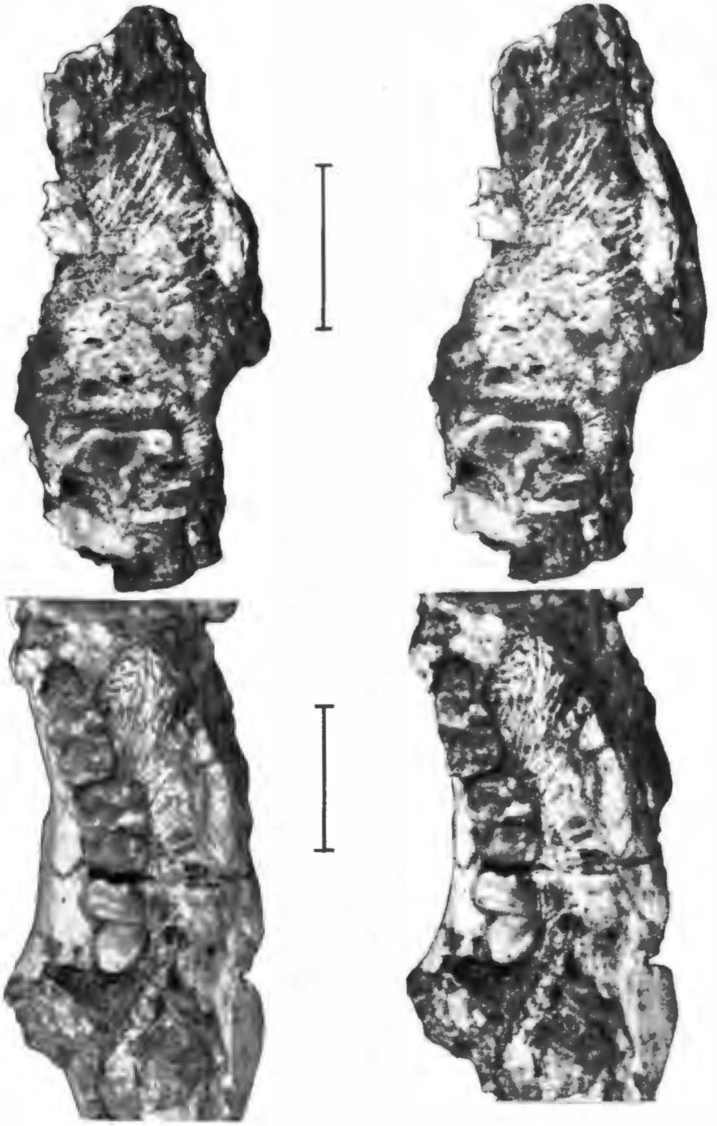

FIG. 8.—Stereophotographs of early Eocene *Apatemys bellus*. Occlusal views of upper and lower dentitions of YPM 23476. Scale units equal 5 millimeters.

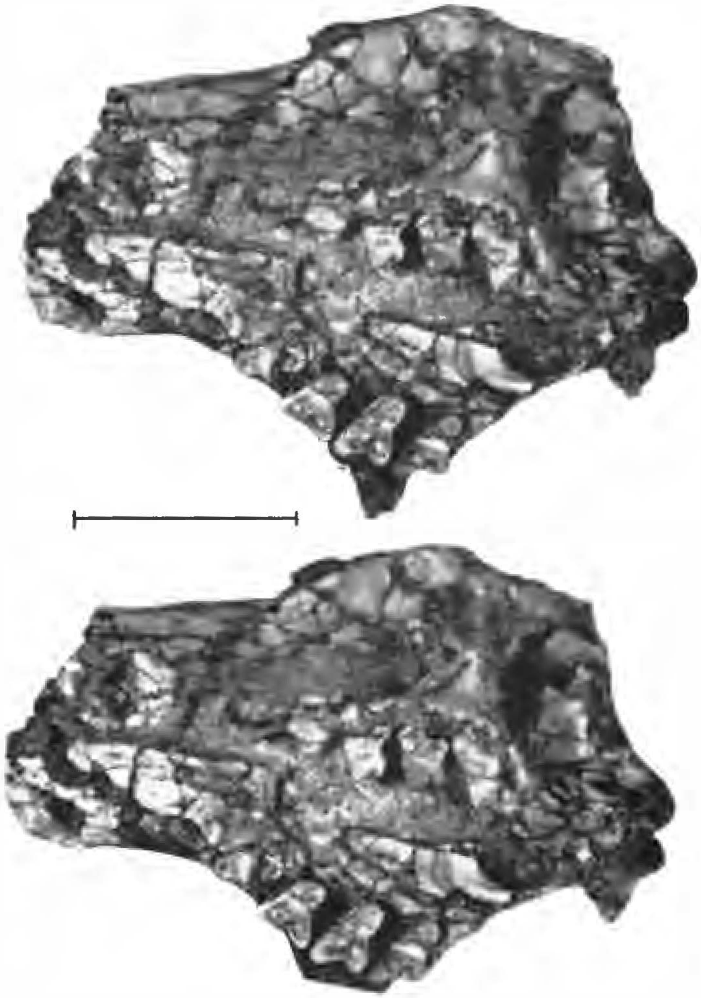

FIG. 9.—Stereophotographs of early Eocene *Apatemys bellus*. Occlusal view of AMNH 48999, rostral part of skull. Scale units equal 5 millimeters.

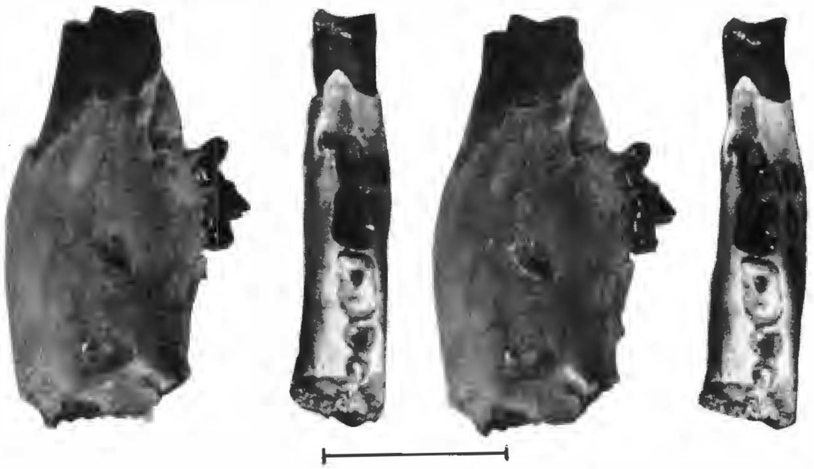

FIG. 10.—Stereophotographs of early Eocene *Apatemys bellus.* Occlusal and labial views of UCR 12203. The lower fourth premolar is in place and the alveolus of p1 is visible. Scale units equal 5 millimeters.

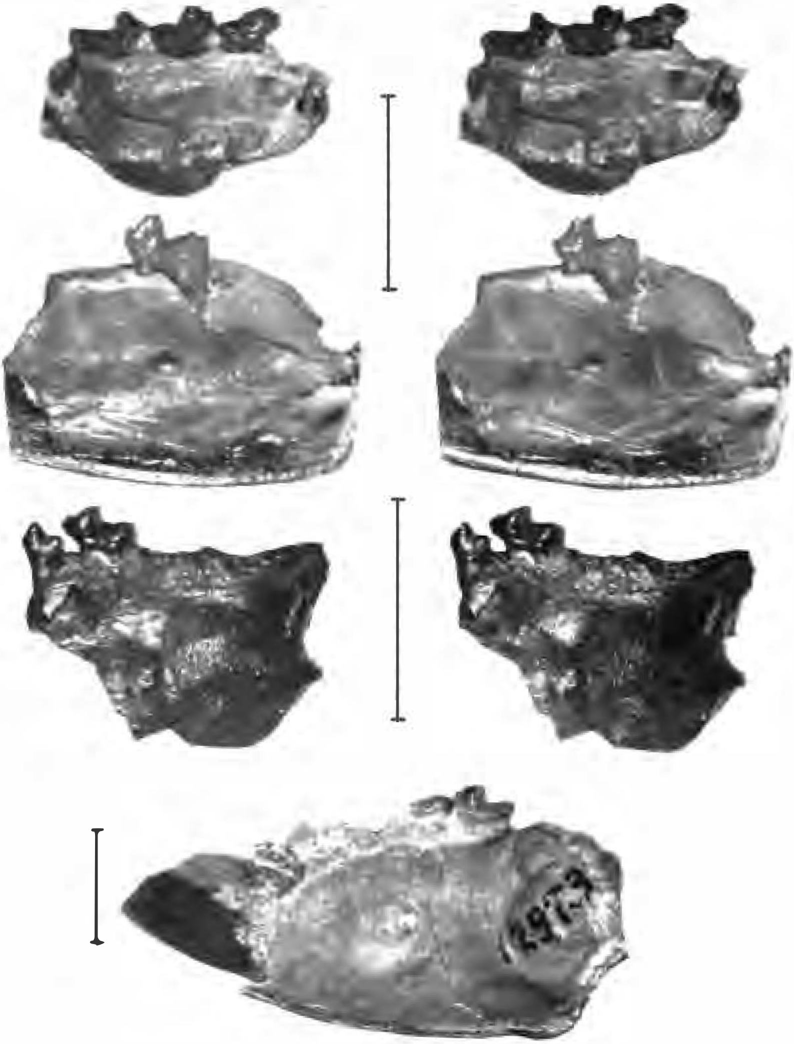

FIG. 11.—Stereophotographs of middle Eocene *Apatemys bellus*: top, YPM 13513, holotype of *Apatemys bellulus* Marsh, 1872; upper center, YPM 13512, holotype of *Apatemys bellus* Marsh, 1872; lower center, AMNH 12060; bottom, YPM 12973, holotype of *Apatemys rodens* Troxell, 1923. Scale units equal 5 millimeters.

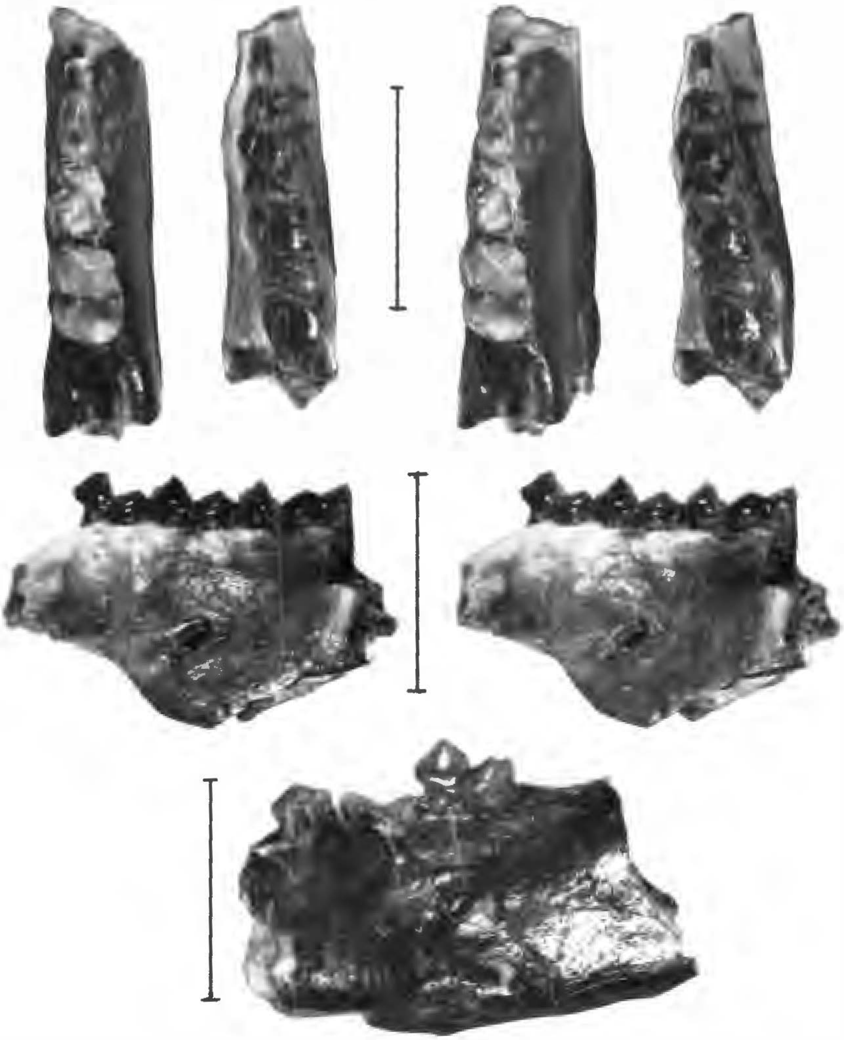

FIG. 12.—Stereophotographs of middle Eocene *Apatemys bellus*: top left and bottom, AMNH 11425, showing a double-rooted p4. Top right and center, AMNH 12047, with the alveolus of a single-rooted p4. Scale units equal 5 millimeters.

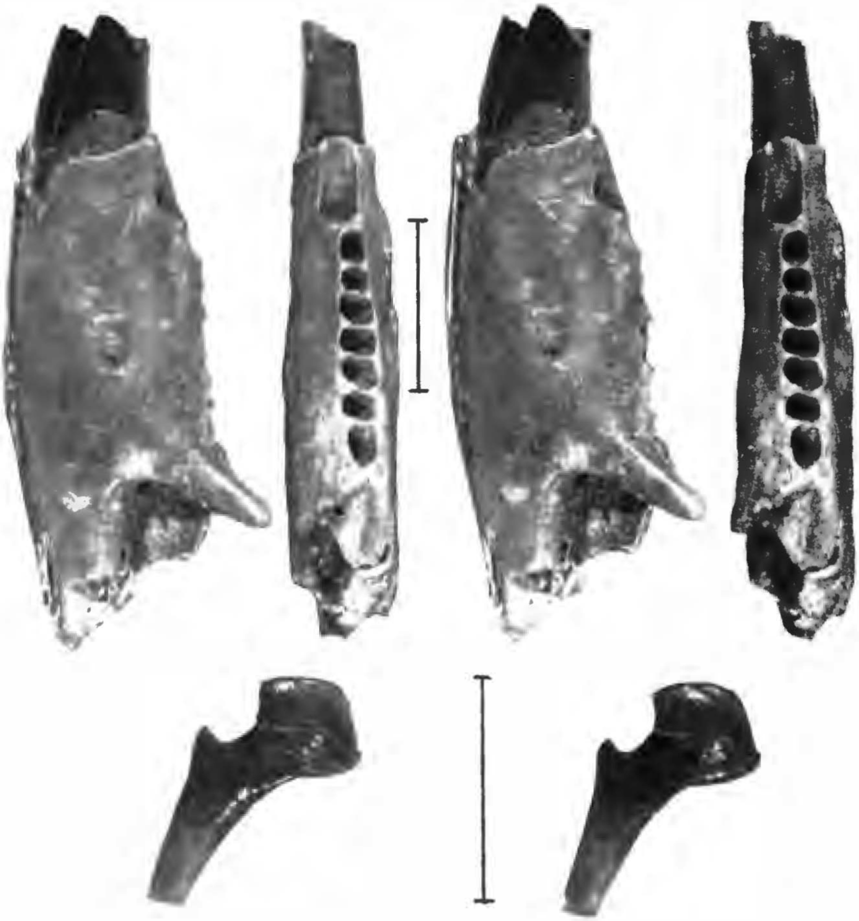

FIG. 13.—Stereophotographs of middle Eocene *Apatemys bellus*: top, labial and occlusal views of CM 6413 showing all the postcanine alveoli; bottom, AMNH 56599, the p1(2) blade. Scale units equal 5 millimeters.

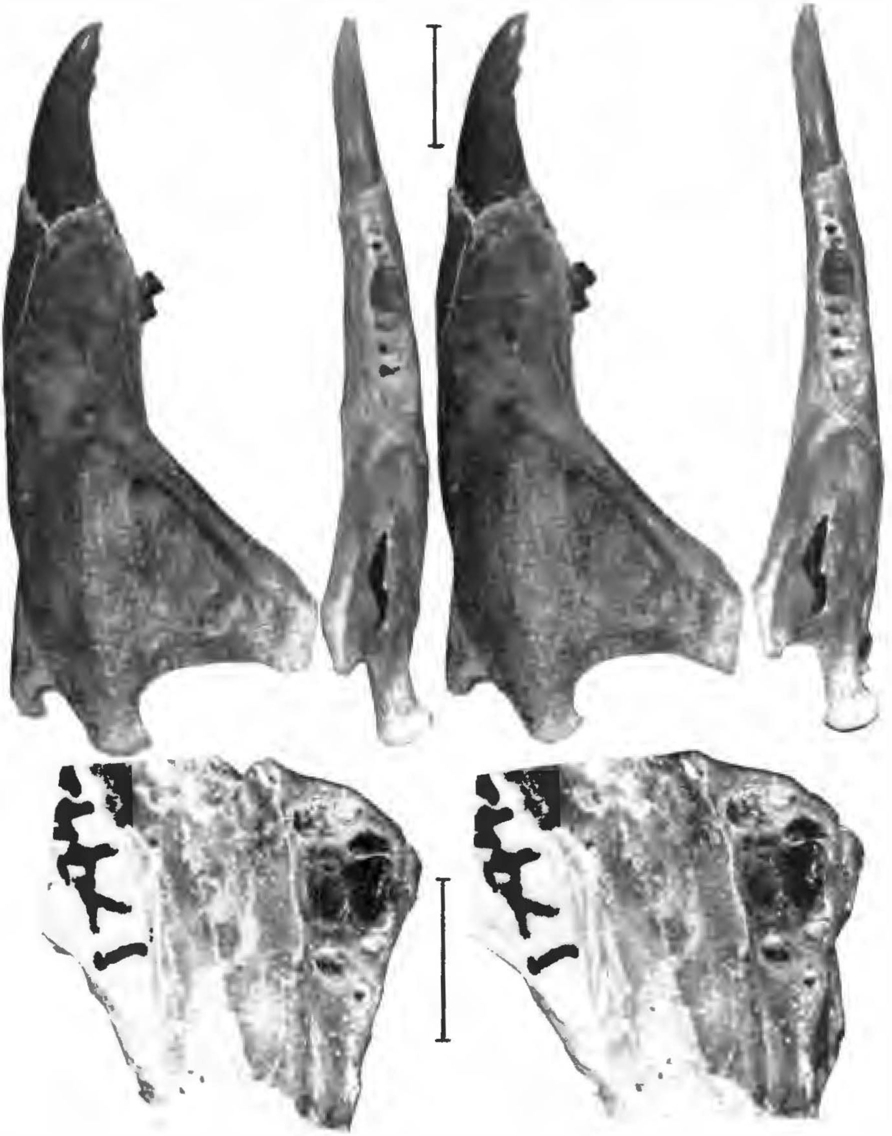

FIG. 14.—Stereophotographs of middle Eocene *Apatemys bellus*, MCZ 17942: top, labial and occlusal views of left dentary; bottom, occlusal view of right maxilla, showing absence of premolars. Scale units equal 5 millimeters.

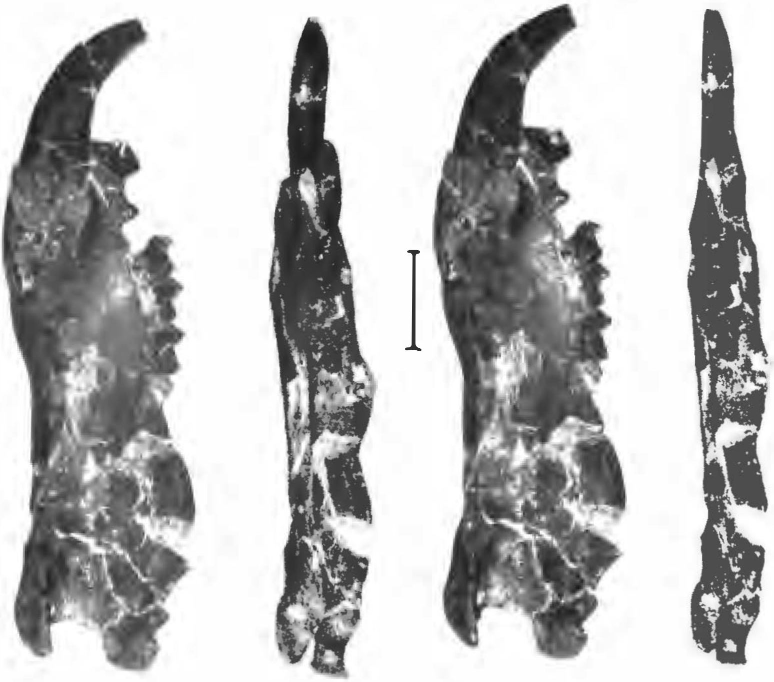

FIG. 15.—Stereophotographs of dentary of AMNH 1903, late Eocene *Apatemys uintensis* (holotype of *Stehlinius uintensis* Matthew, 1921). Scale units equal 5 millimeters.

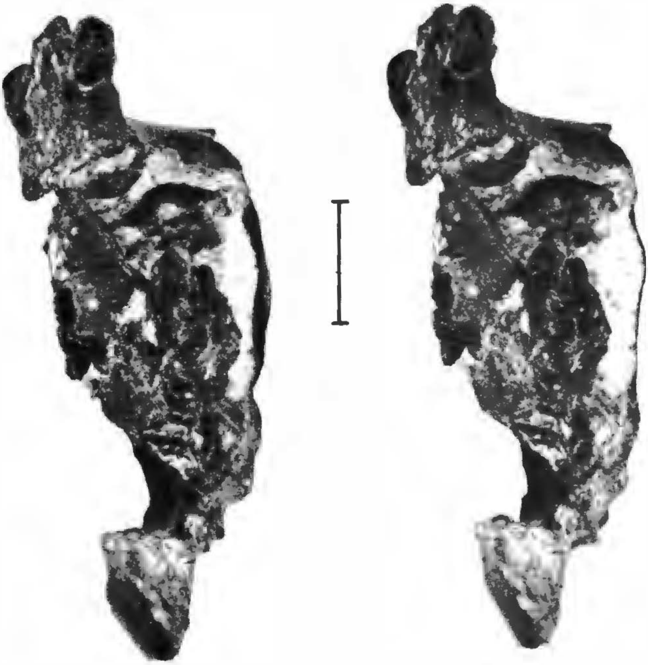

FIG. 16.—Stereophotographs of maxilla of AMNH 1903, late Eocene *Apatemys uintensis* (holotype of *Stehlinius uintensis* Matthew, 1921). Scale units equal 5 millimeters.

FIG. 17.—Stereophotographs of UCMP 86296, late Eocene *Apatemys uintensis*. Scale units equal 5 millimeters.

FIG. 18.—Stereophotographs of dentary of PU 13585, holotype of early Oligocene *Sinclairella dakotensis* Jepsen, 1934. Scale units equal 5 millimeters.

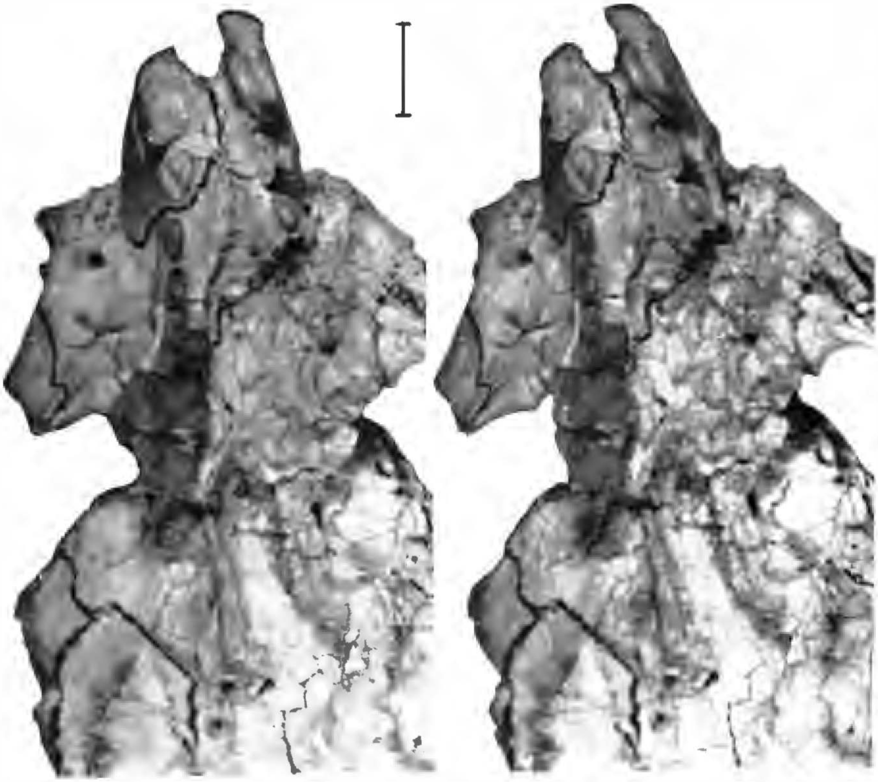

FIG. 19.—Stereophotographs of occlusal view of skull of PU 13585, holotype of early Oligocene *Sinclairella dakotensis* Jepsen, 1934. Scale units equal 5 millimeters.

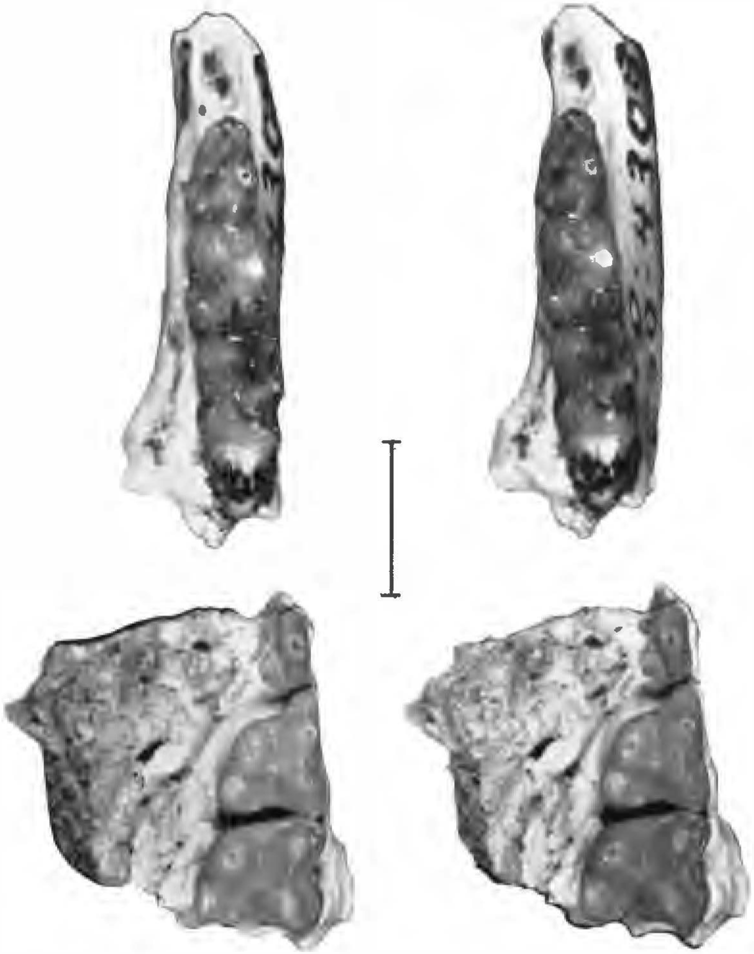

FIG. 20.—Stereophotographs of Oligocene *Sinclairella dakotensis*: top, SDSM 230-4308; left dentary with m1-m3; bottom, KU 11210, left maxilla with p4-m2. Scale units equal 5 millimeters.