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OREOLAGUS AND OTHER LAGOMORPHA (MAMMALIA) FROM THE MIOCENE OF COLORADO, WYOMING, AND OREGON

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INTRODUCTION

Miocene deposits at Split Rock, Wyoming, have yielded an abundant microfauna that includes reptiles, insectivores (Reed, 1960), rodents (Black and Wood, 1956; Black, 1958), and lagomorphs. Investigations on the lagomorphs revealed that an ochotonid, *Oreolagus,* is the most abundant fossil lagomorph in the Split Rock local fauna. *Oreolagus* was previously known from the type species, *O. nevadensis* of middle or upper Miocene deposits at Virgin Valley, Nevada (Kellogg, 1910, p. 435-436; Dice, 1917, p. 182-183), from *O. nebrascensis* of the lower Miocene Marsland Formation of Nebraska (McGrew, 1941), and from species of *Oreolagus* having tentative taxonomic references from two other localities. These are "*Oreolagus* near O. *nebrascensis*" from University of Kansas Quarry A in Martin Canyon, Colorado (Galbreath, 1953, p. 93; Wilson 1960, p. 49), and "*Oreolagus* (?) n. sp." from Beatty Buttes, Oregon (Wallace, 1946, p. 125-126). *Oreolagus* is the most abundant lago-

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morph in the faunas from Quarry A, Split Rock, and Beatty Buttes. This report is a review of the lagomorphs, including *Oreolagus,* from these three Miocene localities.

All measurements are in millimeters. The following abbreviations are used for names of collections:

A.C., Amherst College
C.M., Carnegie Museum
C.N.H.M., Chicago Natural History Museum
C.U., University of Colorado Museum
K.U., University of Kansas Museum of Natural History
L.A.C.M., Los Angeles County Museum
R.O.M., Royal Ontario Museum
U.N., University of Nebraska State Museum
U.W., University of Wyoming

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MARTIN CANYON QUARRY A FAUNA

Sandy silts in University of Kansas Quarry A in the Pawnee Creek Formation exposed in sec. 27, T. 11 N., R. 53 W., Logan County, Colorado, have yielded an interesting fauna studied by Galbreath (1953) and Wilson (1960). The

deposits are considered upper lower Miocene, near the middle or upper parts of the Nebraskan Marsland, and have been correlated with the European Burdigalian, possibly early Burdigalian (Wilson, 1960, p. 13-19; correlations used throughout this paper follow Wilson). Lagomorphs in the fauna are a leporid and the ochotonid, *Oreolagus*.

Family Leporidae

?Hypolagus sp.

No significant information can be added to that previously given for the leporid from Quarry A (Dawson, 1958, p. 44-45; Wilson, 1960, p. 49), which is known by a few isolated teeth, including at least one deciduous tooth. It seems desirable to continue the above reference until more complete material is known of this species, which is either a primitive *Hypolagus* or an advanced *Archaeolagus*.

Family Ochotonidae

Much more abundant than *?Hypolagus* sp. at Quarry A is *Oreolagus*, which Galbreath (1953, p. 93-95) referred to the Ochotonidae and tentatively identified as *Oreolagus* near O. *nebrascensis*. Galbreath's comparisons of the Quarry A specimens with the type of *Oreolagus nebrascensis*, a lower jaw, showed that the lower cheek teeth were relatively longer anteroposteriorly in Quarry A specimens. Additional specimens studied by Wilson (1960, p. 49) confirmed that these proportions were characteristic of *Oreolagus* from Quarry A, but lack of sufficient comparative material of *Oreolagus nebrascensis* from the Nebraskan Marsland did not permit a more definite taxonomic assignment than had been given by Galbreath. Upper and lower jaws from the Marsland of Nebraska referable to *O. nebrascensis* are now available to facilitate comparative studies, which make it clear that the Quarry A *Oreolagus* represents a species distinct from O. *nebrascensis*.

Oreolagus wilsoni,* n. sp.

Figs. 1-11; Table 1

Type specimen. K.U. 9815, nearly complete right jaw having M_{1-2}.

Referred specimens. (All K.U. numbers) 10303, skull fragment including right maxilla, partial palate and zygoma, P^3—M^1; 12050, partial right maxilla, unworn P^{3-4}; 10112, incomplete left jaw having I, P_4—M_2; 10113, incomplete left jaw having M_{1-2}; 12049, fragmentary left jaw having P_4—M_2; 9287, in-

*For Robert W. Wilson in recognition of his work on fossil lagomorphs.

complete left jaw having I, P_4–M_1; 10114, fragmentary right jaw having M_{1-2}. The remaining numbers refer to isolated teeth, often more than one per number: 9338, 9339, 12054, I; 9356, 10109, 10115, 12052, P^3; 9286, ?M^1; 12035, P^3–M^1; 10108, 10117, 12051, P^4–M^2; 9829, 10111, 10118, 12053, P_3; 9285, 9335-9337, 10110, 10116, P_4–M_2; 9340, 12056, d$\underline{P}$; 12055, d$\overline{P}$; 10107, postcranial fragments.

Specific characters. On P^3 anterior loph crosses about half width of tooth. Crescentic valleys present on P^4 and M^1 of adult; lingual hypostria shorter and wider on P^4 than on M^1. Maxillary tuberosity free of zygoma posterior to P^4, contains shaft of M^2 and posterior part of shaft of M^1 in its free portion. Posterior end of lower incisor below talonid of P_4 or trigonid of M_1. Lower molariform teeth usually longer anteroposteriorly than transversely. Posterior mental foramen below trigonid or middle of M_1; coronoid process developed from lateral edge of anterior surface of ascending ramus.

Description and comparisons. Two upper jaws with cheek teeth provide significant information on this species that supplements that from isolated upper teeth. The maxilla, bony palate, and broken zygoma of K.U. 10303 (Fig. 1) represents an adult individual, and K.U. 12050 is the incomplete maxilla of a young individual having P^3 and P^4 unworn and probably unerupted.

Ochotonid characters on the palate in K.U. 10303 include the presence of a premolar foramen, which is in line with the anterior half of P^3, and an incisive foramen that extends back to a line with the posterior wall of P^3. The palatine is longer than the maxilla on the palate, and the palatine foramen pierces the palatine about in line with the middle of P^4. A lateral view of K.U. 10303 shows that the rounded infraorbital foramen is dorsolateral to the shaft of P^2. The anterior surface of the anterior zygomatic root is in line with P^3. The zygoma is concave laterally and thickened anteroventrally in connection with attachments of the masseter muscle. The maxillary tuberosity, in which the shafts of the cheek teeth are situated, contacts the zygoma back to a line approximately between P^4 and M^1, as seen in occlusal view. A dorsal view of K.U. 10303 shows that the part of the maxillary tuberosity containing the shaft of M^2 and the posterior part of the shaft of M^1 is free of the zygoma. Posterior to its contact with the maxillary tuberosity the zygoma extends outward and slightly dorsally as far as preserved.

Compared to *Oreolagus nebrascensis*, *O. wilsoni* has a dorsoventrally narrower zygoma with a slightly more distinct concavity for muscle attachment. In *O. nebrascensis* the zygoma and maxillary tuberosity are in contact to a point in line with the anterior loph of M^1, as seen in occlusal view. Thus, this

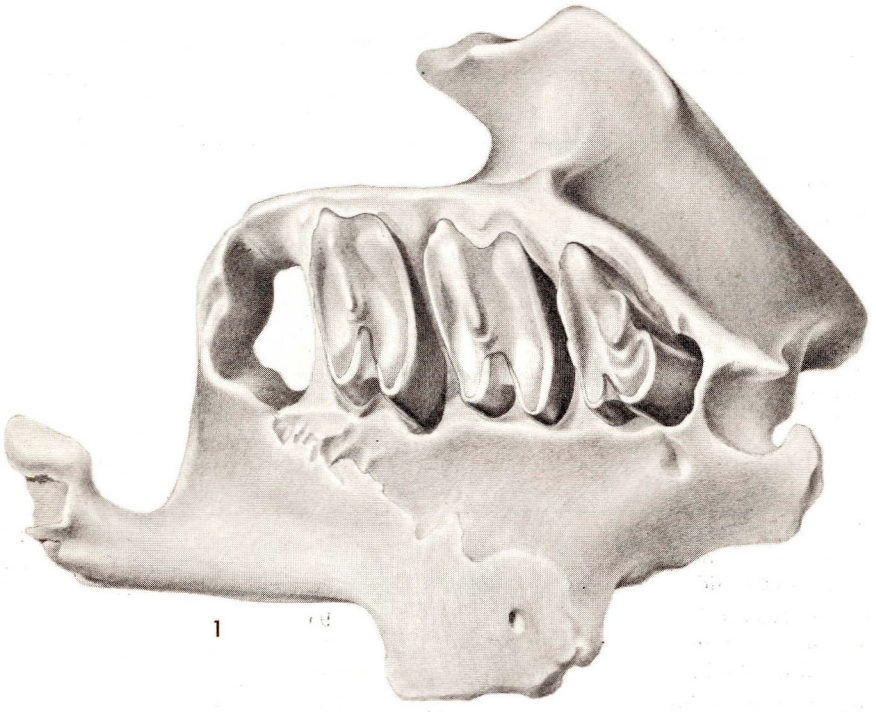


Figure 1. *Oreolagus wilsoni*, skull fragment with right P^3—M^1, K.U. 10303, occlusal view, approx. x8.

contact extends farther posteriorly than in *O. wilsoni*. A still more striking difference between the two species appears in a dorsal view of the tuberosity, for in *O. nebrascensis* the anteriorly curving dorsal parts of the shafts of M^1 and M^2 are, except for the posterior part of M^2, within the bony structure formed by the united zygoma and maxillary tuberosity. The maxillary tuberosity is higher and the maxilla is steeper anterior to the anterior zygomatic root in *O. nebrascensis*, differences from *O. wilsoni* that reflect greater hypsodonty in the former. Recent *Ochotona princeps* resembles *Oreolagus wilsoni* in having the portion of the maxillary tuberosity containing M^2 free of the zygoma, but differs in having a contact of tuberosity and zygoma that continues to a line with the posterior loph of M^1. Another variant in this structure is shown by an African Miocene ochotonid, *Kenyalagomys*, in which zygoma and tuberosity are in contact along the entire length of the latter (MacInnes, 1953, p. 6).

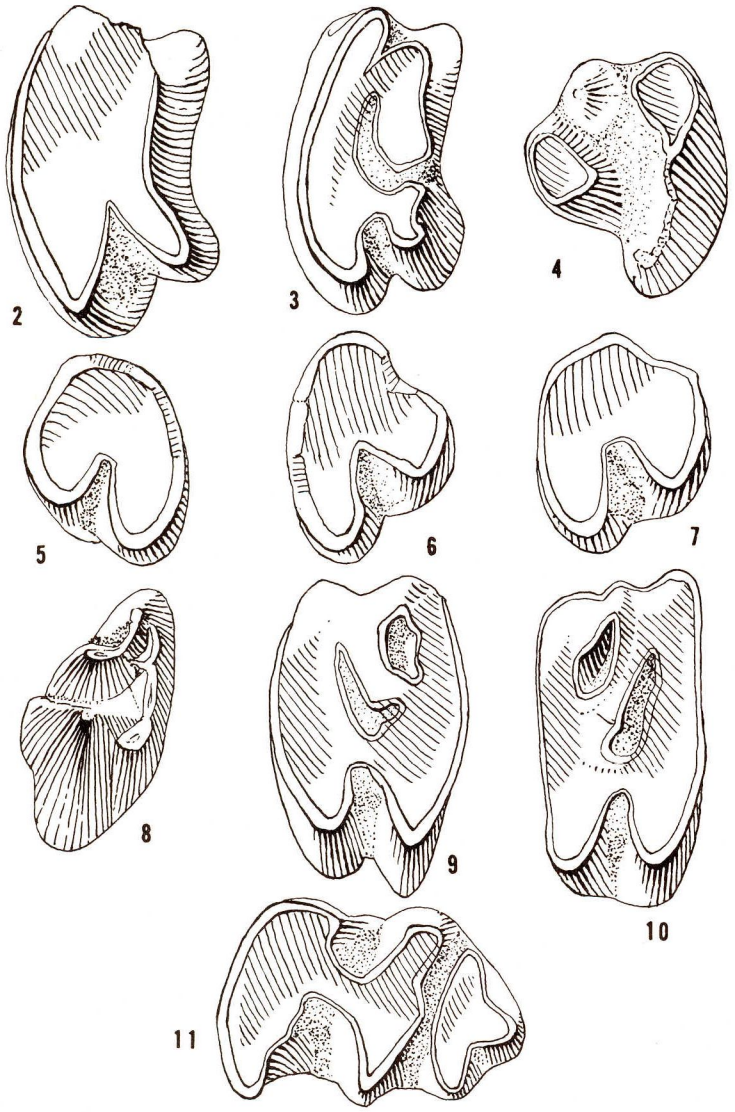
Upper teeth are known except for the posterior incisor and P^2. The anterior incisor has an anterior groove separating a wider lateral portion from a nar-

TABLE 1. Measurements (in millimeters) of *Oreolagus wilsoni*

	K.U. 10303	K.U. 12051
P^3 anteroposterior	1.5	----
transverse	2.3	----
P^4 anteroposterior	1.6	----
transverse	2.9	----
M^1 anteroposterior	1.5	----
transverse	2.9	----
M^2 anteroposterior	----	1.2
transverse	----	2.2
alveolar length, P^3–M^3	7.3	----

	K.U. 9815 Type	K.U. 10112	K.U. 12049	K.U. 9829	K.U. 10111
P_3 anteroposterior	----	----	----	1.1	1.1
width trigonid	----	----	----	1.0	0.9
width talonid	----	----	----	1.3	1.4
P_4 anteroposterior	----	1.95	1.8	----	----
width trigonid	----	1.9	1.7	----	----
width talonid	----	1.75	----	----	----
M_1 anteroposterior	2.0	2.0	1.85	----	----
width trigonid	1.9	1.9	1.85	----	----
width talonid	1.8	1.8	1.55	----	----
M_2 anteroposterior	2.0	1.95	1.9	----	----
width trigonid	1.85	1.8	1.7	----	----
width talonid	1.7	1.55	1.5	----	----
length P_4–M_2	----	6.2	5.6	----	----
inner depth of jaw at M_1	6.4	6.7	6.0	----	----

rower, more anteriorly protruding, medial portion. This structure of the incisor was one of the characters that led Galbreath (1953, p. 93-95, fig. 23D) to refer *Oreolagus* to the Ochotonidae. An ochotonid character is shown likewise by the structure of P^3, which has a short anterior loph crossing about half the width of the tooth, a persistent crescent connected to the anteroexternal wall, and a short wide hypostria directed posterior to the crescent. On unworn P^3 in K.U. 12050 the cuspate middle lobe projects from the cement cover, and the lingual side of the tooth is formed by two cusps. A short distance up the shaft in the alveolus it can be seen that the more anterior of these cusps elongates and would form the anterior loph of a worn tooth. On P^4 in the adult the posterior loph extends farther buccad than the anterior loph. A J-



Figures 2-11. *Oreolagus wilsoni*, occlusal views of teeth. 2. Left M^2, K.U. 10117, approx. x19. 3. Left M^2, K.U. 10108, approx. x19½. 4. Left P_3, K.U. 12053, approx. x22. 5. Left P_3, K.U. 10111, approx. x19½. 6. Right P_3, K.U. 10111, approx. x22½. 7. Right P_3, K.U. 12053, approx. x19. 8. Left dP^2, K.U. 12056, approx. x17½. 9. Left dP^3, K.U. 12056, approx. x20. 10. Right dP^4, K.U. 9340, approx. x18. 11. Right dP_3, K.U. 12055, approx. x20.

shaped crescentic valley, having a longer anterior arm, occurs in the center of the tooth, and a short, wide hypostria is directed slightly anterior to the valley. In the unworn condition shown by K.U. 12050 P^4 is longer anteroposteriorly relative to the transverse width and has a shorter, wider hypostria than in the adult. The enamel of the anterior wall and that of the U-shaped middle lobe protrude from the cement cover in the unworn tooth. The anterior arm of the middle lobe contacts the buccal wall about one-third of the way back from the anterior wall, and the posterior arm of the lobe extends to the posterobuccal corner of the tooth. The crescentic valley in an adult tooth would form from the depression medial to the middle lobe, and the outer depression, which is within the arms of the U, is worn away in an adult. The adult M^1 is relatively shorter anteroposteriorly than P^4, has an anterior and a posterior loph of nearly equal width, and a lingual hypostria that is narrower, deeper, and extends closer to the valley than on P^4. The valley occurs in some form in all known speciments of M^1, ranging from J-shaped in less worn to I-shaped in more worn specimens. Unworn M^1 in K.U. 12035 resembles unworn P^4 in having a prominent anterior wall and middle lobe, but is less well developed posterobuccally and has a J-shaped middle lobe, the longer arm of which contacts the buccal wall near the center of the tooth and the shorter connects by a low ridge to the posterior wall near its center. The last upper cheek tooth, M^2 (Fig. 2), is one of the most distinctive teeth of *Oreolagus,* being composed of a normal appearing anterior loph and an unusual posterior loph that swings posteriorly behind the short lingual hypostria. A relatively little worn specimen of M^2, K.U. 10108 (Fig. 3), has a J-shaped crescentic valley that is connected by the shorter posterior arm to the posterior wall of the tooth. The cement filling the valley of K.U. 10108 can be traced 0.9 mm. up the posterior wall, indicating that some trace of the valley would persist about that far before the pattern without a crescent would appear. The upper cheek teeth in the adult condition have cement in the lingual hypostria, including that on M^2, and the crescentic valley. Transverse enamel ridges that appear to be effective in mastication are formed on P^3 by the anterior wall of the anterior loph and of the middle lobe, on P^4 and M^1 by the anterior wall of the tooth and the posterior wall of the hypostria, with a continuation formed by the posterior wall of the crescentic valley, and on M^2 by the anterior and posterior walls. Although the upper cheek teeth of *O. wilsoni* are similar in general occlusal pattern to those of *O. nebrascensis* from the Marsland Formation of Nebraska, the Nebraska species has a transversely longer, anteroposteriorly narrower hypostria on P^4 and M^1. On M^1 of a specimen of *O. nebrascensis,* U.N. 17726, a small valley occurs buccal to the hypostria, which crosses about one-half the width of the tooth. The valley seems to be

lacking entirely in a second, but somewhat less well preserved specimen of *O. nebrascensis,* U.N. 17723, which has a long hypostria crossing more than half the tooth width.

The most complete lower jaw of *Oreolagus wilsoni* is the type specimen, K.U. 9815, which was described and figured by Galbreath (1953, p. 93-94, fig. 23G) with further details being furnished by Wilson (1960, p. 49). Additional comparisons of lower jaws of *O. wilsoni* with those of *O. nebrascensis* show that the horizontal ramus, though similar in general character, tends to be shallower in depth than in specimens of *O. nebrascensis* from the Marsland Formation. The posterior mental foramen tends to be farther forward in *O. wilsoni,* occurring below the trigonid or middle of M_1, as opposed to a position in *O. nebrascensis* below the middle or talonid of M_1 or in a line between M_1 and M_2. The shaft of the lower incisor terminates below the talonid of P_4 or trigonid of M_1 in *O. wilsoni,* which is slightly farther forward than in *O. nebrascensis,* in which the incisor extends to a line below the middle or talonid of M_1. As in other species of *Oreolagus,* the masseteric fossa in *O. wilsoni* is shallow and its anterior border is a very low ridge that extends forward to a line below the posterior wall of M_2. The coronoid process, known from K.U. 9815, 10112, and 10113, arises from the lateral side of the ascending ramus and bends inward over the concave anterior surface of the ramus. *Oreolagus wilsoni* is the only species of *Oreolagus* for which the ascending ramus is now known, so it is uncertain whether this structure of the coronoid process will prove to be characteristic for the genus as a whole. A coronoid process of this sort resembles that in leporids more closely than that in Recent *Ochotona.* A lateral coronoid process of this general structure is not limited to leporids, however, but occurs also in fossil ochotonids, including *Sinolagomys* (Bohlin, 1942a, p. 81-82), *Kenyalagomys* (MacInnes, 1953, p. 11), and *Paludotona* (Dawson, 1959, p. 162-163), and in relatively primitive lagomorphs generally; it is not a diagnostic character either of ochotonids or of leporids.

The lower incisor, which was described and figured by Galbreath (1953, p. 93; fig. 23C), is triangular in cross section. The first lower cheek tooth, P_3, is composed of narrower trigonid and wider talonid, separated buccally by a persistent fold. Outside of this standard pattern, P_3 is variable (Figs. 4-7). In some specimens there are no extra grooves, but in others there may be a lingual groove or an anterolingual groove. An unworn P_3, included in K.U. 12053, has an anterior and a lingual groove, of which the former seems to be deeper and persists farther down the shaft. The two grooves do not occur together in the more worn specimens. There is some tendency in P_3 of *O. wilsoni* to have a shorter, less flattened lingual wall than in *O. nebrascensis.*

In occlusal pattern the lower molariform teeth, P_4, M_1, and M_2, are general-

ly similar, consisting of two columns, a trigonid and a talonid, which is slightly narrower transversely. Cement unites the columns of each tooth. Prominent transverse enamel ridges are formed by the posterior wall of each column. The anterior wall of M_1 and M_2 has an anterior protrusion that is lacking on P_4. The position of the essentially straight shaft of P_4 lateral to the shaft of the incisor in the horizontal ramus is marked by a prominence on the lateral surface of the jaw. The shaft of M_1 bends posteriorly slightly, and that of M_2 exhibits a more distinct backward curve. These lower molariform teeth are characteristically longer anteroposteriorly than transversely, with few teeth deviating from these proportions. In *O. nebrascensis* the molariform lower teeth are less constant in proportions, and within the species some teeth have approximately equal anteroposterior and transverse dimensions, others have longer teeth, and still others have wider teeth.

Lagomorph deciduous teeth from Quarry A that seem referable to *Oreolagus* rather than to the larger leporid include dP^{2-4} and dP_3. Of these, dP^2 (Fig. 8), dP^3 (Fig. 9), and dP_3 (Fig. 11) are similar in general to the corresponding deciduous teeth of *Oreolagus* from Split Rock (see below). A well worn deciduous tooth, K.U. 9340 (Fig. 10), seems on the basis of its narrower posterior loph to be dP^4. If this assignment is correct, dP^4 in *O. wilsoni* has a much shorter hypostria, not reaching as far buccad as the isolated valley, than in that tooth in *Oreolagus* from Split Rock.

SPLIT ROCK LOCAL FAUNA

Outcrops of the upper porous sandstone sequence in the Split Rock Formation (Love, 1961, p. 14-17, 19) exposed in NW¼ sec. 36, T.29 N., R.90 W., Fremont County, Wyoming, have yielded the fossil reptiles and mammals that compose the Split Rock local fauna. This fauna and the Sheep Creek fauna of Nebraska, which agree in occurrence of the mylagaulid, *Mesogaulus novellus,* seem to be essentially equivalent in age (Black and Wood, 1956, p. 684), and at present the Split Rock local fauna is considered to be early Hemingfordian and thus younger than the faunas from Quarry A and the Nebraskan Marsland.

The Split Rock local fauna resembles the Quarry A fauna in having the ochotonid, *Oreolagus,* present in greater abundance than the leporid, *?Hypolagus.* A very conservative estimate places the number of isolated upper and lower cheek teeth of *Oreolagus* from Split Rock used in this study in the vicinity of 750 to 800 (from collections of Amherst College, Carnegie Museum, Chicago Natural History Museum, Royal Ontario Museum, University of Colorado, and University of Wyoming). *Oreolagus* is one of the most abundant

small mammals from Split Rock, but it is known mostly from isolated teeth; the occurrence of only three known jaws of this ochotonid, one horizontal ramus having P_4–M_2 and two jaw fragments each having one tooth, is an unfortunate contrast to the abundance of teeth. *?Hypolagus,* relatively rare, is known from about 40 cheek teeth and an edentulous palatal portion of a skull. Deciduous teeth that seem referable to *Oreolagus* and *?Hypolagus* have been identified in the collection. Here the relative numbers of specimens present a different picture, about 26 deciduous teeth representing *Oreolagus* and about 19, *?Hypolagus.* The environment sampled at Split Rock seems to have been one in which ochotonids and baby leporids abounded. In addition to *Oreolagus* and *?Hypolagus,* two less well represented lagomorphs, one a leporid and the other an ochotonid, occur in the Split Rock local fauna.

Family Leporidae

?Hypolagus sp.

Figs. 12-14; Table 2

Specimens. A.C. 6400, palatal portion of skull without teeth. Permanent teeth (sometimes more than one per number) : A.C. 6401, 6407, 6413, 6416, 6420; C.M. 13563, 14754, 14759, 14761; C.N.H.M. 2216, 2221; R.O.M. 3918; U.W. 1954, 1955. Deciduous teeth: A.C. 6408, 6419, 6421, 6425; C.M. 13564, 13574, 14762; C.N.H.M. PM 2218, PM 2222; C.U. 21585; R.O.M. 3917.

Description. These leporid specimens represent a species near *?Hypolagus* sp. from Quarry A and *Archaeolagus primigenius,* an upper Rosebud species, in size. The teeth are hypsodont, lacking any trace of roots. A short anterior fold occurs on the anterior surface of P^2, buccal to which a shallow depression is present in C.M. 13563 and U.W. 1955. Two other slightly smaller specimens of P^2, C.M. 13565 and C.N.H.M. PM 2214, have a shorter anterior fold and no trace of the depression, but whether these are referable here or to the smaller leporid discussed below is uncertain. On P^3 a lingual hypostria crosses about half the width of the tooth. In A.C. 6401 the walls of the hypostria on P^3 are wavy but in R.O.M. 3918 are straight. More posterior molariform teeth, P^4 and M^{1-2}, have a hypostria that is relatively a little longer than on P^3, and some variation in its walls, from slightly wavy to essentially straight, is exhibited. On P_3 anteroexternal and posteroexternal folds, characteristics of archaeolagines, occur. The anteroexternal fold is cement-filled and faces mostly externally. The tooth is less elongate anteroposteriorly than in *Hypolagus parviplicatus* and has a shape more similar to that in *H.*

TABLE 2. Measurements (in millimeters) of ?*Hypolagus* sp.

	U.W. 1955	C.M. 13563	A.C. 6401	C.N.H.M. PM 2221*
P^2 anteroposterior	1.3	1.25	----	----
transverse	ca.2.8	2.85	----	----
P^3 anteroposterior	----	----	2.2	----
transverse	----	----	4.4	----
upper molariform tooth				
anteroposterior	----	----	----	2.1
transverse	----	----	----	3.4

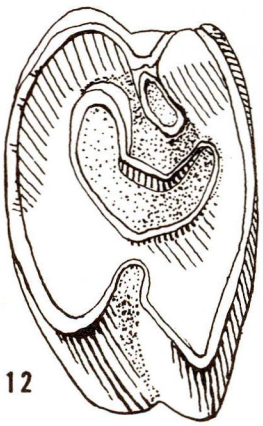
	A.C. 6407*	C.N.H.M. PM 2221*	U.W. 1954
P_3 anteroposterior	2.45	----	----
width trigonid	2.1	----	----
width talonid	ca.2.4	----	----
lower molariform tooth			
anteroposterior	2.8	2.7	2.65
width trigonid	3.0	ca.2.8	2.85
width talonid	----	2.4	----

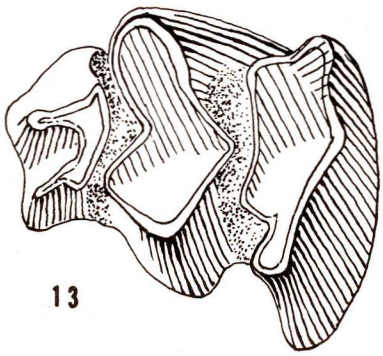
*Isolated teeth, not associated.

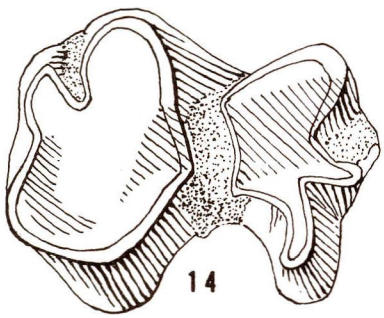
fontinalis. On lower molariform teeth the trigonid is a little wider than the corresponding talonid, and the two columns are joined lingually by the bridge that is found characteristically in advanced leporids.

Both upper and lower deciduous teeth probably referable to this leporid are known. Teeth that represent either dP^3 or dP^4 (Fig. 12) have two small buccal and a large lingual root. A short lingual hypostria directed toward the posterior half of the U-shaped valley on these upper deciduous teeth seems to persist even after considerable wear. The central lobe in a relatively unworn stage on these teeth is oriented mostly anteroposteriorly. Little worn dP_3 (Fig. 13) is formed of three transverse lophs plus a small posterolophid. With wear the posterolophid disappears, and the anterior loph joins the middle loph by a broad dentine connection at approximately the same stage of wear at which a narrow central bridge unites the middle and posterior lophs. A posterolophid occurs on relatively little worn dP_4 (Fig. 14) but becomes worn away, and a lingual bridge appears following wear to join trigonid and talonid of this tooth.

Relationships. The leporid represented by these specimens cannot be referred to any previously described species. The shape of P_3 and stage of development of the anteroexternal fold on that tooth suggest reference to







Figures 12-14. ?*Hypolagus* sp. from Split Rock local fauna, occlusal views of deciduous teeth, C.M. 13564. 12. Left dP^3 or dP^4, approx. x21. 13. Left dP_3, approx. x17. 14. Left dP_4, approx. x18.

Hypolagus, but occurrence of a straight walled or only slightly wavy walled hypostria on upper cheek teeth indicates that if *Hypolagus* is represented, the species is a relatively primitive one. More complete leporid specimens than these from Split Rock are known from the somewhat older Marsland Formation, and it seems desirable to make only a tentative taxonomic reference for this Split Rock leporid until the better materials are studied. The designation "?*Hypolagus* sp." is meant to suggest a possible affinity for this leporid, which, like the leporid from Quarry A, possesses characters transitional between *Archaeolagus* and *Hypolagus.*

Leporidae sp.

A leporid different from ?*Hypolagus* sp. is represented by at least one upper molariform tooth, C.N.H.M. PM 2215. The tooth is smaller (antero-posterior, 1.7 mm.; transverse, 2.8 mm.) than upper molariform teeth of ?*Hypolagus* sp. but larger than those of *Oreolagus*. The tooth contrasts further with the curved upper teeth of the latter in having relatively straight buccal and lingual sides of the shaft, a character suggesting affinities with the leporids. On the occlusal surface a remnant of an isolated valley occurs buccal to a straight walled hypostria that crosses a little less than half the tooth and is directed toward the posterior border of the valley. Another indication of leporid affinity is the presence of slightly thicker enamel on the anterior than on the posterior wall of the hypostria. Another molariform tooth, C.M. 14755, may be referable here, as suggested by similar size, although no isolated valley is present buccal to the hypostria. As mentioned above, two specimens of P^2 that are slightly smaller and have a shorter anterior fold than those referred definitely to ?*Hypolagus* sp. might prove referable to this smaller leporid.

This leporid is more primitive than ?*Hypolagus* sp. in occlusal pattern, and, although very inadequately known, seems to add a shred of evidence that a primitive leporid persisted along with a relatively advanced species at Split Rock. This is not too surprising in view of previous evidence from the late Miocene leporid, *Panolax*, and from lower Pliocene leporids from Avawatz, California (Dawson, 1958, p. 59-60), and from Wolf Creek, South Dakota ("?*Alilepus* sp.", Green, 1956, p. 154), that leporids having relatively primitive dental characters persisted along with the more advanced *Hypolagus*.

Family Ochotonidae

The two species of ochotonid in the Split Rock fauna are very different in abundance, the smaller *Oreolagus* being represented by hundreds of teeth and the larger, more primitive ?*Desmatolagus*, by eleven. The latter is different from any other described Miocene lagomorph from North America, and is hereby named as a new species. It is with hesitation that this is done on such an inadequate record of isolated teeth, but with hope that so doing will call attention to the distinction of this lagomorph from better known North American species.

?*Desmatolagus schizopetrus*,* n. sp.

Figs. 15-18; Table 3

Type specimen. A.C. 6428, left P^3.

Referred specimens. C.M. 14758, broken ?P^4; A.C. 6427, C.M. 13567,

*From Greek, σχιζω, to tear; and πετρα, stone; in reference to the type locality.

14756, C.N.H.M. PM 2220, PM 2226,upper molars; A.C. 6426, C.M. 13566, 14757, C.N.H.M. PM 2225, lower molariform teeth.

Specific characters. Cheek teeth hypsodont but rooted; concave buccal and convex lingual walls indicate unilateral hypsodonty of upper cheek teeth. On P^3 anterior loph crosses about two-thirds width of tooth, crescentic valley connects to anteroexternal wall, lingual hypostria shallow. Upper molars have distinct crescentic valley and hypostria crossing more than one-third occlusal width in early wear; following wear, pattern reduced to remnant of valley and lingual notch. Lower molariform teeth composed of trigonid having relatively straight posterior wall and narrower talonid having anteriorly directed protrusion and curved posterior wall. Smaller than *Desmatolagus robustus* and *D. gazini,* larger than *D. gobiensis.*

Description and comparisons. Compared to other lagomorphs in the Split Rock local fauna, this ochotonid is closer in size to ?*Hypolagus* sp. than to *Oreolagus.* The relatively primitive nature of the dentition is shown by presence of distinct roots on upper and lower cheek teeth, which although hypsodont are less so than those of the other lagomorphs in the fauna. The one known specimen of P^3, A.C. 6428 (Fig. 15), though well worn retains a crescentic valley connected to the anteroexternal wall, and has a wide shallow hypostria. The anterior loph, crossing about two-thirds of the occlusal width, is longer than in *Desmatolagus gazini.* The anterior loph exhibits a groove near the lingual side somewhat similar in position to a deeper groove in *D. gobiensis.* One tooth having a transversely thick shaft, C.M. 14758, may represent P^4. The broken occlusal surface preserves part of a crescentic valley and a wide shallow hypostria. Upper molariform teeth, which have one large lingual and two smaller buccal roots, cannot be classified definitely as M^1 or M^2 on the basis of known specimens. In the early stage of wear shown by A.C. 6427 (Fig. 16), a lingual hypostria crosses more than one-third but less than one-half the occlusal surface. The hypostria is directed toward the anterior wall of a well developed crescentic valley that is connected to the posteroexternal wall. The central lobe, which is bordered by the valley, is transversely elongated. Wear leads to reduction of the hypostria to an isolated lake and a lingual groove and to loss of the external connection of the crescentic valley (Fig. 17). Following still greater wear most traces of pattern are removed except for a lingual notch and a small remnant of the valley. *Desmatolagus vetustus* and *D. gazini* differ from ?*D. schizopetrus* in retaining buccal connections of the crescentic valley after the more linguad parts of the valley are worn away. A relatively primitive North American leporid, *Megalagus,* retained rooted upper molars in the Miocene (Black, 1961, p. 18, fig. 6B), but is differentiated from ?*D. schizopetrus* by a number of leporid

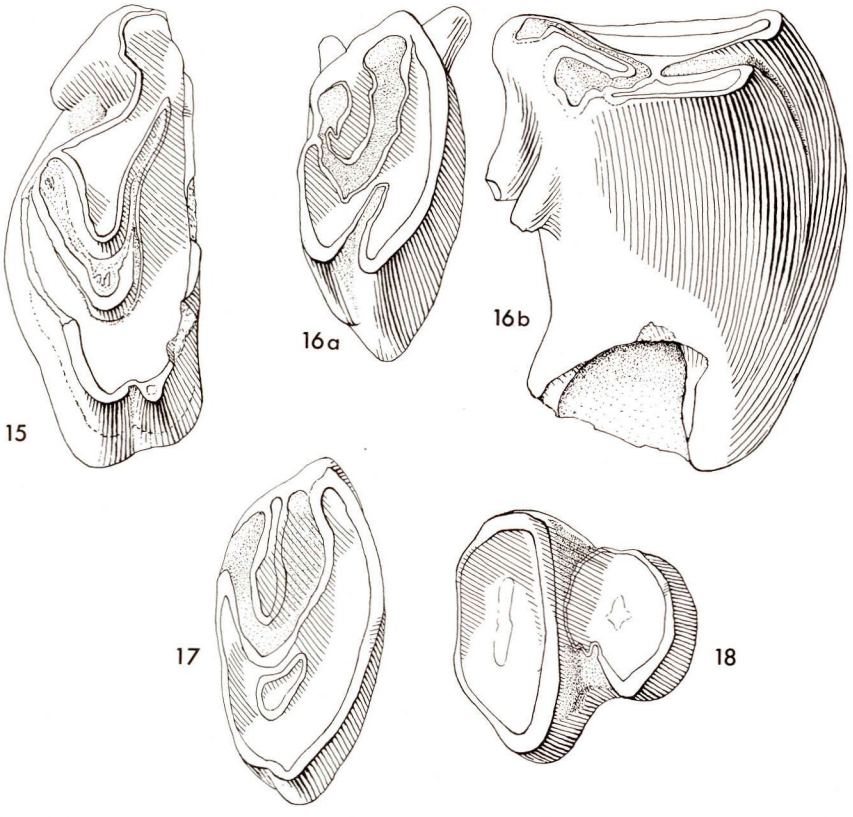
characters in the molars, including presence of a hypostria directed posterior to the crescentic valley, less emphasis on transverse development of crescentic valley and central lobe, and better development of the buccal wall of the molars, which lack the posteroexternal reduction shown by ?*D. schizopetrus.*

Of lower cheek teeth, only molariform teeth are known (Fig. 18). In the lower molariform teeth the trigonid is wider transversely than the corresponding talonid and has a nearly straight posterior wall of thick enamel. The talonid is rounded lingually, slightly tapered buccally, and has an anteriorly directed protrusion of dentine. Trigonid and talonid are separate at the occlusal surface, lacking the lingual bridge between the columns found in Miocene species of *Megalagus* (Dawson, 1958, p. 17) and other later Tertiary leporids. In general structure the molariform teeth resemble those in *D. robustus* and *D. gobiensis,* although the anterior protrusion of the talonid is better developed in ?*D. schizopetrus.* This character is somewhat reminiscent of a still more marked protrusion of the talonid that characterizes *Hesperolagomys,* an early Pliocene ochotonid having rooted cheek teeth (Clark, *et. al.,* 1964, p. 33-39).

Relationships. Within the order Lagomorpha most Oligocene and later genera can be assigned without much difficulty either to the Leporidae or to the Ochotonidae. This has not been the case with *Desmatolagus* and a few other late Eocene and Oligocene genera, such as *Shamolagus* and *Gobiolagus.* A number of generally primitive lagomorph characters are exhibited by the lagomorphs in question, which, no matter what their formal taxonomic assignment, seem to be near the stock that was ancestral to both families. Thorough studies on *Desmatolagus* led Burke (1941) to consider this genus a leporid and Bohlin (1942a), an ochotonid. Illustrative of the morphologically confusing features that complicate classification of *Desmatolagus* is the fact that the type species, *D. gobiensis,* has on its palate the typically ochotonid premolar foramen, whereas that foramen is absent in the contemporary, dentally similar species, *D. robustus,* as well as in the older *D. vetustus.* Future work may show that the species assigned by Burke and Bohlin to *Desmatolagus* should be referred to more than one genus, but for the present and until primitive lagomorphs are more completely understood,* *Desmotolagus* will be used to encompass these species. Bohlin's (1942a) evaluation of *Desmatolagus* as an ochotonid is likewise followed.

Reports of *Desmatolagus* in the North American Oligocene include *D. dicei* (Burke, 1936, p. 149), the affinities of which, whether ochotonid or

*Gureev's (1960) report, although a step toward classification of primitive lagomorphs, does not seem to consider adequately stage of wear, characters of primitive lagomorphs in general, and evidence other than dental. I do not think that his classification is a clear expression of relationships.



Figures 15-18. ?*Desmatolagus schizopetrus*. 15. Left P^3, A.C. 6428, type specimen, occlusal view, approx. x10. 16. Right M^1 or M^2, A.C. 6427, approx. x10: a. occlusal view; b. posterior view. 17. Right M^1 or M^2, C.N.H.M. PM 2226, occlusal view, approx. x11½. 18. Left lower molariform tooth, C.N.H.M. PM 2225, occlusal view, approx. x11.

primitive leporid, are not clear, some inadequately known specimens from Canada (Russell, 1954, p. 97-98) and California (Wilson, 1949, p. 56) that contribute little to phylogenetic understanding, and *D. gazini* of the Nebraskan middle Oligocene (Burke, 1936, p. 150). The last, known by a maxilla having P^3—M^2, has rooted cheek teeth showing general similarity in pattern to those of *D. vetustus, D. gobiensis,* and *D. robustus.* A premolar foramen is absent, as in *D. vetustus* and *D. robustus.* Although comparisons based on the one maxilla of *D. gazini* and the isolated teeth of ?*D. schizopetrus* from Split Rock are limited, there seems to be nothing to bar the former from a position generally ancestral to the latter. Questionable reference of the species

TABLE 3. Measurements (in millimeters) of *?Desmatolagus schizopetrus.*

	P^3 Type A.C. 6428	upper molar A.C. 6427	upper molar C.N.H.M. PM 2226	lower molariform tooth C.N.H.M. PM 2225
anteroposterior	2.1	1.7	1.8	2.4
transverse	3.9	3.3	3.9	----
width trigonid	----	----	----	2.8
width talonid	----	----	----	1.9

from Split Rock to *Desmatolagus* is due to differences from other species of the genus, including longer retention of lingual parts of the crescentic valley on the upper molars and a more distinct anterior protrusion of the talonid on lower molariform teeth. More complete specimens are probably necessary to establish generic reference firmly. For the present, reference to *?Desmatolagus* is meant to indicate that this Split Rock species has affinity with and may have descended from *Desmatolagus.* Relatively primitive rooted cheek teeth and anterior protrusion of the talonid toward the trigonid are characters in common between *?Desmatolagus schizopetrus* and *Hesperolagomys,* a possible descendant of *?D. schizopetrus.* Whether the primitive ochotonid characters of *Titanomys* and *Amphilagus* indicate special affinity between these European ochotonids and *?D. schizopetrus* is uncertain on the basis of known evidence, especially because P_3, a tooth that is often useful in phylogenetic interpretations, is not known for *?D. schizopetrus.* One possible clue in this regard comes from *Hesperolagomys,* in which the structure of P_3 is distinctly different from that in *Titanomys* and *Amphilagus* (Clark, *et. al.,* 1964, p. 37). Carrying this one step farther——very tentatively, if *Hesperolagomys* and *?D. schizopetrus* are allied, the evidence from P_3 of the former suggests that these North American forms are not closely related to the European *Titanomys* and *Amphilagus,* though primitive ochotonid characters are present in all.

Oreolagus nebrascensis

Figs. 19-29; Table 4

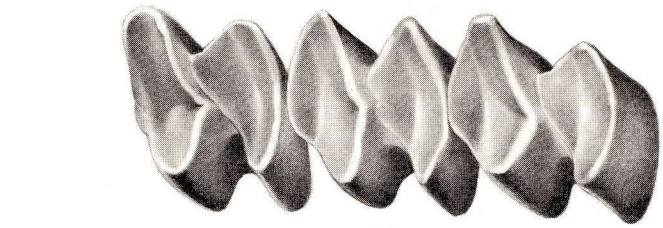
Specimens. U.W. 1949, horizontal ramus of left jaw having P_4—M_2; U.W. 1950, A.C. 6402, jaw fragments having one tooth. Permanent teeth (often more than one per number): A.C. 6403, 6405, 6409, 6412, 6415, 6417, 6422-

6424; C.M. 13555-13560, 13568-13572, 14704, 14763-14766, 14768; C.N.H.M. PM 2217, PM 2224; C.U. 21582; R.O.M. 3916; U.W. 1951-1953. Deciduous teeth: A.C. 6404, 6406, 6410, 6411, 6418; C.M. 13561, 13562, 13573, 14760; C.N.H.M. PM 2219, PM 2223; C.U. 21580, 21581, 21583, 21584, 21587, 21588.

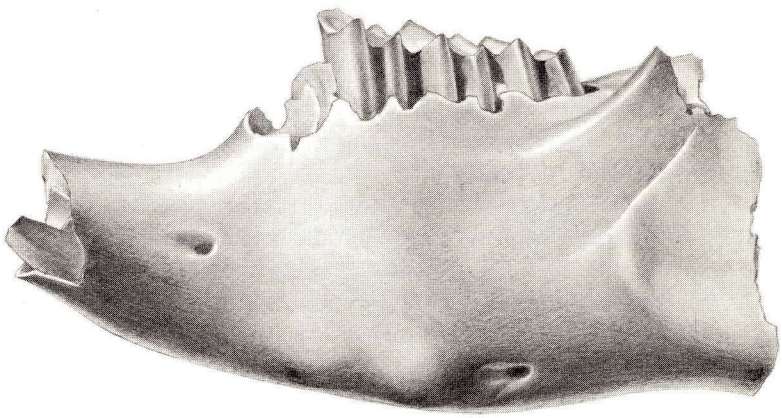
When *Oreolagus nebrascensis* from the Marsland Formation in Dawes County, Nebraska, was named and described (McGrew, 1941), the type and only known specimen was a lower jaw having P_3–M_2, C.N.H.M. P26280. Additional specimens of this species from the Nebraskan Marsland, including upper and lower jaws, are now known. Although it is not the purpose of this paper to describe further the Marsland specimens, they have been used in estimating individual variation within *O. nebrascensis* and in comparing with the known jaws and isolated teeth of *Oreolagus* from the Split Rock local fauna.

The only lower jaw from Split Rock that is more than a fragment, U.W. 1949 (Fig. 19), fits in jaw morphology and general pattern of P_4–M_2 within the range of Marsland specimens of *O. nebrascensis*. In U.W. 1949 the posterior mental foramen is in a line below the talonid of M_1 compared to positions in Marsland specimens varying from below the middle of M_1 to a line between M_1 and M_2. The posterior end of the incisor in U.W. 1949 is below the talonid of M_1, again finding its counterpart in Marsland specimens, among which the incisor terminates below the middle or talonid of M_1. In Marsland specimens of *O. nebrascensis*, P_3 has variably developed grooves on the trigonid and lingual wall in addition to the characteristic buccal fold between trigonid and talonid. The type specimen of *O. nebrascensis* has on P_3 very shallow anterior and lingual grooves, little more than depressions; in referred Marsland specimens of *O. nebrascensis*, U.N. 17719, 17730, and 17733, the lingual wall is essentially flat, and the anterior groove is indistinct in 17730 but relatively well developed in the other two specimens. The shape of P_3 in specimens from Split Rock resembles that in Marsland specimens but more variation in anterior and lingual walls is present. Specimens of P_3 (Figs. 21-24) run the gamut from lacking any grooves on these walls, to having only a lingual groove or an anterior groove, and finally to having both lingual and anterior grooves. Generally comparable variation in P_3 is found among specimens of *O. wilsoni* from Quarry A, and occurrence of some variants among Split Rock specimens not known among the less numerous specimens from the Marsland does not seem to indicate a taxonomically significant difference. In total the morphology of lower jaw and dentition does not preclude reference of specimens of *Oreolagus* from Split Rock to *O. nebrascensis*.

The main difference between known upper cheek teeth from Split Rock,



19a



19b

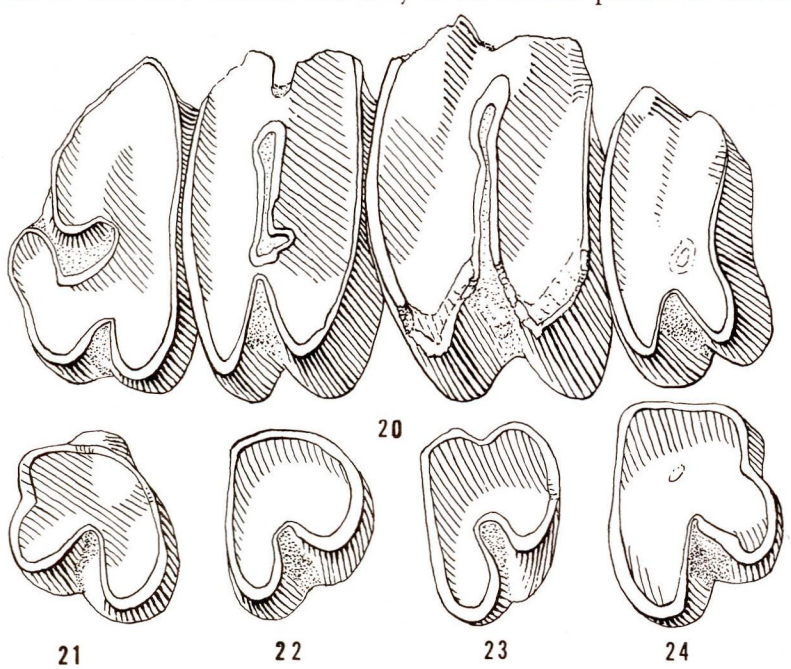
Figure 19. *Oreolagus nebrascensis* from Split Rock local fauna, left lower jaw with P_4–M_2, U.W. 1949: a. occlusal view of teeth, approx. x10; b. lateral view, approx. x5.

which include P^3–M^2 (Fig. 20), and those from the Marsland occurs on M^1. As mentioned in the above description of *O. wilsoni,* the two known Marsland upper jaws having M^1 differ from one another in the occlusal pattern of that tooth; M^1 in U.N. 17726 has a valley buccal to the hypostria but U.N. 17723 has a long hypostria and no trace of the valley. The former variant does not occur in teeth from Split Rock that are definitely referable to M^1, which have only the long hypostria crossing about three-fourths of the width of the tooth.*

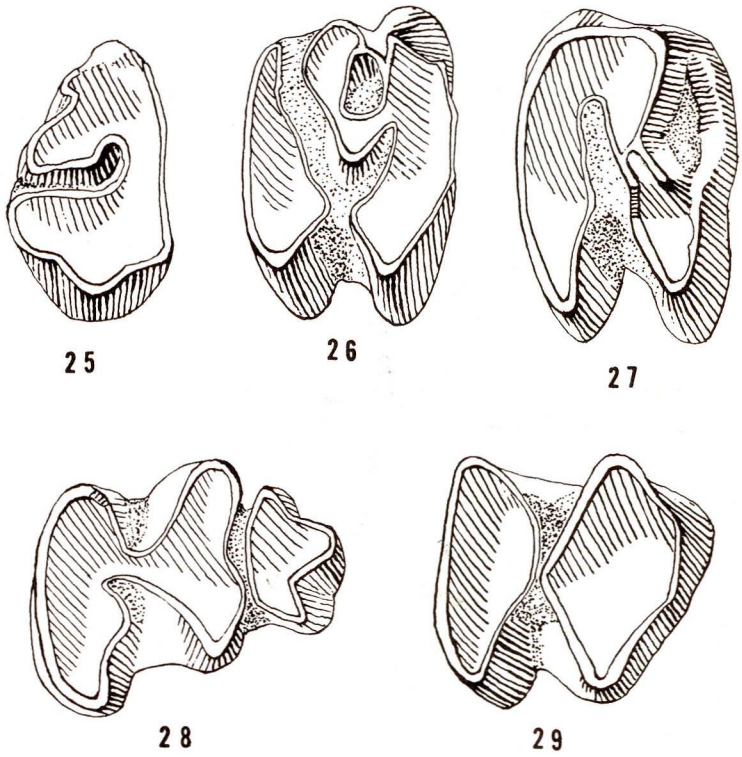
*The posterior loph of P^4 characteristically reaches farther buccad on P^4 than on M^1, and using this criterion all adult specimens from Split Rock having an isolated valley fit into the category of P^4. It is not always simple to distinguish between these teeth.

Except for the absence from Split Rock specimens of this Marsland variant of M^1, the morphology of *Oreolagus* from Split Rock as now known is within the range exhibited by Marsland specimens of *O. nebrascensis*. The difference in M^1 might be indicative of a slightly more advanced level of development of specimens from the geologically younger Split Rock local fauna than of those from the Marsland. The total morphological picture presented by specimens of *Oreolagus* from Split Rock and the Marsland does not seem to support separation into two species, and the Split Rock specimens are here referred to *Oreolagus nebrascensis*. Such morphological differences as are known are regarded as evidence for clinal change toward a slightly more advanced level of *O. nebrascensis* in the Split Rock fauna.

A complete series of deciduous teeth of *Oreolagus* is known from Split Rock. Two anteroposteriorly oriented lobes connected by a transverse posterior loph compose dP^2 (Fig. 25). The more linguad of the anteroposteriorly oriented lobes is notched anterolingually. Two small buccal and a large lingual root support dP^3 and dP^4. General similarity to the occlusal pattern of unworn P^4



Figures 20-24. *Oreolagus nebrascensis* from Split Rock local fauna, occlusal views of teeth. 20. Composite dentition, left P^3–M^2, based on isolated teeth, C.M. 13556-13558, approx. x16. 21. Left P_3, C.M. 13559, approx. x15½. 22, 23. Right P_3, C.M. 13559, approx. x13½. 24. Right P_3, C.M. 13569, approx. x13½.



Figures 25-29. *Oreolagus nebrascensis* from Split Rock local fauna, occlusal views of deciduous teeth. 25. Left dP^2, C.N.H.M. PM 2219, approx. x19. 26. Left dP^3 A.C. 6406, approx. x21. 27. Left dP^4, C.N.H.M. PM 2219, approx. x21. 28. Right dP_3, C.N.H.M. PM 2223, approx. x19. 29. Right dP_4, C.N.H.M. PM 2223, approx. x19½.

is shown by dP^3 (Fig. 26), which has a short, wide hypostria, a U-shaped crescentic valley, and a posteroexternal isolated lake. With wear the hypostria merges with the crescentic valley. The last upper deciduous tooth, dP^4 (Fig. 27), has a long hypostria that extends anterior to the crescentic valley and a posteroexternal isolated lake. Three transverse lophs, each wider than the preceding, form dP_3 (Fig. 28). A persistent anteroexternal fold creases the anterior loph, and a less distinct anterointernal groove may be present. Following wear the middle and posterior lophs join near the middle by a dentine and

TABLE 4. Measurements (in millimeters) of *Oreolagus nebrascensis* from Split Rock.

	C.M. 13570	C.M. 13571*	C.M. 13572	U.W. 1952*
P^3 anteroposterior	1.4	----	----	1.7
transverse	2.3	----	----	2.7
P^4 anteroposterior	----	1.5	----	1.5
transverse	----	2.6	----	2.5
M^1 anteroposterior	----	1.45	----	1.6
transverse	----	2.4	----	2.9
M^2 anteroposterior	----	----	1.0	1.2
transverse	----	----	2.1	2.1

*Isolated teeth, not associated.

	U.W. 1949	C.M. 13559	C.M. 14763
P_3 anteroposterior	----	1.2	1.1
width trigonid	----	1.1	1.1
width talonid	----	1.5	1.5
P_4 anteroposterior	1.8	----	----
width trigonid	2.0	----	----
width talonid	1.8	----	----
M_1 anteroposterior	2.0	----	----
width trigonid	2.0	----	----
width talonid	1.9	----	----
M_2 anteroposterior	2.1	----	----
width trigonid	2.0	----	----
width talonid	1.7	----	----
Length P_4–M_2	5.8	----	----
Inside depth of jaw at M_1	8.3	----	----

enamel bridge, and following greater wear the anterior and middle lophs are united also. In contrast, the anterior and middle lophs of dP_3 in *?Hypolagus* sp. unite at an earlier stage of wear relative to the union of middle and posterior lophs. A posterointernal notch on the posterior loph of some specimens of dP_3 in *O. nebrascensis* suggests a tiny posterolophid. The two rooted dP_4 (Fig. 29) shows general similarity to P_4 but has a more distinct anterior protrusion. None of the known specimens of dP_4 has any trace of a posterolophid, as opposed to the presence of this lophid on dP_4 in *?Hypolagus* sp.

BEATTY BUTTES FAUNA

Tuff beds bordering the north side of Beatty Buttes, a volcanic cone in Harney County, Oregon, have yielded a fauna of fossil mammals described by Wallace (1946). The Beatty Buttes fauna shows similarity to faunas from Skull Spring, Sucker Creek, Virgin Valley, and Mascall (Wallace, 1946, p. 119-120), and is considered to have an age approximately transitional between middle and late Miocene (Downs, 1956, p. 325-326).

As in the faunas from Quarry A and Split Rock, the ochotonid of the Beatty Buttes fauna is more adequately represented than is the leporid, although neither family could be considered abundant at Beatty Buttes on the basis of available material. It is tempting to suggest that ecological conditions at Beatty Buttes were more favorable to ochotonids than to leporids and thus similar in some way to conditions at Quarry A and Split Rock, but the very limited evidence cannot give much weight to such a speculation.

Family Leporidae

Leporid sp.

A single, poorly preserved, hypsodont lower molariform tooth having the talonid narrower than the trigonid, L.A.C.M. 4880, represents a leporid about the size of *Hypolagus fontinalis* (anteroposterior, 2.4 mm.; width talonid, ca. 2.2 mm.). The specimen allows no more than reference to the Leporidae, but adds a record of this family that was previously unreported in the Beatty Buttes fauna.

Family Ochotonidae

Similarity of a fragmentary lower jaw, L.A.C.M. CIT 3088, to that in *Oreolagus nevadensis* led Wallace (1946, p. 125-126) to refer ochotonid specimens from Beatty Buttes questionably to *Oreolagus,* while recognizing that an undescribed species was probably represented. Upper jaws are not known for *Oreolagus nevadensis,* the type species, but are for the referred species, *O. wilsoni* and *O. nebrascensis.* If these species are correctly referred generically, Wallace's reference of the species from Beatty Buttes to *Oreolagus* is strengthened by its similarity to these other species of *Oreolagus* in characters of upper as well as lower cheek teeth. Thus, the tentative generic assignment given by Wallace seems to be correct, and the species from Beatty Buttes is now named.

*Oreolagus wallacei,** n. sp.
Figs. 30-31; Table 5

Type specimen. L.A.C.M. CIT 3088, fragmentary right jaw having M_{1-2}. A specimen of P_4 having an adherent piece of jaw fits into the broken anterior end of the jaw fragment and is believed to be part of the same individual.

Referred specimens. (All L.A.C.M. numbers) CIT 3074, left maxilla having P^3—M^2; CIT 3081, fragment of right maxilla having P^4—M^2; 4866, fragment of right maxilla having P^4; CIT 3075, right P_4 (the P_4 believed to be associated with CIT 3088 was catalogued originally with this specimen); 4867, diastemal region of right jaw.

Specific characters. Upper cheek teeth more hypsodont than in *O. wilsoni.* Anterior loph of P^3 crosses less than half of tooth width. On P^4 lingual hypostria relatively longer and narrower than in *O. wilsoni.* Lingual hypostria on M^1 crosses about three-fourths of tooth width; dorsal part of shaft of M^1 less twisted toward anterior than in *O. nebrascensis.* M^2 small, having very shallow lingual fold. Maxillary tuberosity free of zygoma posterior to P^4. Lower incisor terminates below trigonid of M_1. Lower molars longer anteroposteriorly than transversely. Posterior mental foramen below talonid of M_1.

Description and comparisons. The maxilla and anterior zygomatic root in *Oreolagus wallacei* (Fig. 30) resemble more nearly those in *O. wilsoni* than in *O. nebrascensis.* As in *O. wilsoni,* the zygoma is thickened anteroventrally, but the lateral concavity on the zygoma extends farther anteriorly in *O. wallacei,* suggesting some difference in muscle attachment. An occlusal view shows that the maxillary tuberosity is free from the zygoma posterior to a line approximately between P^4 and M^1. As seen from above, the shaft of M^2 and that of the posterior loph of M^1 occupy the part of the tuberosity that is free of the zygoma. In these features of the zygoma and tuberosity *O. wallacei* is similar to *O. wilsoni,* although a higher maxillary tuberosity indicates that the former has somewhat more hypsodont teeth. The dorsal part of the shaft of M^1 in L.A.C.M. CIT 3081 is less twisted in an anterior direction than in *O. nebrascensis* from Split Rock, a dental feature that seems to be correlated with the morphology of maxillary tuberosity and zygoma. The infraorbital foramen, through incomplete in L.A.C.M. CIT 3074, seems to have been slit-like and elongated dorsoventrally, differences from the rounded foramen in *O. wilsoni* that might be related to the greater hypsodonty in *O. wallacei.* On the palate the premolar foramen occurs in line with the posterior wall of P^3.

Upper cheek teeth, known with the exception of P^2, fit into the general *Oreolagus* pattern suggested by *O. wilsoni* and *O. nebrascensis,* but differ in

*For Robert E. Wallace in recognition of his work on the fauna from Beatty Buttes.

various features from those geologically older species. The anterior loph of P^3 extends a relatively shorter distance across the anterior side of the tooth. The lingual hypostria of P^4, the largest upper cheek tooth, nearly contacts the crescentic valley, which has the shape of a J or shallow U, and that on M^1 crosses about three-fourths of the occlusal surface. No crescentic valley occurs on M^1 of the known specimens of *O. wallacei,* all of which represent adults. In proportions P^4 and M^1 are relatively longer anteroposteriorly than in *O. nebrascensis.* Buccally, the anterior and posterior lophs of M^1 form rounded,

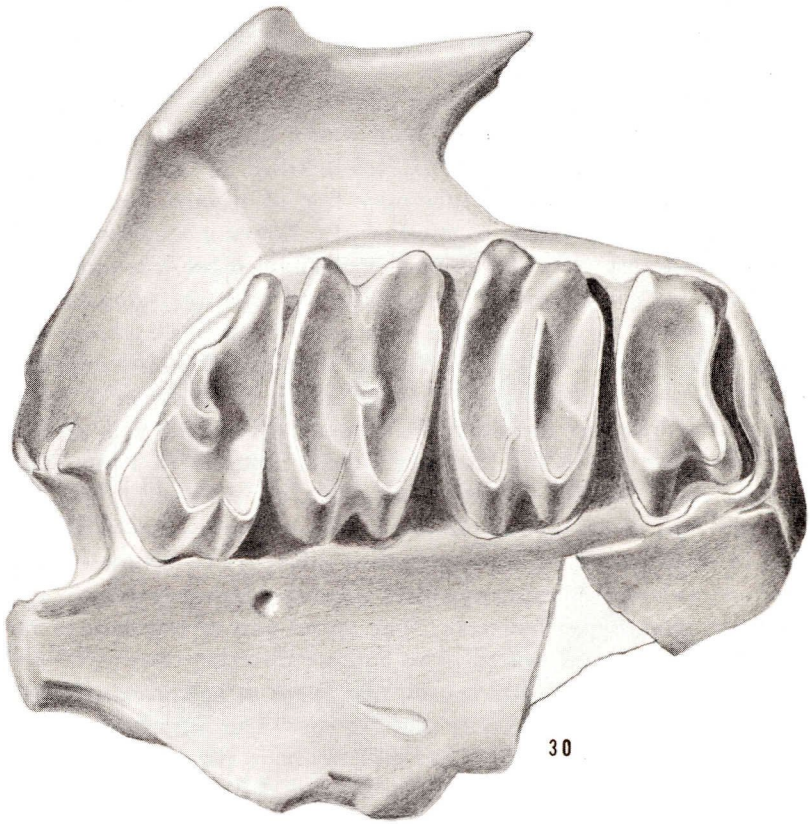


Figure 30. *Oreolagus wallacei,* left maxilla with P^3–M^2, L.A.C.M. CIT 3074, occlusal view, approx. x10⅔.

TABLE 5. Measurements (in millimeters) of *Oreolagus wallacei.*

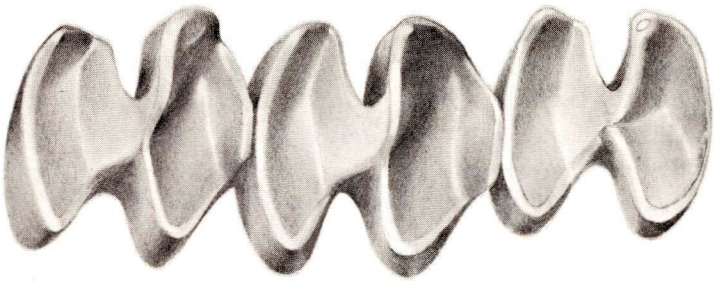
	L.A.C.M. CIT 3074	L.A.C.M. CIT 3081
P^3 anteroposterior	1.4	----
transverse	2.7	----
P^4 anteroposterior	1.7	1.8
transverse	2.8	ca.2.4
M^1 anteroposterior	1.6	1.7
transverse	2.7	2.6
M^2 anteroposterior	1.2	1.2
transverse	2.2	2.3
length P^3–M^2	6.4	----

	L.A.C.M. CIT 3088 Type
P_4 anteroposterior	1.7
width trigonid	1.6
width talonid	1.6
M_1 anteroposterior	1.9
width trigonid	1.8
width talonid	1.75
M_2 anteroposterior	1.9
width trigonid	1.75
width talonid	1.6
length P_4–M_2*	ca.5.6
inner depth of jaw at M_1	6.5

*See description of specimen.

somewhat cuspate, prominences, posterior to which grooves of wear cross the tooth. The last upper tooth, M^2, has a shallow lingual groove, which seems to lack a cement filling. Posterior to the groove the posterior loph swings back. This tooth shows less clearly than do those in *O. wilsoni* and *O. nebrascensis* its derivation from a tooth resembling M^1 in general features.

No complete lower jaw of *O. wallacei* is known, but a general indication of jaw morphology is provided by the incomplete horizontal ramus of the type specimen, L.A.C.M. CIT 3088, and a fragment of the diastemal part of the ramus, L.A.C.M. 4867. In shape and in occurrence of the anterior mental foramen at about mid-depth of the jaw anterior to P_3, the ramus resembles those of *O. wilsoni* and *O. nebrascensis.* The posterior mental foramen is in a line below the middle of M_1, approximately as in *O. nevadensis.* The shaft



31

Figure 31. *Oreolagus wallacei,* right P_4–M_2, L.A.C.M. CIT 3088, type specimen, occlusal view, approx. x15.

of the incisor extends to below the trigonid of M_1 and is thus shorter than in *O. nebrascensis* but longer than in *O. nevadensis,* in which the incisor terminates in a line between P_4 and M_1.

Unfortunately P_3 is not represented among known specimens. As in other species, the shaft of P_4 is straighter than those of M_1 and M_2, and the trigonid of P_4 lacks the anterior protrusion shown by the molar trigonids. Comparisons between occlusal surfaces of *O. wallacei* (Fig. 31) and *O. nevadensis* lack accuracy because the surfaces in *O. nevadensis* are broken and natural wear surfaces are not present. In *Oreolagus wallacei* the teeth are larger and the anterior protrusion of the trigonid and seemingly also of the talonid of M_1 is less distinct on the buccal side of the tooth. In lateral view M_1 of *O. nevadensis* has a distinct crease along the shaft marking the contact of the protrusion with more posterior parts of the trigonid. This crease is absent in *O. wallacei.* Characteristically, the lower molars of *O. wallacei* are longer anteroposteriorly than transversely, a point of resemblance to *O. wilsoni.*

CHARACTERS AND RELATIONSHIPS OF *OREOLAGUS*

Kellogg's (1910, p. 435-436) *Palaeolagus nevadensis,* later made the type species of *Oreolagus* (Dice, 1917, p. 182), is known only from a lower jaw having P_3–M_2. McGrew (1941) referred to the genus another species, *Oreolagus nebrascensis,* also based originally on a lower jaw, and two more species, *O. wilsoni* and *O. wallacei,* are added here. Similarities in characteristics of

the lower jaw and teeth of these referred species must provide the grounds for uniting them with *Oreolagus nevadensis* until more of that species is known. In the absence of known upper jaws and teeth of *O. nevadensis,* it may be hazardous to give generic characters of *Oreolagus* that include these structures. However, presence of certain characters in common among the three referred species lends weight to the opinion that these characters could be expected to occur in *O. nevadensis* also. Accordingly, the generic characters given below include features not known in the type species, but it is recognized that modification may be necessary when *O. nevadensis* becomes more completely known.

Oreolagus Dice, 1917

Generic characters. Ochotonids near Recent *Ochotona* in size range. Dental formula, $\frac{(2)}{1}, \frac{0}{0}, \frac{3}{2}, \frac{2}{2}$. Permanent cheek teeth hypsodont, not rooted. On P^3 anterior loph crosses half or less of tooth width, not reaching buccal side, crescentic valley retains anteroexternal connection, lingual hypostria is short. On P^4 hypostria crosses less than half tooth width, is directed anterior to but does not extend past crescentic valley. Primitively M^1 has crescentic valley and longer hypostria than P^4; progressively valley is absent in adults and hypostria lengthens until it crosses about three-fourths of tooth width. M^2 smaller than M^1, has shallow lingual fold, lingual part of posterior loph swinging posteriorly. Lower incisor terminates below P_4 or M_1. On P_3 buccal fold crosses about half tooth width between trigonid and wider talonid, shallow grooves present or absent anteriorly and lingually. P_4, M_1, and M_2 composed of trigonid and slightly narrower or equally wide talonid; talonid has narrow anterior protrusion; columns of each tooth joined by cement. Two mental foramina on lateral surface of lower jaw: one anterior to P_3; second lower, below molars.

Type species. Palaeolagus nevadensis Kellogg, 1910.

Referred species. Oreolagus nebrascensis McGrew, 1941; *Oreolagus wilsoni,* n. sp.; *Oreolagus wallacei,* n. sp.

Distribution: Late early Miocene (late Arikareean) to late middle Miocene (late Hemingfordian) or early late Miocene (early Barstovian); Nebraska, Colorado, Wyoming, Nevada, Oregon.

One of the most striking dental characters of *Oreolagus* is the development of M^2 into a somewhat reduced tooth, having a shallow lingual fold, that is different from M^2 in any other known ochotonid. Essentially the tooth is a

TABLE 6. Comparisons of species of *Oreolagus*.

	O. wilsoni	*O. nebrascensis*	*O. nevadensis*	*O. wallacei*
1. age	late early Miocene	late early to early middle Miocene	late middle or early late Miocene	late middle or early late Miocene
2. contact of zygoma and maxillary tuberosity	to line between P^4 and M^1	extends farther posteriorly than in other species, to line with anterior loph of M^1	----------	approximately as in *O. wilsoni*, to line between P^4 and M^1
3. length of anterior loph of P^3	about half width of tooth	about half width of tooth	----------	less than half width of tooth
4. pattern on P^4 in adult	crescentic valley and relatively short wide hypostria	crescentic valley and longer hypostria than in *O. wilsoni*	----------	crescentic valley and relatively longer hypostria than in other species
5. pattern on M^1 in adult	persistent crescentic valley buccal to hypostria	variable: small crescentic valley present or absent buccal to hypostria, which is longer than in *O. wilsoni*	----------	no crescent; hypostria crosses about three-fourths of tooth width
6. pattern on M^2 in adult	distinct lingual fold, posterior to which loph swings backward	essentially as in *O. wilsoni*	----------	shallower lingual fold, posterior to which posterior loph swings backward
7. length P^3–M^2	----------	7.4–7.9	----------	6.4
8. position of posterior end of lower I	below talonid of P_4 or trigonid of M_1	below middle or talonid of M_1	below line between P_4 and M_1	below trigonid of M_1
9. pattern and shape of P_3 in adult	accessory folds present or absent; when present one anterior or one lingual	relatively long lingual wall; accessory folds present or absent; when present one anterior and/or one lingual	relatively compressed antero-posteriorly; no accessory folds	----------

10. shape and proportions of lower molariform teeth	usually longer antero-posteriorly than transversely	proportions variable but tending toward greater transverse width than antero-posterior length	anterior protrusion of trigonid of M_1 prominent; variable proportions of width to length	longer antero-posteriorly than transversely
11. position of posterior mental foramen	below trigonid or middle of M_1	variable from below middle of M_1 to below line between M_{1-2}	below middle of M_1	below talonid of M_1
12. length P_4–M_2	5.6–6.2	5.6–6.4	5.0	ca. 5.6

single, transversely elongated basin bordered by two strong transverse enamel ridges that are formed by the anterior and posterior walls. Occlusal relations are such that the anterior wall of M^2 would occlude with the talonid basin of M_2, the posterior wall of M_2 with the basin of M^2, and the posterior wall of M^2 would fit down behind M_2. In Recent *Ochotona,* in which M^2 has a long hypostria and a well developed posterior loph having an additional posterior protrusion and M_3 is retained, it is the posterior enamel wall of the hypostria that occludes behind M_2, in this case with the basin of M_3, and the posterior wall of M^2 that fits behind M_3. The relatively complex posterior loph of M^2, with its protrusion, in *Ochotona* superficially resembles the entire M^2 in *Oreolagus.* The functional unit formed by the posterior-most teeth seems to have been similar in these two genera, although of course *Ochotona* has one more transverse loph when the entire cheek tooth battery is considered. These two relatively distantly related ochotonids seem to have achieved a functional parellel based on different structures. *Oreolagus* resembles the European *Piezodus-Prolagus* line in loss of $M\frac{3}{3}$. In this late Oligocene to Pleistocene line, however, it is M_2 that changes following loss of M_3 by retaining through life a posterolophid, or "third lobe," on M_2. The functional result of this would seem to be essentially the same as that achieved through retention of M_3. *Titanomys visenoviensis* is a relatively primitive Aquitanian ochotonid that usually lacks $M\frac{3}{3}$ and seems to have developed something similar to the functional pattern of the *Piezodus-Prolagus* line through persistence of the posterolophid of M_2. Different solutions to the problem of posterior occlusion in ochotonids lead one to speculate that *Oreolagus* may have descended from

a line of ochotonids lacking a persistent posterolophid on M_2, and thus occlusal relations were developed in a fashion different from that adopted by the European *Titanomys* and the *Piezodus-Prolagus* line. It is interesting that ochotonids have gone to some lengths to maintain or improve effectiveness of occlusion of the posterior teeth after having lost M^3 or $M\frac{3}{3}$.

Oreolagus nebrascensis and *O. wallacei* differ in relations of maxillary tuberosity to zygoma, the contact between the two being longer in *O. nebrascensis,* which also has greater anterior torsion of the upper molar shafts. *Oreolagus* is not the only genus of ochotonid showing variation in the problem of housing hypsodont teeth, however, but is joined by *Ochotona,* among which a Pontian species, *Ochotona lagreli,* has a longer contact of maxillary tuberosity and zygoma than do Recent species (Bohlin, 1942b, p. 149-150). The Miocene African *Kenyalagomys* (MacInnes, 1953, p. 6) and *Prolagus sardus* from the Pleistocene of Sardinia also have a longer contact of tuberosity and zygoma than does Recent *Ochotona.* Just what morphological and developmental factors are behind these different relationships between tuberosity and zygoma are not yet clear.

Within the genus *Oreolagus, O. wilsoni* has more primitive characters than do other species, including its shorter hypostria and persistent crescentic valleys on the upper cheek teeth. The contemporary or near contemporary *O. nebrascensis* is more advanced in these characters. That *O. wilsoni* is more closely allied to *O. wallacei* than is *O. nebrascensis* is suggested by similarity between the first two in the contact between maxillary tuberosity and zygoma, relatively long teeth anteroposteriorly, and relatively short shaft of the lower incisor. The shafts of the upper molars in *O. wilsoni* seem to twist anteriorly a little more than in *O. wallacei,* suggesting either that there is not a direct ancestor-descendant relationship between these species or that there has been a reversal toward a seemingly more primitive condition in *O. wallacei.* Little can be said in regard to the position of *O. nevadensis,* the type species, relative to the others except that the short shaft of the incisor and proportions of the cheek teeth offer faint evidence for closer affinity to *O. wilsoni* and *O. wallacei* than to *O. nebrascensis.* These suggested relationships make little paleogeographic sense, but perhaps this is not unexpected in view of the incomplete state of knowledge of earlier Miocene Great Basin and later Miocene Great Plains microfaunas.

Previous workers (McGrew, 1941, p. 40; Galbreath, 1953, p. 94; Wilson, 1960, p. 49-51) have recognized that *Desmatolagus* could be near the ancestry of *Oreolagus,* a conclusion with which this study is in agreement. *Oreolagus*

seems to have been a widespread and locally successful ochotonid during the Miocene but no later representatives of this line are known.

OCHOTONIDS IN THE NORTH AMERICAN TERTIARY

Although there are many gaps in the fossil record of ochotonids in North America, a brief review of their occurrence and suggestions as to their relationships may be in order at this time. The middle Oligocene *Desmatolagus gazini* is considered here to be the oldest North American species having characteristics relating it clearly to Old World *Desmatolagus* and probably represents the result of an invasion from Asia. Two later North American species, ?*Desmatolagus schizopetrus* from the middle Miocene and *Hesperolagomys galbreathi,* share with *D. gazini* certain dental characters including rooted cheek teeth and persistent crescentic valleys on the upper teeth. Based on known evidence, these three North American species could represent a roughly ancestor-descendant series. However, very little is known of Miocene Asian microfaunas, and, though seeming less likely, the possibility cannot be excluded that these North American forms were derived from separate invasions from Asia.

Another branch of North American ochotonids is represented by the Miocene *Oreolagus,* which is advanced in hypsodonty and pattern of the cheek teeth, and exhibits specialization of M^2. Dental characters suggest that *Oreolagus* could be a descendant of *Desmatolagus,* but whether from North American or Asian species of that genus remains an open question. Two lines of evidence, one morphological and the other distributional, lend a little more probability to origin from Asian members of the genus. The morphological factor is presence in *Oreolagus* and *D. gobiensis,* but not in *D. gazini,* of a premolar foramen. Unless the foramen developed more than once in ochotonids, this feature allies *Oreolagus* and the Asian species. Distributionally, occurrence of *Kenyalagomys* and *Austrolagomys,* ochotonids probably derived from Asian species, in the Miocene of Africa suggests that the Miocene may have been a time of radiation of this family from an Asian center. Perhaps the line leading to *Oreolagus* reached the New World during such a radiation. That other Old World groups moved into North America around the time of the first appearance of *Oreolagus* in North America is shown by presence with *Oreolagus* at Martin Canyon Quarry A of some insectivores and rodents having Old World affinities (Wilson, 1960).

When *Ochotona* appears in the Hemphillian, it is an immigrant from Asia. *Ochotona* lacks a Blancan record in North America, and whether Pleistocene

and Recent *Ochotona* resulted from the same immigration is not known (Shotwell, 1956, p. 727).

Miocene pikas in North America occur in deposits that probably represent stream border accumulations (Wilson, 1960, p. 7), and *Ochotona,* when it appears in the Hemphillian, is a member of a stream bank community but is absent from woodland and meadow habitats (Shotwell, 1958). During the Pleistocene, *Ochotona* extended into the eastern United States, occurring in Cumberland Cave, Maryland (Gidley and Gazin, 1938, p. 68-69). The often encountered interpretation of ochotonids and of *Ochotona* in particular as being restricted to and specially adapted for life in mountains and rocky areas breaks down when the fossil record is considered, and even Recent *Ochotona* occurs in Asia in the open Gobi and in forested areas and grasslands, as well as in rocky regions and mountains (Allen, 1938, p. 524). Any explanations of the Recent distribution of *Ochotona* and of its adaptations should take into account evidence such as this from the fossil record.

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