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PALEONTOLOGY AND GEOLOGY OF THE
BADWATER CREEK AREA, CENTRAL WYOMING

Part 7. Rodents of the Family Ischyromyidae

CRAIG C. BLACK¹

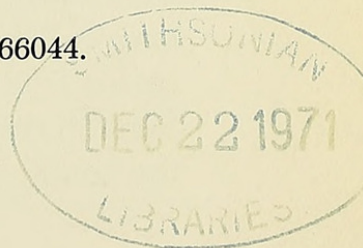
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INTRODUCTION

All ischyromyids described in this report are from the Tepee Trail formation and are of late Eocene age. Nine species of ischyromyids are recognized as occurring at one or more of six different localities within the Tepee Trail formation. Approximately 180 isolated teeth, one jaw with P⁴-M², and two maxillary fragments with two or three teeth form the basis for the present study. One genus of ischyromyid, *Microparamys*, is not considered in the Systematic Review of this report, but is discussed by Mary Dawson in Part 8 of this series. In all, there are nine species of ischyromyids belonging to at least six, and possibly seven, genera.

As always when dealing with a sample composed primarily of isolated teeth, there is considerable risk of error in determining which deciduous premolars and permanent premolars are associated with which molars, and in deciding which upper molars are associated with which lower molars. This problem is less difficult when the isolated teeth from single localities only are considered at one time. No more than five species of ischyromid are known from any one locality in the Tepee Trail formation. Difference in size and in morphology between these five species at any locality has made it possible to separate and recognize taxonomic groups with some certainty. In some cases, e.g., *Leptotomus guildayi*, a considerable amount of variation is recognized for one species. This procedure is considered preferable to recognizing a number of different variants, or species, of a single genus as occurring at one locality. In several cases, only tentative generic assignments have been given, and in two in-

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stances, I have not named new species because the material does not allow for an adequate description of either population.

The association of upper and lower cheek teeth referred to any one species at any single locality is based upon the following assumptions:

1. That, as a number of tons of mudstone have been processed from localities 5, 5A, 6, and Wood, a representative sample of all species preserved at each locality has been obtained.
2. That at each locality there is only a single species in any one size-group exhibiting the same morphology (see Table 1.).
3. That the upper and lower teeth of similar size and similar morphology belong to the same species.. If this is not so, then there would be one species based upon upper teeth alone and another species based upon lower teeth alone.

Abbreviations used in this paper are: ACM, Amherst College Museum; CM, Carnegie Museum; LACM (CIT), Los Angeles County Museum (California Institute of Technology collection); UCM, University of Colorado Museum; a-p, anterior posterior; tr, transverse width (two measurements, the first of which is the width of the upper teeth or the anterior width of the lower teeth, and the second, the posterior width of the lower teeth); N, number; OR, observed range; M, mean; R, Rodent locality; W, Wood locality.

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CLASSIFICATION

I have given my reasons elsewhere (Black, 1968a) for including within the Family Ischyromyidae all rodents considered by Wood (1962) to belong to the Family Paramyidae. In working up the late Eocene ischyromyids from Badwater, it has been necessary to review all late Eocene ischyromyid material as well as to make a brief survey of all members of the family. This study does not review (and it would not be feasible to do

so here) all the rodent material that Wood (1962) studied and reported on in such comprehensive detail. However, during the course of this study a number of changes have had to be made in taxonomic assignments of late Eocene ischyromyid material. This, in turn, has led to a re-evaluation of the classification of all rodents here considered to be members of the Family Ischyromyidae.

The classification proposed below and followed in this paper is similar in some regards to those of Simpson (1945) and Wilson (1949). It differs from those two classifications in recognizing as distinct the families Sciuravidae and Cylindrodontidae, both of which Wilson and Simpson considered subfamilies within the family Ischyromyidae. Reasons for recognizing these families, given in an early paper (Black, 1968a), are based primarily on the major radiations seen in each of the two groups, radiations that depart markedly from the morphological pattern seen in members of the family Ischyromyidae.

Family Ischyromyidae Alston, 1876

Cheek teeth basically low-crowned and tritubercular with hypocone, when present, secondary in importance to protocone; lophate condition rare, found only in a few advanced forms; talonid basins generally large and undivided; infraorbital foramen generally small, rounded, not compressed; zygoma heavy; masseter arises from ventral surface of zygoma; skull quite narrow in postorbital region; nasals usually long; temporal fossa large; brain case small, not inflated; bulla coossified only in a few species; tibia and fibula separate; humerus with entepicondylar foramen.

Subfamily Ischyromyinae Schlosser, 1911

U. Eoc.—U. Oligo., N.A.

Most advanced group in family; partially to completely lophate cheek teeth; four crests developed in upper and lower cheek teeth; hypocone distinct but subordinate to protocone; no mesoconid or mesostylid; hypolophid well developed.

Subfamily Paramyinae Simpson, 1945.

U. Paleo.—?L. Oligo., N.A.; L. Eoc.—

U. Eoc. Eur.; U. Eoc., L. Oligo.,

As.

Least specialized group in family; medium-to-large-sized rodents; cheek teeth generally simple in pattern, particularly in largest forms; enamel of cheek teeth often finely wrinkled to rugose; hypocones when present are small; mesoconids and mesostylids usually absent; entoconids generally continuous with posterolophids; anterior cingula of lower cheek teeth short.

Subfamily Reithroparamyinae Wood, 1962

L. Eoc.—U. Eoc., N.A.; L. Eoc.—M.

Eoc., Eur.

Small-to-medium-sized rodents; cheek teeth tending to become more complex;

hypocone usually present and large; mesoconid generally present; mesostylid small to absent; entoconid usually separated from posterolophid; anterior cingulum of lower cheek teeth elongate; short hypolophid crest commonly present.

Subfamily Prosciurinae Wilson, 1949

U. Eoc.—L. Mio., N.A.; M.—U. Oligo., Eur.; U. Oligo., As.

Small-to-medium-sized rodents; cheek teeth moderately complex; hypocone absent or small; mesoconid large; mesostylid commonly crested; entoconid often separated from posterolophid; trigonid basin reduced; anterior cingulum quite short; hypolophid always present.

Order Rodentia Bowdich, 1821

Suborder Sciuromorpha Brandt, 1855

Superfamily Ischyromyoidae Wood, 1937

Family Ischyromyidae Alston, 1876

U. Paleo. L. Mio.

Subfamily Ischyromyinae Schlosser, 1911

Ischyromys Leidy, 1856.

[Including *Titanotheriomys* Matthew, 1910.]

U. Eoc.—?U. Oligo., N.A.

Subfamily Paramyinae Simpson, 1945

Paramys Leidy, 1871.

U. Paleo.—M. Eoc., N.A., L. Eoc., Eur.

Leptotomus Matthew, 1910.

[Including *Tapomys*¹ Wood, 1962.]

L.—U. Eoc., N.A.

Thisbemys Wood, 1959.

M.—U. Eoc., N.A.

Ischyrotomus Matthew, 1910.

M.—U. Eoc., N.A.

Pseudotomus Cope, 1872.

L.—M. Eoc., N.A.

Manitsha Simpson, 1941.

?L. Oligo., N.A.

Mytonomys Wood, 1956.

U. Eoc., N.A.

¹For discussion of this synonymy see *Tapomys* in Systematic Review.

Rapamys Wilson, 1940.

U. Eoc., N.A.

Pseudoparamys Michaux, 1964.

L. Eoc., Eur.

Plesiarctomys Bravard, 1850.

M.-U. Eoc., Eur.

Hulgana Dawson, 1968.

L. Oligo., As.

Subfamily Reithroparamyinae Wood, 1962

Reithroparamys Matthew, 1920.

[Including *Uriscus*² Wood, 1962.]

L.-U. Eoc., N.A.

Franimys Wood, 1962.

L. Eoc., N.A.

Microparamys Wood, 1959.

L.-U. Eoc., N.A.; L.-M. Eoc., Eur.

Lophiparamys Wood, 1962.

L. Eoc., N.A.

Janimus Dawson, 1966.

U. Eoc., N.A.

Subfamily Prosciurinae Wilson, 1949

Cedromus Wilson, 1949.

M. Oligo., N.A.

Pelycomys Galbreath, 1953.

L.-M. Oligo., N.A.

Prosciurus Matthew, 1903.

L.-Oligo.—L. Mio., N.A.

Spurimus, new genus.

U. Eoc., N.A.

Plesispermophilus Filhol, 1883.

M.-U. Oligo., Eur.; U. Oligo., As.

Ischyromyidae *incertae sedis*

Decticadapis Lemoine, 1891.

L. Eoc., Eur.

²The type, and only known specimen, of *Uriscus* is a lower jaw (LACM; CIT 2194) with worn M₁-M₃. The dental pattern is similar to that of *Reithroparamys gidleyi*. Because of its small size the California specimen probably represents a distinct species of *Reithroparamys*, *R. californicus*.

Ailuravus Rüttimeyer, 1891.

M. Eoc., Eur.

Maurimontia Stehlin and Schaub, 1951.

M. Eoc., Eur.

Meldimys Michaux, 1964.

L. Eoc., Eur.

SYSTEMATIC REVIEW

Order Rodentia

Family Ischromyidae

*Leptotomus guildayi*¹, new species

Figures 1-12

?*Rapamys* sp., Wood, 1949a, :557; ?*Rapamys* sp. B., Wood, 1962 :153.

TYPE: CM 14627, LM₃.

HYPODIGM: Type and P⁴, CM 14621, 15347, 15353, 18230; DP⁴, CM 16065; M¹ or 2, CM 14620, 14625, 15339, 15343, 15349, 15350, 16064, 16068, 18235, 18238, 21980; M³, CM 14622, 15346, 19774; P₄, 14626, 15342, 16769, 18231, UCM 24793; M₁ or 2, CM 14628, 15340, 15341, 16067, 16770, 18197, 18227, 21976-21979, UCM 24739; M₃, CM 16066-16068, 16767, 16768, 18234, UCM 24722, ACM 10014.

DISTRIBUTION: Type from Rodent locality (Black and Dawson, 1966, fig. 1). All other specimens from either Rodent or Wood locality. The Amherst College specimen (Wood, 1949a; 1962:153) is from the Wood locality.

DIAGNOSIS: Protoconid of P₄ crowded backwards and lingually into metaconid; hypolophid complete on P₄-M₃ but generally low, not as strong as in *Ischyromys*, but better developed than in *Rapamys*; trigonid basins of M₁-M₃ generally large, shallow, closed by strong metalophids; buccal valley wide on M₁-M₃; no mesoconid; hypocone distinct on M¹-M², absent on P⁴; single metaconules on P⁴-M³; anterior cingulum short on P⁴-M³.

DESCRIPTION: There is only one tooth that appears to be a deciduous upper premolar, CM 16065 (fig. 1). This tooth is slightly smaller than the permanent P⁴ and displays a distinct hypocone, which is not present on P⁴. The metaconule of dP⁴ is as large as the metacone; it is connected to the internal face of the protocone near its base. There is a distinct protoconule on dP⁴ and a large mesostyle. The anterior cingulum of dP⁴ is wider than that of P⁴.

The permanent fourth premolars are triangular in occlusal outline (figs. 2 and 3) with high, rather sharp protocones, but no hypocones. The anterior cingula are wider than the posterior, and curve back into the anterior slopes of the paracones. The metaconules are very large, possibly more bulbous than the metacones. There is no distinct metaloph on

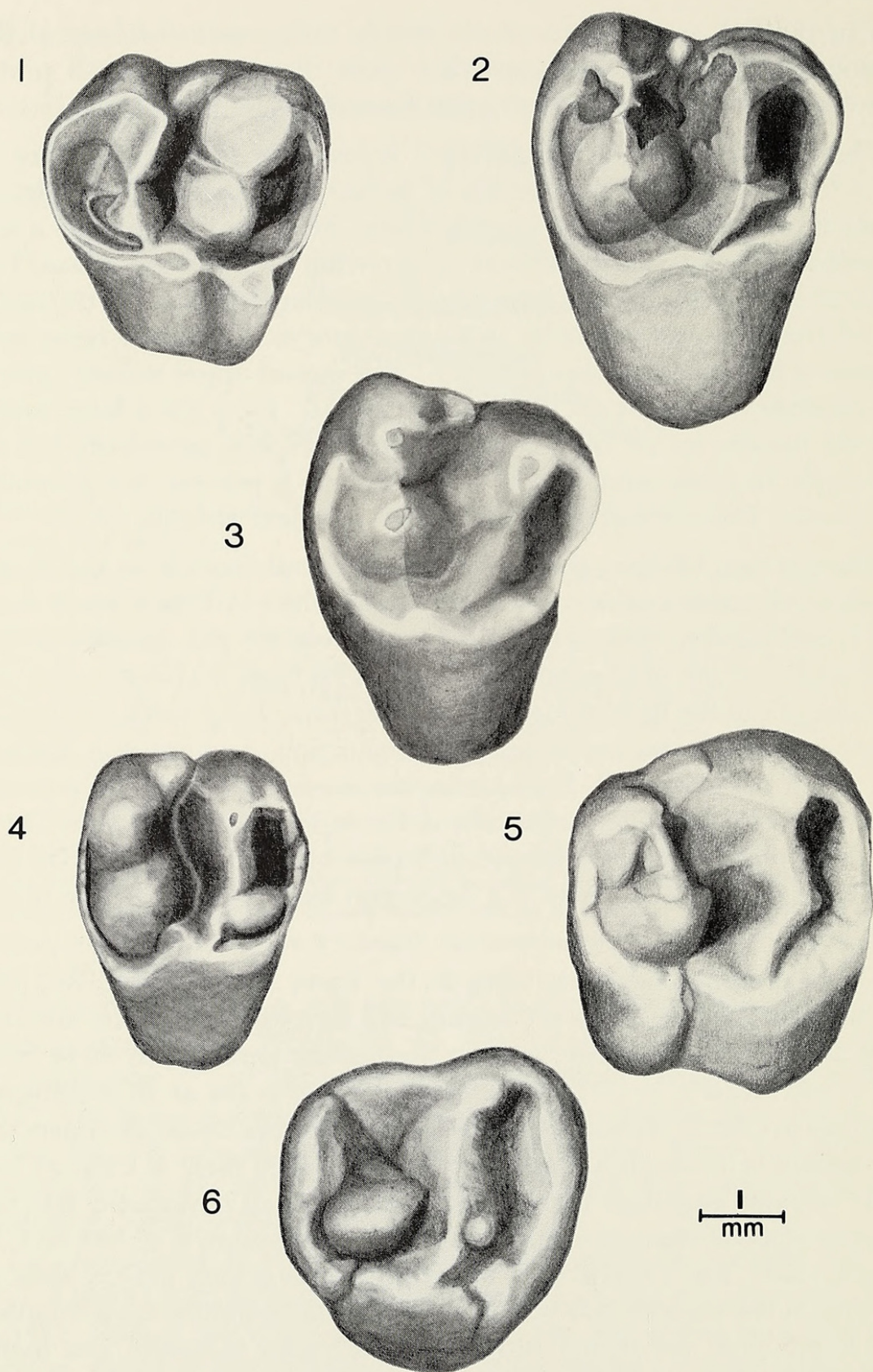
¹Named for John E. Guilday in appreciation of his valued advice and criticism.

any of the P^4 s, as the metaconules simply merge into the base of the protocone. Protolophs are somewhat more distinct, and small protoconules are present. Each P^4 has a small mesostyle.

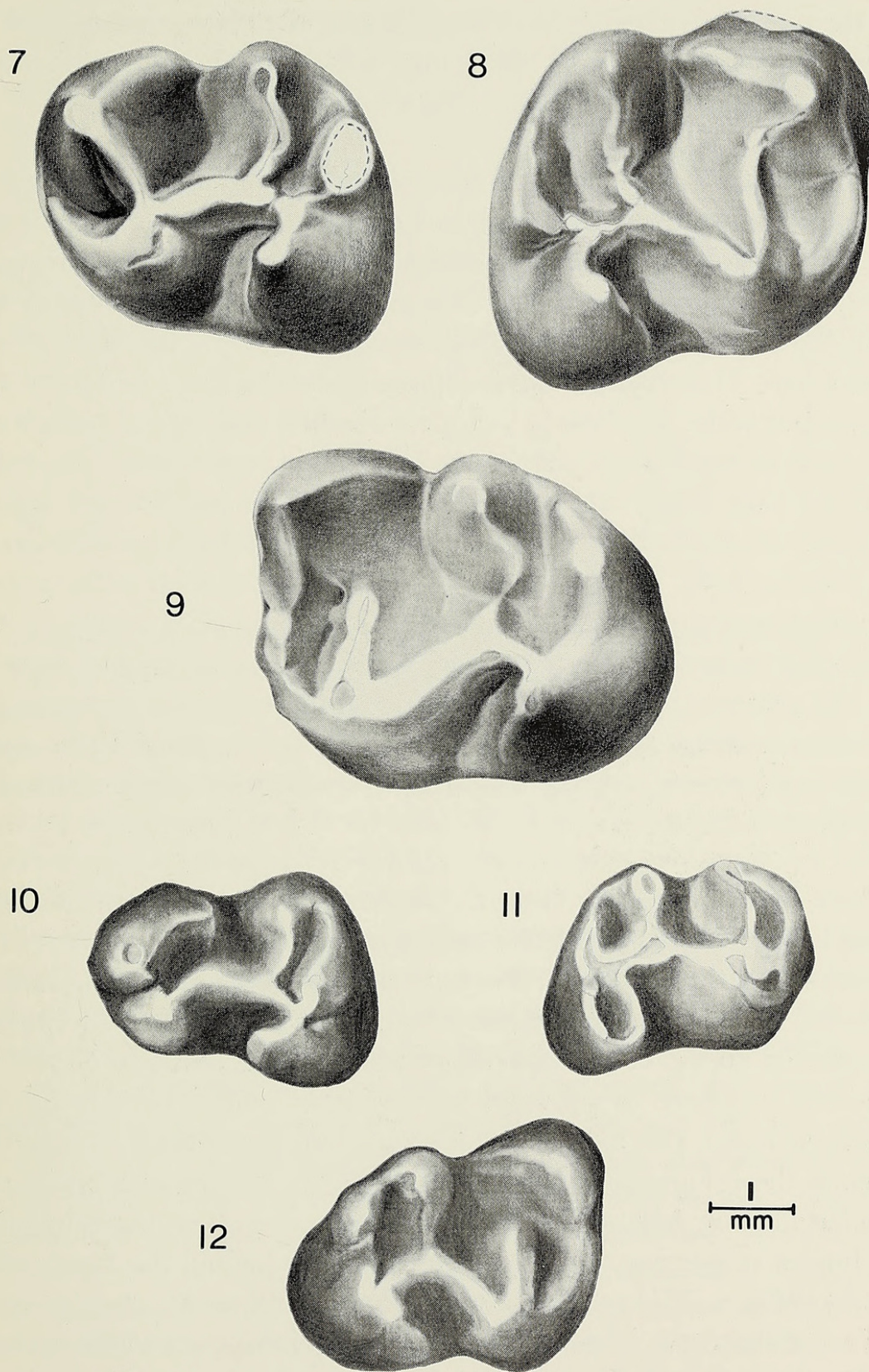
There are two somewhat different types of teeth grouped here as M^1 or 2 . One type (fig. 4) consists of molars that are slightly wider in relation to their length than are the others. Also, these teeth have a less prominent hypocone with little or no grooving of the internal face. The squarer teeth of the second type (fig. 5) have large hypocones distinctly set off from the protocones by an internal groove. These two types may represent first upper molars (group 1) and second upper molars (group 2). In other characters the teeth are all similar. Each has a large metaconule, usually set off from the protocone, complete protoloph, but no metaloph. In some cases (fig. 4) a protoconule is present, but generally it is absent. The size and position of the mesostyle is variable.

There is one M^3 from the Rodent locality, and three from the Wood locality. All teeth are circular in occlusal outline. All three teeth from the Wood locality have a distinct protoconule set just anterior to the protoloph and not incorporated within it. This cusp is absent in the one specimen from the Rodent locality. In other respects the teeth are similar. There is no hypocone and little, if any, indication of a metacone. Rather, the entire posterior loph from protocone around through the postero-external corner is swollen, especially in the region of the metacone. There is a large, partially isolated metaconule present on all specimens. On one specimen (CM 19774) there is a short crest from the metaconule to the protoloph.

There is considerable variation in the lower fourth premolars, particularly in the size of the protoconid and development of the anterior cingulum. There are three P_4 s from the Rodent locality and three from the Wood locality. In CM 14626 the protoconid is not at all prominent, whereas in CM 15342 and 18231 it is distinct. In the other premolars the protoconid is moderately developed. In CM 14626 there is a strong but short anterior cingulum that passes from the small protoconid into the anterior slope of the metaconid. The anterior cingulum is absent on CM 15340, 18231, and UCM 24793, but is present as a very narrow shelf at the base of the anterior face of CM 15342. On all premolars the ectolophid and hypolophid are strong and the buccal valley is broad. The hypolophid passes directly across the occlusal surface from entoconid to ectolophid. There are no metastylids or mesoconids present. The hypoconulids are distinct on all premolars, and the posterior cingula merge



Figs. 1-6. *Leptotomus guildayi*. 1. CM 16065, LdP⁴. 2. CM 14621, RP⁴. 3. CM 15353, RP⁴. 4. CM 21980, LM¹⁻². 5. CM 15350, RM¹⁻². 6. CM 15346, RM³.



Figs. 7-12. *Leptotomus guildayi*. 7. CM 14626, LP₄. 8. CM 14628, RM₁₋₂. 9. CM 14627, LM₃, Type. 10. CM 18231, LP₄. 11. CM 15340, RM₁₋₂. 12. CM 10014, RM₃.

into the posterior slopes of the entoconids near their base. One or more of these teeth, particularly CM 15342, may be a deciduous premolar, but it is impossible to be certain of this in the absence of roots on the teeth.

There is very little variation in the occlusal pattern of the ten first and second lower molars here assigned to *Leptotomus guildayi*. They all display large trigonid basins with complete metalophids posteriorly and strong anterior cingula anteriorly. The anterior cingula lie well below the tip of the protoconids and generally somewhat below the level of the metalophids. The trigonid basins enclosed between these two lophs are shallow but wide. The buccal valleys of the first and second molars are wide, and swing slightly posteriorly behind the hypoconids. The ectolophs are long, heavy crests on all teeth. The hypoconulids are always large and are distinctly set off from the hypoconids by a constriction in the posterior loph. This loph, or posterior cingulum, then either passes from the hypoconulid into the base of the entoconid (CM 14628; fig. 8), or ends before reaching the entoconid, leaving a postero-internal opening into the posterior valley (CM 16770). Hypolophids are strong on all specimens, passing almost directly across the crown towards the ectolophid and curving sharply anteriorly just as they merge with the ectolophid.

There are six M_3 s, four from the Rodent locality and two from the Wood locality. As with the first and second molars, there is very little variation in occlusal pattern. The third molars are, in fact, quite similar to M_1 and M_2 , differing only in the enlargement of the hypoconid, hypoconulid, and the valley between the hypolophid and posterior crest. The entoconid is isolated as a prominent cusp, with a notch between it and the hypoconulid. The hypolophid is strong and runs directly across the crown to the ectolophid. As in the other molars, the trigonid basins are wide but shallow, with well-developed anterior cingula and metalophids. The buccal valleys are wide, and curve slightly behind the hypoconid. Wood (1949a, p. 557) referred a single cheek tooth, an M_3 , to ?*Rapamys* sp. Two of the above M_3 s come from the exact locality at which Wood's specimen was found. They match Wood's specimen completely (figs. 9 and 12), as do the other specimens referred here to *Leptotomus guildayi* from the Rodent locality just to the east.

MEASUREMENTS IN MM., *Leptotomus guildayi*

		N	M	OR	M _R (N)	M _W (N)
dP ⁴	a-p	1	3.44
	tr	1	3.68
P ⁴	a-p	4	3.76	3.50-4.00	3.88(2)	3.60(2)
	tr	4	4.75	4.30-4.95	4.96(2)	4.56(2)
M ¹ or ²						
	a-p	10	3.85	3.50-4.15	4.05(3)	3.80(7)
	tr	10	4.75	4.00-5.30	5.00(3)	4.65(7)
M ³	a-p	3	3.97	3.75-4.00	4.00(1)	3.96(2)
	tr	3	3.84	3.70-4.00	3.84(1)	3.84(2)
P ⁴	a-p	6	4.26	4.00-4.50	4.27(3)	4.24(3)
	tr	4	2.96	2.80-3.05	3.00(2)	2.92(2)
	tr	5	3.62	3.35-4.00	3.68(2)	3.60(3)
M ₁ or ₂						
	a-p	10	4.22	4.00-4.50	4.30(3)	4.20(7)
	tr	10	3.58	3.20-3.85	3.75(3)	3.50(7)
	tr	9	3.90	3.50-4.15	4.00(3)	3.90(6)
M ₃	a-p	6	4.65	4.50-4.95	4.63(4)	4.60(2)
	tr	6	3.92	3.85-4.00	3.92(4)	3.92(2)
	tr	6	3.60	3.45-3.75	3.59(4)	3.68(2)

AFFINITIES: It is extremely difficult to justify assignment of this species to any of the ischyromyid genera as diagnosed by Wood (1962), yet there are no characters that, in my opinion, warrant recognition of a new genus for this material. The dentition is in general rather simple, as in *Leptotomus* and *Ischyrotomus*, in contrast with the more complex dentitions of *Mytonomys* and *Rapamys*. *Tapomys*, also known from the late Eocene, appears to be referable to *Leptotomus* as discussed in a following section.

Leptotomus guildayi is placed in *Leptotomus* primarily because of the lack of specializations in the upper and lower molars. In *Leptotomus*, as defined by Wood (1962:64, 68), the cusps are high; there is little or no crenulation in the dentition; a ridge develops, in some later species, from the entoconid toward the hypoconid; the protoconid of P₄ seems to be displaced into and behind the metaconid; hypocones are progressively developed on M¹ and M²; and there are no accessory conules in the upper molar loph. These characters are all to be found to some degree in *Leptotomus guildayi*. *Leptotomus* is also characterized, however (*op. cit.*), as having reduced basins, a tendency for migration of the anterior cingulum around onto the buccal side of the paracone on P⁴-M³, and well-developed mesoconids on the ectolophids of M₁-M₃. These characters are not found in *Leptotomus guildayi*.

Additionally, this Badwater species is distinct in having a low but complete loph extending from the entoconid to the posterior end of the

ectolophid, in having very large and enclosed trigonid basins, and in having wide buccal valleys on M_1 - M_3 . The upper dentition does not show any particular specializations, and there is no indication of buccal migration of the anterior cingulum.

The dentition of *Mytonomys* (Wood, 1962, fig. 84; Black, 1968b) is much too complex to bear any close relationship to that of *Leptotomus guildayi*. This is also true for the dentition of *Rapamys* (Wood, 1962, fig. 52; figs. 25-40, this paper). In addition, the hypolophid is a much more complete crest in *Leptotomus guildayi* than in either *Mytonomys* or *Rapamys*. Wood (1949a; 1962) referred an isolated M_3 , part of an M_1 or 2 , and an incisor from Badwater (from the Wood locality) to *Rapamys* sp. In 1949, he stated that more material might show that a distinct genus should be recognized for this species. Reason for reference of the Badwater specimen to *Rapamys* hinged on the separation of entoconid and posterolophid, and presence of a hypolophid in both forms. Now that the complete dentition of the Badwater form is known, reference of this species to *Rapamys* does not appear possible. A species of *Rapamys* is present at some of the Badwater localities, but it was not represented in Wood's 1948 collection.

It seems best, therefore, to consider the present sample as belonging to a species of *Leptotomus* possibly derived from *Leptotomus bridgerensis*. The incipient development of a hypolophid seen in some other species of *Leptotomus* was carried much further in *Leptotomus guildayi*, as was the strengthening of the metalophid and enlargement of the trigonid basin. In *L. bridgerensis*, the metalophid is complete on M_1 - M_3 , but the trigonid basin is not enlarged. This is essentially the condition in *Leptotomus tapensis*, although that species is larger than *L. bridgerensis*. *L. tapensis* thus differs from *L. guildayi* in having a smaller trigonid basin and much less development of the hypolophids. While these changes were taking place in the lower dentition, the upper cheek teeth of *L. guildayi* changed little from those of *L. bridgerensis*. There was only a slight increase in size from *L. bridgerensis* to *L. guildayi*. The populations from localities 5 and 6 described below would seem to be intermediate between *Leptotomus bridgerensis* and *L. guildayi*.

It does not now appear likely that *Leptotomus guildayi* gave rise to any later ischyromyids. Earlier (Black, 1968a:299) I had thought that this material might be referable to *Rapamys* and that this species might have been ancestral to *Ischyromys*. I no longer believe this to be so, however, as some specimens of ?*Ischyromys* contemporaneous with *Lepto-*

tomus guildayi are present at the Wood locality. Also, I now restrict *Rapamys* to those forms having complex upper dentitions with doubled metacones or metaconules with accessory lophs or both. This type of dentition is not at all what one would expect in the ancestry of *Ischyromys*. In 1967 (Black, 1968a) I had not recognized in the Badwater collection the *Rapamys* population described below, but was following Wood (1962) in his identification of ?*Rapamys* sp. from Badwater. His material is certainly referable to *Leptotomus guildayi* and does not pertain to *Rapamys*.

Leptotomus near *L. guildayi*

Figures 13-24

MATERIAL: CM 16875, LP⁴-M¹; CM 14569, RM¹-M²; CM 16873, LP₄-M₂; dP⁴, CM 16869, 16874, 16877; P⁴, UCM 24741, 24764; M¹ or ², CM 14510, 15320, 15325, 15563, 16876, 19746, 25352; M³, CM 15575; dP₄, CM 16868; P₄, CM 16791, 16870, UCM 24799; M₁ or ₂, CM 14508, 14568, 15331, 15337, 15576, 16872, 16880, 16885, 19764, UCM 24728, 24744, 24789; M₃, 14507, 15330, 15417, 16794, 16871.

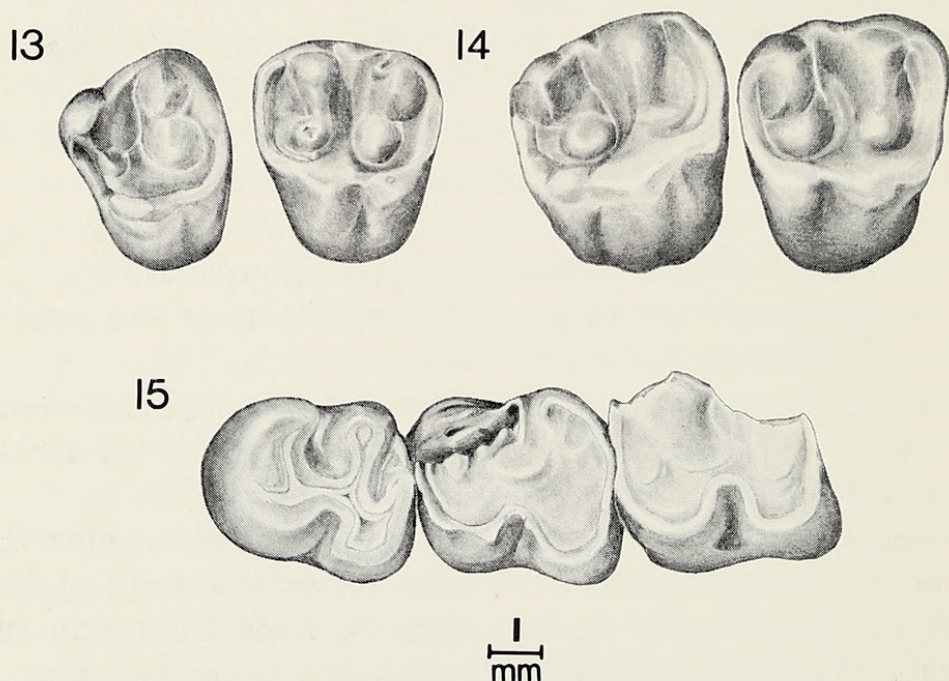
DISTRIBUTION: Localities 5, 5A, and 6.

DESCRIPTION: The deciduous fourth upper premolars are all triangular in occlusal outline. The protocone is a high, rather sharp antero-posteriorly compressed cusp, and there is little or no indication of a hypocone posterior to it. The anterior cingulum is broad, but there is no parastyle. The paracone, protocone, metacone, and metaconule are all distinct cusps that rise well above the rest of the surface of the tooth. A small protoconule is discernible within the protoloph, but it is neither as large nor as distinctly isolated as the metaconule. There is a very low loph from the protoconule to the anterior cingulum dividing the anterior shelf into two parts. Posteriorly, the posterior cingulum curves around the outside of the metacone and onto the buccal face of the tooth.

The two upper permanent P⁴s from locality 5 differ somewhat from the one P⁴ known from locality 6. Those from locality 5 are somewhat larger and more triangular in occlusal outline than the single tooth from locality 6. This difference in occlusal outline is due primarily to the anterior and somewhat internal position of the paracone on the specimen from locality 6 (CM 16875). In all other morphological details these teeth are quite similar. The protocone is the only internal cusp and it is situated anteriorly more or less directly internal to the paracone. The metaloph diverges from the protocone postero-buccally to reach the metacone, and the protoloph passes almost directly from the protocone buccally to the paracone. There is a small protoconule, but a large, separate metaconule. The metaconule in all instances is equal in size to

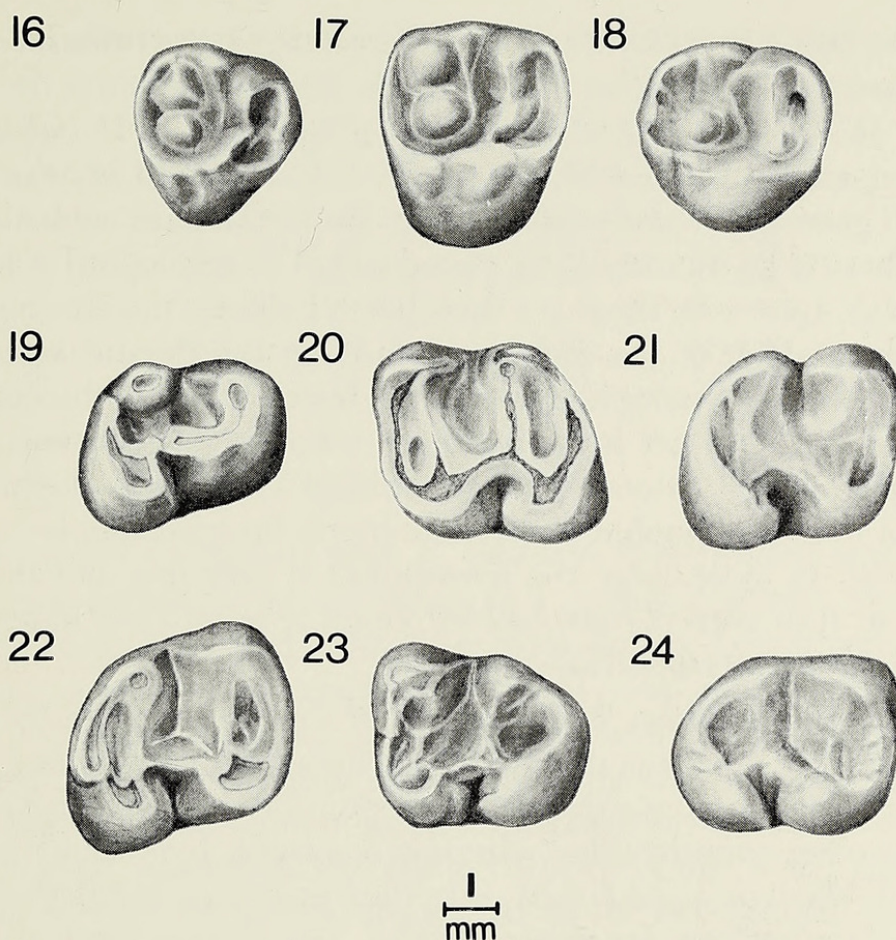
the metacone. The anterior cingulum is short and narrow. There is no mesostyle on any of the P^4 s.

There is one maxillary fragment that preserves M^1 - M^2 (CM 14569) and one maxillary fragment (CM 16875) with P^4 - M^1 . Otherwise, all the upper first and second molars are isolated teeth. On these teeth, the hypocone is generally large and is separated from the protocone by a distinct groove down the internal face of each tooth. The anterior cingula are wide but low, and do not rise into prominent parastylar areas anterior to the paracones. The protoloph is generally complete, with a thin, low ridge connecting the protoconule to the face of the protocone. In contrast, the metalophs are incomplete, ending in an enlarged metaconule which is distinctly separated from the hypocone. Mesostyles are generally present, although small. The posterior cingula are narrow and short, failing to reach the buccal margins of the teeth. The upper first and second molars from locality 5 are somewhat larger than those from locality 6, but in details of morphology, the two samples agree closely.



Figs. 13-15. *Leptotomus* near *L. guildayi*. 13. CM 16875, LP^4 - M^1 . 14. CM 14569, RM^1 - M^2 . 15. CM 16873, LP_4 - M_2 .

Only one M^3 in the collection is believed to represent this species. This tooth is circular in occlusal outline, with a very broad protocone. The protoloph is very low and there is a distinct protoconule abutting against the internal face of the protocone. The metaconule is distinct and is isolated in the talonid basin. The posterior half of M^3 is ringed by a



Figs. 16-24. *Leptotomus* near *L. guildayi*. 16. CM 16877, RdP₄. 17. CM 19746, RM₁₋₂. 18. CM 15575, RM₃. 19. CM 16870, RP₄. 20. CM 16885, LM₁₋₂. 21. CM 19764, RM₁₋₂. 22. CM 15337, RM₁₋₂. 23. CM 15417, LM₃. 24. CM 16794, RM₃.

thin, curving loph, which passes from the posterior slope of the protocone around and into the base of the paracone. There is no distinct swelling of this ridge in the area of the metacone.

The deciduous fourth lower premolar is somewhat smaller than the permanent P₄. It also differs from the permanent teeth in having a distinct protoconid with a small notch between the protoconid and metaconid. In addition, the hypolophid is a complete crest on the deciduous P₄, but not on the permanent teeth.

The permanent fourth lower premolars show no indication of a separate protoconid. The metaconid is an extremely high, very massive cusp, occupying the entire anterior margin of the teeth. There is no notch on the anterior face of these teeth, and no sign of a trigonid basin. The hypoconid and entoconid, although bulbous, lie considerably below the top of the metaconid. There is a low, short ridge from the entoconid into the talonid basin, but it does not reach the ectolophid.

The first and second lower molars are rectangular in occlusal outline, being somewhat longer than they are wide. The metaconid is the largest cusp on M_1 - M_2 and projects well above the tops of the entoconid, hypoconid, and protoconid. The trigonid basin on M_1 and M_2 is relatively small and generally closed posteriorly by the metalophid, which is quite heavy. There is no mesostylid or mesoconid. The ectolophid is low and rather weak. Internally there is a deep notch between the entoconid and the posterior slope of the metaconid, leaving the talonid basin open lingually. The posterolophid between the hypoconid and the entoconid is elevated into a rather heavy crest, with no notch between the posterolophid and the entoconid. Development of the hypolophid from entoconid to the ectolophid is variable, but in no specimen is it a high, strong crest. In most cases, the hypolophid is very low, but does pass buccally to fuse with the ectolophid. There is no distinct hypoconulid on any of the first or second lower molars.

The third lower molar is the largest of the lower cheek teeth, and resembles M_1 - M_2 in general pattern. It differs from the first and second molars in having a more expanded posterior portion of the tooth with a heavy, swollen posterolophid curving from the hypoconid into the entoconid. The hypolophid on M_3 is low but complete, passing from near the base of the entoconid to the ectolophid. The trigonid basin is variable in size, being relatively large on one specimen (CM 16794) but small on another (CM 15417).

The incisor (CM 16873) is compressed laterally and is very deep antero-posteriorly. The enamel is thin and covers about half the lateral face of the incisor, overlapping just slightly on to the medial face. The portion of the mandible that is preserved is deep below the cheek teeth. There are two mental foramina, a small one lying just below the middle of M_1 and a larger one lying forward at about the middle of the diastema and just below the superior diastema surface.

MEASUREMENTS IN MM., *Leptotomus* NEAR *L. guildayi*

		N	M	OR	$M_5(N)$	$M_6(N)$
dP ⁴	a-p	3	...	2.80-3.20	...	3.03(3)
	tr	3	...	3.10-3.50	...	3.37(3)
P ⁴	a-p	3	3.13	3.00-3.20	3.20(2)	3.00(1)
	tr	3	4.20	4.10-4.30	4.25(2)	4.10(1)
M ¹ or ²						
	a-p	10	3.67	3.40-4.10	3.72(7)	3.53(3)
	tr	10	4.47	4.10-4.90	4.59(7)	4.20(3)
M ³	a-p	1	3.70
	tr	1	3.70

(MEASUREMENTS, *Leptotomus* NEAR *L. guildayi*, CONTINUED)

		N	M	OR	M ₅ (N)	M ₆ (N)
dP ₄	a-p	1	3.10
	tr	1	2.00
	tr	1	2.60
P ₄	a-p	3	3.56	3.50-3.70	3.50(2)	3.70(1)
	tr	3	2.50	2.30-2.80	2.35(2)	2.80(1)
	tr	3	2.97	2.80-3.20	2.85(2)	3.20(1)
M ₁ or 2						
	a-p	12	3.85	3.50-4.20	3.84(9)	3.87(3)
	tr	11	3.48	2.90-4.00	3.54(8)	3.33(3)
	tr	10	3.52	3.10-4.00	3.48(8)	3.70(2)
M ₃	a-p	5	4.18	3.90-4.40	4.15(4)	4.30(1)
	tr	5	3.51	3.10-3.90	3.40(4)	3.90(1)
	tr	5	3.30	3.00-3.50	3.25(4)	3.50(1)

AFFINITIES: *Leptotomus* near *L. guildayi* is somewhat smaller than *Leptotomus guildayi* from the Wood and Rodent localities. These specimens from localities 5 and 6 also differ from those of *Leptotomus guildayi* in having a weaker hypolophid on M₁-M₂ and in having somewhat smaller but deeper trigonid basins on the lower molars. The pattern of the upper cheek teeth is quite similar for samples from all four localities. In all, there does not seem to be enough difference between the populations found at localities 5 and 6 and those from the Wood and Rodent localities to warrant specific separation of the two groups. On present evidence, the population found at localities 5 and 6 was probably ancestral to *Leptotomus guildayi* of the Wood and Rodent localities.

Leptotomus near *L. guildayi* is closer, morphologically, to *L. tapensis* than is *L. guildayi*, particularly in possessing the lower, less robust hypolophid and in having a smaller trigonid basin. *Leptotomus* near *L. guildayi* is considerably smaller than *L. tapensis*, however.

Rapamys wilsoni¹, new species

Figures 25-38

TYPE: CM 15564 RM¹ or 2.

HYPODIGM: Type and P₄, CM 14786, 15420, 15422, UCM 24785; M¹ or 2, CM 14502, 15322, 15328, 15561, 15564, UCM 24798; M³, CM 14787, UCM 24723; dP₄, 15324; P₄, CM 14503, 15326, 15569, 15573, 15574, 16884, UCM 24729, 24771; M₁ or 2, CM 15327, 15329, 15418, 15581, 19763, UCM 24747, 24820; M₃, CM 15332, 16879.

DISTRIBUTION: Type from Locality 5. All other specimens from 5 and 5A except CM 15581, 16878, and 16884, which are from Locality 6.

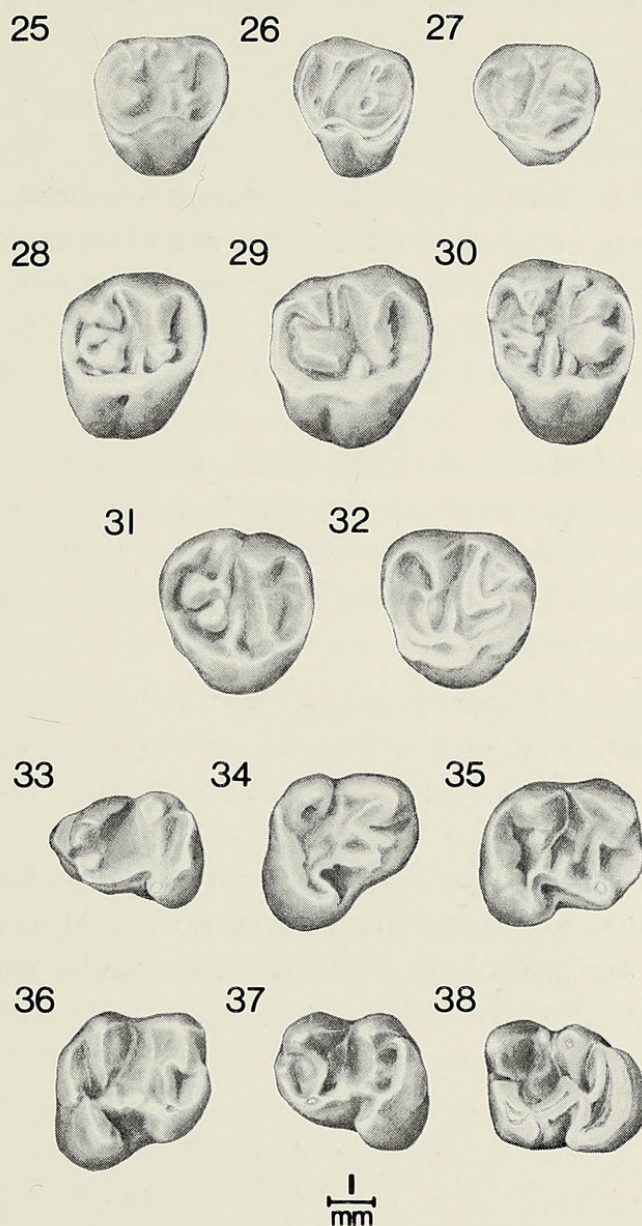
¹Named for R. W. Wilson, for his work on late Eocene rodents of California.

DIAGNOSIS: Smaller than *Rapamys fricki*; metacone single, smaller than doubled metaconule on M^{1-2} ; valley between paracone and metacone open buccally; protocone and hypocone not as deeply separated as in *R. fricki*; lower molars not as elongate as in *R. fricki*; trigonid basins larger and hypolophids somewhat stronger than in *R. fricki*.

DESCRIPTION: The fourth upper premolars are triangular in occlusal outline. The protocone is the main central internal cusp. On one specimen, CM 14786, there is no distinct hypocone. The other specimens have distinct hypocones, although they are considerably smaller than the protocones. The protoloph is weakly developed and the metaloph is incomplete. The paracone is considerably larger than the protoconule, but in the posterior half of the tooth the metaconule is considerably larger than the metacone. On one premolar there is a very small mesostyle, but this cusp is absent on the other premolars. The anterior cingulum is rather narrow and does not rise to a high parastylar ridge at the anterobuccal corner of the teeth.

The first and second upper molars are squarer in occlusal outline than the premolars. This is due primarily to the enlargement of the hypocone. The groove between the hypocone and the protocone along the internal face of the upper molars is not as deep as it is in *Rapamys fricki*, but it is distinct and separates the two cusps. The protoloph on the upper molars is generally well developed and joins the protocone at its antero-internal corner. Between the protoloph and the metaconule, there is a heavy ridge passing from the top of the protocone into the central valley between the protoconule and the metaconule. The metaloph on all first and second molars does not reach the hypocone. In some teeth, it is also interrupted between the metacone and the metaconule, and on others there is a crest between these two cusps. The metaconule is always larger than the metacone, and is generally partially divided into a smaller, anterior cusp and the larger interior portion of the cusp. There is considerable variation in the upper molars in development of the mesostyle. In some cases, e.g. UCM 24798, the mesostyle is barely distinct, while in others it is either a distinct cusp (CM 15322) or is elongated into a ridge passing internally towards the protocone, as in CM 15564. In all cases, however, the central valley between the paracone and the metacone is open internally, with no indication of the posterior paracone buttress seen in *Rapamys fricki*.

The third upper molars are circular in occlusal outline, with no indication of a distinct hypocone. The protoloph is always complete, with the protoconule either completely submerged within the loph or developed



Figs. 25-38. *Rapamys wilsoni*. 25. CM 15420, RP⁴. 26. UCM 24785, LP⁴. 27. CM 14786, LP⁴. 28. UCM 24798, RM¹⁻². 29. CM 15564, RM¹⁻², Type. 30. CM 15322, LM¹⁻². 31. CM 14787, RM³. 32. UCM 24723, LM³. 33. CM 15234, LdP₄. 34. UCM 24771, RP₄. 35. CM 15581, RM₁₋₂. 36. CM 19763, RM₁₋₂. 37. CM 15329, LM₁₋₂. 38. CM 16879, LM₃.

as a very distinct large cusp, as it is in UCM 24723. On the third upper molars there is a heavy ridge passing from the protocone between the protoloph and metaconule, as on the first and second upper molars. The metaconule is distinctly divided into two almost subequal cusps, and joins the ridge from the mesostyle. This ridge and the divided metaconules are distinctly set off from the postero-buccal corner of the tooth,

the metacone area. This area is expanded into a heavy, swollen, semi-circular ridge.

The fourth lower deciduous premolar is smaller and less robust, with smaller, more delicate cusps than the permanent P₄. The metaconid is the largest cusp, with the protoconid, hypoconid, and entoconid of nearly equal size, all lying somewhat lower than the metaconid. The trigonid basin on the deciduous premolar is small, and opens both anteriorly and posteriorly. The hypolophid is also small, appearing to be merely a short ridge passing from the entoconid toward the hypoconid. The principal cusps on the permanent fourth lower premolar are all strong and rounded. The protoconid and metaconid are subequal and appressed to the trigonid basin, appearing as a very narrow slit between the two. The hypolophid is not well developed on the permanent premolar and fails to reach the ectolophid. The hypoconulid is well developed, and is almost the same size as the entoconid.

On the lower first and second molars, the trigonid basins are generally well developed and are closed both anteriorly and posteriorly by narrow crests. The four principal cusps are high and rather bulbous, and the hypoconulid is always strong. The extent of hypolophid development is variable. In some cases it is a complete loph from the entoconid to the ectolophid, whereas in others it just fails to join the ectolophid. The buccal valley on the lower molar is long, and curves posteriorly as it passes into the tooth. The hypoconid is swollen in all teeth, and is pulled anteriorly.

There is only one third lower molar in the collection. The trigonid basin of this tooth is small and is open posteriorly. The hypolophid is well developed, passing all the way across the tooth to the ectolophid. There is no indication of a mesostylid on any of the lower cheek teeth.

MEASUREMENTS IN MM., *Rapamys wilsoni*

		N	M	OR
P ⁴	a-p	4	2.80	2.70-3.00
	tr	4	2.97	2.85-3.20
M ¹ or ²	a-p	6	3.31	3.20-3.70
	tr	6	3.95	3.75-4.35
M ³	a-p	2	3.52	3.50-3.55
	tr	2	3.52	3.45-3.60
dP ₄	a-p	1	3.20	...
	tr	1	2.00	...
	tr	1	2.55	...

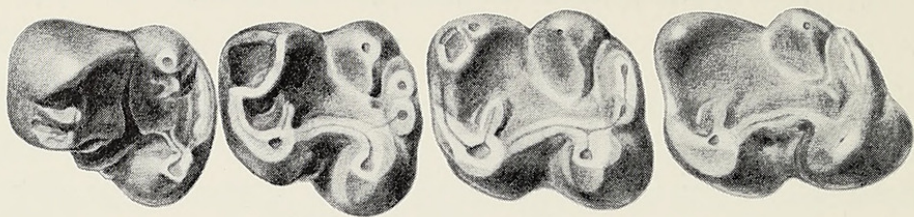
(MEASUREMENTS, *Rapamys wilsoni*, CONTINUED)

		N	M	OR
P ₄	a-p	6	2.97	2.70-3.20
	tr	6	1.98	1.75-2.20
	tr	6	2.51	2.35-2.55
M ₁ or 2	a-p	7	3.60	3.25-3.95
	tr	7	2.75	2.35-2.55
	tr	7	3.30	3.10-3.75
M ₃	a-p	2	3.62	3.55-3.70
	tr	2	2.82	2.80-2.85
	tr	2	2.95	2.90-3.00

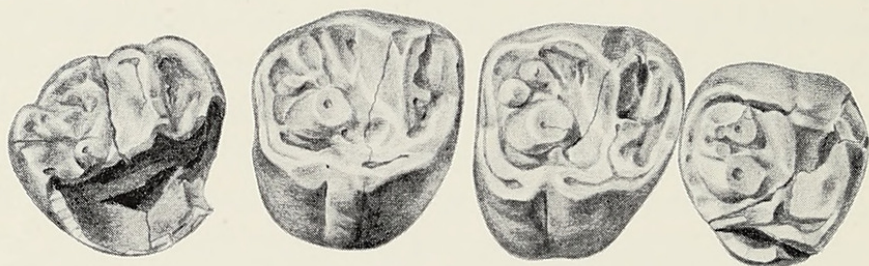
AFFINITIES: Specimens here assigned to a new species, *Rapamys wilsoni*, are all clearly distinct from any other Badwater ischyromyids, but do share a number of characters with *Rapamys fricki*, known from the late Eocene of California (Wilson, 1940). The major points of resemblance between these two species are found in the additional complications of the occlusal pattern of the upper cheek teeth, particularly in the doubling of the metaconules in *Rapamys wilsoni* and the metacones in *Rapamys fricki*. In addition, these two species are similar in having the hypocone and protocone separated in the upper molars; the distinct protoconules in the protoloph of M¹ and M²; the partial hypolophid development in the lower cheek teeth; and the distinct and large hypoconulid set off from the entoconid. The upper and lower dentition of *Rapamys fricki* is here refigured (figs. 39 and 40) to facilitate comparison with the Badwater specimens.

Rapamys wilsoni differs from *Rapamys fricki* in a number of minor details. These include the presence in *R. wilsoni* of a strong ridge from the protocone, which passes between the metaconule and the protoloph; the somewhat larger and more enclosed trigonid basins on the lower molars; and the slightly better-developed ridge from the entoconid towards the ectolophid on M₁-M₂. Perhaps the most striking difference between the two species lies in the doubling of a different cusp on the metaloph of M¹-M². In *Rapamys fricki* the outer or postero-external cusp is doubled. Wood (1962:150) considers this doubled cusp to be the metaconule, whereas Wilson (1940:75) interpreted the doubled cusp as the metacone. Wilson's interpretation is followed here. Thus in *Rapamys fricki*, the metacone is doubled, whereas in *Rapamys wilsoni* it is the internal cusp on the metaloph, the metaconule, that is doubled. The same function, increasing the rugosity or amount of wear surface along the metaloph, is performed in both instances, and I do not believe the dif-

39



40



Figs. 39-40. *Rapamys fricki*. 39. LACM (CIT) 2181, LP₄-M₃, Type. 40. LACM (CIT) 2183, RP⁴-M³.

ference in locus of splitting a single cusp into two parts to be of more than specific importance.

Wood (1962:152-153) considered two other species as possibly belonging in the genus *Rapamys*. These were *Rapamys* sp. A., represented by two teeth earlier referred by Wilson (1940) to *Leptotomus burkei* (an incisor) and *Leptotomus* near *burkei* (an upper molar), and ?*Rapamys* sp. B., based on fragmentary material from Badwater, Wyoming. I have here assigned this Badwater material to *Leptotomus guildayi*. *Leptotomus burkei* (Wilson, 1940:73) is now considered to be a species of *Mytonomys* (Wood, 1956; Black, 1968b). The upper molar [LACM (CIT) 2178] referred by Wilson (1940) to *Leptotomus* near *burkei* and figured by Wood (1962, fig. 52 I as pertaining to *Rapamys* sp. A.), is similar to the upper molars here assigned to *Leptotomus guildayi* and is probably referable to the genus *Leptotomus*. On the basis of size and general morphology, the single tooth [LACM (CIT) 2178] from locality 207 of the Simi Valley, Ventura County, California, might well be an isolated upper molar of the species *Ischyrotomus* (?) *tapensis* Wilson (1940:69). This species was later referred to a new genus, *Tapomys*,

by Wood (1962). In erecting the new genus Wood (1962:154) said, "the cheek teeth of this genus are very similar to those of some of the more primitive species of *Paramys* and even closer in pattern to *Leptotomus*." In the succeeding discussion (Wood, 1962:154-157) of *Tapomys tapensis*, similarities to or differences from *Leptotomus* are not referred to again. The dentition of *Leptotomus* is slightly more complex than that of *Ischyrotomus* in showing trends toward hypolophid development and some accessory crenulation of enamel. In addition, the lower molars of *Leptotomus* are longer than they are wide and not as massive as those of *Ischyrotomus*. In both genera the dentition is much less specialized than in contemporaneous species of *Rapamys*, *Mytonomys*, and *Thisbemys*. The presence of slight crenulations of the enamel, the incipient entoconid cresting, and the elongate lower molars of the cheek teeth of *Tapomys tapensis* are all characters that are also found in species of *Leptotomus*. For this reason it seems likely that the material on which *Tapomys tapensis* is based is indistinguishable, on a generic level, from *Leptotomus*.

To summarize this rather confusing array of species:

Ischyrotomus (?) *tapensis* Wilson, 1940:69

= *Tapomys tapensis* Wood, 1962, p. 154.

= *Leptotomus tapensis*, this paper.

LACM (CIT) 2178 M¹ or ², *Leptotomus* near *L. burkei* Wilson, 1940:75

= *Rapamys* sp. A. Wood, 1962:153.

= *Leptotomus tapensis*, this paper.

Elsewhere in this paper ischyromyids of the California late Eocene are compared in detail with the Badwater assemblage.

Wood (1962:152) discussed the possible relationship of *Rapamys* to the ancestry of the caviomorph rodents of South America. The rodent immigrant into South America from whom the later South American rodents were evolved was probably a member of the Ischyromyidae. On the basis of all available material of this family, there is little reason to suggest that one genus was any more likely to be ancestral to the South American caviomorphs than any other.

Wood (*op. cit.*:152) says, "Certainly no known member of *Rapamys* is ancestral to the South American Caviomorpha, but its dentition unquestionably represents a structural intermediate between that of *Reithroparamys* and that of *Platypittamys*." The dentition of *R. fricki* is much too specialized in the development of accessory small lophs and the presence of doubled cusps in the upper molars to have been ancestral to *Platypittamys* (Wood, 1949b, fig. 3), in which the upper molar pattern

consists of four complete and uncomplicated transverse lophs. In *Rapamys* the trend is toward break-up of transverse lophs into small separate units. It is much easier to derive the general caviomorph ancestral condition from a less highly specialized ischyromyid like *Leptotomus* or *Paramys*.

The fact that the earliest known South American rodents are diverse (Wood & Patterson, 1959, fig. 34; Hoffstetter and Lavocat, 1970), and in their dental pattern clearly specialized beyond the North American ischyromyids suggests a period of occupancy in South America prior to the early Oligocene. Wood and Patterson (1959:396-401) argue convincingly that this colonization probably did not occur before mid-Eocene time. They prefer a late Eocene arrival for the colonizing stock from North America. There are several middle-to-late Eocene lineages of rather generalized ischyromyids known in North America (Wood, 1962, fig. 90), any one of which could be morphologically close to the ancestry of the Caviomorpha. Recently Hoffstetter and Lavocat (1970) described some new rodents from the early Oligocene of Bolivia, noting a number of resemblances of these genera to African phiomorphs. On present evidence it is impossible to be certain of the ancestry of the caviomorphs.

Ischyrotomus cf. *I. eugenei*

MATERIAL: CM 14567, partial left lower I, and 15338, partial right lower I.

LOCALITY: Locality No. 5.

DESCRIPTION: These two incisor fragments match perfectly the description given by Wood (1962:219, fig. 79E) for the lower incisors of *Ischyrotomus eugenei*. As Wood pointed out, the enamel on these incisors is extremely thin. The anterior tip of the incisor is preserved on CM 15338, but not on any of the *I. eugenei* material from Utah. The tip displays a very long wear-face with a distinctly stepped posterior border. Although no cheek teeth referable to *Ischyrotomus* have been found at any of the Badwater late Eocene localities, there can be little doubt that these two incisors should be referred to *I. eugenei*. They are much too large to belong to any other described ischyromyid, and they agree nearly perfectly in pattern with *I. eugenei*.

MEASUREMENTS IN MM.

CM 14567	left lower I	7.60 a-p	6.60 tr
CM 15338	right lower I	7.50 a-p	6.65 tr

?Ischyromys sp.

Figures 41-45

MATERIAL: CM 15385, LP⁴; 16020, LM¹ or ²; 15354, RM¹ or ²; 16016, LM³; 15348, LM₁ or ².

LOCALITY: Wood Locality.

DESCRIPTION: The upper fourth premolar can be separated from the molars, as it displays a more bulbous and more anteriorly projecting parastylar region and has a less obvious separation of the protocone and hypocone. On the molars the protocone and hypocone are set apart by a distinct cleft which passes most of the way down the lingual face of the teeth. On both P⁴ and M¹-M² the protoloph is complete, with no discernible protoconule, and the metaloph is interrupted and set off from the hypocone, terminating in a large metaconule. There is a small mesostyle on P⁴ and on one of the two molars. The lophs are high, and the teeth display a marked unilateral hypsodonty. The M³ is subcircular in occlusal outline, with an enlarged protocone and very heavy posterior border. This postero-internal region of the tooth is divided into three heavy ridges by narrow notches, which break up the heavy crest. There is a distinct metacone and metaloph, but no metaconule. The anterior cingulum is narrow and does not reach the buccal border of M³.

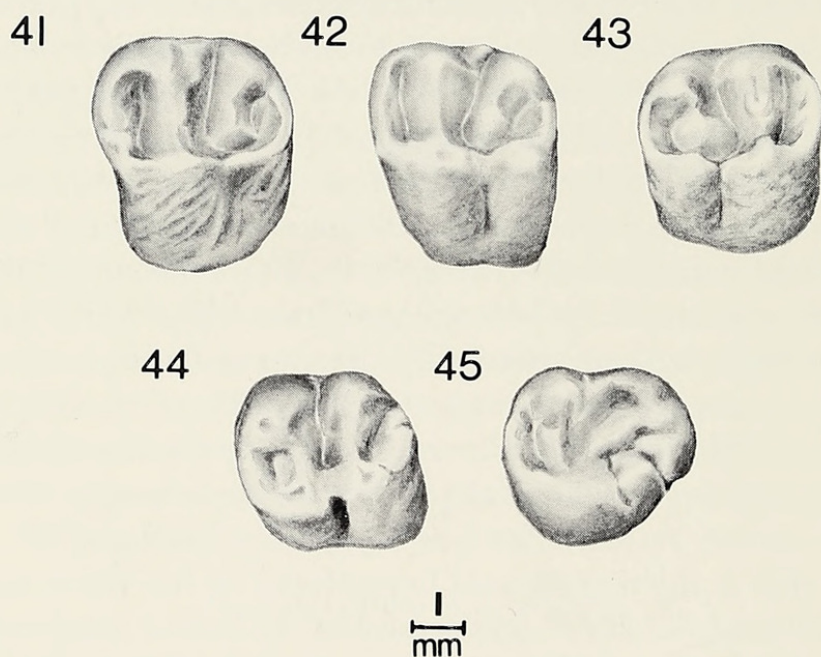
There is only a slight unilateral hypsodonty in the lower molar. The lophs are elevated, however, and separated by rather deep valleys. The trigonid basin is large and closed posteriorly. The hypolophid is prominent and passes to the ectolophid. The posterior cingulum is broad, but does not close off the posterior valley lingually. All major cusps stand above the level of the connecting lophs.

MEASUREMENTS IN MM., *?Ischyromys* sp.

		a-p	tr	tr
CM 15348	LM ₁ or ²	3.35	3.35	3.40
CM 15354	RM ¹ or ²	3.40	3.90	...
CM 15385	LP ⁴	3.60	4.30	...
CM 16020	LM ¹ or ²	3.40	3.85	...
CM 16016	LM ³	3.55	3.25	...

DISCUSSION: The lower molar is similar to that of *Ischyromys douglassi* (Black, 1968a:286), particularly M₁ of CM 10967. However, there is no suggestion in *?Ischyromys* sp. of a small cusp or loph on the posterior side of the metalophid, a structure found occasionally in *I. douglassi*. Also, the lower molars of *I. douglassi* are more rectangular in occlusal outline than the single Badwater tooth. In the upper cheek teeth,

?*Ischyromys* sp. differs from *I. douglassi* in having the metaloph completely separated from the hypocone. In other respects the teeth are similar. There is not enough material of ?*Ischyromys* sp. available to understand the range of variation present in the population. From study based on the few teeth at hand, it appears that the genus *Ischyromys* can be carried back into the late Eocene, and that the Badwater species could well have given rise to the early Oligocene *I. douglassi*.



Figs. 41-45. ?*Ischyromys* sp. 41. CM 15835, LP⁴. 42. CM 16020, LM¹⁻². 48. CM 15354, RM¹⁻². 44. CM 15348, LM₁₋₂. 45. CM 16016, LM₃.

Ischyromyid spp.

Figures 46-50

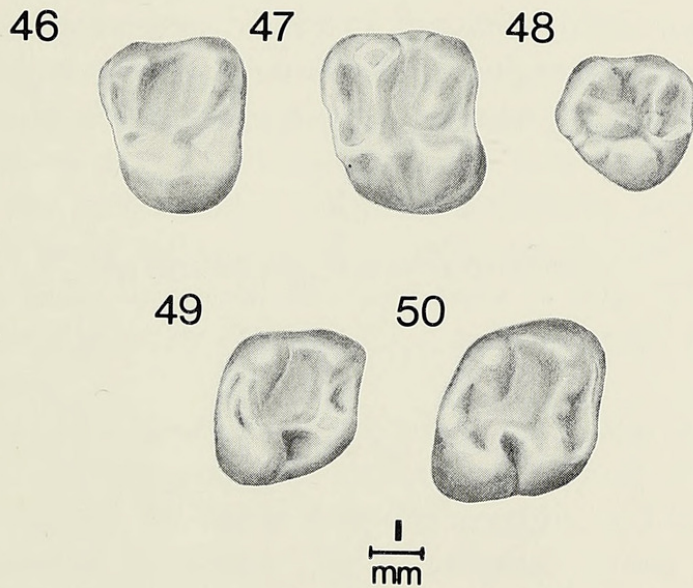
MATERIAL: LP⁴, CM 16014; M¹ or ², CM 15352, 18232; M³, CM 16084 (3 teeth); M₁ or ₂, CM 15345, 16073; M₃, CM 15344.

DISTRIBUTION: All specimens are from the Wood locality except CM 18232, which is from the Rodent locality.

DESCRIPTION: The upper fourth premolar is distinct, with both the protoloph and the metaloph short and incomplete, failing to reach the base of the protocone. The paracone and metacone are widely separated, lying at the anterior and posterior external corners of the tooth. The central valley is therefore wide. Both the anterior and posterior cingula are narrow. There is no indication of a protoconule and there is only a faint swelling in the position of the metaconule. There is no distinct hypocone on this tooth. The mesostyle is absent.

The two upper first or second molars, one from the Rodent locality and one from the Wood locality, are identical in structure. There is a distinct hypocone on both teeth, which is set off from the protocone by a shallow, internal groove. The hypocone is somewhat smaller and set somewhat below the protocone. The protoloph is complete, with no indication of a protoconule. The metaloph fails to reach the protocone, and there is a slight swelling in the area of the metaconule. The central valley is rather narrow. There is no mesostyle at its buccal end.

The three third upper molars are all similar in morphology, although there is considerable variation in size. The teeth are circular in occlusal outline and they all show notching of the posterolophid, the anterior cingulum, and the protoloph. All these lophs are broken up into a series of cusps of various sizes. The protoloph is high and complete. There is a very large, distinct metaconule, buccal to the protocone, which is generally connected to the postero-external corner of the tooth.



Figs. 46-50. Ischyromyid spp. 46. CM 16014, LP⁴. 47. CM 18232, LM¹⁻². 48. CM 16084, LM³. 49. CM 16073, RM₁₋₂. 50. CM 15345, RM₁₋₂.

The two lower first or second molars are different from each other. One, CM 16073, is almost square in occlusal outline, whereas the other, CM 15345, is much wider than it is long. The latter tooth is in many ways reminiscent of the lower molars of some members of the Sciuridae. This tooth, CM 15345, has a rather long anterior cingulum set below the level

of the protocone, metalophid, and metacone. The cingulum and metalophid enclose a long, slit-like trigonid basin. The buccal valley is deep, but quite narrow antero-posteriorly. There is a small hypoconulid immediately posterior to the hypoconid. The posterolophid drops from the hypoconulid to the base of the entoconid. The entoconid is large and high, and there is no indication of a hypolophid from the entoconid into the talonid basin. There is a deep notch between the entoconid and the metaconid. The other tooth (CM 16073) has a very short anterior cingulum and a very small trigonid basin. The buccal valley is wide but not deep. There is no indication of a hypoconulid. There is a distinct, elevated crest crossing from the base of the entoconid to the posterior corner of the ectolophid. As in CM 15345, there is no mesostylid but rather a deep notch between the entoconid and the metaconid, leaving the trigonid basin open internally. It is possible that the smaller, squarer molar represents an M_1 , and the second tooth an M_2 , but the amount of variation in occlusal pattern seems to argue against this interpretation. The M_3 shows a small, enclosed trigonid basin, or pit, and a greatly expanded posterior margin, or posterolophid, which passes into the base of the entoconid. There is a very low crest from the entoconid to the ectolophid.

MEASUREMENTS IN MM., ISCHYROMYID SPP.

		a-p	tr	tr
CM 16014	LP ⁴	2.65	3.20	...
CM 15352	RM ¹ or ²	2.80	3.20	...
CM 18232	LM ¹ or ²	2.85	3.30	...
CM 16084	RM ³	2.70	2.50	...
	RM ³	2.80	2.65	...
	RM ³	3.10	2.95	...
CM 16073	RM ¹ or ²	2.65	2.70	2.60
CM 15345	RM ¹ or ²	2.95	3.20	3.15
CM 15344	RM ³	2.80	2.70	2.55

AFFINITIES: These teeth are different from those of any other ischyromyid known from the Badwater localities. They do not match any of the material known from the late Eocene of California or Utah. As there is not enough material to determine whether there are relationships to other ischyromyids, and as there is no certainty that these teeth represent a single species, no generic allocation can be made at present.

Spurimus¹, new genus

TYPE: *Spurimus scottii*², new species

DIAGNOSIS: Small ischyromyid; hypocone large on M¹-M², absent on P⁴; anterior cingulum narrow, low on P⁴-M³; metaloph generally incomplete ending in small metaconule; trigonid basin small but completely enclosed on M₁-M₂; notch between anterior cingulum and protoconid on M₁-M₂; entoconid separated from posterolophid; hypolophid complete on M₁-M₂.

Spurimus scottii², new species

Figures 51-64

TYPE: CM 16088, RM¹ or 2.

HYPODIGM: P⁴, CM 16085; M¹ or 2, CM 14631, 16088, 18220, 18222, 18262, 21982; M³, CM 16022, 16075; P₄, CM 16015, 21966, 21967, 21968, 21969; M₁ or 2, CM 14629, 14835, 16766, 18233, 21970-21974, 25351; M₃, CM 21975.

DISTRIBUTION: Type from the Wood locality. All other specimens from the Wood or Rodent localities.

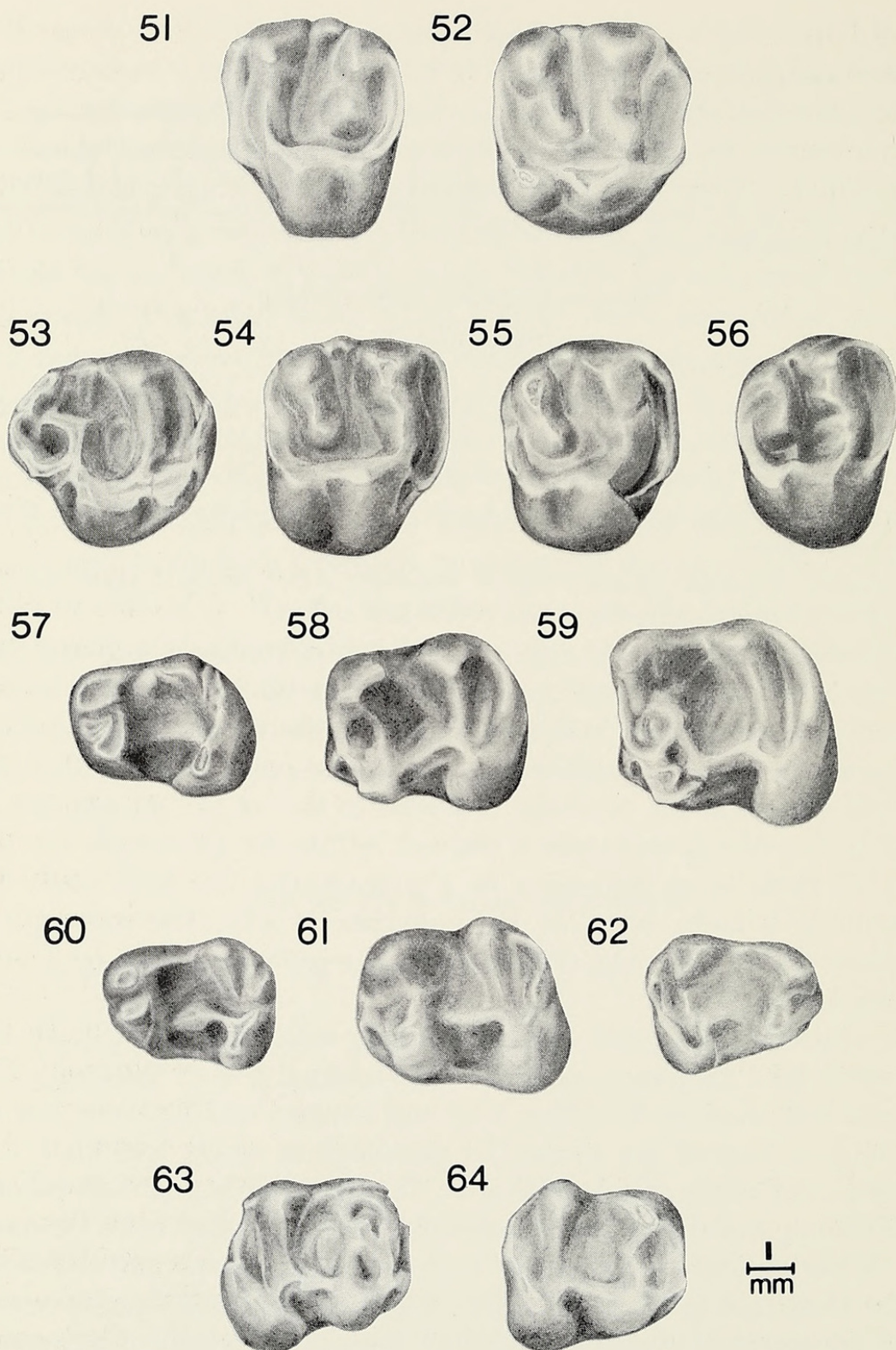
DIAGNOSIS: Hypocone smaller than in *Spurimus selbyi*; trigonid basin smaller, metalophid shorter, and hypolophid lower than in *S. selbyi*.

DESCRIPTION: The fourth upper premolars are similar in occlusal pattern to the first and second upper molars. They differ primarily in the absence of the hypocone on P⁴ and in having a shorter anterior cingulum. The protocone of P⁴ is rather elongate antero-posteriorly, so that the occlusal outline of the premolar is similar to that of M¹-M². On one P⁴ (CM 16086) the protoconule is distinct within the protoloph. On the other P⁴ there is no indication of a protoconule. On both teeth the metaconule is large, equaling the metacone in size. The metaloph is complete on both P⁴s but connected to the protocone only by a very slender, low crest.

All upper M¹-M²s have a large separate hypocone set off from the protocone by a distinct groove down the internal face of the teeth. The anterior cingulum on M¹-M² is long and narrow, and lies very low on the anterior face of the teeth. The protoloph is strong and high, and shows no indication of a protoconule. The metaloph is generally incomplete, ending in a distinct metaconule which is separated from the inner face of the protocone. The valley between the protoloph and the metaloph is deep and is open buccally. On some specimens there is a very small mesostyle at the buccal end of the central valley. The central valley is directed diagonally across the tooth, following the diagonal slope of the metaloph.

¹[L., fr. *spurius* false + *mus* mouse.] False mouse.

²For the late "Scotty" Hendry, who founded the Clear Creek Cattle Company of Badwater, Wyoming.



Figs. 51-64. *Spurimus scottii*. 51. CM 18220, LM¹⁻². 52. CM 14631, RM¹⁻². 53. CM 16075, RM³. 54. CM 16088, RM¹⁻², Type 55. CM 21982, RM¹⁻². 56. CM 16085, RP⁴. 57. UCM 21968, LP₄. 58. CM 21970, LM₁₋₂. 59. CM 21971, LM₁₋₂. 60. CM 21967, LP₄. 61. CM 14835, LM₁₋₂. 62. CM 16015, RP₄. 63. CM 21974, RM₁₋₂. 64. CM 16766, RM₁₋₂.

Third upper molars are nearly circular in occlusal outline, but show a slight notch between the protocone and the postero-external corner of the teeth. There is also an expansion anterior to the protocone where the anterior cingulum curves to come into the protocone slope. There is no distinct metaconule on M^3 but there is a loph which passes from the posterior corner of the protocone into the talonid basin. This loph then forks, one arm passing posteriorly to the postero-external corner of the tooth. The other arm passes directly externally to the buccal side of the tooth. Consequently there are two small, shallow basins that lie between the loph and the slightly elevated postero-external margin of the tooth.

The lower fourth premolars are all long, slender teeth with relatively simple occlusal patterns. The anterior half of the tooth is essentially a single, high ridge with protoconid and metaconid almost completely fused. In unworn specimens there is a very shallow, ephemeral trigonid basin visible, but this is soon obliterated with wear. The posterior slope of this high ridge passes evenly down into the talonid basin, with no break in the region of the ectolophid and no indication of a mesostylid. The hypoconid and entoconid are both rather small, low cusps on P_4 , and the posterolophid is only slightly elevated above the level of the trigonid basin. On one specimen (CM 16015) there is a distinct hypoconulid in the center of the posterior border of P_4 . This cusp is connected by a low ridge to the entoconid. In other specimens this low ridge into the posterolophid is visible, but there is no distinct hypoconulid present.

The molars are considerably larger than the P_4 s, but they also show the elongate, rather slender form. The trigonid basin is a small pit, distinct and rather deep, enclosed between the anterior cingulum and the meta-lophid, which is complete on all M_1 - M_2 s. There is a shallow notch between the anterior cingulum and the anterior face of the protoconid. The anterior cingulum is somewhat swollen, giving the appearance of an incipient anteroconid. The apex of the metaconid rises considerably higher than the tops of any of the other cusps, and there is a very high, steeply sloping, posterior metaconid surface. The ectolophid is rather low on all lower molars and there is no indication of a mesoconid. The posterolophid is elevated from the hypoconid through the region of the hypoconulid, then drops abruptly to pass into the base of the entoconid at the postero-external corner of that cusp. The entoconid is thus set off from the posterolophid, and there is a long narrow valley between the entoconid, hypolophid, and posterolophid. A hypolophid is well developed in all cases from the posterior corner of the ectolophid. There is only one half of an M_3 preserved, but this shows the hypolophid distinctly.

The buccal valley on the lower molars between the protoconid and the hypoconid is long anter-posteriorly, but very shallow.

MEASUREMENTS IN MM., *Spurimus scottii*

		N	M	OR	M _W (N)	M _R (N)
P ⁴	a-p	2	1.95	1.81-2.12	1.95(2)	...
	tr	2	2.43	2.25-2.62	2.43(2)	...
M ¹ or ²	a-p	6	2.06	1.94-2.12	2.09(4)	2.03(2)
	tr	6	2.50	2.37-2.75	2.51(4)	2.47(2)
M ³	a-p	2	2.25	2.25	2.25(2)	...
	tr	2	2.22	2.19-2.25	2.22(2)	...
P ₄	a-p	5	1.77	1.69-1.81	1.77(5)	...
	tr	5	1.24	1.19-1.25	1.24(5)	...
	tr	5	1.45	1.37-1.56	1.45(5)	...
M ₁ or ₂	a-p	10	2.18	2.00-2.44	2.11(5)	2.25(5)
	tr	10	1.73	1.50-2.12	1.67(5)	1.80(5)
	tr	10	1.95	1.69-2.31	1.89(5)	2.01(5)
M ₃	a-p	0
	tr	0
	tr	1	2.00	...	2.00(1)	...

AFFINITIES: *Spurimus scottii* seems to be most closely related to the prosciurine ischyromyids. Within the prosciurines there has been a tendency to enlarge the talonid basin and to develop discrete cusps and short crests along the internal and external margins of this basin. Thus, in *Prosciurus*, *Cedromus*, and *Pelycomys*, the entoconid and the mesostylid are discrete cusps, with short-to-moderately elongate crests that extend into the talonid basin from these cusps. Buccally the hypoconid and the mesoconid also are discrete, sharp cusps. Correlated with the enlargement of the talonid basin is the reduction in size of the trigonid basin and the metalophid. In the upper dentition there has been a loss of the hypocone and antero-posterior compression of the protocone, so that the inner border of the upper cheek teeth is rather short, giving the teeth a triangular occlusal outline.

This type of dentition could have been derived from that of *Spurimus scottii* through reduction and loss of some structures seen in that species. There could have been reduction and shortening of the hypolophid, reduction in the size of the metalophid and trigonid basin, and reduction and eventual loss of the hypocone in the upper molars. The antero-posterior elongation of the lower molars seen in *Spurimus scottii* is similar to the condition found in the Oligocene prosciurines. If *Spurimus scottii* evolved from *Spurimus selbyi* of locality 5, then selection was acting to bring about the type of reduction mentioned above. Between *S. selbyi*

and *S. scottii* this would include reduction in importance and size of the hypocone, and in the lower molars, reduction in the size of the trigonid basin and in the height and importance of the hypolophid. Thus, if this is a natural, phyletic sequence, continuation of these trends would lead easily into the Oligocene prosciurines. If, however, the sequence *Spurimus selbyi* to *Spurimus scottii* is invalid, then neither of these species has any direct relationship to the Oligocene prosciurines.

***Spurimus selbyi*¹, new species**

Figures 65-73

TYPE: CM 15424, LM¹ or 2.

HYPODIGM: Type and P⁴, CM 14511, 15566, 15570, 15571; M¹ or 2, CM 15333, 15334, 15336, 15567; dP₄, CM 15572, 18236; P₄, CM 14784, UCM 24742; M₁ or 2, CM 14783, 15335, 25350, UCM 24730, 24734, 24767, 24801; M₃, CM 14785.

DISTRIBUTION: All specimens from localities 5 and 5A.

DIAGNOSIS: Hypocone large; anterior cingulum on P⁴-M² high; trigonid basin large; hypolophid strong.

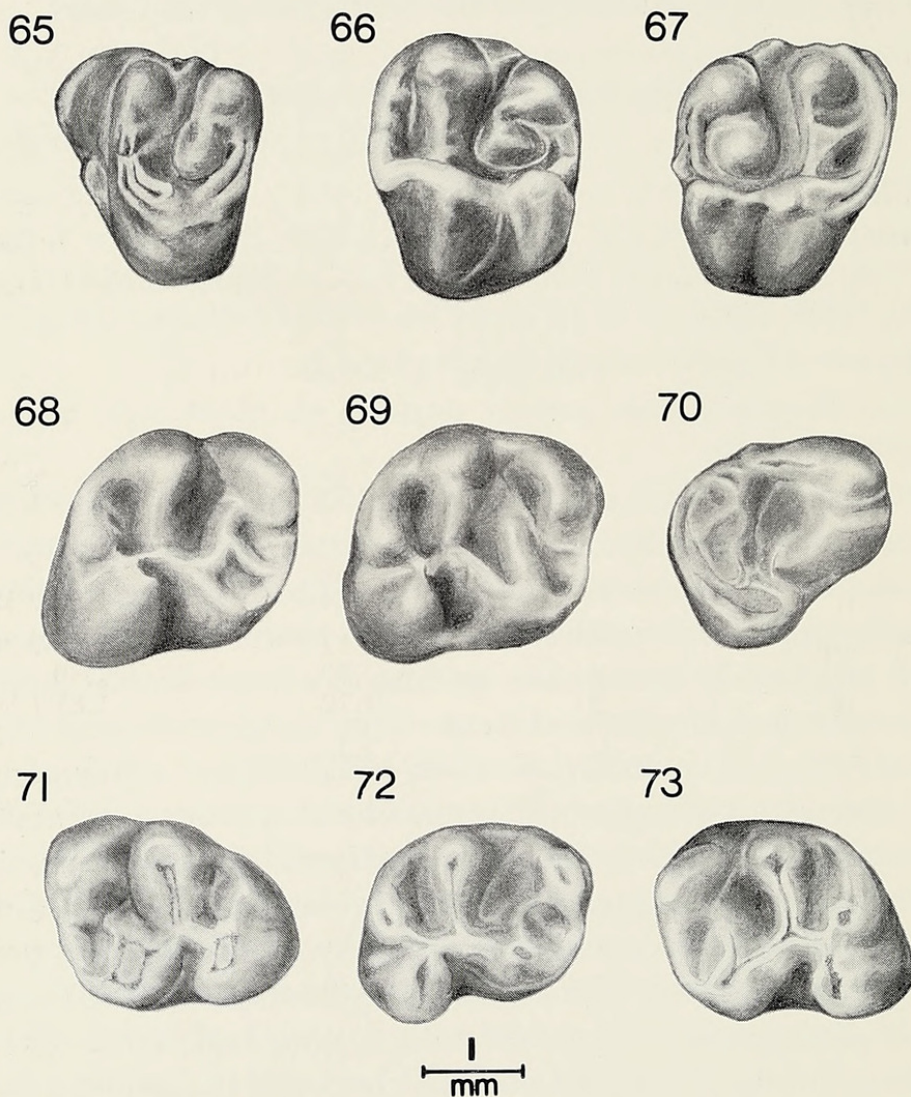
DESCRIPTION: The fourth upper premolars are generally rather triangular in occlusal outline, with antero-posteriorly compressed protocone, no hypocone, and a large, elevated parastyle. The protoloph of P⁴ is complete, with only a faint indication of the protoconule within it. The metaloph is generally incomplete, ending in a large distinct metaconule which is subequal to the metacone. The metaconule and metacone are joined by a thin crest. One P⁴ (CM 15570) shows a thin connection between the metaconule and the protocone. A mesostyle is present, but is very small and fused into the postero-external side of the paracone.

The first and second upper molars are square in occlusal outline, with a large distinctive hypocone that is generally set off from the protocone by a deep, lingual groove. The anterior cingulum is wide and the anterior margin of the cingulum is raised into a thin, high crest. There is a rather deep but narrow valley enclosed between the anterior crest and the protoloph. The protoloph is high but very thin and there is little, if any, swelling in the region of the protoconule. All five M¹-M²s display incomplete metalophs. The metacone and metaconule are subequal in size and are joined by a very thin ridge. The posterior cingulum is short, passing from the hypocone into the postero-internal base of the metacone.

The deciduous P₄ is an extremely thin, elongate tooth with only a shallow notch between the protoconid and metaconid. The postero-

¹Named for Merrill Selby, proprietor of the Big Horn Hotel of Arminto, Wyoming.

lophid is high and thin, and a very shallow, narrow valley lies between the posterolophid and ectolophid. The entoconid is separated from the posterolophid and there is a low, thin crest passing from the entoconid to the posterior end of the ectolophid.



Figs. 65-73. *Spurimus selbyi*. 65. CM 14511, LP⁴. 66. CM 15424, LM¹⁻², Type. 67. CM 15334, RM¹⁻². 68. CM 14783, RM₁₋₂. 69. UCM 24767, RM₁₋₂. 70. CM 18236, RdP₄. 71. CM 14785, LM₃. 72. CM 25350, RM₁₋₂. 73. CM 15335, LM₁₋₂.

The fourth lower premolars resemble M₁-M₂ closely except in the protoconid-metaconid relation. On P₄ these two cusps are set close together, and the trigonid basin is reduced to a mere notch, directed antero-posteriorly between them. The posterior half of P₄ resembles that of M₁-M₂ described below.

The lower first and second molars are long in relation to their width. They are cusplate, and the lophids are extremely thin, although high. Anteriorly, the trigonid basin is large and rather deep, and is enclosed both anteriorly and posteriorly. The protoconid, metaconid, hypoconid, entoconid, and hypoconulid are all high, rather sharp cusps projecting above the level of the lophs. The ectolophid is well developed in all cases, as is the hypolophid, which meets the ectolophid at its posterior corner. There are deep valleys between the posterior slope of the metaconid and the hypolophid, and again between the hypolophid and posterolophid. Both valleys open lingually. There is no mesostylid or mesoconid.

The third lower molar shows essentially the same structure as M_1 - M_2 except that the hypoconid-hypoconulid area is more rounded and swollen, and somewhat more distinctly separated from the entoconid.

MEASUREMENTS IN MM., *Spurimus selbyi*

		N	M	OR
P^4	a-p	4	1.85	1.75-2.00
	tr	4	2.33	2.10-2.60
M^1 or 2	a-p	5	2.08	2.00-2.15
	tr	5	2.44	2.30-2.55
dP_4	a-p	2	2.17	2.15-2.20
	tr	2	1.30	1.30
	tr	2	1.72	1.65-1.80
P_4	a-p	2	2.32	2.25-2.40
	tr	2	1.52	1.50-1.55
	tr	2	1.90	1.80-2.00
M_1 or 2	a-p	7	2.23	2.10-2.40
	tr	7	1.84	1.65-2.10
	tr	7	2.11	1.95-2.35
M_3	a-p	1	2.30	...
	tr	1	2.00	...
	tr	...	1.80	...

AFFINITIES: This species does not seem to be closely related to any other known ischyromyids, with the exception of *Spurimus scottii* discussed earlier. It differs from *Spurimus scottii* in having a stronger hypocone on the upper molars and a much higher anterior cingulum or anterior crest than does *Spurimus scottii*. In the lower molars, the trigonid basin is larger; the cusps are generally sharper, higher, and more distinct; and the talonid basin is much smaller, than in the species from the Wood locality. *Spurimus selbyi* was probably ancestral to *Spurimus scottii*.

DISTRIBUTION OF ISCHYROMYIDS AT BADWATER

It now appears that there actually is an age difference between various late Eocene localities on Badwater Creek. Table 1 shows the distribution of ischyromyid species among five of these localities. Localities 5 and 6 have a similar species association—quite distinct from that found at the Wood and Rodent localities. There appears to be only one species common to these two groupings: *Microparamys dubius*, which is found at the Wood locality as well as at 5 and 6. In two instances, species found at localities 5 and 6 are ancestral to populations found at the Wood and Rodent localities. The population described as *Leptotomus* near *L. guildayi* from 5 and 6 is somewhat more primitive than *Leptotomus guildayi* found at the Wood and Rodent localities. In the other instance, the species *Spurimus selbyi* from localities 5 and 6 is clearly distinct from, but ancestral to, *Spurimus scottii* of the Wood and Rodent localities. Two genera found at localities 5 and 6 are not represented at the Wood and Rodent localities: *Ischyrotomus* and *Rapamys*. Several specimens of the advanced ischyromyid ?*Ischyromys* have been recovered from the Wood and Rodent localities but there has been no suggestion of the presence of this form at the other localities.

Table I: Distribution of Ischyromyids at Badwater

Localities	5	5A	6	W	R
<i>Ischyrotomus</i> cf. <i>I. eugenei</i>	X				
<i>Leptotomus guildayi</i>				X	X
<i>Leptotomus</i> near <i>L. guildayi</i>	X	X	X		
<i>Rapamys wilsoni</i>	X	X	X		
<i>Spurimus selbyi</i>	X	X			
<i>Spurimus scottii</i>				X	X
<i>Ischyromys</i> sp.				X	X
<i>Microparamys dubius</i>	X	X	X	X	
Ischyromyid sp.				X	X

The ischyromyids then, clearly indicate that localities 5 and 6 have a somewhat older fauna than that found at the Wood and Rodent localities. This age difference was suggested earlier (Black, 1970; Dawson, 1970) by the distribution of cylindrodont rodents and by the presence of different species of *Mytonolagus* at the two sets of localities. Some of the

differences noted in total faunal composition between these sets may have been ecologically controlled. However, the ancestor-descendant relationship between species of *Leptotomus* and *Spurimus* certainly indicates that an age difference is also responsible for some of the differences in composition.

DISTRIBUTION OF NORTH AMERICAN LATE EOCENE ISCHYROMYIDS

At first glance the distribution pattern of ischyromyid species and genera among the main late Eocene localities in North America is confusing. Upon closer scrutiny, however, several trends are observable. I have considered here only the well-known late Eocene faunas from Southern California, the Uinta Basin in Utah, and the Badwater localities. Work being done by others on the late Eocene faunas of the Big Bend area in Texas and the Washakie Basin in Wyoming, and our studies in Montana, may modify these patterns somewhat, but I doubt that they will be changed significantly.

On the species level very little can be learned, for each geographic area seems to have its own distinct species complexes. Out of some twenty-four species belonging to 10 genera, there are only two species common to any two of these geographic areas. *Microparamys dubius* is found at Badwater and the Uinta Basin, but not in California. *Ischyrotomus eugenei* is found at Badwater and the Uinta Basin. Because of the specific endemism in these three areas, it is much more profitable to look at the distribution of genera. When this is done, several patterns emerge.

First, three genera, *Leptotomus*, *Ischyrotomus*, and *Microparamys*, are found in all three geographic areas. Two of these genera are the least specialized of all late Eocene ischyromyids. In this regard, *Leptotomus* and *Ischyrotomus* might be considered the late Eocene counterparts of the modern *Sciurus*, showing little variation in dental morphology over a wide geographic area. The third genus, *Microparamys*, found in all three areas, is somewhat more specialized, particularly in its dentition. However, this group had a long history pre-dating the late Eocene, and was probably the most successful of all the small-sized ischyromyids. In this light, its wide geographic occurrence with the larger but unspecialized genera *Leptotomus* and *Ischyrotomus* is not unusual.

Genera endemic to single regions make up the second group or pattern of ischyromyid distribution. Two genera endemic to the Uinta Basin in Utah are *Thisbemys* and *Janimus*. Two other genera, ?*Ischyromys* and *Spurimus*, are found only at Badwater. Under the classification used

Table II: Late Eocene Distribution of Ischyromyids

Geographic area Faunal level	Uinta Basin			Badwater		California		
	A B	C	Randlett	5 6	W R	Poway	Tapo	Pearson
<u>Leptotomus</u>	X	X	X	X	X	X	X	
<u>Ischyrotomys</u>	X	X		X		X		
<u>Microparamys</u>	X			X			X	X
<u>Thisbemys</u>	X	X						
<u>Janimus</u>		X						
<u>Ischyromys</u>					X			
<u>Spurimus</u>				X	X			
<u>Mytonomys</u>	X	X	X				X	
<u>Reithroparamys</u>		X				X		
<u>Rapamys</u>				X		X		

here, there are no endemic genera recognized in the California late Eocene assemblages, as the genus *Uriscus* is considered to be a synonym of *Reithroparamys*, and *Tapomys* of *Leptotomus*. All four of the genera that occur in only one region are highly specialized ischyromyids. The presence of ?*Ischyromys* at the later Badwater late Eocene localities may indicate that this faunal level is somewhat younger than any of the other late Eocene occurrences.

A third and final group of genera may be recognized. This comprises those forms that are found in two of the three geographic regions, but not in the third. In this group are *Mytonomys* and *Reithroparamys*, different species of which are found in Utah and California, and *Rapamys*, with different species in California and at Badwater. Species of *Mytonomys* and *Rapamys* are highly specialized ischyromyids, and perhaps they had narrower ecological tolerances than did species of *Leptotomus* and *Microparamys*. The species of *Reithroparamys* found in California and Utah are both small forms whose dentition is not highly specialized. No members of this genus have been found at Badwater. Members of this third group may offer the best possibilities for insight into the local environments of deposition. Restricted occurrence of these genera to two of the three regions suggests the presence of other associated faunal or environmental factors that were acting to produce differing associations at each locality. Determination of local environments will require a much more detailed knowledge of the physical factors of deposition than is presently available for the localities in California and Utah.

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