Bulletin of the Museum of Comparative Zoology

HARVARD UNIVERSITY

Vol. 131, No. 2

FOSSIL MAMMALS FROM THE LOWER PLIOCENE OF FISH LAKE VALLEY, NEVADA

By

John B. Clark, Mary R. Dawson and Albert E. Wood

CAMBRIDGE, MASS., U.S.A.

PRINTED FOR THE MUSEUM

March, 1964

Bull. Mus. Comp. Zool., Harvard Univ., 131 (2): 27-63, March, 1964

No. 2 — *Fossil Mammals from the Lower Pliocene of Fish Lake Valley, Nevada*

By John B. Clark,[1] Mary R. Dawson[2] and Albert E. Wood[3]

INTRODUCTION

The material on which this study is based was collected by Wood, in 1935, from Hall's locality A (1930c, pl. 37, fig. 1) in the early Pliocene Fish Lake Valley beds, Esmeralda Formation, seven miles north of Arlemont, Nevada.

The material formed the basis for the unpublished Master's thesis, submitted to Amherst College, by Clark. In subsequent years it has proven impossible for him to complete the paper for publication, and the material has now been reworked by Dawson and Wood. Wood has brought up to date and revised Clark's manuscript for the rodents, and Dawson has done the same for the other forms.

The authors are grateful to Drs. J. T. Gregory, Donald Savage and R. A. Stirton for the loan of specimens; to Mrs. Katherine M. Reed and Drs. Claude Hibbard and Peter Robinson for discussions; and to Mrs. Frances W. Wood for critical reading and other assistance in preparation of the manuscript. Figures 6 and 7, B, C and D were drawn by Dr. Florence D. Wood. The material was collected while Wood was Cutting Traveling Fellow in Columbia University. The study has been assisted by the Dorothy Bridgman Atkinson Fellowship of the American Association of University Women awarded to Dawson, and by grants from the National Science Foundation and the Marsh Fund of the National Academy of Sciences to Wood. Abbreviations used are: M.C.Z., Museum of Comparative Zoology; S.D.S.M., South Dakota School of Mines and Technology; U. Cal., University of California Museum of Paleontology. We are grateful to the Museum of Comparative Zoology for undertaking the publication of this paper.

[1] Biology Department, Marietta College, Marietta, Ohio.
[2] Carnegie Museum, Pittsburgh, Pennsylvania.
[3] Biology Department, Amherst College, Amherst, Massachusetts.

Order INSECTIVORA

Family TALPIDAE

DOMNINOIDES cf. RIPARENSIS Green, 1956

Figure 1

Material: M.C.Z. Nos. 17887, incomplete left lower jaw having M_1, M_2-M_3 (broken), alveoli of P_4; 17888, incomplete left lower jaw having M_2, alveoli of P_4, M_1, M_3; 17889, left M_2 (broken).

In size (Table 1) and in most general characteristics these specimens resemble the type and only previously reported specimen of *Domninoides riparensis,* S.D.S.M. No. 53170, from the Clarendonian Wolf Creek faunule of South Dakota (Green, 1956, pp. 152-154). Compared to teeth in the type specimen, M.C.Z. No. 17889 is less worn, M.C.Z. No. 17887 is slightly more worn, and M.C.Z. No. 17888 is much more worn.

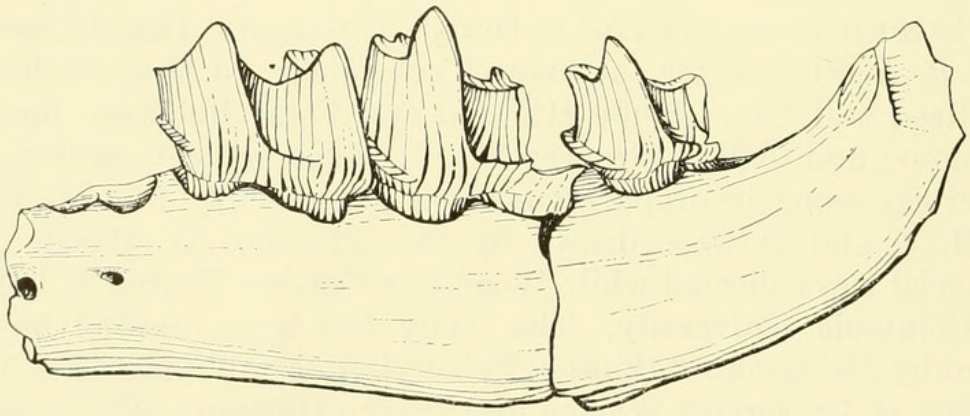

FIG. 1. *Domninoides* cf. *riparensis.* Lateral view of left lower jaw, M.C.Z. No. 17887, × 9.

The most distinct difference from the type specimen is exhibited by M.C.Z. No. 17887 (Fig. 1), which has on M_1 a small but distinct anterior cingulum that connects to the anterolingual cuspule. The anterior wall of M_1 in the type is smoothly convex, lacking a cingulum. Another difference appears on M_3 in M.C.Z. No. 17887, which has an anterior cingulum that is more reduced buccally than in S.D.S.M. No. 53170. Also, in the type specimen the metastylid of M_1 is larger than that of M_2, whereas in M.C.Z. No. 17887 the metastylid of M_2 is prominent and a distinct metastylid is absent on M_1.

The taxonomic significance of these differences is questionable in light of the few available specimens. Possibly the variation in the anterior wall of M_1 is a matter of individual diversity. Somewhat similar individual variation has been reported in another fossil talpid, *Mesoscalops scopelotemos,* in which there is "variable development of a small anterior cingulum, which appears in the majority of specimens" (Reed, 1960, p. 4). That the size of the anterior cingulum may vary with wear in the Fish Lake Valley talpid is shown by the fact that the cingulum on the well worn M_2 of M.C.Z. No. 17888 is narrower than that of M.C.Z. No. 17887. Similarly, stage of wear could account for the difference between the type and M.C.Z. No. 17887 in the cingulum of M_3.

Since wear and individual variation are perhaps responsible for the differences between the Fish Lake Valley talpid and the type of *D. riparensis,* a definite specific assignment should wait until more specimens allow better estimation of the range of variation in either population.

Variation that can be recognized as individual is exhibited by the two jaws from Fish Lake Valley, which differ from one another in the position of the two mental foramina. In both jaws, as in the type, the anterior foramen is below P_3. One specimen, M.C.Z.No. 17888, resembles the type in having the more posterior foramen in line with the posterior wall of the alveolus of P_4, whereas M.C.Z. No. 17887 has the posterior foramen farther forward, in line with the middle of P_4.

TABLE 1

Measurements (in millimeters) of *Domninoides* cf. *riparensis*

	M.C.Z. No. 17887	M.C.Z. No. 17888
M_1 length	*ca.* 2.3	—
width trigonid	1.4	—
width talonid	1.7	—
M_2 length	—	2.4
width trigonid	1.7	1.7
width talonid	—	1.6
alveolar length M_1-M_3	*ca.* 6.5	6.1
outside depth jaw, at middle of M_1	2.2	2.1

Order ?INSECTIVORA

Figure 2

A toothless fragment of a left lower jaw, M.C.Z. No. 17900 (Fig. 2), represents an unidentifiable species of small mammal. The alveoli of the penultimate tooth, with the anterior wall broken away, and of the last tooth indicate that the penultimate tooth was somewhat larger than the last. The alveolus of the last tooth is 1.4 mm long. The alveolus for the root of the trigonid of the last tooth is set obliquely to the long axis of the jaw, directed anterolingually to posterobuccally, and is longer on the lingual side. The alveolus for the root of the corresponding talonid is longer anteroposteriorly and narrower transversely than that of the trigonid. The wall between the two alveoli of the last tooth has an indistinct, shallow groove dorsally, and that between the two alveoli of the penultimate tooth is more distinctly grooved. The deep masseteric fossa is bounded anteriorly by a rounded ridge. Lingually the surface of the jaw is essentially smooth; a dental foramen occurs near the posterior edge of the incomplete specimen. Below the last tooth, the jaw is 1.5 mm deep.

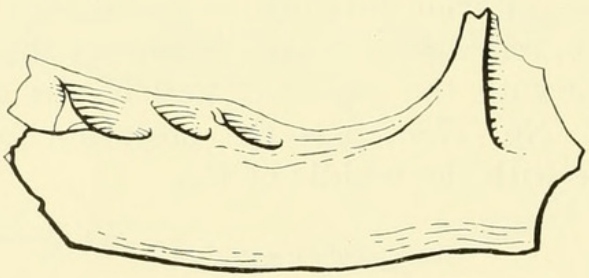

FIG. 2. ?Insectivore. Lateral view of left lower jaw fragment, M.C.Z. No. 17900, × 8.

Compared to other known members of the Fish Lake Valley fauna, M.C.Z. No. 17900 shows closest resemblance to *Mystipterus vespertilio,* the type and only reported specimen of which is a broken fragment of a jaw with M_3 (U. Cal. No. 29604). In both there is a deep masseteric fossa, and lingually both jaw fragments are essentially smooth. The toothless jaw is a little larger than the type of *Mystipterus vespertilio* and seems to have the anterior border of the ascending ramus relatively farther from the last tooth. The specimens are too incomplete to allow more than partial comparisons, and M.C.Z. No. 17900 is regarded as indeterminate.

In the course of these comparisons the question arose again of the taxonomic assignment of *Mystipterus,* originally described as a vespertilionid bat and compared with *Miniopterus* by Hall (1930a, p. 319). Re-examination of the characters of *Mystipterus* and of the differences from *Miniopterus* led Patterson and McGrew (1937, pp. 256-257) to assign the former to the insectivore family Soricidae. The features of *Mystipterus* cited by Patterson and McGrew as characteristic of soricids occur in some other insectivores as well. The deep masseteric fossa, for example, is found also in *Nyctitherium, Micropternodus* (Matthew, 1909, pl. 51, fig. 1), and a geolabidine insectivore, cf. *Myolestes dasypelix* (McKenna, 1960, p. 147). The combination of characters known in *Mystipterus* may not preclude reference to the Soricidae, but at the same time they do not seem to make such a reference the only assignment possible. It would seem necessary to have specimens of *Mystipterus* in addition to the rather inadequate type in order to clarify the taxonomic position of the genus.

Order LAGOMORPHA

Family OCHOTONIDAE

HESPEROLAGOMYS[4] new genus

Type species: Hesperolagomys galbreathi n. sp.

Diagnosis: Cheek teeth hypsodont but rooted; occlusal surface of P^4-M^1 with persistent crescentic valley, hypostria extending almost to crescent, and anteroloph transversely wider than posteroloph; P_3 with buccal fold between trigonid and talonid, anterointernal groove in trigonid, lingual wall short anteroposteriorly; trigonid of P_4-M_2 wider and shorter than talonid, talonid with anterior protrusion directed toward trigonid, and posterolophid present in early stage of wear; large mental foramen below P_3, smaller mental foramina anterior to P_3 and in line between M_1-M_2; lower teeth include M_1-M_3; size near that of *Oreolagus nevadensis;* tooth measurements as given in Table 2.

HESPEROLAGOMYS GALBREATHI[5] n. sp.

Figures 3-4

Type: M.C.Z. No. 17890, incomplete right lower jaw with broken incisor, P_3-M_2, and alveolus of M_3.

[4] From Greek: *hesperos* — west: *lagos* — hare: *mys* — mouse.

[5] For Dr. E. C. Galbreath in recognition of his work on fossil lagomorphs.

Hypodigm: Type; M.C.Z. Nos. 17891, fragmentary left lower jaw with P_3-M_2; 17892, fragmentary left lower jaw with talonid of P_4 to M_2; 17893-17894, upper incisors; 17895-17899, isolated upper cheek teeth; 7651-7652, isolated lower cheek teeth. Probably referable, U. Cal. No. 29633, upper deciduous premolar.

Diagnosis: As for the genus.

Description: The skull, with the exception of a maxillary fragment, is unknown, and the upper dentition is represented by isolated teeth only. The anterior upper incisor has a longitudinal groove slightly medial of center on its anterior surface. The part of the incisor medial to the groove protrudes farther anteriorly than does the lateral part. Of the upper cheek teeth, P^2 and P^3 are not known, but P^4 and probably M^1 are represented. Unilateral hypsodonty is exhibited by these teeth, which are convex lingually (Fig. 3 A, C, D). Two small buccal roots and a larger lingual root are present on the known upper cheek teeth.

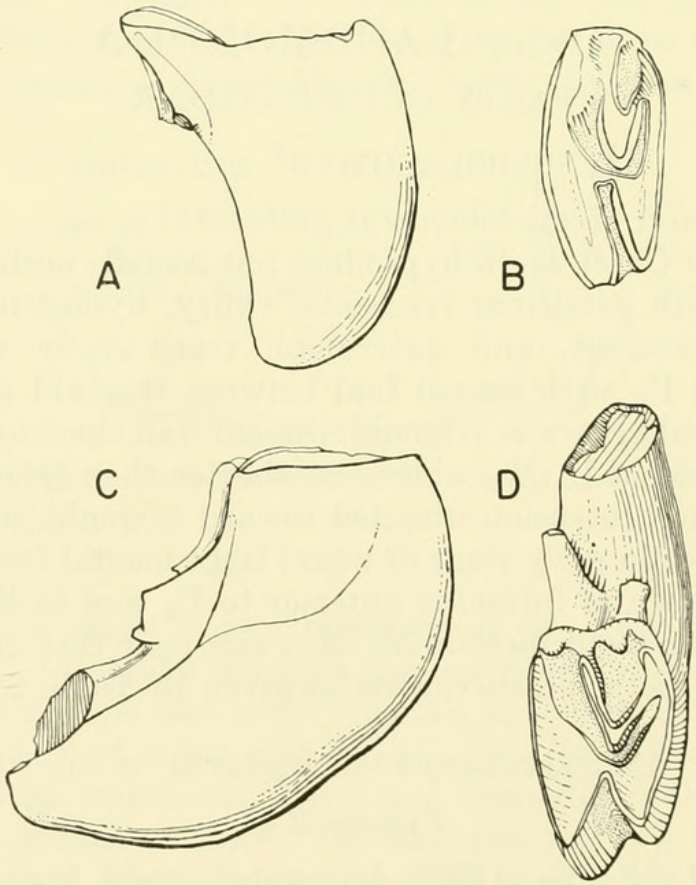

FIG. 3. *Hesperolagomys galbreathi*, n. gen., n. sp. Upper cheek teeth, × 9. Probable M^1, M.C.Z. No. 17898; A, anterior view; B, occlusal view. P^4, M.C.Z. No. 17896; C, anterior view; D, occlusal view.

On a worn P^4, M.C.Z. No. 17895, the anterior loph is wider than the posterior loph. The pattern on the occlusal surface includes an isolated, cement-filled, crescentic valley in the buccal half of the tooth and a cement-filled internal hypostria. The hypostria is directed toward the anterior wall of the crescent and extends almost to its lingual wall. Features of the buccal edge of the occlusal surface cannot be determined due to breakage. Another specimen, M.C.Z. No. 17896 (Fig. 3 C, D), seems to be a relatively unworn P^4. At the occlusal surface the anterior and posterior lophs are nearly equal in width, but farther down the shaft the anterior loph protrudes more medially. A central lobe connects to the buccal wall between two rounded cuspules and extends in a wide V to join the posterior wall of the tooth. Anterior, lingual, and posterolingual to the central lobe is the cement-filled depression that forms the crescentic valley of the more worn tooth. Posterobuccal to the lobe is a second cement-filled depression. The buccal exits of these depressions are blocked by the buccal cuspules. The internal hypostria crosses about one-third of the occlusal surface.

A worn tooth, M.C.Z. No. 17898 (Fig. 3 A, B), probably is a molar. In this specimen the anterior loph protrudes farther lingually than the posterior loph; the complete width of the anterior loph is not shown, owing to its broken lingual wall. The crescentic valley divides anterobuccally into two distinct parts around a transversely elongated cuspule. The anterobuccal part of the valley seems to be better developed than in M.C.Z. No. 17895, a P^4 in an approximately comparable stage of wear. The probable molar lacks the posterobuccal cuspule and is reduced posterobuccally in comparison with M.C.Z. No. 17896, although valid comparisons with the latter are limited by differences in stage of wear. Interpretation of M.C.Z. No. 17898 as a molar is supported by comparisons with *Amphilagus fontannesi,* a late Miocene ochotonid in which M^1 resembles this probable molar and P^4 is more similar to M.C.Z. No. 17896. The closer resemblance of M.C.Z. No. 17898 to M^1 than to M^2 of *A. fontannesi* suggests that it may be the anterior molar, since M^2 is more reduced posteriorly in *A. fontannesi* (Forsyth Major, 1899, pl. 36, figs. 6 of M^2, 7 of M^1, 8 of P^4).

An isolated upper tooth, U. Cal. No. 29633, was tentatively identified as *Entoptychus?* sp. (Hall, 1930c, p. 296) but was subsequently recognized as a deciduous premolar of a lagomorph (Wood, 1936c, p. 25). The tooth is smaller than the permanent

upper teeth of *Hesperolagomys*, but probably represents this ochotonid rather than the much larger leporid of the Fish Lake Valley fauna.

The lower jaw and dentition are more adequately represented than the upper. The ventral border of the horizontal ramus (Fig. 4 B) is essentially straight below the cheek teeth and curves up, below the diastema. The jaw is slightly deeper below the posterior than below the anterior cheek teeth. The shape of the jaw is more similar to that in *Titanomys* and *Oreolagus* than to that in *Ochotona*, in which the jaw is deeper below the anterior cheek teeth and has a more concave dorsal border at the diastema.

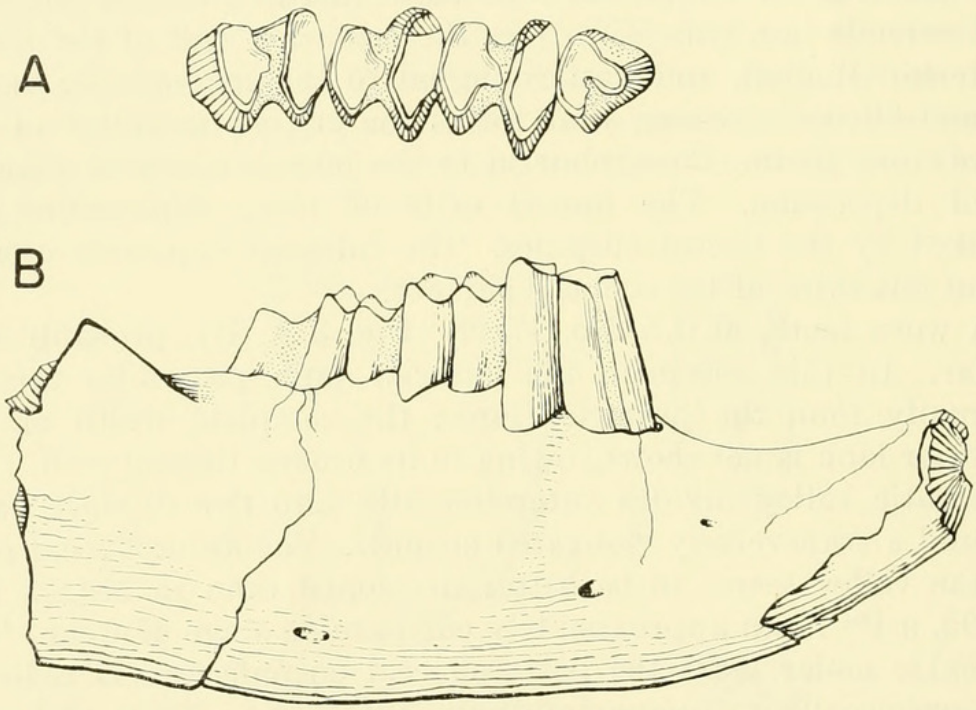

FIG. 4. *Hesperolagomys galbreathi*, n. gen., n. sp. Right lower jaw with P_3-M_2, type, M.C.Z. No. 17890, × 6. A, occlusal view of cheek teeth; B, lateral view.

On the lateral surface of the jaw are several mental foramina; the largest of these is in line with the talonid of P_3 and below mid-depth of the jaw. A smaller foramen occurs anterior to P_3, above mid-depth, and a depression with two small foramina is situated in a line between M_1 and M_2 and lower than the anterior foramina. This disposition of mental foramina, with the middle foramen the largest, differentiates *Hesperolagomys* from other known ochotonids. In *Desmatolagus vetustus*, *D. gobiensis*, and *Sinolagomys* (Bohlin, 1942, pp. 62-63), anterior and posterior

mental foramina are present. Between them there occurs in some specimens another small foramen or foramina approximately in the position of the large foramen in *Hesperolagomys*. Presence of a series of mental foramina seems to be primitive for lagomorphs. Different ochotonids retain and emphasize different foramina of this series. *Hesperolagomys* retains a primitive series, with emphasis on the middle foramen. Another variant on these foramina in an ochotonid is seen in *Kenyalagomys* of the Miocene of Africa, in which the two main mental foramina (MacInnes, 1953, p. 10) seem to correspond to the middle and posterior foramina of *Hesperolagomys*. In *Ochotona* the single mental foramen, probably representing the posterior foramen of *Hesperolagomys*, is situated below M_2.

The shaft of the incisor extends approximately to a line below the middle of M_1, as indicated by a swelling on the medial surface of the jaw. The lower cheek teeth are hypsodont but rooted. For most of their length the trigonid and talonid of P_4-M_2 are connected by cement only, but a short distance above the roots the dentine of the two columns becomes confluent. An isolated tooth, probably a molar, shows two small rootlets for the trigonid and a single root for the talonid. The alveolar portions of P_3 and P_4 are relatively straight anteroposteriorly and extend down lateral to the shaft of the incisor. The lateral surface of the jaw swells out over P_4, thus giving space for that tooth lateral to the incisor. The alveolar portions of M_1 and M_2 curve posteriorly and in this way avoid interfering with the shaft of the incisor.

The most complete lower jaw is the type specimen, M.C.Z. No. 17890 (Fig. 4). On P_3 a cement-filled buccal fold crosses about half the occlusal surface and marks the division between trigonid and talonid. The trigonid is rounded anterobuccally. Anterolingually, P_3 has a wide, shallow groove with a thin coating of cement. This groove is interpreted here as being in the trigonid, and not between trigonid and talonid. The lingual wall of P_3 is short anteroposteriorly.

The trigonids of P_4-M_2 are wider transversely and shorter anteroposteriorly than the corresponding talonids. Each talonid sends forward a narrow protrusion. Enamel is prominent on the external and posterior walls of trigonids and talonids. The alveolus of M_3 is rounded buccally and is narrower transversely than that of the talonid of M_2. The shape of the alveolus suggests that M_3 was probably more rounded and less tapered buccally than is that tooth in *Ochotona*.

A young individual of *Hesperolagomys* is represented by U. Cal. No. 29626, an incomplete lower jaw with P_4-M_1 (Hall, 1930c, p. 311; the specimen was tentatively identified by Hall as *Sylvilagus*? sp.). Small posterolophids, which would be worn away a short distance down the tooth, occur on the talonids of the two teeth. The limited hypsodonty of *Hesperolagomys* is illustrated by this specimen, in which the little worn P_4 shows at its base the confluence of the dentine of the columns that occurs just above the roots.

TABLE 2

Measurements (in millimeters) of *Hesperolagomys galbreathi*

	M.C.Z. No. 17895 P^4	M.C.Z. No. 17896 P^4	M.C.Z. No. 17898 probably M^1
length	1.5	1.5	1.3
width anteroloph	—	2.3	2.9
width posteroloph	—	2.2	2.5

	M.C.Z. No. 17890 type specimen
P_3 length	1.1
width	1.2
P_4 length	1.7
width trigonid	1.9
width talonid	1.4
M_1 length	1.6
width trigonid	1.8
width talonid	1.4
M_2 length	1.6
width trigonid	1.7
width talonid	1.4
alveolar length P_3-M_3	8.1
length P_3-M_2	5.8
length P_4-M_2	4.9
inside depth jaw, at middle of M_1	5.3

Hesperolagomys is an ochotonid that retained into the early Pliocene a number of primitive characteristics, among which are the rooted cheek teeth, persistence of folds in the buccal part of the occlusal surface of P^4 and M^1, and talonids that are narrower transversely than the trigonids on P_4-M_2. Combined with

these primitive characteristics, *Hesperolagomys* exhibits its own peculiar features, including the marked anterior protrusion of the talonids on P_4-M_2 and the disposition of the mental foramina.

Other ochotonids that have been reported from the North American later Tertiary are *Oreolagus* from the Miocene and *Ochotona* which first appears in the middle Pliocene. Among the characters distinguishing *Oreolagus* from *Hesperolagomys* are, in the former, higher crowned cheek teeth, shape and proportions of the lower cheek teeth, in which the trigonids and talonids of P_4-M_2 are more nearly equivalent in width, and absence of M_3. *Ochotona* is distinguished from *Hesperolagomys* by its more hypsodont cheek teeth, absence of a persistent crescentic valley on P^4 and M^1, more complex folds on P_3, and approximately equivalent width of the columns of P_4-M_2. The presence of *Hesperolagomys* with its primitive characteristics in the North American early Pliocene seems to be a parallel to the presence of *Amphilagus fontannesi,* an ochotonid likewise having primitive dental features, in the late Miocene of Europe.

Unless there has been a reversal of evolution affecting several characteristics, which seems unlikely, *Hesperolagomys* was derived from a primitive ochotonid. Of known forms, *Desmatolagus,* which has rooted cheek teeth and a generally primitive level of development, could be near the ancestry of *Hesperolagomys.* More specific evidence for such an affinity, other than the merely primitive features, is afforded by the structure of P_3. In *Hesperolagomys* that tooth has a narrow lingual exposure and an anterointernal groove that seems to be in the trigonid. *Desmatolagus gobiensis* of the late Oligocene of Asia has a somewhat similarly shaped P_3 in some individuals; in late stages of wear the anterointernal groove is worn away in that species. An earlier species, *D. vetustus* of the Mongolian early Oligocene, shows the same general pattern of folding on P_3, but the lingual wall is less reduced anteroposteriorly than in *D. gobiensis* (Burke, 1941, pp. 16-17) and *Hesperolagomys.* A trigonid of P_3, that is divided by an anterior fold, and an internal wall of P_3, that becomes reduced in later species, are among the characters distinctive of Burke's "*Desmatolagus* phylum" (1941, pp. 17, 22). If the folds on P_3 in *Hesperolagomys* have been interpreted correctly, the similar structure of that tooth would seem to indicate affinity with *Desmatolagus.* Whether *Hesperolagomys* is closer to Asian species of *Desmatolagus* or to North American species referred to that genus remains to be determined.

Family LEPORIDAE

Hypolagus fontinalis Dawson, 1958

Material: M.C.Z. Nos. 7640, incomplete left lower jaw with P_4-M_2; 7641, left premaxilla with upper incisors; 7642, isolated teeth; 7643, postcranial fragments including proximal and distal ends of humerus, astragali, calcanea, navicular.

Hypolagus fontinalis, a previously known member of the Fish Lake Valley fauna (Dawson, 1958, p. 48), is represented by these specimens. Lower cheek teeth agree in size (Table 3) and structure with other specimens of this species.

The upper cheek teeth of *H. fontinalis* were previously unknown. Two folds, of which the lingual is longer, occur on the anterior surface of P^2. The internal hypostria crosses somewhat more than half the width of the occlusal surface on P^3-M^2. The walls of the hypostria are strongly crenulated on P^3; on specimens that are probably P^4 or M^1 the walls are less strongly crenulated; and in a specimen that seems to represent M^2 the walls are only slightly wavy. Thus, the folding in the walls of the hypostriae decreases posteriorly in the series of molariform teeth. In general structure the upper cheek teeth resemble those of *H. vetus,* a species averaging larger in size than *H. fontinalis.*

Table 3

Measurements (in millimeters) of *Hypolagus fontinalis*

	M.C.Z. No. 7642	M.C.Z. No. 7640	M.C.Z. No. 7643
P^2 length	1.2		
width	2.6		
P^4 or M^1 length	2.3		
width anteroloph	4.2		
width posteroloph	4.0		
P_3 length	2.6		
width trigonid	2.0		
width talonid	2.5		
P_4-M_2 length		7.4	
astragalus, length proximodistal			10.6
width			5.4
humerus, length proximal end			10.9

The postcranial parts are smaller than corresponding parts of *H. vetus* but suggest similarity to *H. vetus* in general level of development.

Order RODENTIA

Family CRICETIDAE

COPEMYS Wood 1936

Type species: Hesperomys loxodon Cope 1874.

Referred species: C. dentalis (Hall), *C. longidens* (Hall), *C. kelloggae* (Hoffmeister), and *C. esmeraldensis* n. sp.

Distribution: Late Miocene Barstow and Niobrara River to early Pliocene Fish Lake Valley; Nebraska, New Mexico, California and Nevada.

Emended diagnosis: Cricetid in which alternation of buccal and lingual cusps has begun to develop; crowns low; no distinct mesocone or mesoconid, although mesoloph or mesolophid may be well developed; protoconid and metaconid of M_1 unite, after varying amounts of wear, at anterior end of protoconid; metaconid of M_{2-3} at anterior margin of tooth, with anterior cingulum absent or restricted to buccal margin of tooth; paracone of M^1 unites with posterior end of protocone and, sometimes, with its anterior end; metacone of M^1 unites with posteroloph rather than with hypocone; metacone of M^2 tending to unite in this manner; lower incisors broad; mental foramen below or just in front of M_1; masseteric fossa prominent, ending below M_1; deep valley between M_3 and the coronoid process.

One of the striking peculiarities of North American Tertiary rodent history is the record of the cricetids. In the middle Oligocene, *Eumys* is unquestionably the most abundant rodent, and a number of different species have been recognized. *Leidymys* and *Scottimus* have developed from a *Eumys* ancestry. Species of *Eumys* are known from the Oligocene of the Great Plains (Wood, 1937; Galbreath, 1953) and of Montana (Wood, 1937, p. 262; White, 1954, pp. 410-415). In the early Miocene, two species of *Leidymys* and *Paciculus insolitus* are known from the middle John Day (Wood, 1936a). *Eumys eliensis*, from the equivalent Fort Logan of Montana (Black, 1961c, pp. 7-10), seems to be more closely related to *E. brachyodus* of the plains than to the large Montanan species of *Eumys* described by White (1954). It seems possible that *Cotimus* (Black, 1961a) may be

related to *Paciculus*, known only from the upper teeth (Wood, 1936a, pp. 4-6; Black, 1961c, pp. 10-12). *Scottimus kellamorum* is a continuation of the Oligocene *Scottimus* lineage (Black, 1961b).

The only described North American cricetids between the early Miocene and the late Pliocene are: *Horatiomys montanus* (Wood, 1935b, if it is a cricetid), and *Paciculus montanus* (Black, 1961c) from the Deep River of Montana; *Cotimus alicae* from the Flint Creek of Montana (Black, 1961a); *Miochomys niobrariensis* from the Niobrara River (Hoffmeister, 1959); and four species of *Copemys* — *C. longidens* (Hall) from the late Miocene Barstow of California, *C. kelloggae* (Hoffmeister) from the late Miocene Niobrara River of Nebraska, *C. loxodon* (Cope) from the late Miocene or early Pliocene Santa Fé of New Mexico, and *C. dentalis* (Hall) from the early Pliocene Fish Lake Valley. Another species of *Copemys* from the Fish Lake Valley is described below.

The published record would indicate that the cricetids were nearly absent from the Great Plains area during the Miocene and most of the Pliocene, although they survived and evolved in the intermontane areas farther west. Even at such a semi-intermontane area as Split Rock there are no cricetids among the thousands of rodent teeth known. The dominant North American Miocene small rodents were the entoptychine geomyids. In the Pliocene, their place seems to have been taken by the heteromyids. The cricetids do not come back into the picture until the end of the Pliocene, when both hesperomyine and microtine forms become abundant. Perhaps the invasion of the Old World microtines reduced the competing heteromyids, and allowed the native American cricetids to spread eastward once more. The presence of *C. kelloggae* in Nebraska and of cricetids in the Miocene of Florida (Wood, 1947, p. 491), however, shows that they were not completely absent in the great plains and farther east.

The present evidence suggests that the hesperomyines were derived from the eumyines in a manner somewhat similar to that shown in Figure 5, and that the series *Eumys* — *Leidymys* — *Copemys* — *Peromyscus* is not far from a true phyletic sequence. The citation of *Leidymys* in the Oligocene is based on the reference to that genus of *L. vetus* (Wood, 1937, p. 257). Galbreath (1953, p. 72) states that in his opinion *Eumys exiguus* and *Leidymys vetus* represent the same species. In this allocation he is followed by Black (1961b, p. 3). However, *Leidymys* is

characterized by a well-developed hypocone-like cusp on M^3. In *Eumys*, including *E. exiguus*, this cusp is at most an enlarged cingulum. Since *Leidymys* is presumably derived from *Eumys*, the transition must have occurred as individual variants. But *Eumys exiguus* also shows the development of anteroposterior connections between the crests, leading toward *Scottimus* (Black, 1961b, p. 3, transfers it to *Scottimus*, which is just as reasonable as leaving it in *Eumys*), and there is no trace of these in the type of *Leidymys vetus*. The status of the Oligocene eumyine rodents

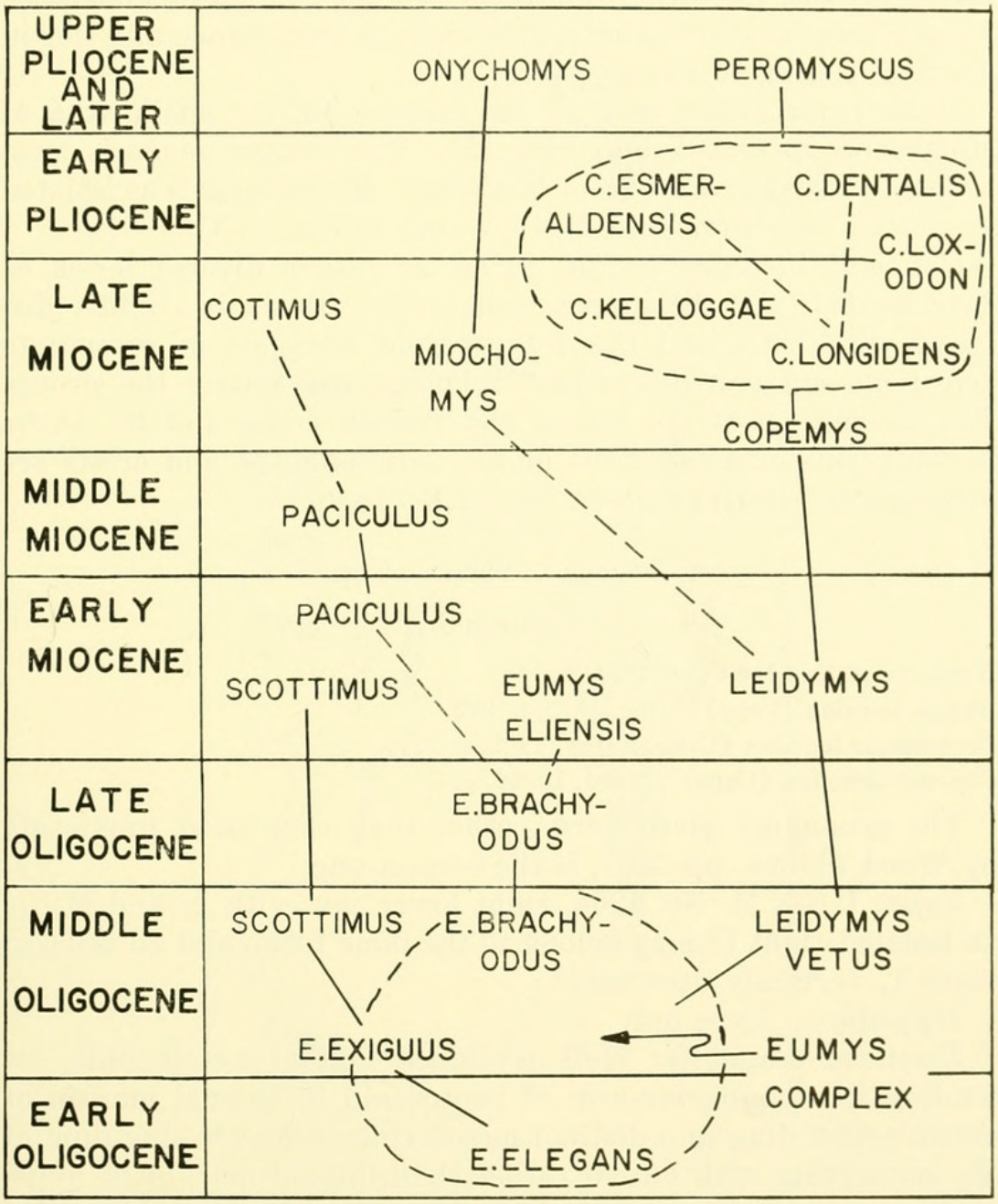

FIG. 5. Phylogenetic relationships of North American Tertiary cricetids.

will have to remain nebulous until the very extensive collections are studied, so that it will become possible to separate individual variations from specific and generic variants. There is so much variation among North American Oligocene cricetids that all possible later trends seem to be represented within a single population, sometimes even in the material from a single ant hill. Very few if any of the described forms can be considered to be adequately categorized and separated from each other.

Cotimus (Black, 1961a, p. 73) is distinct from *Copemys*. It may represent the hitherto undescribed lower teeth of *Paciculus*. At any rate, as stated above, it is close to that genus, and not in the line leading to *Peromyscus*.

Hoffmeister (1959, p. 698) has pointed out the similarities of *Miochomys* to *Onychomys* (Fig. 5). The former genus is most probably also derivable from *Leidymys*. *Horatiomys* is as isolated as when it was first described (Wood, 1935b, p. 3).

Copemys includes several forms at rather diverse levels of development. All the species seem to be evolving in slightly different directions, and the data are not adequate at present to determine ancestor-descendant relationships among the group. The alternation of the buccal and lingual cusps and the shifts in the points of attachment of the various cusps and crests are progressive features foreshadowing *Peromyscus*.

Copemys loxodon (Cope)

Figures 6-7

Hesperomys loxodon Cope, 1874, p. 148.
Eumys loxodon (Cope). Cope, 1875, p. 993.
Peromyscus loxodon (Cope). Hay, 1902, p. 727.
Copemys loxodon (Cope). Wood, 1936a, p. 5.

The synonymy given here, rather than that cited previously by Wood (1936a, pp. 5-6), is the correct one.

Type: U.S.N.M. No. 1204, right lower jaw with I_1 and M_{1-2}; an isolated right I^1 may belong to the same form, and an isolated right I_1 certainly does not.

Hypodigm: Type only.

Emended diagnosis: Well developed lingual mesolophids, extending from posterior arm of protoconid to lingual margin of crown and ending in a distinct mesostylid; posterior cingulum of M_2 connecting with buccal rather than lingual margin of hypoconid; masseteric fossa with everted, overhanging dorsal margin; tooth measurements as given in Table 4.

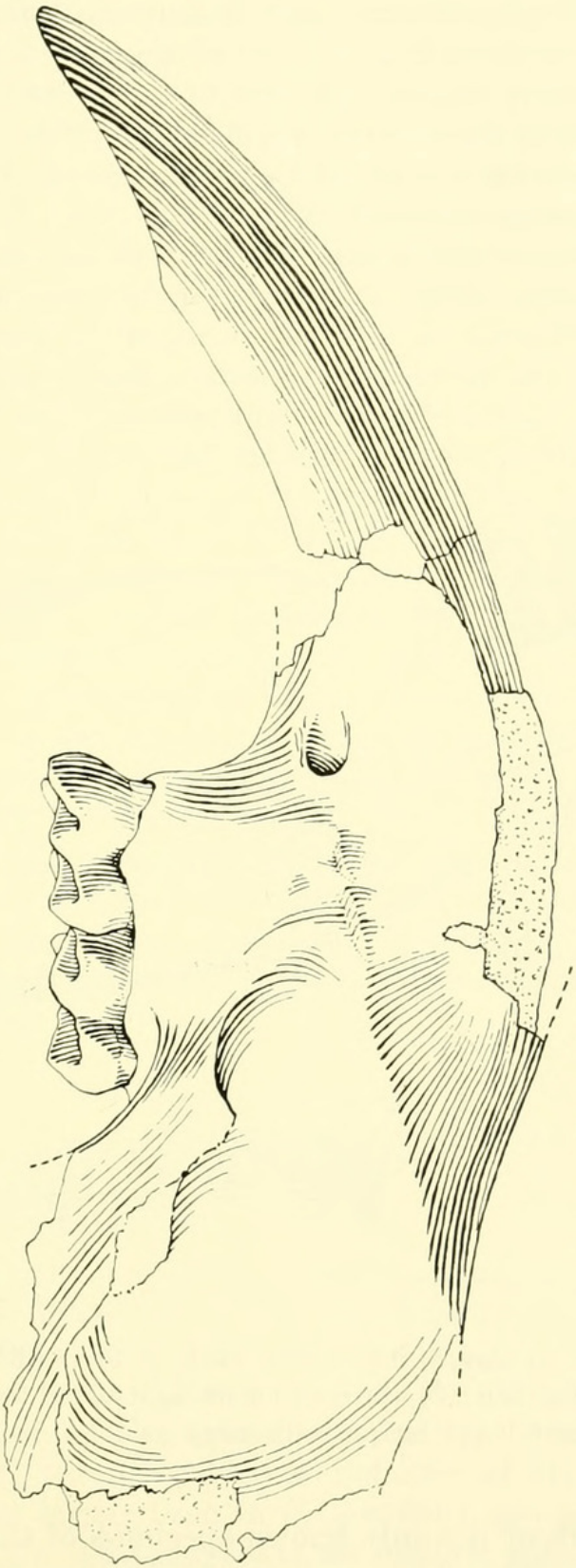

Fig. 6. *Copemys loxodon*, U.S.N.M. No. 1204, lateral view of lower jaw, × 10.

Description: The masseteric fossa is quite unusual, in its overhanging dorsal margin (Fig. 6). No suggestion of such a structure is seen in other species referred to this genus, but there is clearly considerable interspecific variability in this respect (Figs. 8E, 9F). The ventral margin of the fossa extends to the ventral border of the angular process, as in *C. dentalis.* The masseteric knob, at the front of the fossa, lies beneath the middle of M_1, and is more distinct than in *C. dentalis,* but less so than in *C. esmeraldensis.* The mental foramen lies just in front of the anterior root of M_1 as in the other species. There is a pronounced groove between M_3 and the coronoid process. The latter passes the alveolar border by the middle of M_3.

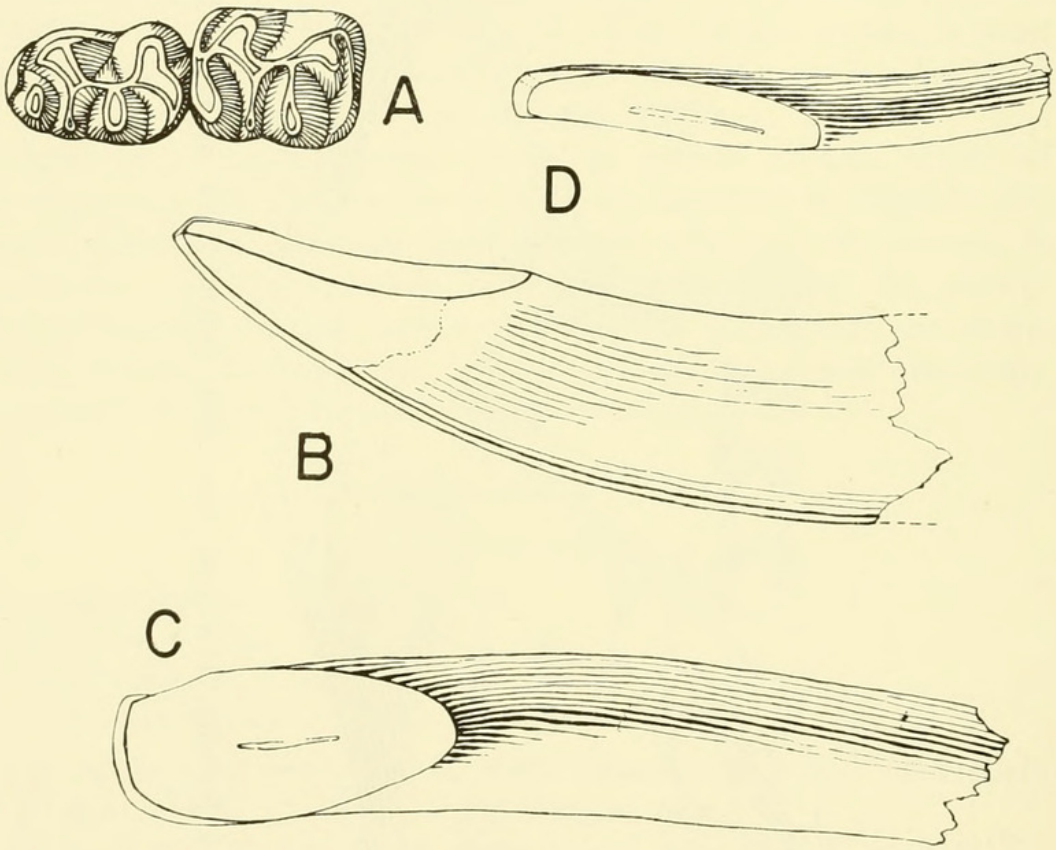

FIG. 7. *Copemys loxodon,* U.S.N.M. No. 1204, × 10. A, RM_{1-2}; B, medial view of right lower incisor; C, ventral view of right upper incisor; D, dorsal view of another right lower incisor with same number.

The cheek teeth of the only known specimen of this species are quite distinctive (Fig. 7A), and are farther removed from the *Peromyscus* pattern than are those of the other members of the genus. As suggested by Wood (1936a, p. 6), the closest relatives of this species seem to be "certain species from the Miocene and

Pliocene of California and Nevada, which have been described as *Peromyscus,*" and which are here referred to *Copemys.* The peculiar position of the posterior cingulum of M_2 is just as unique as it seemed in 1936 (*op. cit.*, p. 6), but Hooper's recent study (1957) of tooth variation in *Peromyscus* shows how much variability can exist within a single living genus, and warns us to be careful about drawing the lines of specific or generic variation too tightly among fossil forms. (The magnification shown for these teeth in Wood, 1936a, fig. 5, is incorrect, that figure being 7.5, rather than 5, times natural size.)

The lower incisor (Figs. 6, 7B) is similar to that of other species of the genus. The anterior face is fairly flat. At the tip of the median side, there is an extensive flat area, where there has been interdental wear with the tooth of the opposite side. This is also present on the type of *C. dentalis,* but all other specimens are too broken to be sure whether this is a generic character, although it probably is. It would probably be associated with a well-developed Transversus mandibulae muscle.

The upper incisor associated with this specimen (Fig. 7C) is of the correct size and general shape to belong here, but it cannot with certainty be referred to this form. Another lower incisor (Fig. 7D) is much too small for *Copemys,* and is too narrow and with too heavy an anterior enamel face to belong to a cricetid. It agrees in size, shape, and shape of the pulp cavity with the incisor of small heteromyids, and presumably is referable to a member of that family.

COPEMYS DENTALIS (Hall)

Figure 8

Peromyscus dentalis Hall, 1930c, p. 306.

Type: U. Cal. No. 29635, a lower jaw with RI_1 and M_{1-2}.

Hypodigm: Type, and U. Cal. No. 29636, edentulous right jaw, and U. Cal. No. 29638, left jaw with M_{1-2}.

Emended diagnosis: Fossa between M_3 and the coronoid process bears small nutritive foramina; mental foramen below diastema as in *C. loxodon;* anteroconid area of M_1 simple as in *C. longidens,* but larger than in *C. loxodon;* mesolophid present or absent, and low when present; no distinct hypoconulid on M_1; metaconid of M_{2-3} far forward, eliminating lingual half of anterior cingulum as in *C. loxodon;* lower incisor narrow; tooth measurements as given in Table 4.

Description: The tooth pattern of this species (Fig. 8 A-B) is more *Peromyscus*-like than is that of the genotype. The teeth show the *Peromyscus* type of alternation of cusps, but the cusps are still less completely integrated with the lophs than in *Peromyscus,* warranting the reference of this species to a genus ancestral to *Peromyscus,* for which *Copemys* is the best name until a great deal more is known about Miocene and early Pliocene North American cricetids.

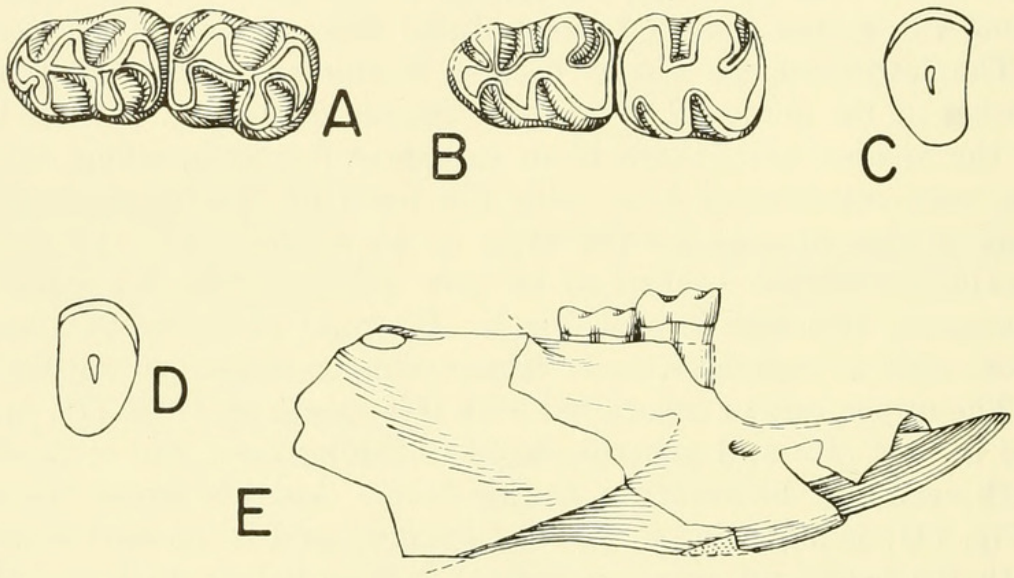

FIG. 8. *Copemys dentalis.* Teeth × 10, jaw × 5. A, U. Cal. No. 29635, RM_{1-2}, type; B, U. Cal. No. 29638, LM_{1-2}; C, U. Cal. No. 29635, type, cross section of right I_1, from rear; D, U. Cal. No. 29636, cross section of right I_1, from front; E, lateral view of lower jaw, anterior half based on U. Cal. No. 29635, type, and rear half on U. Cal. No. 29636.

In M_1, the anteroconid is somewhat larger than in *C. loxodon,* and is close to the metaconid. There are distinct ridges running posteriorly from the protoconid, along the buccal margin of the tooth, in all teeth. These are also present on M_1 of *C. loxodon* (Fig. 7 A), but are less well developed in other species. The mesolophid (or posterior arm of the protoconid) is absent in all teeth except M_1 of U. Cal. No. 29638, where it extends as a faint, low ridge to the buccal margin of the tooth (Fig. 8 B). The hypoconulid seems poorly developed on M_1, but distinct on M_2.

The incisor has a rounded anterior face with a heavy coat of enamel. It is slightly concave on the medial side of the type (Fig. 8 C) which is not shown in the other specimen (Fig. 8 D), and is probably due to crushing, and, at this level, is certainly not due to interdental wear.

The jaw is slender, with no suggestion of a chin process. The mental foramen is below the posterior portion of the diastema. The masseteric fossa is shallower than in other species of the genus, being bounded by faint ridges, especially on the dorsal side (Fig. 8 E). The anterior end of the fossa is beneath the middle of M_1. Posteriorly, the ventral border of the fossa approaches the ventral margin of the angle. The base of the incisor, in U. Cal. No. 29636, forms a knob on the lateral surface of the mandible, at the level of the molar alveoli but well behind them. This knob is broken through on the specimen.

Copemys longidens (Hall)

Peromyscus longidens Hall, 1930b, p. 315.
Peromyscus sp. Hall, 1930b, p. 316.
Peromyscus sp. Hall, 1930b, p. 316.

All of Hall's specimens seem to be within the limits of one variable species, in which variation is no greater than in living species of *Peromyscus* (Hooper, 1957).

There is a single anteroconid on M_1 of the type, as in the previously discussed species. A crest, probably the mesolophid, reaches the lingual margin of the crown in the type. It is much smaller in U. Cal. No. 28503. In U. Cal. No. 28506, the crest is complete but its lingual half is very low. The isolated tooth of Hall's first *Peromyscus* sp. (U. Cal. No. 28517; it is M_1, *not* P_4 as Hall stated) is about ten per cent smaller than the type specimen, and is somewhat (but not significantly) narrower than the other material. The isolated M_2 of U. Cal. No. 28516 is intermediate in size between what would be expected for that of U. Cal. No. 28517 and the rest of the population.

There is a faint trace of an anterolingual cingulum on M_2 of the type, but it is almost eliminated. The mesolophid is very short on this tooth.

The lingual anterior cingulum of M_3 is very small. In the type, the entoconid and mesolophid are minute. There is a lingual marginal ridge connecting the metaconid and entoconid.

The upper teeth show progressive development of lophs. In M^1 of U. Cal. No. 28515 the metaconid unites with the middle of the posterior cingulum. In M^2, there is the beginning of this posterior union (not shown in Hall's figure, 1930b, fig. 7 A), but the union between the metacone and hypocone is still present. The mesoloph (or anterior arm of the hypocone) is well developed. The tooth figured by Hall as M^3 (*op. cit.*, fig. 6) is

actually a specimen of M^2 in which both unions of the metacone are present, and the mesoloph is very long.

The range of variation in tooth size is indicated in Table 4.

The mental foramen lies beneath the diastema, as in *C. dentalis*, and the size and shape of the masseteric fossa is also like that of *C. dentalis*.

Copemys kelloggae (Hoffmeister)

Peromyscus kelloggae Hoffmeister, 1959, p. 698.

This species, from the late Miocene Niobrara River fauna of Nebraska is referable to *Copemys*. The anteroloph is a single cusp, close to the metaconid (Hoffmeister, 1959, fig. 1 B). There is a long mesolophid, reaching nearly to the lingual margin of the crown. The hypoconulid is very well developed.

The upper molar described by Hoffmeister as *Miochomys niobrariensis* does not appear to be referable to the same form as do the lower teeth, although they are of the appropriate size to belong together. The metacone has not shifted its union away from the hypocone, and the posterior cingulum is short. The separation of the tooth into three transverse lobes is not characteristic of *Copemys*.

Copemys esmeraldensis n. sp.

Figure 9

Type: M.C.Z. No. 7644, right jaw with M_1 and M_3 and incisor.

Hypodigm: Type; M.C.Z. No. 7645, right jaw fragment with M_1; M.C.Z. No. 7646, edentulous right jaw; and M.C.Z. No. 7647, left maxillary fragment with M^1.

Diagnosis: Jaw heavier than in *C. dentalis*. with chin process; masseteric fossa not reaching as far ventrad on angle as in *C. dentalis* and upper border of masseteric fossa more pronounced, but much less so than in *C. loxodon;* mental foramen beneath M_1 rather than in front of it; fossa between M_3 and coronoid as in *C. dentalis;* anteroconid area highly complex; mesolophid present and long, though sometimes low; sometimes an accessory crest running buccad from the entoconid to the buccal margin of the tooth; hypoconulid of M_1 distinct; metacone of M^3 uniting with posterior cingulum rather than with hypocone; lower incisor wide; larger than *C. dentalis;* tooth measurements as given in Table 4.

TABLE 4

Measurements (in millimeters) of lower teeth of *Copemys*

	C. loxodon		*C. dentalis*		*C. esmeraldensis*			*C. longidens*		*C. kelloggae*		
	U.S.N.M. No. 1204	U. Cal. No. 29635	U. Cal. No. 29636	U. Cal. No. 29638	M.C.Z. No. 7644	M.C.Z. No. 7645	M.C.Z. No. 7646	U. Cal. No. 28502	O.R. of other specimens (after Hall, 1930a, p. 317)	U. Cal. No. 28517	U. Cal. No. 36105, Type (after Hoffmeister, 1959, p. 698)	U. Cal. No. 36158
	R	Type R	R	L	Type R	R	R	Type R		R	L	L
M_{1-3} alveolar			4.40	4.35	4.85		4.94	4.79	4.54-4.9			
M_1 anteroposterior	1.70	1.50		1.56	1.80	2.13		1.76	1.70-1.90	1.55	1.50	
width, metalophid	1.10	0.94		0.98	1.21	1.19		1.13		0.90	1.06	
width, hypolophid	1.15	1.08		1.08		1.31		1.21	1.13-1.23	1.03	1.16	
M_2 anteroposterior	1.57	1.40		1.37				1.57	1.50-1.70			
width, metalophid	1.22	1.09		1.15				1.28				
width, hypolophid	1.27	1.11		1.20				1.18	1.20-1.30			
M_3 anteroposterior					1.51			1.52	1.32-1.50			
width, metalophid								1.04	1.03-1.10			
width, hypolophid					1.00			0.93				
I_1 anteroposterior		1.27	1.26		1.40		1.44					
transverse		0.76	0.76		1.03		1.02					0.59

Distribution: Lower Pliocene Fish Lake Valley beds, Esmeralda Formation of Nevada. All material came from locality A shown by Hall (1930c, pl. 37, fig. 1).

Description: As shown by the two specimens of M_1 preserved in the present collection (Fig. 9 B, C) there is considerable variability in pattern in this tooth. From what is known of the variability in the Oligocene *Eumys*, and from the detailed studies of *Peromyscus* by Hooper (1957), however, it seems obvious that a great deal of individual variation can be expected within a single species of cricetid. Initially, because the specimens come from a single locality, all the Fish Lake Valley cricetids were referred to a single species. As the study proceeded, however, it became apparent that not only is the material in the present collection all much larger than Hall's material, but there is also the much greater complexity of the anteroconid region and the rather striking difference in the jaw structure, including the masseteric fossa and the position of the mental foramen. These differences make it seem unlikely that this material is conspecific with *C. dentalis*, even though the present collection came from the same spot as the University of California material.

The pattern of M^1 (Fig. 9 A) is fundamentally intermediate between that of *Eumys elegans* (Wood, 1937, fig. 57) and that of such living species of *Peromyscus* as *P. nudipes* (Hooper, 1957, fig. 19). The anterocone is a large cusp, continued both buccally and lingually by narrow ridges. Buccally, there are two such ridges, separated by a groove, as in *P. nudipes*. The anterior arm of the protocone unites with the middle of the anterocone. The posterior arm of the protocone unites with the paracone to form a protoloph as in *Eumys*. In general, in *Peromyscus*, the paracone is behind the protocone, though this is not always the situation. This shift is just beginning in the present form. The mure is longer than in *Peromyscus*. The mesoloph, as in *Eumys*, is a continuation of the anterior arm of the hypocone, instead of appearing more closely related to the paracone, as in *Peromyscus* (Hooper, 1957, figs. 9, 15, 16 and 19). The mesoloph is directed into the base of the metacone, rather than extending freely to or toward the buccal margin of the tooth as in *Paciculus* (Black, 1961c, fig. 4) or some species of *Peromyscus* (Hooper, 1957, figs. 18-19). The most progressive character of this tooth is the union of the metacone with the posteroloph, rather than with the hypocone. In this it resembles *C. dentalis* and is more advanced than *Miochomys niobrariensis*.

Even though this union is characteristic of *Peromyscus,* not all members of that genus are as advanced as is *Copemys dentalis.* The measurements of this specimen are: anteroposterior, 2.27 mm; width protoloph, 1.48; width metaloph, 1.52.

The two specimens of M_1 are rather different, as well as being in very distinct stages of wear. The unworn tooth (Fig. 9 C) shows that the anterolophid is a very complex area, being formed of an anteroconid (partly divided in two), a large lingual cusp, a buccal marginal crest from the anteroconid, and a long, narrow crest from the lingual cusp almost to the buccal margin. The worn specimen (M.C.Z. No. 7644, Fig. 9 B) cannot be shown to have had a different pattern. This area is much more complex than anything seen in any other species of *Copemys,* or in *Eumys,* though the beginnings of subdivision of the anteroconid may be seen in *E. obliquidens* (Wood, 1937, fig. 62) and *E. spokanensis* (White, 1954, fig. 47). This area is much more complicated than is the corresponding area of any of the *Peromyscus* teeth figured by Hooper, though it is approached in *P. nudipes* (Hooper, 1957, fig. 19). The protoconid and metaconid unite at the anterior end of the metaconid, the latter cusp being the more anterior. This condition is typical of both *Copemys* and *Peromyscus,* and is a contrast to *Eumys,* where the primary union is at the posterior side of the protoconid. In *C. loxodon,* the metaconid is more isolated than in *C. esmeraldensis.* The ectolophid (in the sense of Wood and Wilson, 1936; this ridge is called the mure by Hooper, 1957, fig. 1) is much longer than in *Eumys,* being like that of *Peromyscus* in this respect. What may be a mesolophid extends from the middle of the ectolophid almost to the lingual margin of the crown, not being as elevated as is the ectolophid (Fig. 9 C). In M.C.Z. No. 7644 (Fig. 9 B), the mesolophid looks as if it were perhaps more correctly identified as the posterior arm of the protoconid, as in some specimens of *Eumys* (Wood, 1937, fig. 58). There is a connection in this same specimen between this lingual crest and the anterior side of the entoconid (Fig. 9 B). The entoconid connects with the ectolophid in front of the hypoconid, rather than with the anterior arm of the hypoconid as in Oligocene species of *Eumys,* resembling *Eumys eliensis* (Black, 1961c, fig. 3 A) and *Peromyscus* in this respect. There is much more of a hypoconulid than in *Eumys.* An unusual crest that extends buccally from the point where the entoconid meets the ectolophid in one specimen (Fig. 9 C), is completely absent in the other (Fig. 9 B). This

crest is present in many of the species of *Peromyscus* discussed by Hooper, the closest similarity being seen in *P. nuttalli* (Hooper, 1957, fig. 18). This crest, which seems to be fairly important in *Peromyscus,* has been called the ectolophid by Hooper. It is completely unrelated to the ectolophid as that term was used by Wood and Wilson (1936) and does not seem to have been discussed by anyone else. This crest is clearly a neomorph in *Copemys* and *Peromyscus,* and does not arise as a buccal extension of the mesoconid, which Wood and Wilson would have considered to be a buccal part of the mesolophid. Both of these teeth belong to Hooper's pattern type *g* (1957, p. 11). Of the species he studied, pattern *g* occurs in less than ten per cent of all except *P. maniculatus* (20%), *P. truei* (20%), *P. hylocetes* (25%), *P. oaxacensis* (60%) and *P. mexicanus* (50%). A well developed buccal crest (Hooper's ectolophid) is present in all *P. hylocetes* and *P. oaxacensis;* 90 per cent of *P. yucatanensis;* 80 per cent of *P. nasutus* and *P. difficilis;* 70 per cent of *P. boylei;* 30 per cent of *P. leucopus* and *P. mexicanus;* 20 per cent of *P. melanotis* and less than ten per cent of the remainder.

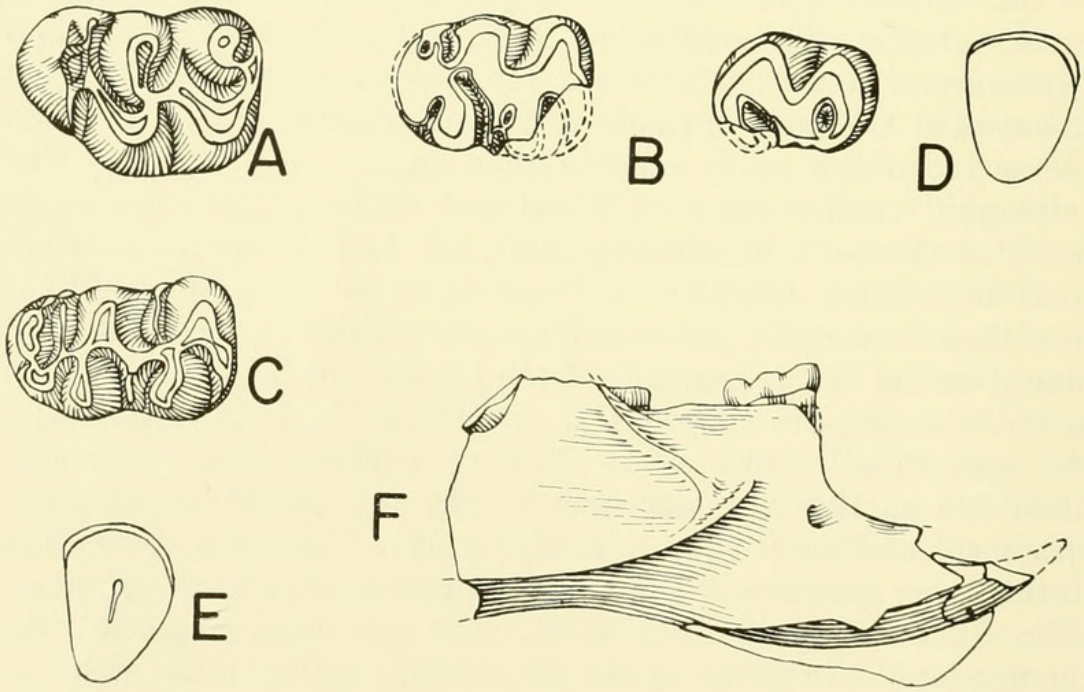

FIG. 9. *Copemys esmeraldensis* n. sp. Teeth × 10, jaw × 5. A, LM^1, M.C.Z. No. 7647; B, type, RM_1 and M_3, spaced as in the specimen, M.C.Z. No. 7644; C, RM_1, M.C.Z. No. 7645; D, cross section of RI_1, M.C.Z. No. 7644, type; E, cross section of RI_1, M.C.Z. No. 7646; F, lateral view of lower jaw, M.C.Z. No. 7644, type. Outline portion restored from M.C.Z. No. 7646. The incisor slid back into the alveolus before fossilization.

Therefore, as far as the available data go, *C. esmeraldensis* seems closest to *P. oaxacensis*, among the species studied by Hooper, in these respects.

The single specimen of M_3 (M.C.Z. No. 7644, Fig. 9 B) is both badly worn and broken. Hooper does not discuss this tooth in *Peromyscus*. This tooth is very different from that of *Eumys*. There is no anterior cingulum, and the metaconid is continuous along the anterior edge of the tooth to the protoconid. From here, a broad ridge runs to the lingual margin of the tooth, showing slight irregularities at the tooth margin, which suggests that it may include a mesolophid and an entoconid, the latter being well forward of the hypoconid. A broad posterolophid extends across the rear of the tooth.

The incisor is broad, with a rounded anterior face, and is proportionately wider and rounder, laterally, than in *C. dentalis*. The enamel is fairly thick, and extends well onto the lateral side of the tooth (Fig. 9 D-E). The pulp cavity enlarges toward the enamel-covered side of the tooth (Fig. 9 E). The base of the incisor is in the ascending ramus behind and at or above the level of M_3 (Fig. 9 F).

Three lower jaws are preserved permitting the composite restoration shown in Figure 9 F. There is a prominent chin process in M.C.Z. No. 7646, not preserved on the other specimens. Such a process does not seem to have been present in *C. dentalis* (Hall, 1930c, fig. 16). This difference may be sexual, but the overall differences in size and in tooth pattern suggest that it is not. The symphysis is weakly ridged, indicating that there may have been a strong Transversus mandibulae muscle and free movement between the mandibles. The alveolar border drops abruptly in front of M_1, as in *C. loxodon*, in contrast to its more gentle slope in *C. dentalis* and *C. longidens*. The prominent mental foramen lies beneath the anterior root of M_1, as in *C. loxodon*, instead of beneath the diastema as in the other species, and opens anterad rather than slightly upward. The masseteric fossa is broad and flat. The masseteric knob is clearly differentiated, beneath the posterior end of M_1, farther to the rear than in *C. dentalis* (Hall, 1930c, figs. 16-17). The masseteric fossa does not extend as far ventrally in the angle as in *C. dentalis*. The coronoid process passes the alveolar border by the middle of M_3. There is a prominent fossa between M_3 and the base of the coronoid, which contains one or more nutritive foramina, as in other species of the genus.

At the present time, little can be said of the interrelationships of the five species of *Copemys*. *C. esmeraldensis* is probably the closest to *Peromyscus*. *C. loxodon* is apparently the most aberrant. *C. longidens* may be ancestral to *C. esmeraldensis*. The differences between *C. longidens* and *C. dentalis* are not great except in size, which may not be very significant, phylogenetically. *Copemys kelloggae* is fairly close to *C. longidens* and *C. dentalis*. These three species are all closer to each other than any is to *C. esmeraldensis* or *C. loxodon*.

Family CASTORIDAE

Eucastor dividerus Stirton, 1935

Figure 10

Aside from lagomorph material, fragmentary remains of this beaver are the most abundant fossils in the collection. The present material adds some features to the full account of this species given by Stirton (1935, pp. 431-437). Two upper premolars, M.C.Z. Nos. 7648 and 7649, show interesting pattern variants, and M.C.Z. No. 7650 is an upper deciduous premolar, hitherto not described.

In both of the permanent premolars, the anteroloph is very long, covering the entire front of the tooth, as opposed to the earliest stage of wear figured by Stirton (1935, fig. 107). The parastria is present in one specimen (Fig. 10 A), but is converted to a parafossette in the other (Fig. 10 B). In each specimen, there is a small enamel lake, of very uncertain homology, in the middle of the paracone. The mesoflexus in the less worn specimen extends across the tooth to the posterior margin of the crown, where it forms a distinct flexus behind the hypocone (Fig. 10 A). In the more worn specimen, this is cut off from the posterior margin of the crown, as in Stirton's specimens. There is considerable variation in the region of the metaflexus. In Stirton's least worn tooth (1935, fig. 107), the metaflexus opens to the rear, and there is a small isolated lake behind it. In M.C.Z. No. 7648, the metaflexus is a triangular valley, opening posteriorly (Fig. 10 A). In the more worn premolar, the metafossette is widely separated from the rear of the tooth, resembling Stirton's second stage of wear (*op. cit.*, fig. 107), but retaining a minute lake behind the fossette.

Presumably these variants indicate that there are numerous minor irregularities at the surface of the unworn crown, and

that these are highly variable, giving a variety of slightly different patterns with wear. The exact angle at which the wear surface cuts the crown may also make appreciable pattern differences.

The upper milk tooth (Fig. 10 C) is clearly deciduous, as it is much lower crowned than are the permanent teeth. There was a large single root under the anterior part of the crown, and two smaller ones under the posterior part. The anterior root, however, is proportionately smaller than in P^4. The hypostria and mesostria extend almost to the base of the crown. The metastria is long, but not quite as long as the other two. The mesoflexus and metaflexus interconnect, isolating a circular buccal mesostyle. The metaflexus runs transversely across the posterior part of the tooth, and is much more extensive than in P^4. The paraflexus is already transformed into a parafossette.

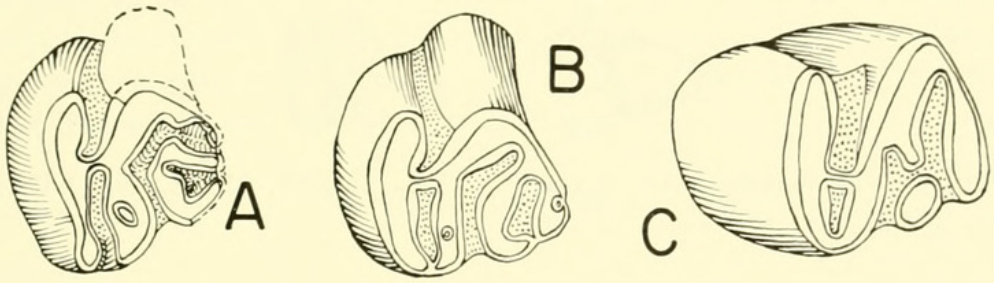

FIG. 10. *Eucastor dividerus*, × 5. A, RP^4, M.C.Z. No. 7648; B, RP^4, M.C.Z. No. 7649; C, RdP^4, M.C.Z. No. 7650.

Family HETEROMYIDAE

DIPRIONOMYS cf. PARVUS Kellogg, 1910

Two isolated and unassociated unworn cheek teeth are perhaps referable to this species: M.C.Z. No. 8535, RP^4, and M.C.Z. No. 8536, RM_2. Since the previously known material is badly worn, they add considerably to our knowledge of this rodent.

The premolar (Fig. 11 A) is clearly that of a heteromyine, in view of the two-cusped protoloph. The buccal cusp is quite small, and distinctly subsidiary to the main cusp. The metaloph forms a crest of nearly uniform height, running from the metacone to the hypostyle, and passing behind the slightly higher hypocone. The hypostyle is at about a right angle with the rest of the metaloph. The valley between the hypostyle and the hypocone curves buccad behind the latter, but would not persist very long with wear.

The molar (Fig. 11 B) is considerd to be M_2 rather than M_1 because of its anteroposterior diameter, which is less than would be expected in M_1 (cf. Wood, 1935a, Table II). Both lophs are strong, and the cusps form only minor enlargements. The protoconid is the only really distinct cusp. There is a prominent valley between the protoconid and protostylid, which would result in the formation of a Y-pattern, a characteristic heteromyine feature (Wood, 1935a, p. 165). The hypolophid is almost a straight crest, the cusps being very indistinct. The least depth of the central valley is between the two stylids, and the valley would thus become closed, buccally, after a moderate amount of wear. Slight further wear would unite the lophs just linguad of the bases of the protoconid and the hypoconid, isolating the buccal part of the valley as a lake. This double union is characteristic of *Diprionomys* (Wood, 1936b, p. 118).

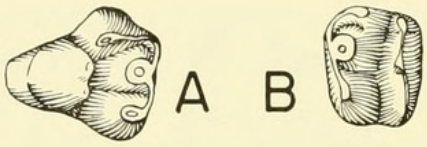

FIG. 11. *Diprionomys* cf. *parvus*, × 10. A, RP^4, M.C.Z. No. 8535; B, RM_2, M.C.Z. No. 8536.

These specimens are the first from the Fish Lake Valley beds that can be referred to *Diprionomys*, Hall's two species (*D. tertius* and *D. quartus*) being perognathines which Wood (1935a, pp. 92-96) placed in a separate genus, *Perognathoides*. The two teeth here described are, however, clearly heteromyines, and seem clearly to be referable to *Diprionomys*. They are the right size to belong only to *D. parvus* among described species, and cannot at the present time be separated from that species, even though the type is appreciably later (Thousand Creek).

The measurements of these specimens are as follows:

	antero-posterior	width anterior crest	width, posterior crest
M.C.Z. No. 8535, RP^4	1.40	0.77	1.43
M.C.Z. No. 8536, RM_2	1.02	1.27	1.23

SUMMARY

A small collection of Pliocene mammals, from the type locality of the Fish Lake Valley local fauna of Nevada, adds appreciably to our knowledge of that fauna. Included are: a talpid, *Domninoides; Hesperolagomys*, a new genus of ochotonid; a new species, *C. esmeraldensis*, of the cricetid *Copemys;* and the heteromyid

Diprionomys. The most abundant material, referable to the rabbit *Hypolagus fontinalis*, and the beaver *Eucastor dividerus*, adds to our knowledge of the dentition of these forms.

These materials permit a discussion of the interrelationships and evolutionary trends among Tertiary North American ochotonids and cricetids. *Hesperolagomys* is an unusually primitive Pliocene ochotonid, apparently representing the survival of a line derived from the primitive stock of the family, perhaps from *Desmatolagus*. The cricetid genus *Copemys* is revised, and three species previously included in *Peromyscus* are referred to it. Although cricetids are abundant in the middle Oligocene, the North American Miocene and Pliocene cricetids are largely limited to intermontane areas, with only two isolated teeth from the late Miocene Niobrara River local fauna of Nebraska and rare specimens from the Thomas Farm local fauna of Florida. They do not appear in numbers in the plains until the late Pliocene. Competition with entoptychine geomyids and with heteromyids may be the factors involved in the reduced numbers of cricetids in the Miocene and early Pliocene.

REFERENCES

BLACK, C. C.

1961a. Fossil mammals from Montana. Pt. I. Additions to the Late Miocene Flint Creek Local Fauna. Ann. Carnegie Mus., **36**: 69-76.

1961b. New rodents from the early Miocene deposits of Sixty-Six Mountain, Wyoming. Breviora, Mus. Comp. Zool., No. **146**: 1-7.

1961c. Rodents and lagomorphs from the Miocene Fort Logan and Deep River formations of Montana. Postilla, Yale Peabody Mus., No. **48**: 1-20.

BOHLIN, B.

1942. The fossil mammals from the Tertiary deposit of Taben-buluk, Western Kansu. Pt. I. Insectivora and Lagomorpha. Palaeont. Sinica, n.s. C, 8 a: 1-113.

BURKE, J. J.

1941. New fossil Leporidae from Mongolia. Amer. Mus. Novitates, No. **1117**: 1-23.

COPE, E. D.

1874. Notes on the Santa Fé marls and some of the contained vertebrate fossils. Proc. Acad. Nat. Sci. Phila., **26**: 147-152.

1875. Report on the geology of that part of northwestern New Mexico examined during the field season of 1874, by E. D. Cope, palaeontologist and geologist. Appendix LL, Ann. Rept. Chief of Engrs., Ann. Rept. Geogr. Expl. & Surv. West of 100th Meridian, Washington: 981-1036.

DAWSON, M. R.
1958. Later Tertiary Leporidae of North America. Univ. Kansas Paleont. Contrib., Vertebrata, **6**: 1-75.

FORSYTH MAJOR, C. I.
1899. On fossil and Recent Lagomorpha. Trans. Linn. Soc. London, (2), Zoology, **7**: 433-520.

GALBREATH, E. C.
1953. A contribution to the Tertiary geology and paleontology of northeastern Colorado. Univ. Kansas, Paleont. Contrib., Vertebrata, **4**: 1-120.

GREEN, M.
1956. The lower Pliocene Ogallala-Wolf Creek vertebrate fauna, South Dakota. Jour. Paleont., **30**: 146-169.

HALL, E. R.
1930a. A new genus of bat from the later Tertiary of Nevada. Univ. Calif. Publ., Bull. Dept. Geol. Sci., **19**: 319-320.
1930b. Rodents and lagomorphs from the Barstow beds of southern California. Univ. Calif. Publ., Bull. Dept. Geol. Sci., **19**: 313-318.
1930c. Rodents and lagomorphs from the later Tertiary of Fish Lake Valley, Nevada. Univ. Calif. Publ., Bull. Dept. Geol. Sci., **19**: 295-312.

HAY, O. P.
1902. Bibliography and catalogue of the fossil Vertebrata of North America. Bull. U.S. Geol. Surv., **179**: 1-868.

HOFFMEISTER, D. F.
1959. New cricetid rodents from the Niobrara River fauna, Nebraska. Jour. Paleont., **33**: 696-699.

HOOPER, E. T.
1957. Dental patterns in mice of the genus *Peromyscus*. Misc. Publ. Mus. Zool., U. Mich., **99**: 1-59.

MACINNES, D. G.
1953. The Miocene and Pleistocene Lagomorpha of East Africa. British Mus. (Nat. Hist.), Fossil Mamm. Africa, **6**: 1-30.

MCKENNA, M. C.
1960. The Geolabidinae. A new subfamily of early Cenozoic erinaceoid insectivores. Univ. Calif. Publ. Geol. Sci., **37**: 131-164.

MATTHEW, W. D.
1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. Mem. Amer. Mus. Nat. Hist., **9**: 291-567.

PATTERSON, B. and P. O. MCGREW
1937. A soricid and two erinaceids from the White River Oligocene. Geol. Ser. Field Mus. Nat. Hist., **6**: 245-272.

REED, K. M.
1960. Insectivores of the middle Miocene Split Rock local fauna, Wyoming. Breviora, Mus. Comp. Zool., No. **116**: 1-11.

STIRTON, R. A.
1935. A review of the Tertiary beavers. Univ. Calif. Publ., Bull. Dept. Geol. Sci., **23**: 391-458.

WHITE, T. E.
1954. Preliminary analysis of the fossil vertebrates of the Canyon Ferry reservoir site. Proc. U.S. Nat. Mus., **103** (3326): 395-438.

WOOD, A. E.
1935a. Evolution and relationships of the heteromyid rodents with new forms from the Tertiary of western North America. Ann. Carnegie Mus., **24**: 73-262.
1935b. Two new genera of cricetid rodents from the Miocene of western United States. Amer. Mus. Novitates, No. **789**: 1-3.
1936a. The cricetid rodents described by Leidy and Cope from the Tertiary of North America. Amer. Mus. Novitates, No. **822**: 1-8.
1936b. Fossil heteromyid rodents in the collections of the University of California. Amer. Jour. Sci., (5) **32**: 112-119.
1936c. Geomyid rodents from the middle Tertiary. Amer. Mus. Novitates, No. **886**: 1-31.
1937. The mammalian fauna of the White River Oligocene. Pt. II. Rodentia. Trans. Amer. Phil. Soc., n.s. **28**: 155-269.
1947. Miocene rodents from Florida. Bull. Mus. Comp. Zool., **99**: 489-494.

WOOD, A. E. and R. W. WILSON
1936. A suggested nomenclature for the cusps of the cheek teeth of rodents. Jour. Paleont., **10**: 388-391.

(Received December 1962)

ADDENDUM

Since this manuscript was completed, three papers, two dealing with Barstovian and Clarendonian, and one with Arikareean, cricetids have appeared. Shotwell (1963, p. 49) refers a lower jaw from the Clarendonian of eastern Oregon to *Peromyscus* cf. *dentalis*. James (1963, pp. 112-129) describes a considerable collection from the Clarendonian of the Cuyama area of California as *Peromyscus russelli*, and refers a single lower jaw from the Barstovian of the same area to *Peromyscus* aff. *dentalis*. Macdonald (1963, pp. 198-201) describes *Eumys blacki* and *E. woodi*, and lists *Scottimus*, sp. indet., from the Arikareean of South Dakota.

Shotwell's specimen is a jaw containing the first lower molar of an animal very similar to the type of *Copemys dentalis* (Fig. 8A). His figure (1963, fig. 52a) suggests an almost complete union of the anterolophid with the protoconid, which is incorrect, as there is a broad but shallow valley in this area, similar to that shown in Figure 8A. The metaconid is close to the anteroconid, also as in *C. dentalis*, to which this specimen clearly should be referred.

James' description of *Peromyscus russelli* indicates that it is very close to its contemporary, *Copemys esmeraldensis*, and that the two are certainly congeneric. The Cuyama form shows a union of the paracone of M^1 with both the anterior and posterior arms of the protocone, a condition more progressive than that seen in *C. esmeraldensis*. This type of union is present on M^{2-3} as well (James, 1963, figs. 47, 52), and this species has thus progressed half way from the *Eumys* condition toward the situation in *Peromyscus*, where the union is exclusively through the anterior arm of the protocone. As in *Copemys*, the metacone of M^1 has shifted its point of attachment from the hypocone to the posteroloph, whereas this shift has not occurred in M^{2-3}. In the lower teeth, the pattern of M_3 is almost identical in the two populations (compare Fig. 9B and James, 1963, fig. 53a). In M_1, the California specimens show the same variation as to the presence or absence of the crest called the ectolophid by Hooper and by James (but *not* that called the ectolophid by Wood and Wilson). The peculiar accessory crests and cusps of the anteroconid region of *C. esmeraldensis* (Fig. 9C) do not seem to be present in the California species.

In spite of the similarity in pattern, there are significant distinctions in size, especially of the first molars. The length and width measurements of M^1 of M.C.Z. No. 7647 exceed those of the mean of *P. russelli* (James, 1963, Table 22) by about six times the standard deviation, and the length of the smaller M_1 of *C. esmeraldensis* exceeds that of *P. russelli* by over five times the standard deviation. The transverse diameter of M_1 of the larger Nevada specimen is larger by nearly 3.5 S.D. The third molar of M.C.Z. No. 7644 is larger than that of any specimen of *P. russelli*, but the difference is not significant. The probability that either measurement of M^1 or of M_1 of *C. esmeraldensis* falls within the limits of variation for the population of *P. russelli* is thus considerably less than .001, and is therefore negligible.

These factors all indicate that *Peromyscus russelli* should be referred to *Copemys*, and that *C. russelli* and *C. esmeraldensis* are closely related but distinct species.

The specimen referred by James to *Peromyscus* aff. *dentalis* is appreciably smaller than are the other specimens of *C. dentalis*, as James indicates (1963, p. 129), with an alveolar length of only 3.6 mm (cf. Table 4, where that of *C. dentalis* is given as 4.35-4.40 mm). It seems probable that this difference is great

enough to place James' specimen outside the limits of *C. dentalis*. It is presumably also referable to *Copemys*.

Peromyscus parvus Sinclair (1905, p. 126) from the middle John Day of Oregon, was included by James as a rather distinctive species of *Peromyscus*, only questionably referable to the modern genus (1963, p. 128). Study of the only known specimen shows that it is clearly a small species of *Leidymys*.

In his paper on Arikareean fossils from South Dakota, Macdonald describes *Eumys blacki* (1963, p. 198, fig. 21), which is clearly congeneric with *Cotimus*, and *E. woodi* (*op. cit.*, p. 199, fig. 22), which is close to *E. eliensis*. He also refers two isolated upper molars to *Scottimus* sp. indet., thus extending the range of this genus into the Arikareean.

ADDITIONAL REFERENCES

JAMES, G. T.

1963. Paleontology and nonmarine stratigraphy of the Cuyama Badlands, California. Part 1. Geology, faunal interpretations and systematic descriptions of Chiroptera, Insectivora and Rodentia. Univ. Calif. Publ. Geol. Sci., **45**: 1-154.

MACDONALD, J. R.

1963. The Miocene faunas from the Wounded Knee area of western South Dakota. Bull. Amer. Mus. Nat. Hist., **125**: 139-238.

SHOTWELL, J. A.

1963. The Juntura Basin: studies in earth history and paleoecology. Trans. Amer. Phil. Soc., n.s. **53**: 1-77.

SINCLAIR, W. J.

1905. New or imperfectly known rodents and ungulates from the John Day series. Univ. Calif. Publ., Bull. Dept. Geol., **4**: 125-143.

Clark, John B. 1964. "Fossil mammals from the lower Pliocene of Fish Lake Valley, Nevada, by John B. Clark, Mary R. Dawson, and Albert E. Wood." *Bulletin of the Museum of Comparative Zoology at Harvard College* 131, 27–63.

View This Item Online: https://www.biodiversitylibrary.org/item/29970
Permalink: https://www.biodiversitylibrary.org/partpdf/32213

Holding Institution
Harvard University, Museum of Comparative Zoology, Ernst Mayr Library

Sponsored by
Harvard University, Museum of Comparative Zoology, Ernst Mayr Library

Copyright & Reuse
Copyright Status: In copyright. Digitized with the permission of the rights holder.
License: http://creativecommons.org/licenses/by-nc-sa/3.0/
Rights: https://biodiversitylibrary.org/permissions

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at https://www.biodiversitylibrary.org.

This file was generated 7 October 2023 at 04:11 UTC