

UNIVERSITY OF KANSAS
PALEONTOLOGICAL CONTRIBUTIONS

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VERTEBRATA

ARTICLE 6

Pages 1-75, Plates 1-2, Figures 1-39

LATER TERTIARY LEPORIDAE OF NORTH AMERICA

By MARY R. DAWSON



UNIVERSITY OF KANSAS PUBLICATIONS

MAY 1, 1958

PRINTED BY
UNIVERSITY OF KANSAS PRESS
LAWRENCE

UNIVERSITY OF KANSAS
PALEONTOLOGICAL CONTRIBUTIONS

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LATER TERTIARY LEPORIDAE OF NORTH AMERICA¹

By MARY R. DAWSON

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¹ A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Kansas.

ABSTRACT

Previous studies of members of the mammalian family Leporidae from the North American Tertiary have made known the morphology and some phylogenetic trends of late Eocene and Oligocene leporids and have resulted in the naming of numerous Miocene and Pliocene species. The study here reported on determines more precisely the relationships between Oligocene and later Tertiary leporids and demonstrates morphologic and phylogenetic trends in Miocene and Pliocene members of the family. Opinions differ regarding the taxonomic validity of certain of the subfamilies that were proposed in the past to show relationships among leporids. Three subfamilies are here recognized, Palaeolaginae, Archaeolaginae, and Leporinae. The content of each subfamily differs somewhat from that proposed by DICE in 1929. The subfamily Archaeolaginae includes the bulk of later Tertiary North American leporids and is the central subject of this study.

All leporids from the North American Tertiary are reviewed. Species of the genus *Palaeolagus* are arranged in three species groups. *Archaeolagus* seems to have descended either from a new middle Oligocene genus or from one of the species groups of *Palaeolagus*. *Archaeolagus* and its descendant *Hypolagus* are differentiated mainly as different levels of development; possibly the level that is taken to characterize *Hypolagus* has been attained by more than one line of *Archaeolagus*. Relationships of some of the numerous Pliocene species of *Hypolagus* are not clear, although two main lines, one including larger leporids and the other smaller, can be traced. Remains of at least thirty-five topotypes of *Hypolagus vetus* illustrate for the first time the variation that might be expected in a relatively homogeneous sample of fossil leporids. In North America, members of the subfamily Leporinae first appear in Blancan times, probably as migrants from the Old World.

Morphologically, most leporids have been conservative and have followed certain general evolutionary tendencies. Evolutionary trends in the cheek-teeth include increase in hypsodonty, molarification of some of the premolars, and replacement of the primitive occlusal pattern by a simpler pattern lacking most traces of primitive tooth cusps. Evolution of the skull and postcranial skeleton has been mostly toward adaptation for improved cursorial locomotion. The primitively flattened skull changed to an arched one having a larger angle between basi-cranial and palatal axes. The arching of the skull

reflects development of a posture in which the head is carried at a greater angle to the vertebral column than in primitive leporids. Several other changes in skull and lower jaws seem to be related to this arching. Trends toward cursorial adaptation in the postcranial skeleton include elongation of the limbs distally and strengthening of articulations and more advantageous placement of muscle attachments in the pelvic girdle and hind limbs, which are important in the half-bound or leaping gallop of leporids. The postcranial skeleton in primitive leporids was probably more flexible laterally than in later leporids, which are specialized for anteroposterior movement. A few leporids departed from the main line of development and paralleled ochotonids in some characters.

Most morphological structures can not be used consistently to determine relationships within the family Leporidae, but P_3 , with certain limitations, seems to reveal relationships, particularly at the subfamilial level.

The subfamily Palaeolaginae is a basal group of persistently primitive leporids and others more progressive. The Palaeolaginae seem to have flourished in the earlier Tertiary of North America, and some Old World lagomorphs have been tentatively referred to that subfamily. The compact subfamily Archaeolaginae seems to have arisen early in Miocene times from one of the more progressive lines of palaeolagines. The main development of the subfamily Archaeolaginae, which includes all or nearly all middle Miocene to middle Pliocene North American leporids, occurred in North America. Archaeolagines reached the Old World late in the Pliocene, flourished until the late Pliocene or early Pleistocene, but became extinct, possibly due to competition with leporines. The subfamily Leporinae is first known from the Pontian of the Old World, seems to have had a successful Pliocene and Pleistocene radiation, reached North America in Blancan times, and includes all living leporids. The ancestry of the leporines is not known from the fossil record, but perhaps a line of palaeolagines reached the Old World and there gave rise to leporines.

Named as new are *Palaeolagus philoi*, n. sp., from the early Miocene; *Litolagus molidens*, n. gen. and sp., from the middle Oligocene; *Archaeolagus acaricolus*, n. sp., from the late early or early middle Miocene; *Hypolagus parviplicatus*, n. sp., from the late middle or early late Miocene; and *Hypolagus fontinalis*, n. sp., from the early Pliocene.

INTRODUCTION

The family Leporidae, rabbits and hares, along with the late Paleocene family Eurymylidae and the late Oligocene to Recent Ochotonidae make up the mammalian order Lagomorpha. The Leporidae are first known from the late Eocene of Asia and North America. Leporids of a primitive type seem to persist throughout the Oligocene in Asia. In North American Oligocene faunas there were some persistently primitive leporids, but also more progressive lines. Most Miocene and Pliocene leporids of North America seem to be descended from one of the more progressive Oligocene lines. Definite leporids are not known from the Miocene of the Old World but reappear there in the early Pliocene. Recent leporids are nearly world-wide in distribution.

The present work is principally a review of Miocene

and Pliocene members of the family Leporidae with the purpose of determining morphologic trends and relationships within the family. Three subfamilies of leporids are recognized here—Palaeolaginae, Archaeolaginae, and Leporinae. Of these, the subfamily Archaeolaginae, which includes the primary or sole North American leporids from middle Miocene through middle Pliocene times, is the central subject of this review. In order to determine the morphologic heritage and ancestry of the later Tertiary leporids, it is necessary also to review the earlier North American leporids, which are included in the subfamily Palaeolaginae. The later Tertiary Leporinae, contemporaries of, and possibly competitors with, the archaeolagines, are also considered.

ACKNOWLEDGMENTS

Sincere thanks are extended first to Professor ROBERT W. WILSON for guidance and encouragement throughout the course of this study and for permitting me to report on several Tertiary leporids on which he had made preliminary studies. Discussions with Assistant Professors EDWIN C. GALBREATH and PETER P. VAUGHN have been appreciated and found profitable. Professor E. RAYMOND HALL has advised and assisted in the preparation of the manuscript. A discussion of leporids with Mr. JOHN J. BURKE was most helpful. Some of the fossil material discussed here has been studied at the institutions where housed, and other material has been made available on loan. I deeply appreciate assistance from the following in making these visits and loans possible: Dr. DONALD BAIRD, Dr. JAMES D. BUMP, Dr. C. LEWIS GAZIN, Dr. JOSEPH T. GREGORY, Dr. CLAUDE W. HIBBARD, Dr. J. LE-

ROY KAY, Dr. JAMES R. MACDONALD, Mrs. RACHEL H. NICHOLS, Mr. BRYAN PATTERSON, Dr. HORACE G. RICHARDS, Dr. ALFRED S. ROMER, Dr. DONALD E. SAVAGE, Dr. ROBERT P. SHARP, Dr. GEORGE G. SIMPSON, Mr. GEORGE F. STERNBERG, Mr. WILLIAM D. TURNBULL, and Dr. ALBERT E. WOOD. Dr. GAZIN generously permitted use of an excerpt from his field notes, and Dr. HIBBARD likewise provided figure 38 by Mr. MICHAEL O. WOODBURN for use here. Other original line drawings were prepared by Mrs. SYLVIA BARR and Mrs. JANE S. MENGEL. Mrs. BARR and Miss HAROLDEAN MURRAY have finished my outline drawings. Mr. JIM SHEPPERD and Miss JANET DAWSON kindly assisted with photography. I am grateful to the University of Kansas for a fellowship in the first year of my study and to the National Science Foundation for fellowships in the two succeeding years.

PREVIOUS STUDIES

In the early, primarily descriptive discussions of Tertiary leporids of LEIDY (1856), COPE (1873, 1884, other papers), MATTHEW (1902, 1903, 1907), and others, Oligocene leporids were included in the genus *Palaeolagus*, and John Day and later leporids were referred to the genus *Lepus*; the phylogenetic connection between primitive and more advanced leporids was considered to be an essentially simple, direct sequence from *Palaeolagus* to *Lepus*. Later, DICE (1917) established the genera *Archaeolagus* and *Hypolagus*, considering them to be morphologically and probably phylogenetically intermediate between *Palaeolagus* and *Lepus*. North American Tertiary leporids became better known and additional leporids were recognized as a result of expansion of the fossil record: WALKER (1931) established the genus *Megalagus* for certain large, relatively unprogressive Oligocene leporids; BURKE described the late Eocene genus *Mytonolagus* (1934) and recognized the Asian genus *Desmatolagus* in North America (1936); WOOD's (1940) study of *Palaeolagus*, *Megalagus*, and *Desmatolagus* of the White River Oligocene is a fundamental work dealing with not only morphological and phylogenetic trends but also tooth development and homology and characteristics of primitive leporids as opposed to ochotonids; numerous Pliocene and Blancan leporids became known through the work of GAZIN (1930, 1934), HIBBARD (1939), WILSON (1937a, 1937b, other papers), and others. Studies of Old World leporids that should be mentioned are those of BURKE (1941) on late Eocene and Oligocene Mongolian leporids, of KORMOS (1934), recognizing the genus *Hypolagus* in the Old World and establishing the genus *Pliolagus*, and of SCHLOSSER (1924), DICE (1929, 1931), and BOHLIN (1942b) on the genus *Alilepus*.

As more specimens accumulated, it became clear that the phylogeny of the leporids was more complex than the simple *Palaeolagus* to *Lepus* sequence. DICE (1929) proposed three subfamilies, on the basis of the structure of P_3 , to express lines of descent within the family: (1) the early Oligocene to Recent Palaeolaginae, characterized by an hour-glass-shaped pattern that was produced by pos-

terointernal and posteroexternal folds of enamel on P_3 , including the Oligocene *Palaeolagus* (later divided into *Palaeolagus* and *Megalagus*) and certain Pliocene to Recent leporids; (2) the extinct subfamily Archaeolaginae, characterized by P_3 lacking an internal fold and having the posteroexternal fold crossing no more than half the occlusal surface, including *Archaeolagus* and *Hypolagus*, which were the main leporids in the later Tertiary of North America; and (3) Leporinae, lacking an internal reentrant on P_3 and having the posteroexternal reentrant crossing nearly the entire occlusal surface, ranging from late Pliocene to Recent and including *Brachylagus*, *Caprolagus*, *Lepus*, *Oryctolagus*, and *Sylvilagus* (*Nesolagus* was added by SCHREUDER in 1936). The peripheral distribution of the living "palaeolagines", *Pentalagus*, *Pronolagus*, and *Romerolagus*, was considered to indicate their antiquity. The subfamily Archaeolaginae was proposed with some reservation, because its characteristics were "seemingly intermediate between those of the other two subfamilies" (DICE, 1929, p. 343). The status of the Archaeolaginae became more uncertain following work by KORMOS (1934), who expressed the opinion that the Villafranchian *Pliolagus*, a leporid having a palaeolagine P_3 in early stages of wear and an archaeolagine P_3 in later stages of wear, showed that the palaeolagines and archaeolagines could not be separated and that only Palaeolaginae and Leporinae should be retained. SCHREUDER (1936) concurred with KORMOS. WOOD (1940) agreed with KORMOS and SCHREUDER in recognizing on the basis of the known evidence two subfamilies, Palaeolaginae (Palaeolaginae plus Archaeolaginae of DICE) and Leporinae. WOOD found evidence for uniting palaeolagines and archaeolagines in the closely related Oligocene genera *Palaeolagus* and *Megalagus*: on the basis of the subfamilial characters used by DICE, individuals of *Palaeolagus* would be palaeolagines for most of their lives but archaeolagines in old age; individuals of the latter genus would be palaeolagines for a short time when young and archaeolagines for most of their lives. Nevertheless, WOOD left the subfamilial classification somewhat tentative, suggesting that a definition

of the palaeolagines as "leporids in which P_3 is divided into two lobes, the anterior of which is simple and without accessory invaginations" (1940, p. 276) might result in a better subfamilial arrangement of genera; it was mentioned that the ancestry of later Tertiary "palaeolagines" and leporines was not definitely known and that further study of Miocene and later leporids might lead to recognition of the Archaeolaginae as a valid phylogenetic unit. Another classification was that of BURKE (1941), who deemed several new subfamilies necessary to show the divergent lines of descent from late Eocene leporids; he mentioned Mytonolaginae, Desmatolaginae, Megalaginae, and Palaeolaginae, and other subfamilies for later leporids were recognized by inference. HIBBARD (1939, 1941b) maintained DICE's subfamilies essentially as proposed; however, his work on Blancan and Recent leporids (1944) suggested that in dental characteristics the Blancan "palaeolagine" *Nekrolagus* led toward *Lepus*, thus seeming to bridge the gap between later "palaeolagines" and leporines. BOHLIN (1942b) set apart the later Tertiary leporids *Alilepus*, "*Caprolagus*" *brachypus*, and *Pliolagus* as a group descended from a common Oligocene ancestor and possibly ancestral to Recent "palaeolagines"; *Hypolagus* was considered to have given rise to *Lepus*. SIMPSON (1945, p. 197) followed KORMOS, SCHREUDER, and WOOD

in recognizing the Palaeolaginae and Leporinae, but mentioned BURKE's subfamilial classification as a valuable analysis that was, however, somewhat impractical due to use of "nearly monotypical subfamilies split both vertically and horizontally". WILSON (1949b, p. 134-139) suggested that if subfamilies be maintained, the definition and content of DICE's subfamilies be revised: the Palaeolaginae should be a primitive basal group of Eocene and Oligocene leporids, the Leporinae should include all living leporids, including certain later Tertiary and the peripheral Recent "palaeolagines"; in line with this arrangement, the Archaeolaginae could be recognized as a compact, extinct group that includes the bulk of North American later Tertiary leporids.

In summary, previous to the present report the status of knowledge of Tertiary leporids was as follows: late Eocene and Oligocene leporids fairly well known and described, and phylogenetic trends of these earlier leporids suggested; some North American Miocene leporids known and species of Pliocene leporids numerous; subfamilial classification somewhat uncertain, although certain Oligocene leporids generally acknowledged to be closely connected to main North American later Tertiary leporids; relationships of Recent leporids, including "palaeolagines" and leporines, to more primitive leporids more uncertain.

METHODS

Relatively complete fossil specimens that were used comparatively throughout most of my study are as follows: *Palaeolagus haydeni*, C.I.T. No. 1402; *Megalagus turgidus*, C.I.T. No. 1563; *Hypolagus vetus*, numerous specimens from C.I.T. locality 63. Specimens from the K.U. collection of Recent mammals that were used comparatively are: *Lepus californicus*, No. 8827; *Romerolagus daiisi*, No. 30815; *Sylvilagus floridanus*, No. 12135; *Ochotona princeps*, No. 54850. Additional specimens were used where possible in order to estimate the limits of individual variation. Unless otherwise noted, comparisons have been between adult individuals.

Names of institutions or collections referred to in the text are abbreviated as follows:

A.E.W.	Collection of Albert E. Wood
Amherst	Amherst College
A.M.N.H.	American Museum of Natural History
A.N.S.P.	Academy of Natural Sciences of Philadelphia
C.I.T.	California Institute of Technology, Collection of Vertebrate Paleontology (this collection has been transferred to the Los Angeles County Museum)
C.M.	Carnegie Museum
C.N.H.M.	Chicago Natural History Museum
F.H.	Fort Hays Kansas State College Museum
K.U.	University of Kansas Museum of Natural History
M.C.Z.	Museum of Comparative Zoology, Harvard
O.M.P.	Oklahoma Museum of Paleontology
S.D.S.M.	South Dakota School of Mines and Technology
U.C.M.P.	University of California Museum of Paleontology
U.M.M.P.	University of Michigan Museum of Paleontology
U.O.M.N.H.	University of Oregon Museum of Natural History

U.S.N.M.	United States National Museum
W.M.	Walker Museum (now in collections of Chicago Natural History Museum)
Y.P.M.	Yale Peabody Museum

In the drawings of teeth, cement is indicated by stippling, and enamel on the occlusal surface is outlined or, in one case, blackened. Breaks are indicated by diagonal lines. Measurements are in millimeters and have been taken with the same instrument and technique. Measurements of teeth individually or in series were taken at the occlusal surface, unless otherwise stated.

The morphologic terminology used is that in general use in the literature dealing with lagomorphs. Terms applied here to the relatively simple structure of the cheek-teeth of adults of more advanced leporids usually are descriptive or positional and do not imply homologies with similarly-named parts in other mammals; in the molariform upper cheek-teeth, *anteroloph* and *posteroloph* are incompletely separated by an *internal hypostria*; in the lower molariform teeth, the columns, termed *trigonid* and *talonid*, are often joined by a *lingual bridge* of enamel and dentine. Other terms used for more primitive leporids and for unworn teeth usually follow WOOD (1940). Skeletal terms follow BENSLEY (1945) in most cases. The term *postalveolar foramen* has been used to designate a foramen for the passage of a vein immediately posterior to M_3 .

WOOD, *et al.* (1941) has been followed in stratigraphic terminology and correlation of North American deposits except in a few cases in which more recent work has shown changes in relative age relationships of faunal units.

SYSTEMATIC REVIEW

Family LEPORIDAE Gray, 1821

Dental formula $\frac{2 \ 0 \ 3 \ 3}{1 \ 0 \ 2 \ 3}$ (except that *Pentalagus*

lacks M^3); P^3 completely molariform in advanced species; snout tapers in width anteriorly; lateral portion of nasal extends farther posteriorly than remainder; supraorbital process of frontal present; in palatine process of maxilla, foramen premolare (BOHLIN, 1942a, p. 59-60) absent.

The combination of characters listed above differentiates the leporids from the other two lagomorph families, Eurymylidae and Ochotonidae. The family Leporidae has a time range of late Eocene to Recent; geographically leporids have a natural distribution that is nearly worldwide, with the exception of Australia.

Subfamily PALAEOLAGINAE Dice, 1929

The subfamily Palaeolaginae, having a late Eocene to early Miocene time range, includes the following genera: from Mongolia—*Shamolagus*, late Eocene, and *Gobiolagus*, late Eocene to early Oligocene and possibly late Oligocene; *Desmatolagus*, early to late Oligocene of Asia and possibly early and middle Oligocene of North America; from North America—*Mytonolagus*, late Eocene, *Megalagus* and *Palaeolagus*, early Oligocene to early Miocene, and the middle Oligocene genus named below on page 32.

The Palaeolaginae are characterized by the following: P^3 and P^4 less molariform than M^1 and M^2 , usually retaining the primitive pattern of crescents between central and lingual lobes and having less persistent internal hypostriae, the buccal ends of which may form isolated lakes; P_3 having a single external reentrant, situated between trigonid and talonid, except in one species, *Palaeolagus hypsodus*, in which P_3 has an additional external reentrant, which is shallow and situated anteroexternally on the trigonid.

Inclusion of *Shamolagus*, *Gobiolagus*, *Desmatolagus*, and *Mytonolagus* in this subfamily is tentative. These genera seem to be closer than are the typical Oligocene North American palaeolagines to the stock that gave rise to both ochotonids and leporids. The similarities of *Shamolagus* and *Gobiolagus* to *Mytonolagus* and, in turn, of *Mytonolagus* to *Megalagus* suggest leporid affinities for the genera in question, but further studies are necessary before their relationships can be stated more precisely. As here conceived of, the subfamily Palaeolaginae is a broad basal group, more primitive than the other subfamilies, ranging from primitive to later, more advanced leporids, and presumably ancestral to the Archaeolaginae and Leporinae.

Genus MYTONOLAGUS Burke, 1934

Mytonolagus BURKE, Carnegie Mus., Annals, v. 23, art. 9, p. 400, November 19, 1934. Type, *Mytonolagus petersoni* BURKE.

Geologic age and distribution.—Late Eocene of Utah, Wyoming, and possibly Saskatchewan.

Generic characters.—Compared with *Megalagus*

brachyodon, cheek-teeth less hypsodont, molarization of premolars less advanced, molars less reduced, and maxilla and mandibular ramus narrower in premolar region; P^3 - P^4 each having shallow hypostria; M^1 largest and transversely widest of upper cheek-teeth; P_3 near M_3 in size, M_1 and M_2 of nearly equal size and transversely widest of lower cheek-teeth; on P_3 , internal reentrant not persistent, and external reentrant not extending more than half-way across occlusal surface; anterior root of zygoma extends outward approximately in line with P^4 , which is more posteriorly than in *Palaeolagus* and *Megalagus*. Known species near *Palaeolagus haydeni* in size.

In addition to *Mytonolagus petersoni* from the Myton Pocket in Utah and *M. wyomingensis* from Badwater Creek, Wyoming, specimens from the Wagonhound member of the Uinta Eocene, the Duchesne River (Randlett horizon), and the Swift Current Creek beds of Saskatchewan have been referred to this genus (BURKE, 1934, p. 399-400, 406-407). Whether these referred specimens are assignable to either of the described species is not definitely established. The faunas from Myton pocket, Randlett, Badwater, and Swift Current Creek, which include *Mytonolagus*, are considered by GAZIN (1956, p. 5-7) to be Uintan and not much different from one another in age.

Mytonolagus is probably close to the lagomorph stock that gave rise to both leporids and ochotonids, but is considered here to be a primitive member of the family Leporidae. *Mytonolagus* seems to be on a line leading toward the genus *Megalagus* and to have especially close affinities with the most primitive species of that genus, *Megalagus brachyodon* of the early Oligocene.

Mytonolagus petersoni Burke

Mytonolagus petersoni BURKE, Carnegie Mus., Annals, v. 23, art. 9, p. 400, November 19, 1934.

Type specimen.—Left maxilla having P^2 - M^2 , right M^3 ; portion of right palatine; left lower jaw having P_3 - M_3 ; fragments of right lower jaw having P_3 - M_2 . C.M. No. 11937, Myton member, Uinta Eocene series of Myton Pocket, Little Pleasant Valley, Uinta County, Utah.

Geologic age and distribution.—Late Eocene of Utah and possibly of Saskatchewan.

Specific characters.— P^3 and P^4 each having only one strong outer rootlet; enamel better developed and more persistent than in *M. wyomingensis*. Hypostria on M^1 and M^2 does not extend to upper limit of enamel lingually (GAZIN, 1956, p. 8).

The specimens referred to *Mytonolagus* from the upper Eocene beds at Swift Current Creek have not been examined in connection with the present study, but BURKE (1934, p. 407) mentions that the specimens may be referable to *Mytonolagus petersoni*.

Mytonolagus wyomingensis Wood

Mytonolagus wyomingensis WOOD, Jour. Paleont., v. 23, no. 5, p. 561, September, 1949.

Type specimen.—Isolated right P^3 , Amherst No.

10022, upper Eocene of Badwater Creek, eastern Wind River Basin, central Wyoming.

Geologic age and distribution.—Late Eocene of Wyoming.

Specific characters.—Well-developed buccal roots in upper teeth; hypocone weak on P^3 - P^4 ; enamel reduced buccally on upper teeth, anteriorly on lowers, and lost after wear (WOOD, 1949, p. 561).

The species *Mytonolagus wyomingensis* resembles *M. petersoni* in general characteristics, but combines features, some presumably primitive and some advanced, that differentiate the two species. *M. wyomingensis* probably is not descended from *M. petersoni* (WOOD, 1949, p. 561). The upper Eocene strata in which *M. wyomingensis* occurs are considered to be Duchesnean in age by WOOD (1949, p. 556), but Uintan by GAZIN (1956, p. 5-7). Thus, according to GAZIN's stratigraphic interpretations the two species of *Mytonolagus* would have been essentially contemporaneous, and hence an ancestor-descendant relationship would hardly be expected.

Genus MEGALAGUS Walker, 1931

Megalagus WALKER, The Aetend, v. 2, no. 4, p. 234, Fall, 1931. Type, *Palaeolagus turgidus* COPE.

Geologic age and distribution.—Chadronian (early Oligocene) to Arikareean (early Miocene), Great Plains.

Generic characters.—Upper molariform teeth having buccal roots; on P^3 and P^4 lingual hypostria shallow; on M^1 and M^2 lingual hypostria deeper and tending to persist as isolated lake following rather early separation from the lingual wall. On P_3 single external reëntrant persists in adult; lingual reëntrants on that tooth tend to disappear at an early stage of wear. Cement not well developed. Size larger than in all but one species of *Palaeolagus* (*P. intermedius*).

Included in the genus *Megalagus* are Oligocene and early Miocene leporids that are characterized by relatively low crowned cheek-teeth and persistent traces of a primitive pattern in the upper cheek-teeth. Although separated generically from *Palaeolagus* in 1931, the genus was not immediately recognized as valid. BURKE recommended that the genus *Megalagus* should be recognized if the species of his *turgidus* group were distinct from species of his *haydeni* group (1934, p. 414); later he used the name *Megalagus*, implying reference of the members of the *turgidus* group to that genus (1936, p. 150-152). BURKE's *turgidus* group included "*Palaeolagus*" *turgidus*, "*P.*" *brachyodon*, and *P. intermedius*. Of the *turgidus* group, *M. brachyodon* and *M. turgidus* do seem to be closely related, but the affinities of *Palaeolagus intermedius* seem to be closer to other species of *Palaeolagus* (WOOD, 1940, p. 327-329). Thus, of BURKE's *turgidus* group only *M. brachyodon* and *M. turgidus* are recognized here as members of the genus *Megalagus*. A third species, *M. primitivus*, is referred below to that genus.

The late Eocene leporid *Mytonolagus* appears to be ancestral to *Megalagus*. The dentition of *Megalagus* retains certain persistently primitive features, including rooted upper cheek-teeth having a primitive pattern, and relatively low crowns in the lower cheek-teeth; these features make it improbable that this genus gave rise to

more advanced leporids. *Megalagus* has been favored by some, for example BURKE (1941, p. 22), as the ancestor of the Archaeolaginae, in part because of the occlusal pattern of P_3 . In *Megalagus* the internal reëntrant on P_3 is lost at an early stage of wear, as it is in the archaeolagines. This early loss is regarded by WOOD (1940, p. 332) as a progressive character of *Megalagus*. Actually, in *Mytonolagus* of the late Eocene the internal reëntrant on P_3 is not persistent, and it disappears at an early stage of wear in the two early Oligocene species *Palaeolagus temnodon* and *Megalagus brachyodon*. Therefore, early loss of the internal reëntrant in *Megalagus* may be the retention of a primitive trend rather than a strictly progressive feature. This interpretation is more in keeping with the otherwise primitive nature of the dentition in *Megalagus* and does not necessitate close relationship of *Megalagus* to the archaeolagines. Further evidence that the archaeolagines did not descend from *Megalagus* is offered by materials of the new middle Oligocene genus and lower Miocene species named below on pages 32 and 29 respectively; these leporids, which combine generally advanced dental characters with early loss of the internal reëntrant on P_3 , show more features suggestive of ancestry to the archaeolagines than does *Megalagus*.

Known evolutionary tendencies in the genus *Megalagus*, of early Oligocene to early Miocene times, tend to parallel tendencies in *Palaeolagus*: on the upper cheek-teeth the primitive pattern of crescents wears away earlier and the hypostriae persist longer in the later species of both genera; the development of palate and zygoma shows trends in the same direction as do those structures in the later species of *Palaeolagus*. Nevertheless, *Megalagus* tends to lag behind *Palaeolagus* in most dental characters. To judge by the known fossil record, *Megalagus* became extinct in the early Miocene and left no descendants.

Megalagus brachyodon (Matthew)

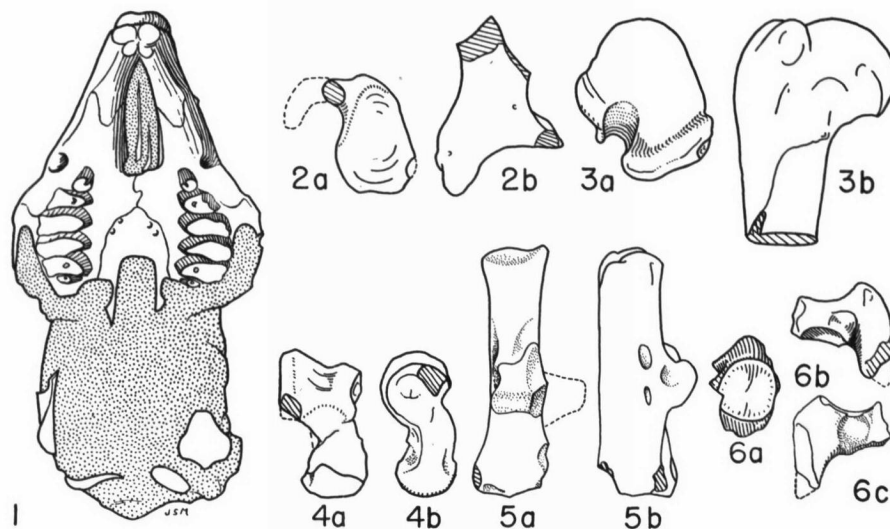
Palaeolagus brachyodon MATTHEW, Amer. Mus. Nat. Hist., Bull., v. 19, art. 6, p. 217, May 9, 1903.
Megalagus brachyodon, WOOD, Amer. Philos. Soc., Trans., v. 28, pt. 3, p. 343, April, 1940 (this assignment is implied by BURKE, 1936, p. 150-152, but the first formal reference is that by WOOD).

Type specimen.—Left maxilla with P^2 - M^2 , A.M.N.-H. No. 9652, Titanotherium beds, Pipestone Springs, Montana.

Geologic age and distribution.—Chadronian (early Oligocene): Pipestone Springs, Montana; ?Cypress Hills, Saskatchewan.

Specific characters.—*M. brachyodon* differs from other species in the genus as follows: cheek-teeth lower crowned; primitive pattern of upper cheek-teeth retained longer and P^3 and P^4 less molariform; M^3 seemingly larger; anterior root of zygomatic arch arises closer to alveolar border.

The late Eocene genus *Mytonolagus* appears to be closely allied and ancestral to this primitive species of *Megalagus*. *M. brachyodon* is probably ancestral to *M. turgidus* (MATTHEW, 1903, p. 218). It is likely that the specimens, seemingly lost, from the Cypress Hills of Saskatchewan referred to *M. turgidus* by COPE were actually referable to this species (WOOD, 1940, p. 340).

FIGURES 1-6. *Megalagus turgidus* (C.I.T. No. 1563).

1. Ventral view of skull, $\times 1$.—2. Apex of left scapula, $\times 2$; 2a, articular surface; 2b, lateral view.—3. Proximal end of left humerus, $\times 2$; 3a, articular surface; 3b, lateral view.—4. Right astragalus, $\times 2$; 4a, dorsal view; 4b, medial view.—5.

Right calcaneum, $\times 2$; 5a, dorsal view; 5b, lateral view.—6. Right navicular, $\times 2$; 6a, proximal view; 6b, medial view; 6c, lateral view.

Megalagus turgidus (Cope)

Plate 1; Figures 1-6

Palaeolagus turgidus COPE, *Palaeont. Bull.*, no. 16, p. 4, August 20, 1873.
Megalagus turgidus, WALKER, *The Aerd*, v. 2, no. 4, p. 234, Fall, 1931.
Palaeolagus triplex COPE, *Palaeont. Bull.*, no. 16, p. 4, August 20, 1873.
Tricium paniense COPE, *Palaeont. Bull.*, no. 16, p. 5, August 20, 1873.

Type specimen.—Part of left lower jaw having broken incisor, P₃-M₃, A.M.N.H. No. 5635, Oreodon beds, Cedar Creek, Colorado.

Geologic age and distribution.—Orellan (middle Oligocene) and probably Whitneyan (late Oligocene) of Great Plains.

Specific characters.—Upper cheek-teeth more hypsodont and with buccal parts of pattern less persistent than in *M. brachyodon*; internal hypostriae on upper molars less persistent and palatine component of palate proportionately longer than in *M. primitivus*.

Description.—Previous descriptions of specimens of this species are based primarily on a nearly complete skull, No. W.M. 1642, described by OLSON (1942, p. 505-511), and parts of skulls, dentitions, and fragmentary portions of the postcranial skeleton discussed by COPE (1884, p. 882-885) and WOOD (1940, p. 332-342). Thus, although the skull is known, the only descriptions of the postcranial skeleton have been based on incomplete material consisting mostly of the ends of limb bones. A specimen of *M. turgidus*, which was available for my study, C.I.T. No. 1563 (Pl. 1), consists of a skull, mandibular rami, and partial postcranial skeleton. The skull offers some additional information to that given by No. W.M. 1642; the postcranial material makes possible a fairly complete description of the structure and proportions of the skeleton. This descriptive information may contribute to a clarification of the phylogenetic position of this large leporid.

Its dentition, which is completely preserved except for right M₃, indicates that C.I.T. No. 1563 is ontogenetically older than No. W.M. 1642. The pattern is almost completely worn away on the upper cheek-teeth: the only remnants remaining are an anteromedial reentrant on P², part of the isolated crescent between central and lingual lobes on P³, and isolated, enamel lined lakes on M²-M³. At this stage of wear, P³-M² are wider transversely than are teeth in younger specimens. External roots are visible on P³-M². In the lower jaw, P₃ lacks an internal reentrant, and the external reentrant does not persist to the alveolar border.

Skull. Some of the sutures of No. 1563 do not agree in position with some described by OLSON in No. W.M. 1642. Reexamination of the latter revealed that cracks obscured the pattern of some of the sutures in that specimen. OLSON (1942, p. 508) describes the suture between the maxilla and the premaxilla lateral to the incisive foramen as passing "medially almost at right angles to the axial plane of the skull". C.I.T. No. 1563, which is better preserved, shows that lateral to the incisive foramen the premaxilla forms a V-shaped process with its apex directed posteriorly, generally resembling that process in *Palaeolagus haydeni*. In *M. turgidus* the part of the maxilla bordering the incisive foramen and medial to that V-shaped premaxillary process is proportionately larger than in *P. haydeni*.

On the palate the incisive foramina terminate in line with the middle of P². The internal nares, which are proportionately wider in *M. turgidus* than in *P. haydeni*, extend forward to a level between M¹ and M². According to OLSON (1942, p. 508), the maxillopalatine suture on the palate "passes anteromedially to the fenestra [incisive foramen] so that the palatine forms a small portion of the posterior border of this structure and the maxillaries fail

to meet". The palate is considerably broken in No. W.M. 1642, and the "suture" mentioned above appears to be due to cracking. Relationships of the maxilla and palatine are more clearly shown in C.I.T. No. 1563 (Fig. 1), which has an essentially unbroken palate. The suture arches anteriorly and extends to a level between P³ and P⁴; the palatines do not completely separate the maxillae nor do they form part of the border of the incisive foramina. The bony bridge of the palate is essentially like that in *P. haydeni*, but the palatine component forms a slightly larger proportion of the palatal length in *M. turgidus* and is proportionately somewhat narrower anteriorly than is that in *P. haydeni*. In proportions of the palate *M. turgidus* may be slightly more primitive. At least two palatine foramina perforate each side of the palate a short distance posterior to the maxillopalatine suture.

The squamosal is incompletely preserved in C.I.T. No. 1563, but a piece of bone and an impression on the matrix indicate that this bone sent back a curved process dorsal to the opening of the external auditory meatus. This process, which is similar to that in *P. haydeni*, covers part of the mastoid. More dorsal portions of the squamosal are not preserved. OLSON (1942, p. 509) states that there is in No. W.M. 1642 along the parietosquamosal suture "a large, elongate temporal foramen, a structure unusual among the leporids". Above the "foramen" in that specimen remnants of both squamosal and parietal are present, and below it is the curved dorsal border of the mastoid. If there were an opening, it must have been between squamosal and mastoid, or within the squamosal, not along the parietosquamosal suture. However, even there an opening may not have existed. Specimens of *Palaeolagus haydeni*, including C.I.T. Nos. 1402 and 1547, show that breakage of the thin squamosal over the mastoid occurs frequently, resulting in the appearance of a temporal opening, but in more completely preserved specimens such an opening does not exist. In No. W.M. 1642 the aperture in the temporal region may be the result of similar breakage. *Megalagus turgidus* probably had no temporal foramen or at most only a small gap between the squamosal and mastoid.

The nasals are broken anteriorly, but an impression on the matrix suggests that these bones extended slightly more anteriorly than do the premaxillae. About half way back, the nasals are deeply pitted along their lateral borders. The dorsal surface of the frontals is rugose and somewhat pitted. The anterior root of the zygoma extends outward approximately in line with the middle of P³.

The auditory bulla in *Megalagus turgidus* is proportionately and absolutely smaller than that in *Palaeolagus haydeni*. The surface of the well-developed mastoid is rugose, and the wide, crested mastoid process contacts the paroccipital process for almost its entire length. These two processes are directed anteroventrally; in *P. haydeni* these processes are oriented more nearly vertically due to the larger size of the auditory bulla, against which the processes lie. The stylomastoid foramen is between the mastoid process and the posterior side of the external auditory meatus. In *P. haydeni* a variably developed ridge crosses the mastoid from its dorsoposterior corner onto the mastoid process. *M. turgidus* lacks this ridge, but the

posterolateral border of the mastoid is ridged; the mastoid extends onto the occipital surface medial to this ridge. The supraoccipital, which reaches only a short distance onto the dorsal skull surface, is pitted and has a medial ridge on the occipital surface from its dorsal margin to the dorsal border of the foramen magnum. *P. haydeni* has a corresponding ridge and also one on each lateral margin of the supraoccipital. These lateral ridges extend upward to the dorsolateral corners of the occiput as buttresses, which are less prominent in *M. turgidus* than in *P. haydeni*. The dorsal and lateral borders of the occipital surface are formed by a ridge that crosses the supraoccipital, posterolateral side of the mastoid, and the paroccipital process. The foramen magnum is wider than it is high, and the occipital condyles are more nearly horizontal in orientation than in *P. haydeni*. The less prominent occipital ridges and more nearly horizontal occipital condyles suggest that the neck muscles were weaker and the head was carried with less flexure at the neck in *M. turgidus* than in *P. haydeni*.

The jugular fossa, bordered medially by the occipital condyle and laterally by the bulla and paroccipital process, is less constricted transversely in *M. turgidus* than in *P. haydeni*, due to the smaller bulla in the former. The condyle is pierced by two foramina that probably transmitted branches of the hypoglossal nerve. The jugular foramen is an elongate opening lateral and anterior to the more ventral of these foramina and ventral to the portion of the exoccipital that extends laterally toward the paroccipital process. Lateral and slightly anterior to the jugular foramen is another opening, probably the external carotid foramen. In *P. haydeni* this foramen is situated more anteriorly and in *Lepus* still more so.

Lower jaw. In general shape the horizontal ramus of the lower jaw in *Megalagus turgidus* resembles that in *P. haydeni*. The swelling over the shaft of the incisor extends to a level below P₄ or to between P₄ and M₁, thus being slightly shorter than in *P. haydeni*. The masseteric fossa is bordered anteriorly by a V-shaped ridge, which is somewhat heavier than the corresponding ridge in *P. haydeni*. In C.I.T. No. 1563 the angular process and an impression on the matrix show that the posterior border of the ascending ramus in *M. turgidus* is less concave than in *P. haydeni*, resulting in the appearance of a less elongate angular process in *M. turgidus*.

Compared to that in *Palaeolagus haydeni*, the skull in *Megalagus turgidus* is much larger, has a heavier muzzle, and much smaller bullae. The angle between the axes of the basicranial segment of the skull and the palate is approximately the same in these two species, or possibly the angle is slightly less in *M. turgidus*. Following study of the skull in *M. turgidus*, OLSON (1942) concluded that *Palaeolagus* and *Megalagus* are on a similar evolutionary plane but differ generically. The present study reveals that in two features relied upon by OLSON to differentiate *Megalagus* and *Palaeolagus*, the shape of the palatine bone on the palate and the position of the maxillopremaxilla suture, the two genera do not differ greatly. Nevertheless, the remaining differences in the skull and dentition appear to be of generic worth. The stages of evolutionary development of *P. haydeni* and *M. turgidus* are difficult to evaluate, but *M. turgidus* is more primitive in denti-

tion and possibly in palatal proportions. The more nearly horizontal orientation of the occipital condyles and seemingly weaker ridges for occipital muscle attachment on the occiput may also be primitive features in *M. turgidus*. The proportionately wider internal nares in *M. turgidus* could be an advanced feature or an adaptive one related to the much greater bulk of this leporid.

Postcranial skeleton. Previous reports on the postcranial skeleton of *Megalagus turgidus* have been based mostly on the ends of various bones and fragments; among such descriptions are those of COPE (1884, p. 884-885) and WOOD (1940, p. 337-339). Postcranial elements of C.I.T. No. 1563 make a more complete description possible. Preserved parts of the specimen are fragmentary vertebrae and ribs; a partial scapula; humeri, radius and ulna; fragments of the pelvis; left femur and tibiofibula; incomplete right femur; astragalus, calcaneum, and navicular. The following description is based mostly on this specimen, although information from additional specimens has been utilized.

In general conformation, the scapula in *Megalagus turgidus* resembles that in *Palaeolagus haydeni*; in both species the supraspinous and infraspinous fossae are subequal, and the neck of the scapula is short and wide. In the Recent leporids the supraspinous fossa is proportionately reduced, the neck is longer and narrower, and the scapular spine is free for a greater proportion of its length. Viewed laterally the glenoid cavity (Fig. 2b) is approximately as concave as are those in *P. haydeni* and *Ochotona*, but less so than in the Recent leporids. The posterior part of the glenoid cavity (Fig. 2a) is slightly expanded transversely, nearly as much as in *Ochotona* but is not so much elongated transversely as in later leporids. A trace of this elongation occurs in *P. hypsodus* from the lower Miocene; the elongation is present in the Recent *Romerolagus*, is more pronounced in *Hypolagus* and *Sylvilagus*, and is still better developed in *Lepus*. This elongated portion of the glenoid cavity is less concave transversely in *M. turgidus* than in the Recent leporids.

In lateral view the humerus is convex anteriorly approximately as in *P. haydeni* and more so than in *Sylvilagus* and *Lepus*. The deltoid crest forms a distinctly raised ridge that extends about half the length of the bone, as do those crests in *P. haydeni* and *Ochotona*, and farther than those in *Sylvilagus* and *Lepus*. About 8.5 mm. below the proximal end of the greater tuberosity the deltoid crest bends onto the lateral side of the shaft at almost a right angle to the more distal portion of the crest. The structure of the crest seems to indicate a larger area for muscle attachment on the humerus in *M. turgidus* than in *P. haydeni*. The proximal end of the greater tuberosity is approximately level with, or a little lower than, the head of the humerus (Fig. 3b); this tuberosity in *P. haydeni* is slightly lower but in Recent leporids is higher. The lesser tuberosity is somewhat more strongly ridged than in *P. haydeni*. On the proximal end of the humerus a series of changes in orientation of greater and lesser tuberosities can be observed when comparing the fossil leporids with the Recent species. In *Megalagus turgidus* (Fig. 3a) the long axis of the greater tuberosity is anteromedial to posterolateral and that of the lesser tuberosity is slightly anterolateral to posteromedial, but mostly anteroposterior.

In *P. haydeni* the greater tuberosity is oriented essentially like that in *M. turgidus*, but the lesser tuberosity is a little more nearly transverse. The series *Romerolagus-Hypolagus-Lepus* shows in increasing development, more anteroposterior orientation of the greater tuberosity and a more nearly transverse orientation of the lesser tuberosity. The bicipital groove is deep, exceeding that in *P. haydeni*. The humeral heads in *M. turgidus* and *P. haydeni* are evenly curved and globular. In the Recent leporids, however, the medial and lateral parts of the head are more distinctly separated by a shallow concavity, which is a continuation of the bicipital groove, the medial portion of the head is more elongate in a medial direction, and the proximal end of the head is more flattened than in *M. turgidus* and *P. haydeni*. In addition, the humeral heads in the Recent leporids overlap the shaft posteriorly more than in the two fossil species. The relatively primitive structure of the head of the humerus in *M. turgidus* and *P. haydeni* suggests greater flexibility at the shoulder than in the Recent leporids, in which the structure of the glenoid cavity and proximal end of the humerus indicate action more restricted to, and specialized for, anteroposterior movement.

The distal end of the humerus is wider, proportional to the length of the humerus, in *M. turgidus* than in *Sylvilagus* and *Lepus*. The supinator crest is well developed, and a supratrochlear foramen is present. No trace of an entepicondylar foramen, which is present in *Palaeolagus*, is seen in this specimen, although the position of the humerus in the matrix may obscure such a foramen. The distal end of the humerus does not have such a distinctly pulleylike appearance as that in the Recent leporids. The medial keel is better developed than the lateral one, and both keels seem to be more distinct than in *P. haydeni* but less so than in *Hypolagus*, *Sylvilagus* and *Lepus*. The medial condyles in *M. turgidus* and *Palaeolagus* are proportionately larger than in Recent leporids; possibly the flexors of the carpus and manus, which originate on that condyle, were stronger in *M. turgidus* and *Palaeolagus* than in the Recent leporids. The structure of the distal end of the humerus in *M. turgidus* indicates an early stage in leporid development in which movement is somewhat restricted to an anteroposterior direction, but specialization is lacking for the highly efficient movement at the elbow seen in the later leporids. The distal end of a humerus referred to *Palaeolagus turgidus* by COPE (1884, p. 884; pl. 67, figs. 22-22c) is not that of a leporid, as was recognized by WOOD (1937, p. 37).

The ulna in *M. turgidus* is well developed and is convex anteriorly as in *Palaeolagus haydeni*. The ulnar shafts in *Sylvilagus* and *Lepus* are more reduced. On the anterior surface of the shaft two ridges, bounding a slightly depressed area, extend from below the semilunar notch toward the distal end of the bone. Similar ridges are present in the Recent leporids, in which the more medial ridge is in contact with the radius. In *M. turgidus* the medial ridge is lower and does not reach so far proximally as in *Sylvilagus* and *Lepus*. The proximal end of the ulna bends medially as does that in *Palaeolagus*. The groove on the olecranon for the triceps is bounded by higher medial and lower lateral ridges; the groove is more concave than in *P. haydeni*, but less so than in *Sylvilagus* or *Lepus*. On

the distal end of the ulna there are two articular surfaces as in *P. haydeni*, an anteromedial facet and a posterolateral styloid process, which forms slightly less than half the distal end. The anteromedial facet becomes reduced in the later leporids; in *Lepus* only a trace of it remains, and the styloid process forms most of the functional articulation surface.

The shaft of the radius is slightly convex anteriorly, approximately as in *P. haydeni*, and its posterior surface has a wide, shallow, longitudinal groove. On the proximal end the notches in which the distal keels of the humerus insert are deeper than in *P. haydeni* and *Ochotona* but less distinct than in Recent leporids. The distal articular surface is slightly concave and essentially three-sided: the anterior border is slightly concave in the middle, the posteromedial and posterolateral borders intersect posteriorly in a wide angle, and the corners are rounded. This articular surface is larger in proportion to the length of the bone and less concave than in *Sylvilagus* and *Lepus*.

Well-developed muscles in the shoulder and forelimb in *Megalagus turgidus* are indicated by the supraspinous fossa, greater tuberosity, and long deltoid crest of the humerus. Not only does the forelimb seem to have been more muscular than those in the Recent leporids, but also it seems to have been capable of a greater latitude of movement, especially at the shoulder, as the configuration of the glenoid cavity and head of the humerus suggests. The Recent leporids are more specialized for efficient anteroposterior movement. *Sylvilagus* and *Lepus* are characterized by reduction of the shaft of the ulna and greater elongation of the radius and ulna in proportion to the length of the humerus; both features are cursorial adaptations. Although *M. turgidus* and *P. haydeni* are on essentially the same level of evolutionary development in the forelimb, *M. turgidus* does seem slightly advanced in the structure of the greater tuberosity, deltoid crest, and elbow. The differences are slight, and possibly some of them were necessitated by the larger size in *M. turgidus*.

Neither side of the pelvic girdle is complete in No. 1563; on the left side, parts of the ilium, acetabulum, and ischium are present; on the right only a few fragments of bone are present, but an impression in the matrix shows the general shape of the inner side of the right innominate. From this impression it appears that in general the ischium and auricular surface on the ilium resembled those structures in *P. haydeni*. The blade of the ilium, like that in *Palaeolagus*, is divided by a rounded crest into two fossae. The dorsal edge of the ilium rises gradually marking the place of sacral articulation; this rise is more gradual than in *P. haydeni*. The tubercle of the ilium in *M. turgidus* is a distinct, raised process, extending out from the ventrolateral border of the ilium in a position similar to that in *P. haydeni*, but is lower and thicker than in the latter. Immediately posterior and slightly dorsal to this tubercle, a distinct, knoblike process fills the space between the tubercle and the anterior border of the acetabulum. This process is similar in general to that in the new genus named on page 32 but is proportionately larger and closer to the tubercle of the ilium and may represent the same thing functionally as the raised area posterior to the tubercle of the ilium in *P. haydeni* and the similarly situated ridge in *Ochotona*.

In lateral view the shaft of the femur in *M. turgidus* is straight, resembling those in *P. haydeni* and *Ochotona* but differing from the anteriorly convex shafts in *Sylvilagus* and *Lepus*. The posterior surface of the bone also resembles that in *P. haydeni* in being somewhat rounded, in contrast to more flattened surfaces in *Sylvilagus* and *Lepus*. The greater trochanter is divided by a ridge into a smaller anterior and a larger posterior portion, and is proportionately higher than in *P. haydeni* but lower than in *Sylvilagus* and *Lepus*. The long axis of the greater trochanter in *P. haydeni* is almost completely anteroposterior, but in *M. turgidus* is more anterolateral to posteromedial; consequently the intertrochanteric fossa is more inclosed in the latter. In this orientation *M. turgidus* shows advance toward the characteristic structure in *Sylvilagus* and *Lepus*, although in these Recent genera the orientation is more nearly transverse and the intertrochanteric fossa is more enclosed. The third trochanter forms a definite process starting about 14.4 mm. below the proximal end of the greater trochanter; a low ridge runs from the proximal portion of the third trochanter toward the greater trochanter. Although matrix covers the lesser trochanter in C.I.T. No. 1563, another specimen, A.M.N.H. No. 5662, shows that the proximalmost part of the third trochanter reaches approximately to a level opposite the middle of the lesser trochanter; this is more proximal than in *P. haydeni* but less so than in the Recent leporids. The proximal end of the femur is not expanded into a flattened plate in *M. turgidus*, whereas it is so expanded in *Sylvilagus* and *Lepus*. The distal end of the femur is massive and generally similar to that in other leporids. On the posterior surface above the condyles a ridge crosses the bone from its lateral side toward, but not quite reaching, the midline. A short ridge on the medial side of the posterior surface parallels the long axis of the femur. Both ridges resemble those in *P. haydeni*; in *Sylvilagus* and *Lepus* the ridge from the lateral side is longer, passing the midline. This difference seems to indicate that the extensors of the foot originating on that ridge were weaker in *Megalagus* and *Palaeolagus* than in *Sylvilagus* and *Lepus*.

The lateral side of the tibiofibula is buried in matrix, and details of the fibula therefore cannot be determined. In anterior view the shaft is slightly convex medially and the proximal condyles face somewhat laterally. This curvature seems to be greater than in *P. haydeni* and much more than in *Lepus*. In medial view the tibiofibula is convex posteriorly, more so than in *P. haydeni* and the Recent leporids, and the distal end bends forward about as in *P. haydeni*. The cnemial crest and proximal end of the bone resemble the corresponding parts in *P. haydeni* in general, except that the tibial tuberosity in *M. turgidus* is proportionately higher and larger. The distal end of the tibiofibula is wider, relative to the length of that bone, than in *Sylvilagus* and *Lepus*. The medial half of the distal end is broken from C.I.T. No. 1563, but other specimens show that the facets for the astragalus are prominent, the keels are higher than in *P. haydeni*, and a faint ridge blocks the anterior margin of the groove that accommodates the medial keel of the astragalus (Wood, 1940, p. 338). The lateral facet for articulation with the calcaneum is less concave than in *Sylvilagus* and

Lepus. The anterolateral border of the facet is curved, as in *P. haydeni* and *Ochotona*, in contrast to the definite anterior and lateral borders, which lie at an angle to one another, that are present in *Sylvilagus* and *Lepus*. The groove for the lateral keel of the astragalus seems to be proportionately deeper than in *P. haydeni* but shallower than in *Sylvilagus* and *Lepus*. The tibiofibula in *M. turgidus* is less elongate in proportion to the length of the femur than in *P. haydeni*: in the former the ratio of tibiofibula to femur is 1.02 and in the latter 1.16. Thus, in proportions of the hind limb *M. turgidus* seems to have been less adapted for cursorial life than was *P. haydeni*.

Of the tarsal bones, astragalus (Fig. 4), calcaneum (Fig. 5), and navicular (Fig. 6) are present in C.I.T. No. 1563. As in *P. haydeni* the astragalus reaches approximately the same distance distally as does the calcaneum; in *Hypolagus* and the Recent leporids the calcaneum extends more distally than the astragalus, making possible a calcaneonavicular contact. On the calcaneum the tuber calcis is proportionately wider and its medial ridge is higher than in *P. haydeni*; the tuber is still wider proportionately and the medial ridge more pronounced in *Sylvilagus* and *Lepus*. The knoblike process for articulation with fibula and astragalus has a lateral facet for fibular articulation which generally resembles that in other leporids in shape. Medially on this knoblike process the facet for the astragalus has a ridge separating two distinct surfaces, one facing more proximally and the other more distally. The corresponding facet for the astragalus in *P. haydeni* forms one continuous, gently rounded surface, proportionately shorter than in *M. turgidus*, whereas that facet in *Hypolagus* and the Recent leporids is more distinctly separated into two surfaces by a sharper ridge than in *M. turgidus*. The facet for articulation with the cuboid approaches the L-shape of that in the later leporids, thus being slightly more advanced than is that facet in *P. haydeni*. The keels of the astragalus are proportionately larger than in *P. haydeni* but smaller than in *Sylvilagus* and *Lepus*. In *M. turgidus* there is a greater difference than in *P. haydeni* between the keels, the lateral being proportionately larger in *M. turgidus*. In the Recent leporids the neck of the astragalus is essentially in line with the long axis of the keels, but in *M. turgidus* and *P. haydeni* the neck bends slightly more medially. The rounded articular surface of the keels extends onto the plantar surface a shorter distance than in Recent leporids. Correlated with the development of the facet for the astragalus on the calcaneum described above, the astragalus has two distinct facets on its plantar surface for contact with that facet of the calcaneum. In *P. haydeni* this articular surface on the astragalus forms a continuous concavity, whereas in *Hypolagus* and the Recent leporids the facets become more distinct and are separated by a deeper groove than in *M. turgidus*. On the lateral side of the head, the rounded process that contacts the calcaneum is proportionately larger than in *P. haydeni*. The head is proportionately wider transversely than in *P. haydeni* or in the Recent leporids, and its articular facet does not extend so far up the dorsal surface of the astragalus as in *Sylvilagus* and *Lepus*. Thus, the astragalus and calcaneum are more advanced than in *P. haydeni*. Contact between these bones was probably less firm than in the Recent leporids. The

structure of the astragalar keels suggests that less anteroposterior bending was possible at the tarsus in *M. turgidus* than in Recent leporids. The navicular is not known in *P. haydeni*. This bone in *M. turgidus* is less elongate proximodistally than in *Hypolagus* and the Recent leporids but is of the same general shape. The facet for articulation with the astragalus is slightly less concave, and is more rounded and less elongate dorsoventrally than in *Hypolagus* and the Recent leporids. On the lateral side of the bone a distinct notch for articulation with the cuboid extends the full distance between proximal and distal articular surfaces. In *Hypolagus* and the Recent leporids the notch for navicular-cuboid contact is limited to the more distal part of the lateral surface, and proximal to this notch an articular surface for contact with the calcaneum is developed. This contact, which is lacking in *Megalagus*, seems to be an adaptation in the later leporids to strengthen the tarsus and reduce movement between proximal and distal tarsal rows. The tarsus in *M. turgidus* is more primitive in this regard. On the medial side of the navicular a rounded knob marks the place of contact with the proximal end of metatarsal II (or with the entocuneiform, which is fused with metatarsal II in *Ochotona*, *Hypolagus*, and the Recent leporids, and probably in *Megalagus*); this knob does not reach so far proximad in the Recent leporids but has a greater development on the distal surface of the navicular than in *M. turgidus*. The facet for articulation with the mesocuneiform is proportionately larger in *M. turgidus* than in *Hypolagus* and the Recent leporids. The structure of the medial knob and the articulation for the mesocuneiform suggest that the medial side of the foot was better developed and that the medial digits were capable of a greater range of movement in *M. turgidus* than in *Hypolagus* and the Recent leporids.

Summary. WOOD concluded, on the basis of a study of the postcranial elements available to him, consisting mostly of ends of long bones and fragments of the pelvis, astragalus and calcaneum, that *Megalagus turgidus* shows advance over *Palaeolagus haydeni* in better developed keels, firmer union of the bones and areas for muscle attachment that indicate stronger muscles, which contracted more rapidly. On this evidence, it was suggested that *P. haydeni* was in approximately the same stage of locomotive evolution as is *Ochotona*, and that *M. turgidus* was in approximately the same stage as is *Sylvilagus* (WOOD, 1940, p. 338-339). Evidence from more complete skeletal parts, however, does not completely support this interpretation. On the basis of this additional evidence, *M. turgidus* does seem to be more muscular than *P. haydeni*: the structure of the scapula shows that this element was as well developed as in *P. haydeni*, and the tuberosities and crest on the humerus suggest strong muscles; the medial condyle of the humerus suggests well-developed muscles to the manus; the heavy iliac tubercle and trochanters of the femur suggest a well-muscled hind limb. The prominent keels and firmer union of the bones mentioned by WOOD are advances toward the structure in later leporids. However, possibly these are adaptations necessary in a larger animal, rather than indications of better cursorial adaptation. In *M. turgidus* the deltoid crest is proportionately as long as in *P. haydeni*, and the third trochanter is

only slightly higher than in the latter; consequently, there is no strong evidence for raised muscular insertions and hence for more rapid movement in the larger leporid. The more pronounced curvature of the tibiofibula in *M. turgidus* is not a cursorial modification. The proportions of the hind limb show that the distal segment is less elongated than in *P. haydeni*; since elongation of the distal elements is an adaptation of more cursorial animals, the proportions of *M. turgidus* suggest that it was less cursorial than *P. haydeni*. Added to the evidence from the postcranial skeleton, the structure of the occipital region of the skull suggests that the head in *M. turgidus* was carried more nearly horizontally than in *P. haydeni*. The latter probably had proportionately greater flexure at the neck, which is a tendency toward the posture of the later leporids and is an adaptation for their bounding mode of locomotion. *Megalagus turgidus* seems to have been a large, muscular leporid that had well-developed ends of the bones, possibly necessitated by its larger size. It was probably no more cursorial than its smaller contemporary, *P. haydeni*, and in general level of postcranial evolution, *M. turgidus* and *P. haydeni* are closer to one another than either is to *Sylvilagus*.

TABLE 1.—Measurements in millimeters of *Megalagus turgidus*, C.I.T. No. 1563

length of skull, estimated	67.3+
width across anterior roots of zygomata	32.5
width nasals posteriorly	13.3
width palate between P ⁴	11.6
length palate	10.5
length palatine on palate	6.6
length maxilla on palate	3.9
width internal nares	4.4
length P ³ -M ³	14.0
length P ³ -M ²	12.0
length P ₃ -M ₃	14.4
length P ₁ -M ₃	9.8
inside depth of jaw below M ₁	11.1
dorsoventral length scapula	ca. 46.8
length humerus	50.2
anteroposterior length proximal end of humerus	11.0
transverse width proximal end of humerus	9.0
transverse width distal end of humerus	ca. 8.9
length ulna	ca. 54.3
length radius	44.4
length femur	70.2
transverse width proximal end femur	ca. 12.6
length tibiofibula	71.5
proximodistal length astragalus	9.6
proximodistal length calcaneum	16.8
proximal width calcaneum	4.5
distal width calcaneum	4.8
greatest proximodistal length navicular	6.3
least proximodistal length navicular	2.8
transverse width navicular	4.5

Megalagus primitivus (Schlaikjer)

Hypolagus primitivus SCHLAIKJER, Mus. Comp. Zool., Bull., v. 76, no. 4, p. 127, May, 1935.

?*Palaeolagus primitivus*, WOOD, Amer. Jour. Sci., v. 33, p. 40, January, 1937.

Type specimen.—Partial skull with right P²-M³, M.C.Z. No. 2887, lower Miocene, approximately 150 feet above Brule-lower Harrison contact, Goshen County, Wyoming.

Geologic age and distribution.—Arikareean (early Miocene), Wyoming.

Specific characters.—Size near that in *M. turgidus*; isolated lakes from hypostriæ tend to be better developed and more persistent than are those in other species of the genus; palatine component of palate proportionately shorter than in *M. turgidus*; orbit relatively large.

Description.—The teeth of the type, which is the only known specimen definitely referred to this species, are in an advanced stage of wear. On the upper cheek-teeth the following remnants of pattern remain: on P² a single anterior reentrant that does not persist throughout the length of the tooth; on P³ a shallow lingual groove representing the internal hypostria and an isolated remnant of the crescentic valley between central and lingual lobes; on M¹ and M² isolated portions of the internal hypostriæ, slightly crenulated; and on M² a shallow groove of the hypostria on the lingual wall. At this stage of wear P³-M² are widened transversely, and P² and M³ are relatively small. Well-developed roots are visible externally on P³-M¹. Cement is not extensive but does seem to fill the isolated crescent and hypostriæ. The bony palate extends between the posterior ends of the incisive foramina, approximately on a line with the posterior edge of P², and the internal nares, about in a line with the middle of M¹. In the midline a long, tapered process formed by the maxillæ extends between the posterior ends of the incisive foramina. The suture between maxillæ and palatines reaches anteriorly to a line between P³ and P⁴; this suture is somewhat less arched anteriorly than in *Megalagus turgidus*. In *M. primitivus* the palatine forms a slightly smaller proportion of the palatal length than in *M. turgidus*. The fragmentary skull of the type specimen of *M. primitivus* differs from that in *M. turgidus* in several features: in *M. primitivus* the orbit is deeper dorsoventrally, the anterior portion of the zygomatic arch is shallower dorsoventrally, and the posterior ends of the frontal processes of the premaxillæ extend to the posterior ends of the nasals, whereas these processes terminate more anteriorly in *M. turgidus*.

Relationships.—That the original reference of this species to the genus *Hypolagus* is incorrect was recognized by WOOD (1937, p. 39-40; 1940, p. 331) who suggested that the species "is referable either to *Megalagus* or to a genus close to that form", but left it provisionally in "*Palaeolagus*". SCHLAIKJER considered the slight crenulations in the hypostriæ of M¹ and M² in *M. primitivus* to suggest that this species represents a primitive member of the genus *Hypolagus* (1935, p. 127-129). However, slight crenulations also occur in the hypostriæ of some specimens of *Palaeolagus* and *Megalagus*; therefore this feature does not prove relationship to *Hypolagus*. *M. primitivus* differs from *Archaeolagus* and *Hypolagus* in the following: presence of roots and of less persistent hypostriæ on the upper cheek-teeth; persistent traces of the primitive leporid pattern of isolated crescents on P³-M², especially on the premolars; less well-developed cement on the teeth; and a more primitive palatal structure. These features are not merely reflections of an early Miocene stage of leporid evolution, for the contemporary leporid named on page 29 is more advanced in dental development and seems closer to the evolutionary line leading to the *Archaeolaginae*. In the presence of buccal roots on the upper cheek-

teeth, the shallow development of the hypostriae on P^8 and P^4 , and the lack of well-developed cement, *M. primitivus* differs from *Palaeolagus*, but resembles the Oligocene species of *Megalagus*. Thus, this early Miocene species should be referred to the genus *Megalagus*. *M. primitivus* is more advanced than *M. turgidus* in somewhat longer retention of the hypostriae on M^1 and M^2 , and in the structure of the palate, in which the palatine forms a shorter portion of the total length, the maxillopalatine suture is slightly less arched, and the internal nares are situated a little more anteriorly. These differences between *M. primitivus* and *M. turgidus* resemble those characterizing different evolutionary levels within the genus *Palaeolagus* and are such as might be expected in a conservative evolutionary series. Resemblances between the species suggest that *M. primitivus* is merely an advanced member of the genus.

The presence of *M. primitivus* along with species of *Palaeolagus* shows that in the early Miocene there was a persistence of advanced species of "typical" Oligocene genera of leporids.

Megalagus cf. *primitivus*

Figure 7

Referred specimens.—The following S.D.S.M. specimens, all lower jaws, are from lower Rosebud beds (lower Miocene) in Shannon County, South Dakota: 53387, NW¼ sec. 24, T. 39 N., R. 43 W.; 54264, NW¼ sec. 20, T. 39 N., R. 43 W.; 54282, SE¼ sec. 31, T. 40 N., R. 43 W.; 54298, SE¼ sec. 18 and NE¼ sec. 19, T. 38 N., R. 43 W.; 5536, SE of Manderson-Pine Ridge road, 3.6 miles southwest of Manderson; 56114, corner sections 13, 14, 23, 24, T. 39 N., R. 43 W.

The six specimens listed above represent a leporid that occurs along with the new species of *Palaeolagus* described below on page 29, which is more abundant in lower Rosebud beds. In size the specimens listed above are close to *Megalagus turgidus*. On the jaw an anterior mental foramen is present on the dorsolateral surface, approximately two-thirds of the way back below the diastema, and one or two posterior mental foramina occur on the lateral surface, approximately below P_4 . Limited pitting is present in some individuals on the lateral surface of the jaw below the diastema, and more extensive pits occur on the surface of the swelling that marks the shaft of the incisor. This swelling extends to below P_3 or the trigonid of P_4 ; in *M. turgidus* the incisor usually terminates more posteriorly, approximately below the talonid of P_4 . Curvature of the line along the ventromedial edge of the horizontal ramus suggests that the rami would diverge outward from one another more than in *M. turgidus*. A well-developed ridge, stronger dorsally than ventrally, forms the anterior border of the masseteric fossa, which reaches forward to below M_3 or the talonid of M_2 .

In some specimens breakage of the jaw exposes the base of the shafts of the teeth, which tend to be somewhat constricted, suggesting the formation of roots. Cement is present, but not extensive, on the teeth. In an adult dentition (Fig. 7b), P_3 has a single external reentrant crossing about half the occlusal surface; this tooth is proportion-

ately shorter anteroposteriorly than in *M. turgidus*; on P_4 , M_1 , and M_2 each, trigonid and talonid are joined by lingual bridges; the anterior wall of the talonid tends to be slightly crenulated. The columns of M_3 , separate in earlier stages of wear, are probably united in the fully adult dentition. Enamel tends to be thick buccally, but in the adult tends to be thinner or absent lingually on P_4 - M_2 , especially on the talonid, and is absent anteriorly on P_4 - M_3 . On P_3 of an adult, enamel is thin posterolingually and on the anterior wall of the talonid in the external reentrant; elsewhere enamel is well developed.

No unworn dentitions are represented, but one specimen of a younger individual, No. 5536 (Fig. 7a), shows an earlier stage of wear on P_3 , in which a small posterolophid is separated from the talonid by a shallow lingual fold. Even in this younger specimen the trigonid and talonid are united lingually without a reentrant intervening, although a shallow groove is present in the place in which this reentrant probably occurred; a second groove on the anterolingual surface may represent a remnant of a fold between the two main cusps of the trigonid. Distinct posterolophids are present on P_4 and M_2 , and at an earlier stage of wear M_1 also probably had a posterolophid. In Nos. 5536, 54264, and 54282, all young indi-

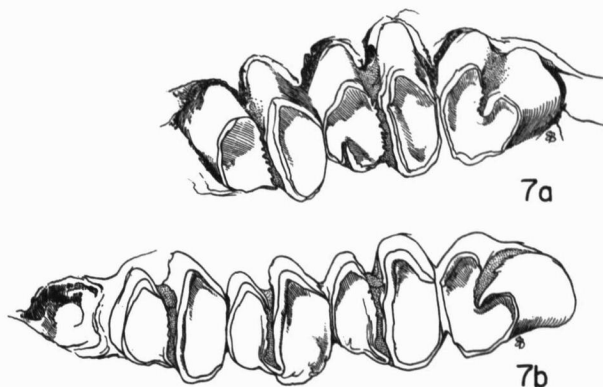


FIGURE 7. Stages of wear in lower cheek-teeth of *Megalagus* cf. *primitivus*.

Occlusal views of cheek-teeth, $\times 4.5$; 7a, left P_3 - M_1 of young individual (S.D.S.M. No. 5536); 7b, left P_3 - M_2 of older individual (S.D.S.M. No. 54298).

viduals, enamel is still well developed on the lingual walls of the talonid of P_3 - M_3 . On the anterior wall of the talonid on P_4 - M_2 and in the external reentrant on P_3 , crenulations in the enamel are better developed in younger individuals than in those having more worn dentitions.

The affinities of this large leporid seem to be with the genus *Megalagus*, as suggested by the general structure of the low-crowned cheek-teeth and short shaft of the incisor. As Wood has shown (1940, p. 336), P_3 in *Megalagus* is characteristically more compressed anteroposteriorly than is that tooth in *Palaeolagus*: in the former the metaconid is rotated backwardly, resulting in close approximation of metaconid and entoconid and early union of these two cusps. *Megalagus* has a small posterolophid on P_3 . In *M. cf. primitivus* P_3 is still more compressed anteroposteriorly, thus seeming to carry further a tendency of the Oli-

gocene species of *Megalagus*, and the posterolophid seems to have been small.

Thus, these specimens are considered to represent an advanced species of *Megalagus*. Whether they are referable to *M. primitivus* is less certain in the absence of associated upper and lower dentitions. However, several lines of evidence favor assignment of these jaws to *M. primitivus*: (1) in stage of evolution both the maxilla of *M. primitivus* and these lower jaws represent an advanced *Megalagus*; (2) the size of *M. primitivus* and these jaws is such that association would be possible; (3) in the lower Miocene beds of Goshen County, Wyoming, three leporids are present—*Palaeolagus hypsodus*, the new species of *Palaeolagus* named below (referred to as *Archaeolagus ennisianus* by SCHLAIKJER), and *Megalagus primitivus*; in the lower Rosebud beds of South Dakota three leporids are present—*P. hypsodus*, the new species of *Palaeolagus*, and the leporid represented by these jaws (a fourth leporid, known from one fragmentary ramus, occurs in South Dakota, but this aberrant form shows no similarity to *Megalagus*); in the lower Miocene (Gering) of Nebraska, *P. hypsodus* and the new species of *Palaeolagus* occur. Occurrence of *P. hypsodus* and the new species in these three areas suggests that a rather uniform leporid fauna may have been widespread; the presence of a third, larger leporid in lower Miocene deposits of Wyoming and South Dakota may be evidence that the maxilla from Goshen County and the lower jaws from South Dakota represent the same species. Due to lack of association it cannot be proved on the basis of known specimens that the jaws in question are *M. primitivus*, but this conclusion seems probable. If these jaws do represent *M. primitivus*, the affinities of that species with other species of the genus *Megalagus* are even clearer than suggested by the type specimen alone.

TABLE 2.—Measurements in millimeters of *Megalagus* cf. *primitivus*

	No. 54298	No. 5536
P ₃ anteroposterior	2.1	2.0
width trigonid	1.8	1.5
width talonid	2.8	2.6
P ₄ anteroposterior	2.9	3.3
width trigonid	3.0	3.0
width talonid	2.6	2.5
M ₁ anteroposterior	3.0	3.2
width trigonid	2.9	2.9
width talonid	2.3	2.6
M ₂ anteroposterior	2.8	
width trigonid	3.0	
width talonid	2.4	
P ₄ -M ₂	8.9	
inside depth of jaw below M ₁	12.0	11.3

Genus *DESMATOLAGUS* Matthew & Granger, 1923

Desmatolagus MATTHEW & GRANGER, Amer. Mus. Nat. Hist. Novitates, no. 102, p. 8, December 31, 1923. Type, *Desmatolagus gobiensis* MATTHEW & GRANGER.

Geologic age and distribution.—Oligocene of Mongolia, China and possibly of Great Plains of North America; possibly late Eocene or early Oligocene of British Columbia and late Oligocene of California.

Generic characters.—MATTHEW and GRANGER (1923, p. 10) characterized this genus as a leporid having P², P₃, M³ and M₃ greatly reduced. WOOD (1940, p. 345) added the following characters: cheek-teeth persistently low

crowned, and buccal openings of valleys in upper molars retained throughout a large part of life.

There is some question regarding the affinities of the genus *Desmatolagus*. MATTHEW and GRANGER (1923, p. 8-10) placed *Desmatolagus* in the family Leporidae on

the basis of the number of cheek-teeth, which is $P \begin{smallmatrix} 3 \\ 2 \end{smallmatrix}$, $M \begin{smallmatrix} 3 \\ 3 \end{smallmatrix}$

as in the leporids; BURKE (1936, p. 149-153) and WOOD (1940, p. 345-350) subscribe to this assignment. However, TEILHARD DE CHARDIN (1926, p. 23), BOHLIN (1942a), and others regard *Desmatolagus* as a member of the family Ochotonidae. Some evidence suggests that the type species, *D. gobiensis*, is an ochotonid, whereas the North American species referred to the genus seem to have characteristics of leporids. The problem of the affinities of *Desmatolagus* and of other ochotonid-like leporids or leporid-like ochotonids is outside the scope of this paper, as is that of the status of *Amphilagus* and *Piezodus*, European genera possibly near *Desmatolagus* (BURKE, 1936, p. 151-152), but the North American species referred to *Desmatolagus* are included here for the sake of completeness. The genus probably did not give rise to any known post-Oligocene leporids in North America.

A worn, isolated upper molar from British Columbia (RUSSELL, 1954, p. 97) and a fragmentary ramus having P₃-M₂ from the upper Oligocene Sespe beds, California (WOOD, 1940, p. 350; WILSON, 1949a, p. 56), have been referred to the genus *Desmatolagus*. These references are tentative at best, and it may be more reasonable to refer the specimens to more common genera of leporids or to regard them as being indeterminate.

Desmatolagus? dicei Burke

Desmatolagus dicei BURKE, Carnegie Mus., Annals, v. 25, art. 16, p. 149, December 12, 1936.

Type specimen.—Left maxilla having P³-M², right lower jaw having P₄-M₃, left lower jaw having M₁-M₂, C.M. No. 814, lower Oligocene of Pipestone Springs, Jefferson County, Montana.

Geologic age and distribution.—Chadronian (early Oligocene) of Montana.

Specific characters.—Larger than *Desmatolagus robustus*, premolars less well developed, and molars less reduced (BURKE, 1936, p. 149).

Desmatolagus? dicei is difficult to distinguish from its early Oligocene contemporary, *Megalagus brachyodon*, but BURKE (1936) and WOOD (1940) have emphasized the distinctions between the two.

Desmatolagus? gazini Burke

Desmatolagus gazini BURKE, Carnegie Mus., Annals, v. 25, art. 16, p. 150, December 12, 1936.

Type specimen.—Left maxilla having P³-M², C.M. No. 37, middle Oligocene of Oreodon beds, Badland Creek, Sioux County, Nebraska.

Geologic age and distribution.—Orellan (middle Oligocene) of Nebraska.

Specific characters.—Size between that in *Desmatolagus gobiensis* and that in *D. robustus*; premolar-molar proportions nearly as in those species. Differs from *D.*

gobiensis and *D. robustus* in having anterior face of P³ less compressed transversely, posterior wall on M² shorter, and external roots on upper cheek-teeth stronger (BURKE, 1936, p. 150).

Unlike *D. dicei*, *Desmatolagus? gazini*, although known from the type specimen only, seems to be clearly distinct from other middle Oligocene leporids in North America.

Genus PALAEOLAGUS Leidy, 1856

Palaeolagus LEIDY, Acad. Nat. Sci. Philadelphia, Proc., v. 8, p. 89, April, 1856.
Type, *Palaeolagus haydeni* LEIDY.
Trictium COPE, Palaeont. Bull., no. 16, p. 4, August 20, 1873.
Protolagus WALKER, The Aerenid, v. 2, no. 4, p. 230, Fall, 1931.

Geologic age and distribution.—Chadronian (early Oligocene) to Arikarean (early Miocene) of Great Plains; Chadronian of Saskatchewan; possibly Whitneyan (late Oligocene) of California and Arikarean of Texas and Oregon.

Generic characters.—Cheek-teeth more hypsodont and having better developed cement than in *Mytonolagus* and in contemporary species of *Megalagus* and *Desmatolagus?*; teeth in later species of the genus more hypsodont than in earlier species. On P³-M² isolated crescent between central and lingual lobes usually retained, especially on premolars, which are less molariform than in *Archaeolagus*; internal hypostria uncrenulated or having a few small irregularities, usually shorter transversely and worn away more rapidly on premolars than on molars. Lower incisor extends posteriorly along ventromedial edge of lower jaw to below M₁ in primitive species and to below talonid of P₃ in advanced species. On P₃ antero-external groove of trigonid usually lacking, or, if present, shallow and associated with internal reentrant between trigonid and talonid. Anterior root of zygomatic arch situated slightly more posteriorly and extends laterally less abruptly than in *Archaeolagus*. In species in which skull is known, angle between basicranial axis and palate smaller than in *Archaeolagus*.

The limits of the genus *Palaeolagus* are set broadly both horizontally and vertically. As a result of this procedure, several lines of development and several evolutionary levels are included within the genus, and the characterization of the genus must be based in part on trends rather than on absolute characters. The known species of *Palaeolagus* can be divided into three species groups, each of which includes two species that are seemingly more closely allied to one another than either is to any of the other species of the genus. The groups are: the *P. temnodon* group for *P. temnodon* and *P. haydeni*; the *P. burkei* group for *P. burkei* and *P. hypsodus*; and the *P. intermedius* group for *P. intermedius* and the lower Rosebud species named and described below on page 29.

The *P. temnodon* group, having an early to middle Oligocene time span (possibly into the late Oligocene for *P. haydeni*), is geologically oldest and has more primitive characters than the other groups. Among the characters uniting the species in this group are the following: isolated crescents between central and lingual lobes on P³-M² more persistent in general than in other groups; buccal end of internal hypostria on P³ and P⁴ and of internal reentrant on P₃ retained as isolated lakes following sepa-

ration from lingual wall; and on P₄-M₂, trigonid united, following wear, to corresponding talonid by lingual bridge of enamel and dentine.

The other two groups first appear in the higher levels of the middle Oligocene and persist into the lower Miocene. The *P. burkei* group is characterized by the flattened skull, large bullae, long and persistent hypostria on P⁴-M², a crescentic lake on P³ that retains a buccal connection, retention of the internal reentrant between trigonid and talonid on P₃, and union of trigonid and talonid on P₄-M₂ solely by cement during most of life. In this group there is a tendency toward formation of a shallow anteroexternal groove on the trigonid of P₃. The characteristics of the *P. intermedius* group are: larger size than other species of the genus; relatively shallow hypostria on P³ and P⁴ and deep, persistent hypostria on M¹ and M²; early loss of internal reentrant between trigonid and talonid on P₃; and trigonid and talonid on P₄-M₂ joined by lingual bridge following wear.

Although the characteristics of each group set it apart from the other two, resemblances between the species of *Palaeolagus* are marked in relatively young individuals having unworn teeth: for example, immature individuals of *P. haydeni* and *P. burkei* are difficult to differentiate from one another on the basis of tooth pattern alone. The dental differences between the groups seem to be mostly, although not entirely, matters of retention or loss of various parts of the immature tooth pattern. The species of *Palaeolagus* tend to parallel one another in certain trends: the later member in each species group has more hypsodont teeth, a shorter shaft of the lower incisor, and tends to retain the hypostria on M¹ and M² longer than the earlier member. The *P. burkei* and *P. intermedius* groups, which have essentially the same known time range, parallel one another in progressive shortening of the palate, especially of its palatine component. The similarity between immature individuals and parallelism in some characters evidence the close relationships between the species groups of *Palaeolagus*.

The late Eocene or early Oligocene ancestors of all three groups probably resembled one another in general, may have had many of the characteristics that were retained in the *P. temnodon* group, and perhaps, if known, would be included in that group. The *P. burkei* group diverges from the centralized stock in having adaptations that possibly are ochotonid-like; this group does not seem to be ancestral to either the Archaeolaginae or the Leporinae. The *P. intermedius* group has certain advanced characteristics and seemingly leads toward the Archaeolaginae.

Palaeolagus temnodon Douglass

Palaeolagus temnodon DOUGLASS, Amer. Philos. Soc., Trans., v. 20, p. 250, 1901.

Type specimen (lectotype).—Right maxilla having P²-M³, C.M. No. 725a, Pipestone Springs Oligocene, Pipestone Springs, Montana.

Geologic age and distribution.—Chadronian (early Oligocene) of Pipestone Springs and Three Forks, Montana, and possibly of Cypress Hills, Saskatchewan.

Specific characters.—Cheek-teeth lower crowned,

maxillary tuberosities correspondingly lower, and cement less well developed than in other species of the genus. From *P. haydeni*, *P. temnodon* differs as follows: upper cheek-teeth narrower transversely; buccal lobe on P² more persistent; premolars less molariform; buccal portion of internal hypostria on M¹ and M² isolated at earlier stage of wear; on P³-M² crescents between central and lingual lobes retained longer. Shaft of lower incisor extends posteriorly to below M₁. On P₃ following wear internal reentrant forms isolated lake that still later becomes completely worn away. Size near that in *P. haydeni*.

Palaeolagus temnodon is closely allied to *P. haydeni*, and, although possibly not a direct phylogenetic ancestor, is an approximate structural ancestor of *P. haydeni* (WOOD, 1940, p. 320).

Palaeolagus haydeni Leidy

Figures 8-9

Palaeolagus haydeni LEIDY, Acad. Nat. Sci. Philadelphia, Proc., v. 8, p. 89, April, 1856.

Palaeolagus agapetillus COPE, Palaont. Bull., no. 15, p. 1, August 20, 1873.

Tricium avunculus COPE, Palaont. Bull., no. 16, p. 5, August 20, 1873.

Tricium leporinum COPE, Palaont. Bull., no. 16, p. 5, August 20, 1873.

Tricium annae COPE, Washington, Gov't. Printing Office, p. 4, October, 1873.

Protolagus affinis WALKER, The Aerenid, v. 2, no. 4, p. 231, Fall, 1931.

Archaeolagus striatus WALKER, The Aerenid, v. 2, no. 4, p. 236, Fall, 1931.

Type specimen (lectotype).—Right lower jaw having P₃-M₃, A.N.S.P. No. 11031, Turtle bed, head of Bear Creek, Nebraska.

Geologic age and distribution.—Orellan (middle Oligocene) and possibly Whitneyan (late Oligocene) of Great Plains; possibly uppermost Chadronian (early Oligocene) of northeastern Colorado.

Specific characters.—Cheek-teeth higher crowned, on P³-M² crescents between central and lingual lobes less persistent, and internal hypostria tends to retain lingual connection longer than in *P. temnodon*. On P₃ following wear internal reentrant between trigonid and talonid forms isolated lake, which tends to be retained longer than in *P. temnodon*, but which is absent in heavily worn teeth. Anterior root of zygomatic arch farther from alveolar border than in *P. temnodon*.

Palaeolagus haydeni is the common leporid in certain middle Oligocene localities, and its skull and postcranial skeleton are relatively well known. COPE (1884, p. 875-880; pl. 66, figs. 1-27) described and figured skeletal elements of this species, but knowledge of the morphology is based mostly on descriptions by DICE (1933) and WOOD (1940, p. 278-316) of U.M.M.P. No. 14317, a relatively complete specimen. Two specimens utilized in the present study, C.I.T. Nos. 1547 and 1402, offer some additional evidence on the morphology of this species; both specimens are Orellan in age, having come from the lower nodular layers of the Oredon beds, eight miles southeast of Douglas, Wyoming. No. 1547 is a nearly complete skull, and No. 1402, preserved in a "sitting" position, includes the skull and lower jaws, partial vertebral column, including the sacrum and most of the lumbar region, ribs, scapulae, humeri, radii, ulnae, femora, tibiofibulae, pelvic girdle, and metapodials.

In No. 1547 parts of the basicranial region are well preserved. The jugular fossa is deep and transversely constricted, due to the large size of the bulla and the orienta-

tion of the occipital condyle. A single hypoglossal foramen perforates the anterolateral surface of the occipital condyle, in a position similar in general to that in *Lepus*. The jugular foramen occurs dorsal and anterolateral to the hypoglossal foramen, and ventral to the arm of the exoccipital that extends laterally to the paroccipital process. The external carotid foramen is present ventral and slightly anterior to the jugular foramen. In *Lepus* the jugular foramen is essentially on a level with the hypoglossal foramen, rather than dorsal to it, and the external carotid foramen is more anteriorly situated on the medial side of the bulla.

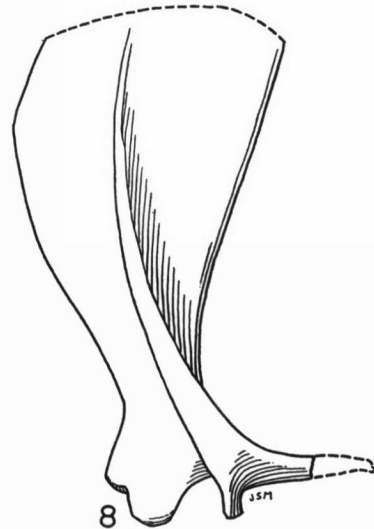


FIGURE 8. *Palaeolagus haydeni* (C.I.T. No. 1402).

Left scapula, lateral view; composite from left and right sides, $\times 2$.

Evidence from No. 1402 adds to knowledge of the postcranial skeleton. On both scapulae parts of the scapular spines, with acromion and metacromion processes, are present. The neck of the scapula is short and wide, and the well-developed spine arises proportionately closer to the glenoid cavity than in *Romerolagus*, *Sylvilagus*, and *Lepus*, and still closer proportionately than in *Ochotona*, in which the spine arises about two-thirds of the distance up the scapular blade from the glenoid cavity. The ventral end of the scapular spine forms distinct acromion and metacromion processes (Fig. 8). Relative to the glenoid cavity the ventral end of the spine is more anteriorly situated than in *Sylvilagus*, *Lepus*, and *Ochotona*. Although possibly incomplete in No. 1402, the acromion process is proportionately longer than in *Sylvilagus* and *Lepus*; this process is lacking in *Ochotona*. The acromion in *P. haydeni* reaches ventrally about as far as the anterior rim of the glenoid cavity, and the metacromion, which is longer than the acromion, is directed posteroventrally. In contrast, the ventral portion of the spine does not reach so far ventrally and the metacromion tends to bend slightly upward in *Sylvilagus* and *Lepus*. DICE (1933, p. 305, fig. 10) described and figured the metacromion of U.M.M.P. No. 14317, but in WOOD's later description it was stated that the metacromion of DICE "does not appear to me to be a part of the scapula, but if it should prove to be the meta-

acromion, I believe that it must have been rotated about ninety degrees from its proper position" (1940, p. 305). Reëxamination of that specimen and the C.I.T. specimen show that DICE's description of a metacromion that is "remarkably long for the size of the scapula" (1933, p. 305) is correct. The acromion is broken from the U.M.-M.P. specimen. The structure of the scapular blade, especially the proportions of the supraspinous and infraspinous fossae, suggests that the forelimb was more muscular in *P. haydeni* than in the living lagomorphs (WOOD, 1940, p. 306). Well-developed acromion and metacromion processes seem to suggest the same thing, with the possibility of stronger muscle attachment on these processes. *Palaeolagus haydeni* probably possessed a stronger forelimb, capable of a greater range of movements, than in *Sylvilagus* and *Lepus*.

A slender bone, about 14 mm. long, lies in the matrix anterior to the head of the humerus, near which its lateral end terminates. In cross-section the lateral part of the shaft of this bone is rounded and the medial part is flattened, and the shaft is slightly curved. Position of this bone in the matrix, the rounded shaft, and lack of pronounced curvature indicate that this bone may be a clavicle. The lateral end is broken, so it is not possible to determine whether the bone had a flattened, hooklike termination as does the clavicle in *Ochotona*. If a clavicle, it is propor-

tionally long for a leporid: although this element is incomplete in length, the ratio of length of humerus to its length is about 2.6 in contrast to ratios of length of humerus to length of clavicle of 3.2 in *Romerolagus* and 4.0 in *Sylvilagus* (LYON, 1904, p. 374). It is proportionately shorter than in *Ochotona*, in which the ratio is about 1.7. A longer clavicle may be correlated with other evidence for a more muscular forelimb in *P. haydeni* than in the Recent leporids. Possibly the bone described here may be a displaced rib, although position and general shape do not seem to support this interpretation.

The distal end of the ulna has two distinct facets for articulation with the carpus: posterolaterally there is a small globular styloid process, which forms slightly less than half of the distal end; anteromedially there is a flattened, or slightly concave, more proximal facet. Reëxamination of U.M.M.P. No. 14317 shows a similar development although WOOD does not describe such a condition (1940, p. 308). *P. haydeni* shows an early stage in the development of the styloid process; this process forms almost

the entire functional distal articular surface on the ulna in *Lepus*.

On the innominate bone (Fig. 9) the process termed the tubercle of the ilium by WOOD (1940, p. 309) is high and distinct, and a faint ridge runs forward from it into the middle of the inferior fossa. Posterior to the tubercle, between it and the acetabulum, an oval facet is raised above the general level of the ilium. Possibly this posterior facet furnished a place for muscle attachment supplementary to that on the tip of the tubercle. A similarly situated, but more distinct, process occurs in *Megalagus turgidus* and the new genus described below on page 32.

In *Ochotona* the anterior portion of the tubercle of the ilium is lower than the tubercle in *P. haydeni*; posterior to the tubercle a raised ridge extends to the anterior rim of the acetabulum. *Hypolagus*, *Sylvilagus*, and *Lepus* have a compact, rounded iliac tubercle, which is lower than in *P. haydeni* and *Ochotona*, and lack a posterior facet or ridge. Near the posterior end of the ischium the dorsal border bends upward, and the compact ischial tuberosity is divided by a low, longitudinal ridge into two facets, one facing dorsolaterally and the other dorsomedially. Ventral to the tuberosity, the descending ramus of the ischium is relatively thick transversely for a short distance and then tapers to a narrower width. The tuberosity bends laterally. In *Romerolagus*, *Sylvilagus*, and *Lepus* the ischial tuberos-

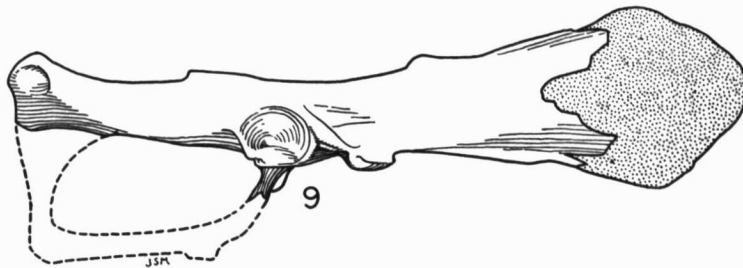


FIGURE 9. *Palaeolagus haydeni* (C.I.T. No. 1402).

Right innominate bone, $\times 2$ (restored part after WOOD, 1940, pl. XXXV, fig. 5a).

ity is proportionately stronger than in *P. haydeni*, the strengthening having taken place as thickening of the lateral and ventral portions of the tuberosity, and the tuberosity is elongated anterolaterally to posteromedially. In *P. haydeni* and *Romerolagus* the ischium is not elongated posteriorly, and the descending ramus is at almost a right angle with the horizontal ramus of the ischium. In *Sylvilagus* and *Lepus* the ischia are more elongated, and the descending ramus forms a more acute angle with the horizontal ramus. The ischial tuberosity in *Ochotona* is proportionately longer than in *P. haydeni* and is slightly strengthened by medial expansion but is proportionately weaker than the tuberosities in the Recent leporids. The condition of the tuberosity in the fossil seems to be more primitive than that in either *Ochotona* or the Recent leporids. Weak development of the ischial tuberosity in *P. haydeni* suggests a corresponding weakly developed biceps femoris, which may have been incompletely separated into anterior and posterior parts as in *Ochotona* (CAMP & BORELL, 1937, p. 321).

Study of C.I.T. No. 1402 and reëxamination of

U.M.M.P. No. 14317 shows that in the sacral region of *P. haydeni* four vertebrae are fused together, agreeing in number with those in the Recent leporids and *Ochotona*, rather than "a single sacral, as in modern forms, and two pseudosacrals" (Wood, 1940, p. 305; pl. 35, fig. 5). In C.I.T. No. 1402 anterior to the "sacral" of Wood, a vertebra, which is fused with Wood's sacral and which has a well-developed spine, is present. This is the first vertebra of the sacrum, whereas the vertebrae described and figured by Wood are actually the second, third, and fourth sacral vertebrae. In *Lepus* a dorsal median foramen occurs between the first and second sacral vertebrae; this foramen is lacking in *P. haydeni* and *Sylvilagus*. Between second and third, and between third and fourth sacral vertebrae, a large foramen occurs in the dorsal mid-line, proportionately larger than corresponding foramina in *Sylvilagus* and *Lepus*. The spines of the posterior three sacral vertebrae are lower than that of the first. *Ochotona* has on the sacral vertebrae lower spines, which are fused together, and lacks dorsal foramina between the vertebrae. In *P. haydeni* the transverse processes of the first and second sacral vertebrae, which fuse to form the articular process for the pelvis, extend slightly farther posteriorly than in *Sylvilagus* and *Lepus*. The auricular surface is more nearly vertical, the two arms of the surface form a more acute angle than in the Recent leporids, and the transverse processes have less outward expansion anteriorly (Wood, 1940, p. 305); these characteristics indicate a less firm sacral articulation in *P. haydeni* than in the Recent leporids.

Of the characters discussed above, those of the scapular spine and possible clavicle can be added to the evidence for a more muscular forearm in the fossil than in the Recent leporids. The distal end of the ulna is primitive but foreshadows later developments in leporids. Presence of four fused vertebrae in the sacrum is a resemblance to the Recent leporids, although the iliosacral articulation is of a more primitive nature. These additions to knowledge of skeletal morphology of *P. haydeni* do not change essentially Wood's conclusions regarding the level of skeletal development of that species as "more primitive and less adapted for the leaping habitus than are the skeletons of the later forms", nor the opinion that "presence of the initial stages of the leporid specializations suggests that the fossil was able to hop in a similar manner, though the great relative weakness of the skeleton and particularly of the attachments for the muscles definitely indicates that *Palaeolagus* was not an animal which sought safety by sustained flight" (Wood, 1940, p. 315).

GALBREATH (1953, p. 50) referred certain specimens from the Horsetail Creek and "Horsetail Creek or Cedar Creek" members of the White River formation of northeastern Colorado to *P. intermedius*. Compared to specimens of *P. haydeni* from Wyoming and Nebraska, these northeastern Coloradan specimens are similar in tooth pattern, equal or slightly larger in size, and probably should be referred to that species. Specimens of *P. haydeni* from the higher, Cedar Creek member in northeastern Colorado tend to be smaller than typical specimens of the species from Wyoming or Nebraska. Differences between the Horsetail Creek and Cedar Creek specimens

are of a magnitude that might be expected within a gradually changing chronocline: the geologically older specimens are larger on the average and have slightly less hypsodont teeth, which approach the crown height but are slightly higher crowned than in *P. temnodon*; the geologically younger specimens tend toward smaller size but retain the tooth pattern of *P. haydeni*. Possibly the northeastern Coloradan specimens indicate that the ends of the cline represent paleontological subspecies.

Palaeolagus burkei Wood

Palaeolagus burkei Wood, Amer. Philos. Soc., Trans., v. 28, pt. 3, p. 325, April, 1940.

Type specimen.—Skull having complete dentition, A.M.N.H. No. 8704, White River formation, Castle Rock, Logan County, Colorado. From the upper levels of the White River beds according to MATTHEW (1902, p. 308).

Geologic age and distribution.—Orellan and Whitneyan (middle and late Oligocene) of Great Plains.

Specific characters.—Small angle between basicranial axis and plane of palate, muzzle narrow, auditory bullae well developed, elongate anterior to meatus. Teeth hypsodont. On P³-M² internal hypostria persistent, usually straight-walled or having one or two crenulations; on P³ crescent between central and lingual lobes persists and retains connection with anteroexternal side of tooth for most of length of tooth; on P⁴-M² primitive pattern of crescents and lakes disappears at early stage of wear. On P₃ persistent external and internal reentrants between trigonid and talonid; on P₄, M₁, and M₂ each, trigonid and talonid tend to remain separate, not being joined by lingual bridge for most of length of tooth.

The ancestry of *Palaeolagus burkei* is not definitely known. There are some leporids from the lower Oligocene of Montana, including M.C.Z. No. 4778 from Black Butte, Madison County, and specimens from Pipestone Springs in the collections of the Carnegie Museum, that are smaller than *P. temnodon* and tend to retain the internal hypostria on P³-M² longer than in *P. temnodon*. Possibly these specimens represent a line of leporids leading toward *P. burkei*. However, further study of these Chadronian specimens is necessary in order to determine their affinities more precisely. The new middle Oligocene leporid named on page 32 might also be expected to have a Chadronian ancestor having persistent internal hypostriae on the upper cheek-teeth.

Variation within the species *Palaeolagus burkei* has been studied in specimens from the middle and upper levels of the Cedar Creek member (Orellan) and from the Vista member (Whitneyan) of the White River formation in northeastern Colorado. In a typical or "average" specimen of *P. burkei*, the posterior end of the incisor extends to the space below the talonid of P₄ or the trigonid of M₁; as a variant the shaft is shorter, terminating in the space below the trigonid of P₄ or between P₃ and P₄. On P₃ of an adult the trigonid is usually rounded. In some specimens, however, the trigonid is oblique, with the long axis anterointernal to posteroexternal. A shallow, anteroexternal fold on the trigonid of P₃ appears as a second variant on that tooth. These variants in the incisor and in P₃ may or may not accompany one another in a

single specimen. The variants from the more usual condition in *P. burkei* seem to be more common in specimens from the Vista member, although leporids from that level are too rare to allow a reliable estimate of frequency of the variants. The significance of these variants is discussed below in connection with the relationship of *P. hypsodus*.

auditory bullae greatly inflated, larger than in any other known leporid. From *P. burkei*, *P. hypsodus* differs as follows: size larger; palatine component of palate proportionately shorter; teeth more hypsodont; shaft of incisor usually shorter, terminating below P_3 or the trigonid of P_4 ; on P_3 shallow anteroexternal groove on trigonid,

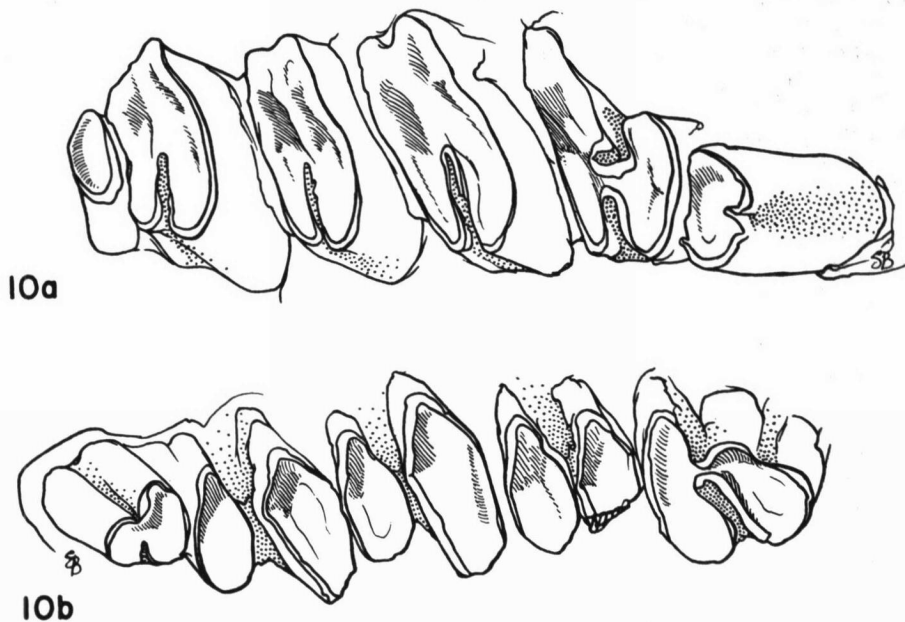


FIGURE 10. *Palaeolagus hypsodus* (M.C.Z. No. 3720).

Occlusal views of cheek-teeth, $\times 9$; 10a, right P^2 - M^3 , 10b, left P^3 - M^3 .

Palaeolagus hypsodus Schlaikjer

Plate 2, figure 1; Figure 10

Palaeolagus hypsodus SCHLAIKJER, Mus. Comp. Zool., Bull., v. 76, no. 4, p. 126, May, 1935.

Type specimen.—Right maxilla having P^3 - M^2 , M.C.Z. No. 2889, lower Miocene, approximately 150 feet above Brule-lower Harrison contact, NW $\frac{1}{4}$ sec. 21, T. 20 N., R. 62 W., Goshen County, Wyoming.

Referred specimens.—M.C.Z. No. 3720, nearly complete skull, left lower jaw, partial postcranial skeleton, lower Miocene, 30 feet above Brule-lower Harrison channel deposit, Bear Mountain, SE $\frac{1}{4}$ sec. 17, T. 20 N., R. 62 W., Goshen County, Wyoming. The following S.D.-S.M. specimens from the lower Rosebud formation of Shannon County, South Dakota: 53386-maxilla, 54244, 5539-lower jaws, NW $\frac{1}{4}$ sec. 24, T. 39 N., R. 43 W.; 5531-maxilla, 5530-lower jaw, corner sections 13, 14, 23, 24, T. 39 N., R. 43 W.; 5540-maxilla, 5543, 56102-lower jaws, N $\frac{1}{2}$ sec. 17, T. 39 N., R. 43 W.; 54314, 54315-lower jaws, NW $\frac{1}{4}$ sec. 35 and S $\frac{1}{2}$ sec. 26, T. 41 N., R. 43 W.; 53424-maxilla, SE $\frac{1}{4}$ sec. 31, T. 40 N. and NE $\frac{1}{4}$ sec. 6, T. 39 N., R. 43 W.; 54321-maxilla, NW $\frac{1}{4}$ sec. 30, T. 40 N., R. 43 W.; 5545-lower jaw, SW $\frac{1}{4}$ sec. 26, T. 38 N., R. 44 W.

Geologic age and distribution.—Arikareean (early Miocene) of Wyoming, South Dakota (probably approximate Gering-Monroe Creek equivalents), Nebraska (Gering).

Specific characters.—Skull flat, muzzle narrow,

long axes of internal reentrant and of trigonid anterointernal to posterolateral.

Description.—The only previously reported specimen of *Palaeolagus hypsodus* is the type, but the species is now known by more complete material, including the above referred specimens, which permit a more complete description and clarification of the phylogenetic position of this leporid.

Dentition. The following description of dental characteristics of the species is based on the type specimen, M.C.Z. No. 2889, on M.C.Z. No. 3720 (Fig. 10), which has complete upper and left lower teeth, and on the other specimens referred to this species, all of which have moderately worn teeth unless otherwise stated. Unfortunately no milk teeth or unworn permanent teeth are known at present.

The anterior upper incisor is more curved, its tip is directed more posteriorly, and the sulcus, which is approximately in the midline, is wider and shallower than in *P. haydeni* and the Recent leporids. The posterior upper incisor is wider transversely than anteroposteriorly and smaller than the corresponding tooth in *P. haydeni*. The height of the alveolar process of the maxilla indicates that the upper cheek-teeth in *P. hypsodus* are more hypsodont than in *P. haydeni* and *P. burkei*. The upper teeth in *P. hypsodus* are larger than in *P. burkei*, but following moderate wear the pattern on the upper teeth in these two species is similar in general. P^2 has a single anterior re-

reëntrant, which crosses one-third to one-half of the occlusal surface. The reëntrant is persistent to the base of the tooth in all specimens examined. On this tooth enamel is well developed lingually and is reduced buccally and posteriorly. The anterior loph of P^3 is narrower transversely than the posterior loph. Following moderate wear, this tooth has an internal, straight-walled hypostria crossing about one-third of the occlusal surface and a J-shaped crescent having a persistent connection to the anteroexternal side of the tooth. Following greater wear the hypostria becomes shortened and the crescent completely worn away. P^4 , M^1 , and M^2 resemble one another in pattern. In occlusal view each of these teeth has an internal, straight-walled hypostria crossing one-half or slightly less of the occlusal surface. In the most worn specimen available, the hypostria on P^4 is slightly shorter than are those on M^1 and M^2 . M^3 is a simple cylinder, wider transversely than anteroposteriorly. That the premolars have not become completely molariform is indicated by retention of the crescent on P^3 and greater shortening of the internal hypostria with wear on the premolars than on the molars. On P^3 - M^3 , following moderate wear, enamel is thickest anteriorly and lingually, is thinner posteriorly, and is absent externally and sometimes posteroexternally; enamel tends to be thicker on the anterior wall of the hypostria than on its posterior wall. Cement is well developed and fills the anterior reëntrant on P^2 , the crescent on P^3 , and the hypostria on P^3 - M^2 . In addition, cement extends onto the lingual and sometimes onto the antero-lingual sides of the shafts of P^3 - M^2 .

In cross section the lower incisor is trapezoidal, slightly higher than wide, and its shaft extends to below P_3 or the trigonid of P_4 . Except for larger size in *P. hypsodus*, following moderate wear P_4 - M_3 resemble the corresponding teeth in *P. burkei*. However, P_3 is more easily distinguished by its different pattern from that in the latter species. As in *P. burkei* the talonid is united to the trigonid by a narrow bridge, which is between an external reëntrant crossing about one-third of the occlusal surface and an internal reëntrant extending about halfway across the tooth. In all specimens examined, both reëntrants are persistent the full length of the tooth. In addition to these reëntrants a shallow fold, also persistent to the base of the tooth, enters the anteroexternal wall of the trigonid. The trigonid and the internal reëntrant tend to be elongated anterointernally to posterobuccally. Each of the more posterior cheek-teeth, P_4 - M_2 , consists of two columns, the posterior of which is narrower than the anterior. In all specimens examined the columns of each tooth are connected at the occlusal surface by cement only; that is, the trigonid and talonid are not joined lingually by the bridge characteristic of many leporids. In a narrow strip on the anterior side of the trigonid enamel is absent; it is absent also on both columns lingually but is present posteriorly and externally, being especially well developed posteriorly on the trigonids. In relatively early stages of wear, the columns of M_3 are separated at the occlusal surface by cement, but with wear the dentine of the columns becomes confluent. As on the upper teeth, cement is well developed on the lowers: it fills the reëntrants on P_3 and in No. 5530 covers the buccal and anterior walls of this tooth; cement is

present between the trigonid and talonid on each of the more posterior cheek-teeth.

Skull. The skull of M.C.Z. No. 3720 (pl. 2, fig. 1) is nearly complete, lacking only parts of the right zygoma, the right bulla, and the ventral wall of the braincase, and is almost undistorted, except for possible lateral compression of the snout. This skull of *Palaeolagus hypsodus*, which is that of an adult, is approximately the same in size as that of an adult *P. haydeni*. The huge bullae, anteriorly tapered muzzle, wide, flat braincase, and a seemingly smaller angle between basicranial and palatal axes are characteristics of the skull in *P. hypsodus* that distinguish it from the skull in *P. haydeni*.

The muzzle is elongate, tapered anteriorly, and is proportionately narrower posteriorly than in *P. haydeni*. The anterior end of the nasals extends farther forward than the anterior face of the incisors, thus seeming to extend farther forward than do the nasals in *P. haydeni*. The nasals, which are pitted along their lateral borders, are wider posteriorly than anteriorly. Although some compression may alter the muzzle in M.C.Z. No. 3720, the anterior tapering of the nasals seems to be more pronounced than in *P. haydeni* and *P. burkei*. The nasals are slightly convex dorsally, a condition that, coupled with the anterior elongation, results in a somewhat "tubular" appearance of the anterior part of the nasals. The frontals, which have a lightly pitted dorsal surface, form a medial, V-shaped embayment between the posterior ends of the nasals. The maxillary process of the frontal is in contact with the orbital process of the maxilla at the anterodorsal border of the orbit, continues anteriorly between the frontal process of the premaxilla and the fenestrated region of the maxilla for about half the length of the muzzle, and tapers anteriorly. The supraorbital process arises gradually anteriorly, without a free anterior process, and extends laterally; its posterior end forms a hooklike process directed posteromedially. On both sides of the midline the frontoparietal suture crosses the roof of the skull transversely for a short distance about on a level with the anterior margin of the zygomatic process of the squamosal; laterally the suture bends forward into the orbit. The parietal extends a short distance into the orbit but does not exclude the frontal from a short contact with the squamosal. The braincase is wide, and its dorsal surface is slightly concave in the midline in the region of the frontal-parietal contact; lateral to this depression the parietals are slightly convex. More posteriorly, at a level with the opening of the external auditory meatus, the parietals are concave, resulting in a "dished-in" appearance of this part of the roof of the skull. A low lambdoidal crest is formed at the parietal-squamosal contact. The supra-occipital sends a flattened plate of bone a short distance onto the dorsal skull roof. In contrast to the braincase in *P. hypsodus*, that in *P. haydeni* is narrower transversely, and in lateral view the parietals are more domed and lack the pronounced posterior concavity. The frontal in *P. haydeni* does not extend so far posteriorly, and the parietal sends into the orbit a wider process, which excludes the squamosal from superficial frontal contact. *P. burkei* is intermediate between *P. haydeni* and *P. hypsodus* in the structure of the frontal-parietal contact: in the first the frontals extend farther posteriorly than do

those in *P. haydeni*, and the process of the parietal in the orbit is narrower and shorter than in *P. haydeni*. In *P. haydeni* the supraoccipital does not extend so far onto the dorsal skull roof as in *P. hypsodus*.

The premaxilla in *P. hypsodus* is proportionately lower dorsoventrally than in *P. haydeni* and is slightly pitted over the shaft of the incisor. The frontal process of the premaxilla parallels the lateral edge of the nasal for the full length of that bone and does not taper in width posteriorly.

On the lateral side of the snout, the maxilla sends forward a V-shaped process into the premaxilla, but this process does not reach so far anteriorly as in *P. haydeni*. Although some breakage obscures the details, dorsal to this process the fenestrated region of the maxilla seems to extend about as far forward as does the process. The infraorbital foramen is ventral to the fenestrated region and is separated from that region by a well-developed rim of bone. The alveolar process of the maxilla is proportionately higher than in *P. haydeni* and *P. burkei*, indicating the progressive development of hypsodonty for which *P. hypsodus* was named. The anterior rim of the orbit, formed by the orbital process of the maxilla, bends slightly outward as it rises dorsally; near the anterodorsal border of the orbit it bends medially and is in contact with the maxillary process of the frontal, whereas the orbital process in *P. haydeni* bends slightly medially as it ascends and does not project so far laterally at the frontal contact.

The width of the skull across the anterior roots of the zygomatic arches is proportionately less than in *P. haydeni*. The zygomatic arches diverge outward posteriorly, and the zygomatic plate is inclined from a vertical plane, having the dorsal rim more lateral than the ventral. In contrast, the zygomatic arches in *P. haydeni* parallel the long axis of the skull, and the zygomatic plate is essentially vertical. The anterior zygomatic root is about on a line with the anterior loph of P³; the anterior root arises slightly closer to the alveolar border than in *P. haydeni*. The anteroventral border of the zygoma forms a thickened ridge. A distinct crest extends vertically from the anterior edge of this ridge to the alveolar border, which is intersected in line with the middle of P³. Anterior to this crest the maxilla is slightly concave. The lateral side of the zygomatic plate is concave, and a pit enters the anterior zygomatic root near the anterior end of this concavity. A similarly placed, but shallower, pit is present in *P. burkei*, but the pit is absent in *P. haydeni*. The zygomatic plate becomes narrower dorsoventrally below the zygomatic process of the squamosal and continues posterior to this process. The skull is widest at the zygomatic process of the squamosal, which extends laterally almost at right angles to the long axis of the skull. In *P. haydeni* this process inclines forward at less than a right angle with the long axis of the skull, is proportionately shorter transversely, and has a more definite anterodorsal groove for the temporalis muscle. In *P. hypsodus* the outward deviation of the zygoma from the skull, inclination of the zygomatic plate, and long zygomatic process of the squamosal combine to form an orbit that seems to be larger than in *P. haydeni*. However, vision in *P. hypsodus* may have been directed mostly laterally or dorsolaterally, due to

the restriction of anterior vision by the orbital process of the maxilla.

On the palate the incisive foramina extend a short distance between the posterior incisors. The bony bridge of the palate is shorter and narrower than in *P. haydeni* and extends between the posterior ends of the incisive foramina, which are about in line with the anterior edge of P², and the internal nares, which reach forward to a level between P⁴ and M¹. The palatine processes of the maxillae, which form the part of the palate between the incisive foramina and the maxillopalatine suture, send forward a narrow medial projection between the incisive foramina. The maxillopalatine suture is slightly convex in an anterior direction and reaches to a line between P³ and P⁴ in M.C.Z. No. 3720. There seems to be some variation in palatal structure in *P. hypsodus*: a referred specimen, S.D.S.M. No. 5531 from the lower Rosebud beds of South Dakota, has a short palate, but the palatine component is more posterior than is that of M.C.Z. No. 3720, extending approximately from opposite the middle of P⁴ to the posteroloph of M¹. The available specimens are too few in number to determine whether this variation represents a real difference between populations from South Dakota and Wyoming or is individual variation. The suture between maxilla and palatine is more arched anteriorly and the palatine forms a larger proportion of the palate in *P. haydeni* and *P. burkei* than in *P. hypsodus*. Two palatine foramina are present on each side of the palatal midline posterior to the maxillopalatine suture, and a short, median process from the palatines is directed posteriorly into the internal nares. The nares are approximately as narrow anteriorly as in *P. haydeni* and are constricted in width opposite the posterior end of the tooth-row.

The optic foramina in the orbitosphenoids are confluent, as in all leporids in which this structure is known. In M.C.Z. No. 3720 the foramen is elongate anterodorsally to posteroventrally; the specimen is slightly broken but distortion seems not to be responsible for this shape. In *P. burkei* and the Recent leporids the foramen is more rounded. On the alisphenoid an elevated ridge that terminates in a ventrally tapered process marks the place of origin of the superior head of the external pterygoid muscle. This ridge is better developed than in *P. burkei*, but is less elongate than in the Recent leporids.

On the dorsolateral surface of the roof of the skull the squamosal extends as a thin plate of bone to, or almost to, the lambdoidal crest. In M.C.Z. No. 3720 the squamosal, which is slightly broken, does not make contact with the crest, but there probably was contact in the unbroken condition. Due to the widening of the parietals, the squamosals are more restricted to the lateral portions of the skull and cover a smaller proportion of the roof of the skull in *P. hypsodus* than in *P. haydeni*. A process of the squamosal arches dorsally over the external auditory meatus and terminates slightly posterior to the opening of the meatus. This process is separated from the more dorsal parts of the squamosal by a notch through which part of the mastoid is exposed.

Perhaps the most striking characteristic of the skull of *Palaeolagus hypsodus* is the inflation of the auditory bullae, which are proportionately and absolutely larger

than are those in any other leporid in which this region is known. The inflation involves all parts of the bulla, and the structure of the posterior part of the skull, as well as the posture of the head, was probably affected by this enlargement. The wide, short, external auditory meatus is directed dorsoposteriorly. The mastoid has a considerable lateral, and some dorsal, exposure, and the mastoid process extends down behind the meatus at least to its ventral edge. A stylomastoid foramen is present between the mastoid process and the meatus, near the posteroventral edge of the latter. The surface of the mastoid is not pitted, but is slightly rugose. From the dorsoposterior part of the mastoid a ridge that is in line with the lambdoidal crest crosses the mastoid in a vertical direction. Posterior to this ridge the surface of the mastoid faces posterolaterally. The lateral edge of the supraoccipital and a portion of the mastoid form a second vertical ridge, which originates dorsally just posterior to that mentioned above. Only a small plate of the mastoid is present on the occipital surface medial to this second ridge. In *P. haydeni* both ridges are present but are variable and generally less well developed, and the mastoid has a larger expanse on the occipital surface. The short, wide paroccipital process is in contact with the bulla and is well separated from the mastoid process. The nuchal crest, paralleling the lambdoidal crest, crosses the supraoccipital nearly horizontally at the dorsal margin of the occipital surface. In the midline of the occiput a low but distinct ridge leads from the nuchal crest toward the foramen magnum but is separated from the latter by a flattened plate of bone. Part of the surface of the supraoccipital is slightly rugose. The foramen magnum is wider than high. The occipital condyles are partly ventral to the foramen magnum and are more horizontal than in *P. haydeni*, resembling those in *Megalagus turgidus* in general orientation. With the skull oriented in a seemingly natural position, the occipital surface is nearly vertical. Correlated with the inflated bullae, the width of the skull across the ventral part of the mastoids is greater in *P. hypsodus* than in *P. haydeni*. In *P. haydeni* the dorsal margin of the occiput is narrower and more arched, the foramen magnum is slightly higher than wide, the occipital condyles are more vertically oriented, and the occipital surface faces ventrally slightly more than does the essentially vertical occipital surface in *P. hypsodus*. The character of the occiput suggests that *P. hypsodus* carried its head more horizontally than did *P. haydeni*.

On the ventral surface between the bullae, the basioccipital is narrow. Due to the inflation of the bulla and the orientation of the occipital condyle, the jugular fossa is narrow. Although the posterior foramina of the skull are obscured in No. 3720 due to breakage, it can be determined that the external carotid foramen, jugular foramen, and hypoglossal canal must have opened in this fossa, for no openings are present medial to the bulla or dorsal to the occipital condyles. The external carotid foramen must have been situated, as in *P. haydeni*, more posteriorly than it is in the Recent leporids.

Lower jaw. Although somewhat smaller, the lower jaw in *P. hypsodus* resembles that in *P. haydeni* in general shape. The greatest difference from *P. haydeni* is in the posterior part of the jaw: in *P. hypsodus* the ascending

ramus is proportionately narrower anteroposteriorly; the posterior border of the ascending ramus is more concave with the result that the angular process is longer; the lower border of the masseteric fossa projects farther ventrally. The anterior border of the masseteric fossa is marked by a V-shaped ridge, at the apex of which is a small knob below M_3 . Despite the smaller area for insertion of the masseter muscle in *P. hypsodus* than in *P. haydeni*, the ridges bounding the masseteric fossa and the elongate angular process suggest that the insertion may have been as strong as in *P. haydeni*, although weaker in both these species than in the Recent leporids. Possibly the short anteroposterior dimension and the posterior concavity of the ascending ramus are correlated with the inflated bullae, with which a longer ramus might have interfered mechanically. The coronoid process is low, and its anterior edge bends medially, but less than in the Recent leporids. The pterygoid depression is bounded anteriorly and ventrally by distinct ridges. This depression is proportionately deeper than in the Recent leporids. A low ridge marking the separation of the insertions of internal and external pterygoid muscles crosses the depression obliquely. The surface of the jaw is pitted medially over the shaft of the incisor; the extent of the incisor is marked by a swelling along the ventromedial side of the jaw that varies in length, extending from below P_3 posteriorly to below the middle of P_4 . On the lateral surface of the jaw a single mental foramen occurs below the diastema; pitting is present below P_3 and P_4 in the region where a second mental foramen occurs in *P. haydeni*. The dental foramen is situated on the medial side of the mandible immediately dorsal to the intersection of the anterior margin of the pterygoid depression and the ridge separating the places of insertion of external and internal pterygoid muscles. In the Recent leporids a postalveolar foramen pierces the jaw posterior to M_3 . *P. hypsodus* lacks this foramen, but small perforations in the area may indicate incipient fenestration.

Postcranial skeleton. A partial skeleton is associated with the skull of M.C.Z. No. 3720; included are the atlas, parts of the sacrum, isolated vertebrae and ribs, left scapula, distal ends of left radius and ulna, one left metacarpal, nearly complete pelvic girdle, distal ends of both femora, proximal end and most of the shaft of the right tibiofibula, right navicular, and several isolated phalanges. The skeletal parts are about the same size as those of an adult specimen of *P. haydeni*, C.I.T. No. 1402.

Viewed anteriorly, the outline formed by the edges of the atlas is roughly diamond-shaped. The transverse axis of the diamond is the longer. The articular surfaces for the occipital condyles form the two ventral arms of the diamond and the neural arch, the two dorsal arms. This configuration differs from that of the atlas in the Recent leporids, in which the outline of the anterior edges is roughly rectangular, with the lateral sides of the rectangle formed by the articular surfaces for the occipital condyles. This difference is correlated with orientation of the occipital condyles, which are more nearly horizontal in *P. hypsodus* than in the Recent leporids. Both the anterior articular surface for the condyles and the posterior surface for articulation with the axis are less con-

cave than in the Recent leporids. The transverse processes of the atlas are short transversely and not expanded anteroposteriorly, contrasting with the long, expanded processes in the Recent leporids. The transverse processes in *Ochotona* are proportionately longer transversely than in *P. hypsodus*. Those parts of the rectus capitis and obliquus capitis muscles that originate on the transverse processes of the atlas and insert on the occiput were probably weaker in *P. hypsodus* than in the Recent lagomorphs.

The medial side and glenoid region of the left scapula are exposed in No. 3720. The neck of the scapula is short, and the anterior border flares anteriorly above the neck. The subscapular fossa is divided by a groove that parallels the long axis of the scapula. This groove marks the place of attachment of the scapular spine on the lateral surface of the scapula and divides the fossa into two surfaces that reflect the shape of the subequal supraspinous and infraspinous fossae. Thus, in proportions these fossae resembled those in *P. haydeni* more than those in the Recent leporids. The surface of the axillary border is set almost at a right angle with the surface of the subscapular fossa, is separated from that fossa by a definite ridge that is more pronounced toward the vertebral border, and is narrower dorsally than toward the glenoid region. The posterior part of the glenoid cavity in *P. hypsodus* is more expanded transversely than in *Megalagus*, but slightly less than in *Romerolagus*. The coracoid process extends medially a short distance from its origin; its distal end bends ventrally and terminates slightly ventral to the anterior lip of the glenoid cavity, thus extending farther ventrally than in *Megalagus turgidus* and the Recent leporids.

The distal articular facet of the radius is slightly longer transversely than anteroposteriorly, the outer edges of the facet are essentially parallel, and the surface is slightly concave. The corresponding facet in *Megalagus turgidus* is proportionately wider transversely than in *P. hypsodus*; those in the Recent leporids are proportionately still wider and have a more concave surface than do those in either *P. hypsodus* or *Megalagus*. Toward its distal end, the shaft of the ulna in *P. hypsodus* is flattened anterolaterally to posteromedially. Similar flattening occurs in *Romerolagus* and *Sylvilagus*, but in these genera this part of the ulna is more reduced in width, and reduction has proceeded even further in *Lepus*. The distal articular surface on the ulna for the cuneiform is composed of two facets: posterolaterally a knoblike styloid process forms about half the distal surface; the anteromedial half is formed by a flattened facet. These facets indicate a more advanced level of development than in *Megalagus turgidus* and *Ochotona*, but a more primitive level than in the Recent leporids.

The pelvic girdle of No. 3720 is preserved having the lateral aspect of the left ilium and medial aspect of the right innominate exposed. Anteriorly the iliac blade bends outward and its border is thickened. The iliac blade is divided into two concave fossae by a rounded ridge that begins at the anterior border of the ilium and parallels its long axis. The ridge becomes lower posteriorly and terminates dorsal to the tubercle of the ilium. The ridge separating the fossae and the concavity of the fossae ex-

tend farther posteriorly in *P. hypsodus* than in *P. haydeni*. A faint ridge, beginning anteroventrally, crosses the lower fossa in a longitudinal direction and terminates near the anterior margin of the tubercle of the ilium. The rise of the dorsal margin at the place of sacral articulation is more gradual and begins farther posteriorly than in *P. haydeni*, and the iliac blade in *P. hypsodus* seems to have offered a slightly larger surface for muscle attachment than did that in *P. haydeni*. The tubercle of the ilium stands out sharply from the ventral edge of the ilium and has a slightly thickened tip. The surface between the tubercle and the anterior border of the acetabulum is slightly raised into a rugose ridge. On the ilium the auricular surface forms a V with the apex directed posteriorly. The angle at which the two arms of the V intersect is more acute and the surface is not so distinctly ridged as in *Sylvilagus*. Toward its posterior end the dorsal ramus of the ischium rises to the ischial tuberosity. This rise is greater in *P. hypsodus* than in *P. haydeni*. In No. 3720 the ischial tuberosities are broken. The inferior ramus of the ischium is expanded anteroposteriorly. The obturator fenestra is elongate and of nearly equal depth throughout its length, resembling that in *P. haydeni*. In general, the innominate in *P. hypsodus* resembles that in *P. haydeni* but is advanced in having slightly larger fossae on the ilium and higher ischial tuberosities. The parts of the femora preserved in No. 3720 resemble those in *P. haydeni*. The tibiofibula is incompletely preserved and only its posterior portion is exposed. In general the proximal end of the tibiofibula resembles that in *P. haydeni*.

The navicular in *P. hypsodus* resembles that in *Megalagus turgidus* in general, except that in the former this bone is smaller, has a proportionately shallower notch for the cuboid, and the medial knob for articulation with metatarsal II reaches less far proximally. The navicular lacks a distinct articular facet for the calcaneum, and the latter probably did not extend much farther distad than did the astragalus. In this character the tarsus in *P. hypsodus* resembles those in *P. haydeni* and *Megalagus turgidus* and differs from those in the Recent leporids, all of which have a well-developed calcaneonavicular articulation.

Adaptations. The incisors in *Palaeolagus hypsodus* seem to indicate that gnawing ability was weak, but the pattern and hypsodonty of the cheek-teeth suggest that the ability to grind food was well developed. The essentially vertical occipital surface, orientation of the occipital condyles, and evidence that neck muscles were relatively weakly developed suggest that the flat skull was carried essentially horizontally, in contrast to a posture with greater flexion at the neck in most other leporids. In addition, the enlarged bullae may have acted mechanically to prohibit depression of the head. The postcranial skeleton gives evidence of some advance over *P. haydeni*, although probably the mode of locomotion was still essentially scampering. Thus, *P. hypsodus* may have resembled the ochotonids in posture of the head and mode of locomotion. If increased size of auditory bulla indicates improved sound reception, as seems likely, the ability to hear was probably well developed in *Palaeolagus hypsodus*. Size of bulla is not necessarily directly correlated with length of external ear; for example, *Brachylagus idahoensis* has larger bullae but shorter ears than does

TABLE 3.—Measurements in millimeters of *Palaeolagus hypsodus*

	M.C.Z. No. 3720	S.D.S.M. No. 54321
(right side for teeth)		
P ² anteroposterior	1.0	1.1
width	1.5	1.8
P ³ anteroposterior	1.9	1.8
width anteroloph	2.0	2.2
width posteroloph	3.4	2.6
P ⁴ anteroposterior	1.6	1.6
width anteroloph	3.4	3.3
width posteroloph	3.2	3.1
M ¹ anteroposterior	1.6	1.7
width anteroloph	3.0	3.1
width posteroloph	2.9	2.8
M ² anteroposterior	1.5	1.5
width anteroloph	2.6	2.9
width posteroloph	2.3	2.1
M ³ anteroposterior	0.7	0.7
width	1.3	1.5
length P ² -M ³	9.3	9.5
length P ³ -M ²	7.9	7.5
length skull	54.6	
width across anterior roots of zygomatic arches	22.0	
width posterior to zygomatic process of squamosal	28.1	
length nasal	23.6	
posterior width nasals	ca. 9.8	
medial length frontal	19.6	
medial length parietal	15.0	
width palate between P ⁴	6.8	
length palate	5.6	
length palatine on palate	2.2	
length maxilla on palate	3.4	
width internal nares	2.4	
dorsoventral depth anterior root of zygoma	5.1	
length zygoma	21.1	
length bulla	ca. 14.6	
dorsoventral height occiput	ca. 12.3	
width across paroccipital processes ..	17.0	

	M.C.Z. No. 3720	S.D.S.M. No. 54314	S.D.S.M. No. 54244
P ₃ anteroposterior	2.2	2.0	2.1
width trigonid	1.6	1.5	1.6
width talonid	2.0	1.8	1.8
P ₄ anteroposterior	2.0	2.0	2.0
width trigonid	2.2	2.2	2.1
width talonid	1.8	1.8	1.6
M ₁ anteroposterior	2.3	2.1	2.2
width trigonid	2.4	2.2	2.1
width talonid	1.9	2.0	1.9
M ₂ anteroposterior	2.1	2.1	2.1
width trigonid	2.3	ca. 2.1	ca. 2.1
width talonid	1.8	1.7	1.8
M ₃ anteroposterior	1.3		
width trigonid	1.2		
width talonid	0.9		
length P ₃ -M ₃	9.8		
length P ₄ -M ₂	6.4	6.4	6.3
inside depth of jaw below M ₁	7.4	7.3	8.3
transverse width distal radius	2.8		
length innominate	ca. 45.9		
length ilium	ca. 26.0		
transverse width proximal tibiofibula	8.3		
length tibia from proximal end to union with fibula ..	29.5		

Lepus californicus. Thus, it does not need to follow from the inflated bullae of *P. hypsodus* that the external ears were long.

Relationships. *Palaeolagus hypsodus* appears to be a descendant of *P. burkei*. In both species the skull is flat and the bullae are large. In dental characters the two species resemble one another in most features, including retention of relatively long hypostriae on the upper cheek-teeth, a persistent crescent on P³, retention of an internal reentrant on P₃, and continued separation of trigonid and talonid on P₄-M₂. In certain features, including proportions of the palate and greater hypsodonty, *P. hypsodus* is advanced over *P. burkei*. In *P. burkei* the bullae tend to be large; this tendency is carried to an extreme in the enlargement of those structures in *P. hypsodus*. The main differences in tooth pattern from *P. burkei* seem to be the presence of an anteroexternal reentrant and the oblique orientation of the trigonid on P₃ in *P. hypsodus*. As mentioned above (under *P. burkei*), variants among Orellan and Whitneyan specimens of *P. burkei* have a tendency toward development of both these characters, although they are not so well developed as in *P. hypsodus*. It may be difficult in cases of individual specimens and incomplete material to recognize on the basis of morphology alone which of the two species is represented. The line that must be drawn between the two species at the place where the type of P₃ and other characters typical of *P. hypsodus* become the usual condition in a population, rather than variants from the norm, is placed, on the basis of the known specimens, at the transition from Oligocene to Miocene.

The line of leporids represented by *P. burkei* and *P. hypsodus* does not seem to lead toward either the archaolagines or the leporines. The general pattern of an isolated P₃ referred to ?*Alilepus* (GREEN, 1956, p. 154-155, fig. 5A), from the late Clarendonian of Wolf Creek, South Dakota, resembles that in *P. hypsodus*. Possibly this resemblance indicates that the *P. burkei*-*P. hypsodus* line persisted later than early Miocene times in North America, although the evidence is too incomplete to allow more than a suggestion that this was the case.

Palaeolagus intermedius Matthew

Palaeolagus intermedius MATTHEW, Amer. Mus. Nat. Hist., Bull., v. 12, art. 3, p. 53, March 31, 1899.

Type specimen.—Nearly complete skull, A.M.N.H. No. 8722, Oredon beds, White River formation, Castle Rock, Logan County, Colorado.

Geologic age and distribution.—Orellan (middle Oligocene) and possibly Whitneyan (late Oligocene) of northeastern Colorado. Matthew lists the species from horizons B and C of the White River in Colorado; specimens have been referred to this species from other localities in the Great Plains.

Specific characters.—Size larger than *P. haydeni*. Angle between basicranial and palatal axes near that in *P. haydeni*, greater than in *P. burkei*; muzzle long and heavy; auditory bulla proportionately smaller than in *P. haydeni* and *P. burkei*. Teeth hypsodont. On P³-P⁴ crescents retained longer than on molars, but absent in heavily worn teeth; hypostria shallow, not forming isolated lake

after wear. On M^1 - M^2 crescents between central and lingual lobes worn away at earlier stage of wear than in *P. haydeni*; hypostria relatively long and persistent. Shaft of lower incisor terminates below P_3 . On P_3 internal reentrant between trigonid and talonid probably lost at early stage of wear.

It is difficult to differentiate *Palaeolagus intermedius* from *Megalagus* on the basis of lower jaws alone. The pattern of the lower cheek-teeth seems similar in the two; in both, P_3 tends to lose the internal reentrant between the trigonid and talonid at an early stage of wear. However, the lower cheek-teeth in *P. intermedius* are slightly smaller and more hypsodont.

As mentioned in the discussion of *Palaeolagus haydeni*, the specimens referred to *P. intermedius* by GALBREATH (1953, p. 50) from Horsetail Creek and Horsetail Creek or Cedar Creek seem actually to represent *P. haydeni*. His specimens of *P. intermedius* from Cedar Creek are correctly referred. Known specimens of *P. intermedius* are restricted to middle and possibly late Oligocene age; the known appearance of *P. intermedius* is later in the Oligocene than the appearance of *P. haydeni*.

Palaeolagus philoi,² n. sp.

Figures 11-14

Type specimen.—Incomplete right maxilla having P^3 - M^2 , P^2 broken at alveolus, alveolus of M^3 without tooth, and part of palatine, S.D.S.M. No. 53389. Lower Rosebud beds, SE $\frac{1}{4}$ sec. 31, T. 40 N., R. 43 W., Shannon County, South Dakota.

Referred specimens.—Partial left maxilla and palatine having P^2 - M^2 , M.C.Z. No. 2888, lower Miocene, NW $\frac{1}{4}$ sec. 36, T. 20 N., R. 62 W., Goshen County, Wyoming, "approximately 200 feet above the Brule-lower Harrison contact" (SCHLAIKJER, 1935, p. 129; referred therein to *Archaeolagus ennisianus*). The following, all S.D.S.M. specimens, are from lower Rosebud beds in Shannon County, South Dakota. Lower jaws: 54283, 54284—SE $\frac{1}{4}$ sec. 31, T. 40 N., R. 43 W. and NE $\frac{1}{4}$ sec. 6, T. 39 N., R. 43 W.; 53388, 54123—NW $\frac{1}{4}$ sec. 24, T. 39 N., R. 43 W.; 5529—corner sections 13, 14, 23, 24, T. 39 N., R. 43 W.; 53385, 53428, 5541, 5544—N $\frac{1}{2}$ sec. 17, T. 39 N., R. 43 W.; 53427, 54269, 54276, 54277—SW $\frac{1}{4}$ sec. 9, T. 39 N., R. 43 W.; 53384—SE $\frac{1}{4}$ sec. 6, T. 39 N., R. 43 W.; 5537—NW $\frac{1}{4}$ sec. 20, T. 39 N., R. 43 W.; 5535—NW $\frac{1}{4}$ sec. 30, T. 39 N., R. 43 W.; 53383—SW $\frac{1}{4}$ sec. 36, T. 38 N., R. 44 W.; 54259—NW $\frac{1}{4}$ sec. 30, T. 40 N., R. 43 W.; 54313—SE $\frac{1}{4}$ sec. 18 and NE $\frac{1}{4}$ sec. 19, T. 38 N., R. 43 W. Fragmentary maxilla having P^3 - M^3 , No. 54325 and lower jaws, 5526, 5527, 5528, 5538—SW $\frac{1}{4}$ sec. 32, T. 39 N., R. 44 W.

Geologic age and distribution.—Arikareean (early Miocene) of South Dakota, Wyoming, probably Nebraska (Gering). Most of the specimens from South Dakota and Wyoming come from strata that appear to be approximately equivalent to Gering-Monroe Creek beds of Nebraska.

Specific characters.—Size near that in *Palaeolagus*

intermedius. Differs from *P. intermedius* in having more hypsodont upper cheek-teeth and a proportionately shorter palatine component on the palate.

Although the known maxillae and lower jaws were not found in direct occlusal association, reference of both to one species is favored by several factors. At some localities in the lower Rosebud beds in Shannon County, South Dakota, the small *P. hypsodus*, the large *Megalagus* cf. *primitivus*, and the maxillae and jaws referred here to *P. philoi* are associated. Neither maxillae nor lower jaws could be referred to either of the other lower Rosebud species, and if not associated, there would be maxilla-less mandibles and mandible-less maxillae representing different leporids in the Rosebud beds. The maxillae and jaws fit one another in size and are in comparable levels of evolutionary development. In view of this evidence, reference of the maxillae and lower jaws to one species, *P. philoi*, seems to be correct.



FIGURE 11. *Palaeolagus philoi* (S.D.S.M. No. 53389).

Ventral view of fragment of skull (type specimen) having P^3 - M^3 , $\times 4$.

Description.—Unfortunately the upper cheek-teeth are known only from relatively old individuals in which most of the tooth pattern has been worn away. The shafts of the hypsodont upper cheek-teeth extend into a well-developed maxillary tuberosity, which is slightly higher than in *P. intermedius*. In M.C.Z. No. 2888, a single anterior reentrant is present on P^2 ; this tooth is broken at the alveolar level in the type specimen, S.D.S.M. No. 53389 (Fig. 11), and lacks an anterior reentrant, seemingly because of wear. In the known, relatively worn specimens each of the next four teeth, P^3 - M^2 , has an internal, straight-walled hypostria; in the known stages of wear these hypostriae are deeper on the molars than on the premolars, indicating incomplete molarization of the premolars. The hypostriae persist into the alveoli, are cement filled, and their buccal portions do not seem to form isolated lakes. M^3 is a simple, cylindrical tooth lacking reentrants.

Unworn as well as worn lower cheek-teeth are known. In specimens with the adult pattern in the cheek-teeth (Fig. 12), P_3 has a single buccal reentrant, which is be-

² Named for Philo G. Macdonald, in appreciation of his field work in the lower Rosebud beds for the South Dakota School of Mines.

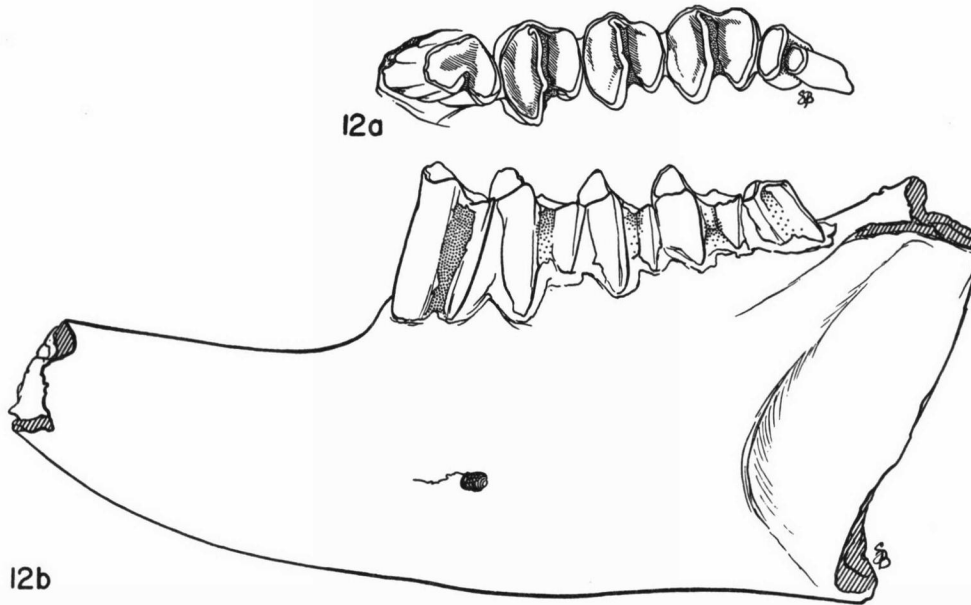


FIGURE 12. *Palaeolagus philoi* (S.D.S.M. No. 5526, adult).

12a, Occlusal view of left P₃-M₃, ×4; 12b, lateral view of left lower jaw, ×4.

tween trigonid and talonid and crosses approximately half the occlusal surface. P₃ varies in shape at the occlusal surface, seemingly due to individual and age differences (Fig. 14). On P₄, M₁, and M₂ trigonid and talonid are joined by a lingual bridge. Crenulations occur in the anterior wall of the talonid in some specimens and seem to reflect an early ontogenetic age, for immature animals have crenulations better developed than do older animals. In moderately worn specimens, on P₃ enamel is well developed buccally but is thin or absent lingually on the talonid; on P₄-M₃ enamel is absent along an anterior strip on the trigonid, tends to be thinner lingually than buccally, and seems to be especially thin or absent lingually on the talonid. Cement fills the reëntrant on P₃ and is present between trigonid and talonid on each of the more posterior cheek-teeth. No trace of roots appears in the known specimens.

The pattern of the teeth in immature specimens (Fig. 13) is more complex than in the older individuals. Unworn P₃ is composed of three transverse lophs. The anterior loph, the trigonid, is composed of one buccal and one lingual cusp, probably protoconid and metaconid respectively; of these the buccal is larger and extends farther anteriorly. Between the cusps is a shallow groove which persists a short distance down the anterior surface of the tooth. A buccal and a lingual groove enter the crown between trigonid and talonid: the deeper, buccal groove persists in the adult; the lingual groove is shallow and continues down the shaft approximately as far as does the anterior groove on the trigonid. Two lophs make up the talonid. Although cement covers most of the larger anterior loph, or hypolophid, obscuring most details, a variable number of small cusplules can be seen to line its posterior wall, which is slightly convex posteriorly. One of the cusplules occurs at the point at which the more

posterior loph of the talonid, the posterolophid, diverges posteriorly. In the youngest available specimen of P₃, No. 54283, cement is present between the cusps of the trigonid and extends a short distance down the anterior groove; between trigonid and talonid cement fills the buccal groove and extends into the shallow lingual groove; most of the surface of both lophs of the talonid is cement covered. On P₃ of two slightly older specimens, Nos. 53384 and 5535, in which P₃ is still essentially unworn, cement is absent on the trigonid and in the lingual groove. Individual and age variation seems to affect deposition of cement and details of the cusps. On unworn P₄ the trigonid is composed of a buccal and a lingual cusp; these cusps are compressed, in contrast to the rounded cusps on the trigonid of P₃. A crest from each cusp joins that of the other to form a posteriorly directed V at the posterior edge of the trigonid. Buccal and lingual grooves are present between trigonid and talonid. The posterior wall of the hypolophid is essentially transverse and is lined with small cusps. The posterolophid appears to be better developed than on P₃ and diverges more abruptly from the hypolophid. Cement fills the anterior basin between the compressed cusps of the trigonid, the buccal and lingual grooves between trigonid and talonid, and covers most of the occlusal surface of the talonid. Following wear the cement is worn away from the occlusal surface, and the posterolophid forms a more prominent part of that surface. At this stage crenulations are present in the enamel of the anterior wall of the talonid. Greater wear leads to the adult condition. No unworn molars are known; in the youngest specimens available, M₁ and M₂ resemble a slightly worn P₄ in showing the presence of a posterolophid and crenulations on the anterior wall of the talonid. Cement fills buccal and lingual grooves between trigonid and talonid and between hypolophid and



FIGURES 13, 14. *Palaeolagus philoi*.

13. Occlusal view of left P₃-M₂ of immature individual having unworn P₃ and P₄ (S.D.S.M. No. 54283), ×6.7.—14. Occlusal surface of P₃, showing variation in shape, ×6.7; 14a, left P₃ (S.D.S.M. No. 54276); 14b, left P₃ (S.D.S.M. No. 53427); 14c, right P₃ (S.D.S.M. No. 5537).

posterolophid. At this stage the posterior wall of the trigonid forms a more pronounced V than in more worn specimens. The youngest specimen having M₃ exhibits some wear on that tooth; the talonid is elongate anteroposteriorly, suggesting that a remnant of a posterolophid may have been present at an earlier stage of wear. The unworn lower cheek-teeth in *P. haydeni* differ from those in *P. philoi* as follows: the trigonid of P₃ has a proportionately smaller protoconid and a less persistent groove between protoconid and metaconid, cement does not occur in the basin between these cusps; the lingual groove between trigonid and talonid on P₃ is deeper and more persistent, the lingual cusps on trigonid and talonid tend to be farther from one another, and the posterolophid diverges less abruptly from the hypolophid; on P₄-M₂ the posterolophid tends to be proportionately smaller, and crenulations on the anterior wall of the talonid are indistinct or absent. Compared to that in *P. philoi*, the unworn P₃ in *Megalagus turgidus* has a proportionately larger protoconid, the lingual cusps on trigonid and talonid are more closely approximated, resulting in a small lingual groove that is eliminated at an early stage of wear, and the posterolophid is proportionately smaller.

The known parts of the skull consist of partial maxillae having zygomatic, alveolar, and palatine processes and the palatine component of the palatal bridge. The anterior zygomatic root extends laterally approximately in line with the middle of P³. Anterior to this root the maxilla is lightly pitted. The lateral surface of the zygoma is slightly concave, and the anteroventral edge of the zygoma is thickened; a ridge extends ventrally from the anterior edge of this thickening to intersect the alveolar border posterior to P³. Anterior to this ridge the maxilla is concave. The bony palatal bridge extends from the posterior ends of the incisive foramina, approximately in line with the posterior half of P², to the internal nares, in line with the posteroloph of M¹. The maxillopalatine suture is slightly convex in an anterior direction and crosses the palate about in line with the anteroloph of P⁴. Two palatine foramina occur on each side of the palate posterior to the suture. In *P. intermedius* the palatal bridge is longer, extending approximately from in line with the middle of P² to between M¹ and M²; the maxillopalatine suture is more arched anteriorly, and its anteriormost extent is about in line with the posteroloph of P³. Thus, the palatine component of the palate is longer anteroposteriorly in *P. intermedius*, which is a more primitive leporid feature.

The shape of the horizontal ramus, the only completely known part of the lower jaw, resembles those in

TABLE 4.—Measurements in millimeters of *Palaeolagus philoi*

	No. 53389	No. 54325		No. 5526	No. 54277	No. 54283 (immature)
P ² anteroposterior	1.5					
width	1.9					
P ³ anteroposterior	1.9	2.0				
width anteroloph	3.2	3.1				
width posteroloph	3.6	4.0				
P ⁴ anteroposterior	2.0	2.1				
width anteroloph	4.0	4.2				
width posteroloph	4.2	4.0				
M ¹ anteroposterior	1.9	2.1				
width anteroloph	3.9	3.8				
width posteroloph	4.0	3.9				
M ² anteroposterior	1.9	1.9				
width anteroloph	3.4	3.4				
width posteroloph	ca. 3.6	3.1				
M ³ anteroposterior		1.1				
width		1.8				
P ³ -M ²	8.8	8.8				
length palate (lateral)	6.8					
length palatine on palate	3.0					
length maxilla on palate	3.8					
dorsoventral depth, anterior root of zygoma	4.7					
P ₃ anteroposterior	2.2	2.5	1.9			
width trigonid	1.7	1.8	1.4			
width talonid	2.0	2.2	1.9			
P ₄ anteroposterior	2.6	2.5	2.2			
width trigonid	2.8	2.7	2.2			
width talonid	2.1	2.2	1.8			
M ₁ anteroposterior	2.5	2.6	2.4			
width trigonid	2.7	2.7	2.2			
width talonid	2.1	2.2	2.0			
M ₂ anteroposterior	2.5	2.7	2.4			
width trigonid	2.6	2.5	2.0			
width talonid	2.1	2.3	1.9			
M ₃ anteroposterior	1.4					
width trigonid	1.5					
width talonid	0.9					
P ₃ -M ₃	11.3					
P ₄ -M ₂	7.6	8.0	7.3			
inside depth of jaw below M ₁	10.9	11.2	ca. 8.7			

other species of *Palaeolagus* and of *Megalagus* in general. The lateral surface of the ramus tends to be pitted below the diastema, and the medial surface also is pitted, especially on the swelling over the shaft of the incisor, which extends to the space below P₃-P₄ or the trigonid of P₄. An anterior mental foramen pierces the dorsolateral surface of the ramus below the diastema; a posterior mental foramen may be present on the lateral surface below P₄, although in some lower jaws a number of pits, rather than a single foramen, occur in this region. On the

dorsal surface of the ramus immediately posterior to M_3 , a series of small pits are present, suggesting incipient fenestration in this region. The ridge marking the anterior border of the masseteric fossa reaches anteriorly to below M_3 or the talonid of M_2 .

Relationships.—The closest affinities of *Palaeolagus philoi* seem to be with *P. intermedius*. On the basis of the known material, *P. philoi* resembles *P. intermedius* in general but is advanced in the greater hypsodonty of the upper cheek-teeth and the shorter palatine component of the palate. The known specimens of *P. intermedius* show most stages of wear for the upper teeth, but the lower cheek-teeth are poorly known; the reverse is true of *P. philoi*—known specimens show various stages of wear of the lower cheek-teeth but only well-worn upper cheek-teeth. As a result it is difficult to compare the two species. However, the known specimens are adequate to show that *P. philoi* is closely related to *P. intermedius* but is slightly more advanced. As now known, the *P. intermedius*—*P. philoi* line seems to be a progressive series developing in a direction leading toward the Archaeolaginae.

Palaeolagus? sp.

Several specimens that have been tentatively referred to *Palaeolagus* are significant as representing possible extensions of the geographic range of the genus. C.I.T. No. 1512, an incomplete ramus having P_3 — M_2 from the upper Oligocene of the Sespe beds of California, was tentatively referred to *Desmatolagus* by Wood (1940, p. 350); WILSON'S earlier provisional reference (1934, p. 16) of this specimen to *Palaeolagus* sp. may be more accurate. An isolated lower cheek-tooth from the lower Miocene of the Texas Gulf Coastal Plain, A.M.N.H. No. 30089, may represent a species of *Palaeolagus* (Wood & Wood, 1937, p. 139), although the incomplete material permits no more than tentative reference.

In the lower Miocene John Day beds of Oregon, *Archaeolagus ennisianus* is the common leporid, but COPE (1884, p. 881) mentioned that specimens indistinguishable from *Palaeolagus haydeni* were also present in his collections from Oregon. However, MATTHEW (1901, p. 376-377) stated, following examination of the COPE collection, that all the John Day leporids have the typical archaeolagine P_3 composed of three lobes and that *Palaeolagus* does not occur in the John Day beds. Reexamination of materials from the John Day beds in the COPE collection shows that in a mandibular fragment included under A.M.N.H. No. 7219 P_3 , the only cheek-tooth present, has the characteristic palaeolagine shape: only one external reentrant, between trigonid and talonid, occurs, resulting in a two-lobed tooth; an isolated enamel-lined lake remains as a remnant of the internal reentrant between trigonid and talonid. Although evidence from this one specimen is not conclusive, the presence of *Palaeolagus* in the John Day beds is suggested.

Further evidence for the presence of a palaeolagine in the John Day beds is furnished by C.I.T. No. 5182 from C.I.T. locality 246, John Day beds, Oregon. This specimen, a fragmentary right lower jaw having part of the incisor and P_3 — M_2 , has a typical palaeolagine P_3 composed of two lobes. A short internal reentrant is present between

trigonid and talonid. This reentrant is lined with enamel, filled with cement, and loses its connection with the lingual wall above the alveolar level; it cannot be determined from the present state of wear whether a trace of this reentrant would persist as an isolated lake. The trigonid and talonid of M_1 are united by a lingual bridge, but absence of a complete bridge on P_4 and M_2 indicates that the fully adult pattern of the cheek-teeth is not present in this specimen. The incisor is nearly triangular in cross-section, and the swelling over the shaft of the incisor extends to below P_3 — P_4 . No. 5182 is larger than *P. haydeni*; it is close to *A. ennisianus* in size of the teeth but has a dorsoventrally shallower jaw. In earlier stages of wear *A. ennisianus* may have an internal reentrant or isolated lake on P_3 as does No. 5182, but typical specimens of *A. ennisianus* differ from No. 5182 as follows: P_3 is composed of three lobes, the lower incisor is more flattened dorsoventrally, and the swelling over the lower incisor terminates below the trigonid of P_3 . However, variation within *A. ennisianus* must be considered before the affinities of No. 5182 can be determined, because not all specimens of *A. ennisianus* have the "typical" characteristics. For example, A.M.N.H. No. 7199 appears to be *A. ennisianus* on the basis of an archaeolagine P_3 , but the swelling over the lower incisor extends to below P_3 — P_4 . Despite the differences of No. 5182 from typical *A. ennisianus*, possibly it is an aberrant archaeolagine. However, the combination in that specimen of at least three palaeolagine features that are differences from most specimens of *A. ennisianus*, the palaeolagine P_3 , the shape of the incisor, and the length of the shaft of the incisor, casts considerable doubt on reference of No. 5182 to *A. ennisianus*. On the basis of C.I.T. No. 5182 and of A.M.N.H. No. 7219 it seems probable that *Palaeolagus* does occur in the lower Miocene John Day beds, although *A. ennisianus* is more common. If No. 5182 belongs to the genus *Palaeolagus*, it seems not to be referable to one of the known species.

TABLE 5.—Measurements in millimeters of *Palaeolagus?* sp.

	C.I.T. No. 5182
P_3 anteroposterior	2.3
width trigonid	1.8
width talonid	2.2
P_4 anteroposterior	2.6
width trigonid	2.5
width talonid	2.0
M_1 anteroposterior	2.6
width trigonid	2.5
width talonid	2.1
M_2 anteroposterior	2.7
width trigonid	2.4
width talonid	2.0
P_1 — M_2	8.0
inner depth of jaw below M_1	9.7

*Litolagus*³ *molidens*,⁴ n. gen. and n. sp.

Plate 2, figures 2-3; Figures 15-17

Type specimen.—Partial skull, lower jaws, associated partial postcranial skeleton, C.I.T. No. 1568. Lower nodular layer of Oreadon beds, Oligocene, about six and one-half miles southeast of Douglas, Wyoming.

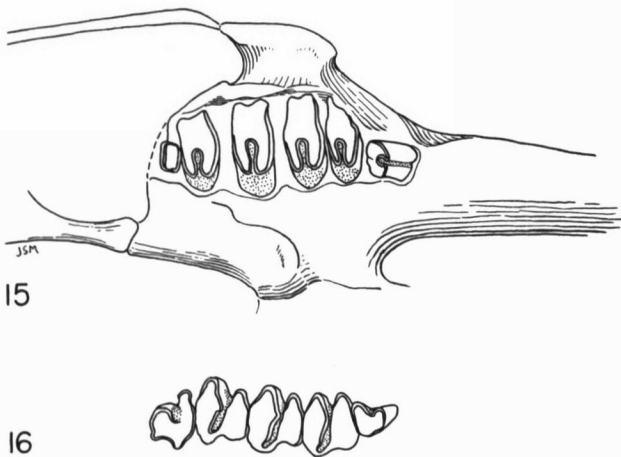
³ From Greek, *litos*, simple, and *lagos*, hare, referring to the simple folds on the upper cheek-teeth.

⁴ From Latin, *molo*, to grind, and *dens*, tooth.

Referred specimen.—Partial skull and lower jaws, F.H. No. 10283. Locality and horizon as for type.

Geologic age and distribution.—Orellan (middle Oligocene) of Wyoming.

Generic and specific characters.—Size larger than *P. haydeni*, smaller than *P. intermedius*. Cheek-teeth hypodont and having well-developed cement. On P^3 - M^2 relatively long, straight-walled internal hypostria; primitive pattern of crescents on these teeth presumably lost at early stage of wear. Shaft of lower incisor extends posteriorly to below P_4 . P_3 composed of two lobes, separated by single buccal reentrant between trigonid and talonid; internal reentrant lost at early stage of wear. On P_4 - M_2 , trigonid and talonid joined by lingual bridge. Palatine component of palate shorter, anterior root of zygoma extends laterally less abruptly than in *P. haydeni*.



FIGURES 15, 16. *Litolagus molidens* (C.I.T. No. 1568).

15. Ventral view of skull fragment (type specimen) having right P^2 - M^3 , $\times 3$.—16. Occlusal view of right P_3 - M_3 , $\times 3$.

In the type specimen of *Litolagus molidens*, C.I.T. No. 1568 (Pl. 2, fig. 3), right upper and lower cheek-teeth are complete; on the left the cheek-teeth are present but broken. The remains are those of an immature individual, as shown by the presence of unfused or only partly fused epiphyses on the proximal end of the humerus, proximal and distal ends of the ulna, distal end of the radius, distal end of the tibiofibula, and ischial tuberosity. That the individual was approaching maturity, however, is suggested by fused epiphyses on the proximal radius and distal humerus, and by the dentition, which consists of somewhat worn permanent teeth. The type specimen is slightly smaller than F.H. No. 10283 (Pl. 2, fig. 2), the skull and jaws of an adult. The two specimens are from the same locality and resemble one another in the pattern of the teeth and in most known characteristics of the skull and jaws. The palate and dentition are more completely known in the type than in the referred specimen, although the skull of the latter is more complete in general. Despite its slight immaturity, No. 1563 has been selected as the type: the characters judged to be of generic value are present, and the specimen, which has associated postcranial material, is the more complete of the two

known specimens. The following description of the skull and dentition is based on both type and referred specimens.

Description.—Dentition. In the row of upper cheek-teeth (Fig. 15), P^2 is wider transversely than M^3 and has a single anterior reentrant that crosses about one-third of the occlusal surface. Enamel is well developed lingually but thinner or absent buccally. The posteroloph of P^3 is wider than the anteroloph, and an internal straight-walled hypostria crosses slightly less than half the occlusal surface of this tooth. On the anterior wall of the anteroloph near its buccal side there is a shallow notch in No. 1568 that may represent the last remnant of a crescent similar to that on P^3 in *Palaeolagus burkei*. P^4 , M^1 , and M^2 resemble one another in general pattern. On each an internal, straight-walled hypostria crosses slightly less than half the occlusal surface. On P^3 - M^2 enamel is well developed anteriorly, lingually, and on the borders of the hypostriae, is thinner posteriorly, and is reduced or absent buccally. M^3 consists of a single loph without reentrants and has an enamel development similar to that of the more anterior teeth. Cement is well developed: it fills the fold on P^2 ; on P^3 - M^2 it fills the hypostria and in No. 1568 extends onto the lingual and anterolingual sides of the shafts. In No. 10283 M^2 is the only tooth in which the lingual side is visible; on that tooth cement spreads onto the shaft as in the type specimen. Unfortunately the pattern of more worn teeth is unknown at present, so it cannot be determined whether the hypostriae persist, become shortened, or form isolated lakes. In pattern and proportions P^3 and P^4 in *Litolagus* are more molariform than in *Megalagus* and *P. haydeni*.

Two lobes compose P_3 (Fig. 16): the trigonid is narrower than the talonid, a single external reentrant between trigonid and talonid crosses about half the width of the tooth, and the dentine of the columns is confluent on the lingual half of the tooth. A furrow, shallower in No. 10283 than in the type, is present on the lingual side of P_3 ; this seems to be a remnant of an internal reentrant, most of which was lost at an earlier stage of wear. A similar early loss of the internal reentrant occurs in *Palaeolagus intermedius* and *Megalagus*. Enamel is thick buccally on both columns and is thin or absent on the lingual side of the talonid. In general P_4 , M_1 , and M_2 resemble one another: each consists of a trigonid and a slightly narrower talonid, which are united lingually by a bridge of enamel and dentine. The enamel is well developed buccally on both columns and posteriorly on the trigonid, is present, but thin, posteriorly on the talonid, is absent on a narrow anterior strip on the trigonid, and is absent or thin lingually. The columns of M_3 are joined in the type, but their former separation is indicated by a shallow lingual groove and a deeper external fold. Cement is present between the columns on P_4 - M_2 and fills the external reentrants on P_3 and M_3 .

Skull. The incomplete skull of No. 1568 includes most of the maxillae, the zygomata, right bulla and mastoid, and the palate. The skull of No. 10283 is more complete but lacks the posterior part of the roof, the occiput, and most of the bullae. The skull is slightly smaller than in *Palaeolagus intermedius* and *Archaeolagus ennisianus*. The anterior root of the zygomatic arch projects laterally

proportionately less far than in *P. haydeni*. Anteroventral to the root there is a slight depression in the maxilla. The anteroventral border of the zygoma projects downward as a thickened ridge. The zygomatic plate is essentially vertical, and the lateral surface of the zygoma is concave, more deeply so anteriorly.

On the palate the incisive foramina are long, reaching posteriorly to a level with the posterior half of P². The internal nares reach forward to a level with the posteroloph of M¹. The maxillopalatine suture, which crosses the palate in line with the posteroloph of P⁴, extends across the palate more nearly transversely and is less arched anteriorly than in *P. haydeni*. Posterior to the maxillopalatine suture, two or three palatine foramina, having nearly confluent openings, pierce the palatine on each side of the midline. In *Litolagus* the shorter length of the palate and its proportionately shorter palatine component indicate that this genus was more advanced in the structure of the palate than *Megalagus* and the Oligocene species of *Palaeolagus*.

The small supraorbital process of the frontal resembles that in *P. haydeni*. The posterior end of the frontals is approximately in line with the middle of the zygomatic process of the squamosal, and a process of the parietal extends into the orbit. *Palaeolagus haydeni* is more primitive in having shorter frontal bones, which terminate anterior to the zygomatic process of the squamosal, and a longer process of the parietal in the orbit. The anterior portion of the braincase seems to be proportionately narrower transversely than in *P. haydeni*. The bulla is proportionately about as large as in *P. haydeni* but larger than in *Megalagus turgidus*. The mastoid is a well-developed, rugose element having a dorsal border that is convex anteriorly and concave posteriorly, resembling that in *P. haydeni*.

Lower jaw. The lower jaw, although larger, resembles that in *P. haydeni* in shape. The ventral portions of the horizontal ramus are somewhat pitted laterally and medially, especially on the swelling over the shaft of the incisor. On the lateral surface of the jaw, one mental foramen occurs below the diastema and a second below P₄. The low ridge that marks the anterior border of the masseteric fossa extends forward to a line below the trigonid of M₃ or talonid of M₂.

Postcranial skeleton. Preserved in the type specimen, C.I.T. No. 1568, are about seven lumbar vertebrae, sacral and probably caudal vertebrae; scapulae, humeri, radii, and ulnae, portions of the right carpus, and right and left metacarpals; partial right innominate; right femur lacking proximal and distal ends, and left tibiofibula lacking proximal end. One of the more noticeable differences between the skeleton in this species and that in *P. haydeni* is size; long bones of the immature specimen are 23 to 35 per cent longer. The size difference between an adult of this species and *P. haydeni* would be more.

Except for being larger, the lumbar vertebrae resemble those in *P. haydeni* in general. As in that species, the transverse processes, especially those of the more anterior lumbar, are short and anteroposteriorly expanded. The transverse processes of the lumbar vertebrae in both *Palaeolagus* and *Litolagus* resemble those in *Romerolagus*

more closely than they resemble the proportionately longer, more slender processes in *Sylvilagus* and *Lepus*.

Although the dorsal part of the scapular blade is broken, the more ventral parts suggest that the suprascapular and infraspinous fossae are approximately equal in size. The anterior border of the scapula flares anteriorly above the rather short neck, and the scapular spine merges with the blade proportionately closer to the glenoid region than in *Sylvilagus* and *Lepus*. In the characteristics of the scapula just mentioned, *Litolagus* resembles *P. haydeni* and *Megalagus*. The posterior part of the medial side of the scapula, not visible in known specimens of *P. haydeni*, is exposed in No. 1568. The axillary border is wide and flattened. Toward the vertebral border of the scapula the axillary border narrows somewhat and is set off from the subscapular fossa by a distinct ridge; more ventrally the axillary border is wider, and a ridge separating it from the subscapular fossa is lacking, so the two surfaces intersect with a slight outward convexity. The posterior half of the subscapular fossa is gently convex above the neck of the scapula but becomes flattened or even slightly concave dorsally. In contrast to the structure in *Litolagus*, the axillary borders in *Palaeolagus hypsodus*, *Romerolagus*, *Sylvilagus*, and *Lepus* are sharply set off from the subscapular fossa along the entire length of contact by a definite ridge, and the posteroventral part of the subscapular fossa is more flattened or slightly concave. Although the lack of a pronounced ridge between the axillary border and the subscapular fossa may possibly be a characteristic of immaturity, this does not seem to be the case in the Recent leporids, so the lack in *Litolagus* may be a real difference from the Recent leporids. The axillary border and subscapular fossa in *Ochotona* are more nearly like those in the Recent leporids than those in *Litolagus*.

Although presence of unfused epiphyses on the ends of some of the long bones makes comparison with adult specimens of other leporids somewhat difficult, limited comparisons can be made. The humerus is slightly straighter, in lateral view, than in either *P. haydeni* or *Megalagus turgidus*. On the anterior side of the humerus the deltoid crest extends about halfway down the bone but seems to be a little less pronounced distally than in *P. haydeni* and *M. turgidus*, a difference possibly due to ontogenetic age. The greater tuberosity is slightly higher than the head of the humerus, thus being a little higher than in *P. haydeni*. Distally there is a distinct supinator crest, an entepicondylar foramen, and a supratrochlear foramen. The medial keel and the medial condyle seem to be a little larger in proportion to the size of the distal end of the humerus than in *P. haydeni*.

Viewed laterally the ulna and radius are somewhat less convex anteriorly than in *P. haydeni*. Distally the ulna widens, especially anteroposteriorly. The epiphysis of the distal end of the right ulna is missing, and the unfinished end is concave. The left ulna has the unfused distal epiphysis in place, but due to its position in the matrix, only the posterior side is visible. In this view the epiphysis is slightly wider proximally and tapers toward the distal end. The posterolateral part reaches somewhat more distally than the anteromedial, forming a styloid process that probably formed slightly less than half of the distal surface. The proximal end of the radius is somewhat grooved

as in *P. haydeni*, but in *Litolagus* and *P. haydeni* the distinct notches for articulation with the humerus, which characterize the proximal end of the radius in the Recent leporids, are lacking. The distal epiphysis of the radius, which is displaced in this specimen, is slightly concave both proximally and distally. The medial side of the epiphysis is longer than the lateral, and anteriorly the epiphysis has two distinct ridges paralleling its long axis. In proportions, the radius and ulna in *Litolagus* are slightly more elongate relative to the length of the humerus than in *P. haydeni*; in the former the proportion of radius to humerus is 0.96 and in the latter 0.90.

No part of the carpus has been described previously in an Oligocene leporid, and although the carpus in No. 1568 is not complete, scaphoid, lunar, pisiform, centrale, and magnum are present (Fig. 17). Both scaphoid and lunar are slightly convex proximally, concave distally, and have flattened anterior surfaces. Viewed anteriorly the proximodistal and transverse dimensions of the lunar are subequal, and its posterior portion curves down over the centrale and magnum. In *Romerolagus*, *Sylvilagus*, and *Lepus*, the anterior surfaces of the scaphoid and lunar are more curved, forming a continuation of the proximal convexity, rather than being flattened. The cuneiform is not preserved, but considering the well-developed distal end of the ulna and its relatively small styloid process, the cuneiform probably resembled that in *Ochotona* in forming a larger proportion of the proximal carpal row than in Recent leporids and in having two distinct proximal articular facets, a posterolateral one for the styloid process

and another situated anteromedially for the flattened facet of the distal ulna. However, the styloid process in *Litolagus* seems to be proportionately longer proximodistally and to have a shorter posterolateral extension than in *Ochotona*; probably, therefore, the cuneiform in *Litolagus* was more deeply socketed and less elongate posterolaterally than in *Ochotona*. The facet on the anterior face of the pisiform, which is concave for contact with the styloid process, forms a proportionately smaller part of that face, and that portion of the bone medial to this facet is proportionately longer than in Recent leporids. The pisiform is more elongate anteroposteriorly than in Recent leporids. The centrale, which fits between lunar, magnum, and the proximolateral end of metacarpal II, is approximately trapezoidal in outline and its anterior face is flattened. The magnum fits between the laterodistal side of the lunar and the proximal end of metacarpal III. The anterior face of the centrale is larger than that of the magnum; a similar size relationship between these bones occurs in *Ochotona* and *Romerolagus*, but the reverse is true in *Sylvilagus* and *Lepus*. In the latter two genera the proximal carpals seem to be proportionately larger and the distal carpals smaller than in *Litolagus*, *Romerolagus*, and *Ochotona*.

All metacarpals except the first are preserved in this specimen, seemingly in a relatively "natural" position with metacarpal III reaching most distally, followed by IV, II, and V. Metacarpal II is actually slightly longer than IV. In the lagomorphs a series showing progressive shortening of metacarpal IV in relation to the other metacarpals can be traced: in *Ochotona* metacarpal IV is actually longer and reaches more distally than metacarpal II; in *P. haydeni* metacarpals II and IV are approximately equal in length and IV probably reached more distally; in *Litolagus* metacarpal IV is shorter but reaches more distally than II; in Recent leporids metacarpal IV is shorter and does not reach so far distally as II. There is no indication of the level of development of metacarpal I. The notch for the trapezoid on the proximal end of metacarpal II seems to be a little deeper than in Recent leporids. The facets on the proximal end of metacarpal V resemble those in *Ochotona* and are better developed than in the Recent leporids. Viewed anteriorly, the shaft of metacarpal II is slightly convex laterally. *Litolagus* shows an early stage in development of the leporid carpus and metacarpus. The facets on the proximal ends of the metacarpals in *Litolagus* suggest that the manus was better adapted for movement in several planes and more flexible than in the Recent leporids; in the latter the extension of the proximal convexity onto the anterior face of the proximal carpals suggests better development of hingelike movement about a transverse axis at the wrist. The ulnar side of the manus is well developed in *Litolagus* in correlation with the essentially unreduced ulna. The shaft and distal end of the ulna are reduced in Recent leporids, a cursorial adaptation, and correspondingly the ulnar side of the manus is proportionately smaller than in *Litolagus*.

The innominate is not complete, for the anterior part of the iliac blade is broken, and the pubis and ventral parts of the ischium, if present, are obscured by matrix. The blade of the ilium, which has the two fossae separated by a distinct, rounded ridge, generally resembles that in



FIGURE 17. *Litolagus molidens* (C.I.T. No. 1568).

Part of right forelimb (type specimen), $\times 3$, showing proximal ends of ulna and radius, carpus with scaphoid, lunar, centrale, and magnum (pisiform present but not visible), and metacarpals II, III, IV, V (missing parts restored in dashed lines from *Romerolagus*).

P. haydeni, but the rise of the dorsal rim of the ilium at the place of sacral articulation is gradual, in contrast to a more abrupt rise in *P. haydeni*. The tubercle of the ilium extends outward from the lateroventral border of the ilium as in *P. haydeni* but is somewhat lower and thicker. A small, knoblike protuberance occurs posterodorsal to the tubercle and immediately anterior to the anterior rim of the acetabulum. In function, this may be similar to the raised and roughened area posterior to the tubercle of the ilium in *P. haydeni*. The exact position of the ischial tuberosity is not clear, due to displacement of its unfused epiphysis, but the tuberosity seems to resemble that in *P. haydeni* in forming a distinctly raised knob and in consisting of two facets.

Proximal and distal ends of the femur are missing from the specimen, possibly due to loose attachment of the epiphyses. Its shaft is straight as in *P. haydeni*. The grooves in the distal end of the tibiofibula for tarsal articulation seem to be proportionately a little deeper than in *P. haydeni*. In an attempt to determine the proportions of the tibiofibula in *Litolagus* in comparison to *P. haydeni* the distance between the distal end and the separation of the fibula from the tibia was utilized: in this measurement the tibiofibula in *Litolagus* is about 53 per cent longer than is that in *P. haydeni*. This far exceeds the difference in length of the other long bones of 23 to 35 per cent. The excess could be due to union of the fibula with the tibia more proximally or to distal elongation of the tibiofibula in *Litolagus*. Possibly both factors contributed, although the latter may be responsible for more of the difference.

Summary. *Litolagus molidens* is more advanced than its smaller contemporary, *Palaeolagus haydeni*, in the following characters of the upper cheek-teeth: greater molarization of the premolars, on P³-M² earlier loss of the crescentic lakes between central and lingual lobes, longer internal hypostriae, and more cement. Early loss of the internal reentrant on P₃ is a character in which *Litolagus* is more nearly like the Archaeolaginae. Cranial characters in which *Litolagus* is more advanced than *P. haydeni* are: palatal structure, in which *Litolagus* is approximately intermediate between *P. haydeni* and *Archaeolagus ennisianus*; more posterior position of frontals and shorter process of parietal on the posterior wall of the orbit. Nevertheless, the anterior root of the zygoma in *Litolagus* shows less resemblance than does that in *P. haydeni* to the condition in more advanced leporids. Thus, presumably advanced characters in dentition and skull are combined with seemingly primitive characters. In most postcranial characters *Litolagus* is close to *P. haydeni*, although in the type specimen of *Litolagus* the radius is proportionately longer relative to the length of the humerus and the tibiofibula seems to be relatively longer than in *P. haydeni*. This may indicate more cursorial adaptation for *Litolagus*, but immaturity of the type may cause the distal segments to be proportionately more elongate than in an adult and thus be responsible for the differences from *P. haydeni*. Probably definite conclusions about the level of cursorial development of *Litolagus* should not be made solely on the basis of the type specimen.

Relationships.—In the middle Oligocene of North America four genera of leporids are known, *Desmatolagus*, *Megalagus*, *Palaeolagus*, and *Litolagus*. American species of *Desmatolagus* are poorly known and of questionable status but may be most closely related to certain Mongolian leporids. *Megalagus*, which appears to be a descendant of *Mytonolagus*, a North American late Eocene genus, is persistently primitive in most characters of the cheek-teeth. Within the genus *Palaeolagus* there is a diversity of species, all of which have more progressive characters in the teeth than does *Megalagus*; the stock leading toward *Palaeolagus* may have been separate from that ancestral to *Megalagus* at least since late Eocene times. Considering *Palaeolagus* as a structurally central type in the middle Oligocene, *Megalagus* diverges in the direction of more primitive development of the cheek-teeth, whereas *Litolagus* diverges toward more progressive dental characters. *Litolagus* appears to be closest to those species of *Palaeolagus*, such as *P. intermedius*, in which the internal hypostriae on the upper cheek-teeth are becoming a persistent part of the pattern and the internal reentrant on P₃ is eliminated at an early stage of wear. Of late Eocene and early Oligocene leporids, *Mytonolagus* and *Megalagus brachyodon* appear to be most closely allied to *M. turgidus*, and *Palaeolagus temnodon* to *P. haydeni*; the Mongolian leporids with that time range do not seem closely allied to the later North American genera with the exception of *Desmatolagus*. As mentioned above (under *P. burkei*), there are specimens of an incompletely-known early Oligocene leporid having persistent internal hypostriae on P³-M². These specimens might represent a line leading toward *Litolagus*, although relationships of this early Oligocene leporid to *P. burkei* seem more probable. In the absence of other known pre-Orellan leporids, remarks as to the ancestry of *Litolagus* will be speculative. Possibly *Litolagus* is the descendant of a late Eocene or early Oligocene stock near that leading toward *Palaeolagus intermedius*; from such a stock *Litolagus* would seem to have evolved relatively rapidly in the advanced characters of teeth and palate but to have been somewhat less progressive in the zygomatic structure and to have essentially paralleled *Palaeolagus* in postcranial development.

The advanced characters of the palate and dentition in *Litolagus* make this genus a possible candidate for ancestry of some later leporids; the Archaeolaginae, for example, might be expected to have descended from an ancestor with well-developed internal hypostriae in the upper cheek-teeth and early suppression of the internal reentrant on P₃, a combination of characters found in *Litolagus*. However, certain later leporids suggest that *Litolagus* may actually be too advanced in dentition to be ancestral to the Archaeolaginae; furthermore, its unprogressive zygomatic structure does not suggest affinity to the archaeolagines. On the basis of currently known leporids, *Litolagus* may be leading phylogenetically toward the archaeolagines, but more probably *Litolagus* was a palaeolagine that was near the *P. intermedius*-*P. philoi* line of *Palaeolagus* and that showed tendencies of advance toward the Archaeolaginae but was not ancestral to that subfamily.

TABLE 6.—Measurements in millimeters of *Litolagus molidens*

	C.I.T. No. 1568	F.H. No. 10283
P ² anteroposterior	1.0	ca. 1.1
width	1.7	
P ³ anteroposterior	1.5	1.9
width anteroloph	2.4	
width posteroloph	3.0	
P ⁴ anteroposterior	1.7	2.1
width anteroloph	3.1	
width posteroloph	3.0	
M ¹ anteroposterior	1.7	2.0
width anteroloph	3.1	
width posteroloph	3.0	
M ² anteroposterior	1.5	1.9
width anteroloph	2.5	
width posteroloph	2.4	
M ³ anteroposterior	0.9	1.2
width	1.2	
length P ² -M ²	9.6	11.8
length P ³ -M ³	7.8	8.7
skull width across anterior roots of zygomata	ca. 23.8	ca. 24.1
width braincase posterior to zygomatic process of squamosal		ca. 17.0
width palate between P ⁴	ca. 8.2	
length palate	ca. 5.3	
length palatine on palate	ca. 2.4	
length maxilla on palate	ca. 2.8	
P ₃ anteroposterior	1.9	
width trigonid	1.4	
width talonid	2.2	
P ₄ anteroposterior	2.1	
width trigonid	2.4	
width talonid	1.9	
M ₁ anteroposterior	2.4	
width trigonid	2.5	
width talonid	2.2	
M ₂ anteroposterior	2.5	
width trigonid	2.4	
width talonid	2.0	
M ₃ anteroposterior	1.2	
width trigonid	1.4	
width talonid	0.9	
length P ₃ -M ₃	9.8	
length P ₄ -M ₂	7.0	
inside depth of jaw below M ₁	9.7	
length right humerus	45.0	
length left ulna	50.8	
length right radius	43.4	
length right metacarpal II	13.4	
length right metacarpal III	15.0	
length right metacarpal IV	12.5	
length right metacarpal V	8.1	
length tibiofibula approximately from place of union with fibula to distal end	ca. 44.4	

Palaeolaginae?

Figure 18

Specimen.—Fragment of left lower jaw having P₃-P₄, S.D.S.M. No. 5542, lower Rosebud (lower Miocene), N $\frac{1}{2}$ sec. 17, T. 39 N., R. 43 W., Shannon County, South Dakota.

The single specimen concerned was found in a lower Rosebud locality along with specimens of *Palaeolagus hypsodus* and *P. philoi*. In No. 5542 P₃ is composed of two distinct columns that seem to be connected to one another solely by cement. The anterior column, seemingly the trigonid, is similar in shape to the complete P₃ in *P. philoi*: the anterior lobe of this column is narrower

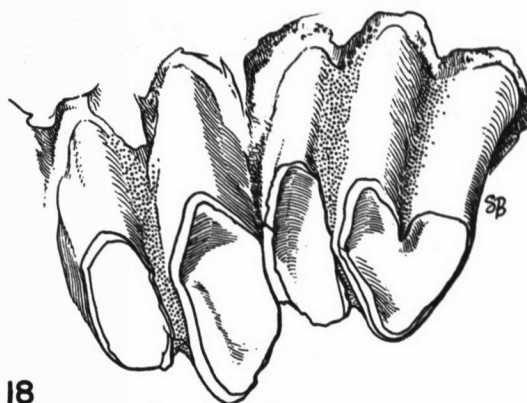


FIGURE 18. Species doubtfully assigned to Palaeolaginae.

Occlusal view of left P₃-P₄ (S.D.S.M. No. 5542), $\times 9$.

than the posterior; a single external reentrant, which has a thin cement filling, enters the occlusal surface; the dentine of the two lobes of the column is confluent lingually. Cement completely fills the space between the trigonid and the posterior column, or talonid; this complete separation of the columns persists as far as it can be traced into the alveolus. The talonid resembles that of an adult *P. philoi* in general shape but lacks a lingual enamel and dentine bridge connected to the trigonid. Enamel is thin or absent lingually on the talonid. The trigonid and talonid of P₄ resemble those in *P. philoi* in general, but here again the two columns are united only by cement. Enamel is absent anteriorly on the trigonid and is thin or absent lingually on the talonid. The pattern of the occlusal surfaces of these teeth and the reduction of enamel indicates that this is not an immature individual. The fragment of the jaw in which the teeth are situated is incomplete but does show pronounced ridges at the symphysis. On the lateral surface of the jaw is an anterior mental foramen below the diastema, a posterior mental foramen below the talonid of P₃, and possibly another foramen below P₄. The swelling over the shaft of the incisor extends to a line below the middle of P₄ and has a pitted surface. Connection of the columns by cement only gives the cheek-teeth an ochotonidlike cast. However, connection of the columns by cement only is found also among the leporids in *Palaeolagus burkei* and *P. hypsodus*, and No. 5542 seems to be referable to the Leporidae on the basis of the general structure of incisor, cheek-teeth, and lower jaw and the development of the enamel.

No. 5542 differs from *Palaeolagus philoi* as follows: presence of deep anteroexternal reentrant on the trigonid of P₃; lack of a lingual connection of dentine and enamel between the columns on P₃ and P₄; slightly shorter diastema; more posterior position of anterior mental foramen; slightly longer shaft of the incisor; and slightly smaller size. Possibly the specimen is an aberrant individual of the species *P. philoi*. Several of the differences listed above, such as the connection of cement between the columns of both P₃ and P₄, might accompany one another as the result of abnormal development or mutation. However, the sum of the differences listed above strongly suggests

that No. 5542 is not an aberrant individual of *P. philoi* but is a previously unknown (and unexpected!) leporid.

If No. 5542 is not an aberrant *P. philoi*, its relationships within the Leporidae are unknown; it is tentatively referred to the Palaeolaginae primarily as a matter of convenience. Among later leporids a separation of trigonid and talonid on P_3 similar to that in No. 5542 occurs in some stages of wear in *Hypolagus? browni* and *?Pratilepus progressus* and throughout most of life in *Brachylagus* and *Nesolagus*. Thus, No. 5542 seems to be curiously advanced in the structure of P_3 toward some members of the subfamily Leporinae, although the later fossil record indicates that the leporines are probably not derived from such an ancestor. A more definite statement of the affinities of this leporid must await more complete material.

TABLE 7.—Measurements in millimeters of Palaeolaginae?

	No. 5542
P_3 anteroposterior	2.8
width trigonid	2.0
width talonid	2.1
P_4 anteroposterior	2.4
width trigonid	2.6
width talonid	2.1

Subfamily ARCHAEOLAGINAE Dice, 1929

Three genera are included in the subfamily Archaeolaginae: *Archaeolagus*, known in time from early Miocene to early middle Miocene; *Hypolagus*, later middle Miocene to early Pleistocene; *Notolagus*, middle Pliocene to Blancan (early Pleistocene?). Geographically the archaeolagines seem to have undergone their greatest development in North America, but *Hypolagus* reached Asia and Europe in the later Pliocene. Derivation of the Archaeolaginae from the Palaeolaginae probably occurred in North America. *Archaeolagus* and *Hypolagus* seem to be separated mainly as different levels of evolutionary development; *Notolagus* is more sharply differentiated than *Hypolagus* and constitutes a side-branch from the *Archaeolagus—Hypolagus* line.

The following dental characteristics unite the archaeolagines: cheek-teeth hypsodont; only persistent fold on upper molariform cheek-teeth formed by internal hypostria having straight or crenulated walls; upper molariform premolars usually more molariform than in palaeolagines; two external reentrants on P_3 , anterior of which is usually shallower than posterior; posterointernal reentrant on P_3 between trigonid and talonid not persistent, usually lost at early stage of wear. Skull seemingly more advanced than in palaeolagines: angle between basicranial and palatal axes larger; palatine forming proportionately shorter part of bony palatal bridge; anterior zygomatic root situated more anteriorly.

Genus ARCHAEOLAGUS Dice, 1917

Archaeolagus DICE, Univ. California Pub., Bull. Dept. Geol., v. 10, no. 12, p. 180, March 23, 1917. Type, *Lepus ennisianus* COPE.

Geologic age and distribution.—Arikareean (early

Miocene) to early Hemingfordian (early middle Miocene); Oregon, California, South Dakota.

Generic characters.—In adult, single, shallow, anterior reentrant on P^2 ; internal hypostria on P^3 - M^2 usually straight walled; P^3 and P^4 less molariform than molars and less than corresponding premolars in *Hypolagus*. On P_3 two external grooves: anterior groove shallow and usually lacking cement; posterior groove between trigonid and talonid deeper and cement filled. Anterior root of zygoma situated more anteriorly and extending outward more abruptly, where known, than in *Palaeolagus* and *Megalagus*.

The leporids here included in the genus *Archaeolagus* have reached a level of evolutionary development in which the characters of the Archaeolaginae are established, but certain primitive characteristics, such as lack of crenulations in the internal hypostriae of the upper cheek-teeth and less molarization of P^3 and P^4 than in *Hypolagus*, are still present. It is possible, using the characteristics of the archaeolagines, to differentiate *Archaeolagus* from the palaeolagines, but it may be difficult, especially in incomplete specimens, to differentiate advanced species of *Archaeolagus* from primitive species of *Hypolagus*. Nevertheless, the combination of characters given above does serve to unify the leporids in the genus *Archaeolagus*.

On the basis of the known fossil record, the species of *Archaeolagus* can be divided into two lines; the species in each line seem to be more closely related to one another than to the species in the other line, although this is based primarily on the structure of P_3 and may place undue weight on that character. In one line, which includes *Archaeolagus* sp. from upper Sespe beds, the new species, from Tick Canyon, named below on page 39 and *A. primigenius* from the upper Rosebud, P_3 is proportionately shorter anteroposteriorly and tends to be nearly triangular in outline; in the second line, composed of *A. ennisianus* from John Day beds and *A. macrocephalus* from the upper Rosebud, P_3 is anteroposteriorly elongate. In the first line, P_3 is closer in shape to that in *Palaeolagus* and seems closer to the shape that might be expected for that tooth in a primitive archaeolagine than does the elongate P_3 in the second line. The two groups essentially parallel one another in time. *Archaeolagus* sp., *A. primigenius*, and *A. macrocephalus* are known only from lower teeth and jaws, but the new species from Tick Canyon in the first line and *A. ennisianus* in the second line are known from upper teeth and parts of the skull. These remains indicate that the two lines are similar in general level of development of the upper cheek-teeth, although different in the shape of P_3 . Possibly the two groups represent parallel lines that developed independently from palaeolagine ancestors and reached essentially similar evolutionary levels; if such were the case perhaps the lines should be considered to be two genera. However, the characters in common between the lines seem to suggest close relationships, and the lines are recognized here as members of one genus, thus emphasizing horizontal relationships that seem to be real. Leporids seemingly near *Archaeolagus* that retained primitive characteristics, such as the late Miocene or early Pliocene leporid *Panolax*, seem to have persisted along with *Hypolagus*, the more progressive descendant of *Archaeolagus*.

Archaeolagus sp.

Archaeolagus(?) sp., WILSON, Carnegie Inst. Washington Pub. 584, pt. 3, p. 57, June 22, 1949.

Specimen.—Fragment of left lower jaw having P_3 - P_4 , C.I.T. No. 3538, upper Sespe beds (about 100 feet below Sespe-Vaqueros contact) of north side of Simi Valley, north of Alamos Canyon, southern California.

Naming of this species, which seems to be distinct from other known species of *Archaeolagus*, should await more complete material. The teeth are smaller than in *Palaeolagus philoi*. A wide, shallow trough occurs on the anteroexternal wall of the trigonid of P_3 ; this indentation suggests an early stage of development of the anteroexternal fold that is characteristic of the Archaeolaginae. On the anterointernal wall of the trigonid a small groove may be the groove between the buccal and lingual cusps that usually occur on the trigonid of an unworn P_3 ; if so, the groove is more lingual in position than the corresponding groove in *P. philoi*. In general shape P_3 resembles those in *P. philoi*, the new species of *Archaeolagus* named below from Tick Canyon, and *A. primigenius* more closely than those in *A. ennisianus* and *A. macrocephalus*.

According to WILSON (1949a, p. 63-64) the upper Sespe deposits of Simi Valley are in part equivalent to the Promerycochoerus? zone of the upper Sespe at South Mountain, and about the same age as, or slightly older than, the upper John Day. SCHULTZ & FALKENBACH (1949, p. 151), however, consider this part of the upper Sespe at South Mountain to be equal to the Monroe Creek of Nebraska, or older than the middle and upper John Day. Thus, the stratigraphic relationships of *Archaeolagus* sp. to other lower Miocene leporids cannot be more precisely stated than as near or slightly higher than *Palaeolagus philoi* and near or slightly lower than *A. ennisianus*.

Archaeolagus sp. seems to be the most primitive known species of the genus. Structurally, No. 3538 represents a leporid approximately intermediate in the character of P_3 between *P. philoi* and the new species of *Archaeolagus* named below. *Archaeolagus* sp. may be too late in time to represent the phylogenetic intermediate between palaeolagines and archaeolagines but possibly is near such a transitional stock. The structure of P_3 suggests that the relationships of *Archaeolagus* sp. are closer to the new species of *Archaeolagus* and *A. primigenius* than to *A. ennisianus*, although the latter could conceivably be descended from a leporid such as that discussed here.

Archaeolagus acaricolus,⁵ n. sp.

Figures 19-21

Type specimen.—Incomplete left lower jaw having incisor, P_3 - M_3 , C.I.T. No. 5171, C.I.T. locality 201, Tick Canyon formation, near narrows of Vasquez Canyon, approximately 10 miles by road from town of Saugus, southern California (JAHNS, 1940, p. 151 and fig. 4).

Referred specimens.—The following, all C.I.T. specimens, are from the type locality: incomplete right lower jaw having P_3 - M_3 , No. 5172; right maxilla having

P^2 - M^3 , No. 5173; left maxilla having P^2 - M^3 , No. 5174; fragmentary left lower jaw having P_4 - M_3 , No. 5175; fragmentary right lower jaw having essentially unworn P_3 and P_4 - M_2 , No. 5176; incomplete left innominate and proximal end of femur, No. 5177; postcranial fragment, ?tibiofibula, No. 5178.

Geologic age and distribution.—Late Arikareean (late early Miocene), or early Hemingfordian (early middle Miocene), southern California.

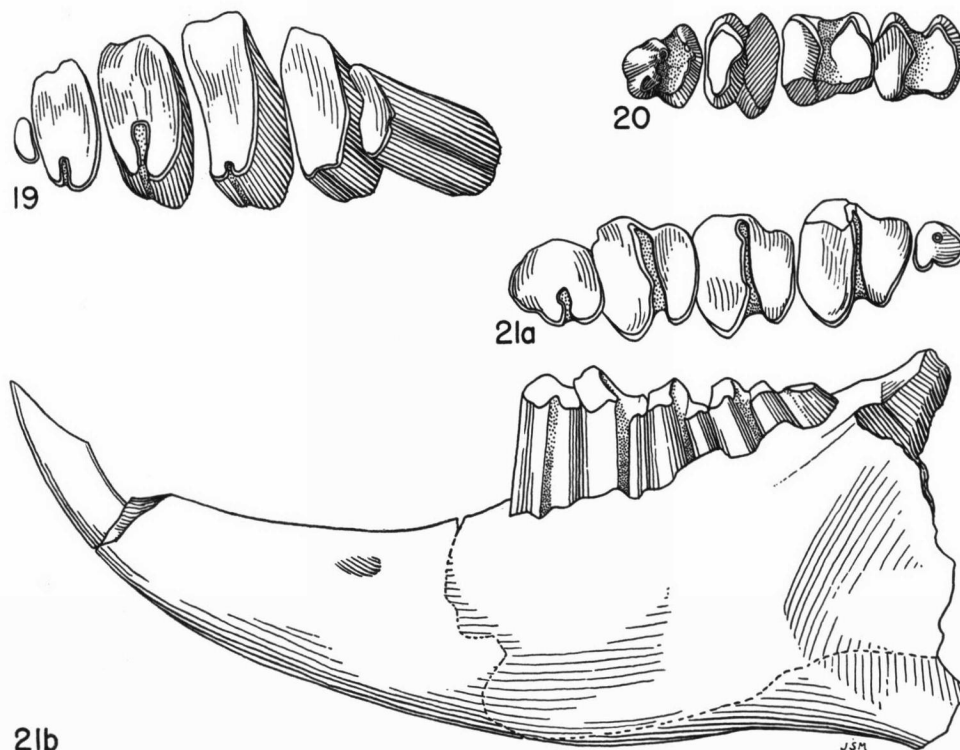
Correlation of the Tick Canyon beds, in which *Archaeolagus acaricolus* occurs, with other early or middle Miocene localities is not definite. The fauna from the Tick Canyon beds is small but, according to JAHNS (1940, p. 175-178), suggests a position approximately equivalent to upper Rosebud, Marsland, and lower Hawthorn deposits. However, SCHULTZ & FALKENBACH (1947, p. 188), in a study of oreodonts, considered the Tick Canyon deposits to be approximately equivalent to the Harrison formation of Nebraska. Further, SCHULTZ & FALKENBACH (1949, p. 93) correlated beds of the middle and upper John Day with the Harrison. This problem of correlation bears on the stratigraphic relationships of *Archaeolagus ennisianus* from the John Day, *A. acaricolus* from Tick Canyon, and *A. primigenius* from the upper Rosebud, to one another. Tentatively, perhaps the Tick Canyon beds should be regarded as higher than the John Day but lower than typical upper Rosebud and Marsland deposits; accordingly, *A. ennisianus* may be geologically slightly older and *A. primigenius* slightly younger than *A. acaricolus*.

Specific characters.—The following pattern occurs on the occlusal surface in moderately worn upper cheek-teeth: on P^2 single anterior reentrant; on P^3 - M^2 straight-walled internal hypostria; hypostria on P^3 and P^4 reduced in length at earlier stage of wear than on M^1 and M^2 ; M^3 without reentrants. Lower incisor less flattened dorsoventrally than in *Archaeolagus ennisianus*. P_3 convex lingually, proportionately shorter anteroposteriorly and having anteroexternal groove, which is shallow and essentially without cement, facing more anteriorly than in *A. ennisianus*. Posterolophids small on unworn P_3 and P_4 . Anterior zygomatic root extends outward abruptly from rostrum. Slightly smaller than *A. ennisianus*.

Description.—Dentition. The teeth in the two known maxillae, Nos. 5173 (Fig. 19) and 5174, are moderately worn, and the adult tooth pattern seems to be present. P^2 has a single, shallow, anterior fold slightly medial of the midline. On each of the two succeeding premolars, P^3 and P^4 , a shallow internal hypostria is present. The internal hypostria on M^1 crosses slightly more than one-third and that on M^2 approximately one-third of the occlusal surface. The walls of the hypostriae lack crenulations. M^3 is wider transversely than anteroposteriorly and lacks folds. Cement seems to be absent in the anterior fold on P^2 but fills the hypostriae on P^3 - M^2 . On the upper cheek-teeth the enamel is well developed anteriorly and lingually, thin posteriorly, and thin or absent buccally.

In cross section the lower incisor is more flattened dorsoventrally than in *Palaeolagus haydeni* but less flattened than in *Archaeolagus ennisianus*. The posterior extent of the incisor cannot be determined due to crushing of the jaws. In three lower jaws, Nos. 5171 (Fig. 21), 5172, and 5175, the cheek-teeth are moderately worn. At

⁵ From Latin, *acarus*, mite or tick, and *-cola*, dweller, referring to the type locality.

FIGURES 19-21. *Archaeolagus acaricolus*.

19. Occlusal view of right P_2 - M_2 (C.I.T. No. 5173), $\times 6$.
 —20. Occlusal view of right P_2 - M_2 of immature individual having unworn P_2 (C.I.T. No. 5176), $\times 6$. —21. Type specimen,

adult (C.I.T. No. 5171); 21a, occlusal view of left P_2 - M_2 , $\times 6$;
 21b, lateral view of left lower jaw, angle of incisor distorted, $\times 4$.

this stage of wear, P_3 has two external reentrants: the anterior reentrant is shallow and faces anteroexternally; the posterior reentrant, which is between trigonid and talonid, crosses slightly less than half the occlusal surface. Both reentrants lack crenulations. The lingual border of P_3 is convex. The anteroexternal groove faces more anteriorly and that portion of the trigonid anterior to the anteroexternal groove extends less far externally than in *A. ennisianus*. In general P_4 , M_1 , and M_2 are similar to one another: each consists of a trigonid and a talonid that is transversely narrower than the trigonid and is connected lingually to the trigonid by a bridge of dentine and enamel. In worn specimens the trigonid and talonid of M_3 are connected by dentine and enamel, but probably the columns were separate in earlier stages of wear. Cement is absent in the anteroexternal reentrant but fills the posteroexternal reentrant on P_3 and is present between the trigonid and talonid on P_4 - M_3 . Development of the enamel is similar to that in most leporids: on P_3 and M_3 the enamel is thicker buccally than lingually; on P_4 - M_2 the enamel is thick buccally and on the posterior wall of the trigonid, is thinner or absent lingually and on the posterior wall of the talonid, and is absent on the anterior wall of the trigonid.

No. 5176 (Fig. 20) is the lower jaw of an immature individual having an essentially unworn P_3 . In this tooth buccal and lingual reentrants are present between trigonid and talonid. The buccal reentrant persists the length of

P_3 ; the lingual reentrant, which is absent in adults, persists somewhat below the alveolar border, although crushing obscures its exact extent. Two main cusps, one buccal and one lingual, compose the trigonid. The buccal cusp, which is the larger of the two, has an irregular surface and, on its anteroexternal side, a shallow groove that persists the length of the shaft; this groove, forming the anteroexternal reentrant, is more distinct in the adult. The anterior portion of the groove between buccal and lingual cusps is shallower at the alveolar level than on the unworn crown and continues only a short distance below the alveolar border. The surface of the lingual cusp of the trigonid is broken but appears to have been regularly rounded. A small cuspule protrudes into the posterior portion of the groove between the main cusps of the trigonid. The talonid is wider transversely than the trigonid and has a convex posterior wall. Three distinct cuspules are present in a transverse line on the posterior wall; the most medial of these cuspules, which occurs slightly lateral to the midline of the tooth, is the posterior-most portion of the talonid and may be a much reduced posterolophid. Medial to the cuspules the posterior wall of the talonid is a relatively even ridge. Cement covers most of the surface of the talonid and is present throughout the length of the buccal reentrant between trigonid and talonid. Enamel seems to cover both cusps of the trigonid; on the exposed portions of the occlusal surface of the talonid enamel seem to be very thin. The trigonid of P_4 is worn

and has an essentially adult pattern except that its posterior wall forms a more definite V, having a posteriorly directed apex, than in the adult. The talonid of P₄ is broken in No. 5176. On M₁ and M₂ signs of immaturity persist: the posterior wall of each trigonid forms a wide V; lingual enamel is thicker than in the adult; on M₂ the trigonid and talonid are not yet united by a lingual bridge (M₁ is broken lingually, so existence of a bridge cannot be ascertained); the talonid of M₂ is proportionately longer anteroposteriorly than in the adult, suggesting the presence of a posterolophid in a tooth that is less worn.

Skull. Fragments of zygoma and palate are present in Nos. 5173 and 5174. Although possibly slightly distorted, the anterior portion of the zygoma does seem to be proportionately deeper dorsoventrally than in *Palaeolagus philoi* and *Archaeolagus ennisianus*. The lateral surface of the zygoma is slightly concave. The anterior zygomatic root juts outward abruptly from the rostrum, having its anterior surface approximately on a level between P² and P³. A distinct ridge extends from the anteroventral edge of the zygoma to the alveolar border; the ridge intersects that border approximately in line with the metaloph of P³. The surface of the maxilla is concave anterodorsal to the ridge. Portions of the palate are fragmentary, but the maxillopalatine suture seems to be present approximately at a level between P³ and P⁴.

Lower jaw. The known lower jaws are all somewhat crushed. In Nos. 5171 and 5172, specimens of adults, the masseteric fossa is bordered anteriorly by a V-shaped ridge that has an anteriorly-directed apex and reaches to below the metaloph of M₂. In No. 5176, the lower jaw of an immature individual, the masseteric fossa lacks this ridge. A mental foramen is present on the dorsolateral surface of the jaw below the diastema; breakage makes it impossible to determine whether a more posterior mental foramen or foramina, present in most leporids, occur below the premolars. The medial surface of the ramus is lightly pitted below the diastema and cheek-teeth. On the medial surface of the jaw posterior to the cheek-teeth, there seem to be two foramina: the more ventral foramen is probably the dental foramen; the more dorsal foramen appears to communicate with a tiny postalveolar foramen on the dorsal surface of the jaw posterior to M₃. Recent leporids have similarly situated foramina; the postalveolar foramen is larger.

Relationships.—*Archaeolagus acaricolus* differs from *A. ennisianus* as follows: size slightly smaller; internal hypostria on P³ and P⁴ less persistent; lower incisor less flattened dorsoventrally; P₃ anteroposteriorly shorter, having more convex lingual border and more triangular outline of the occlusal surface. The anterior zygomatic root juts outward abruptly in both species, but the root is situated slightly more posteriorly, and anterior to the root the maxilla is more concave in *A. acaricolus* than in *A. ennisianus*. Earlier reduction of the internal hypostria on P³ and P⁴ indicates less molarification of the premolars, a primitive character, in *A. acaricolus* than in *A. ennisianus*. *A. acaricolus* seems to be closer to *Hypolagus* in the structure of the anterior zygomatic root and rostrum than is *A. ennisianus*. *A. acaricolus* resembles *Archaeolagus* sp. and

A. primigenius of the upper Rosebud in the general shape of P₃, which is more nearly triangular in shape and proportionately shorter anteroposteriorly than in *A. ennisianus* and *A. macrocephalus*.

On the basis of the known material, the affinities of *A. acaricolus* seem to be with *Archaeolagus* sp. from the upper Sespe and with *A. primigenius*. *Archaeolagus* sp. could be near the ancestry of *A. acaricolus*, which, in turn, could have given rise to *A. primigenius*.

In his preliminary description of the Tick Canyon leporid, WILSON (in JAHNS, 1940, p. 182) suggested that the leporid was "an advanced *Archaeolagus* or a very primitive *Hypolagus*". The Tick Canyon leporid, which is considered here to be a species of *Archaeolagus*, seems to be more primitive than *A. ennisianus* in some characters, such as the lack of persistent hypostriae on P³ and P⁴. In other respects, such as the triangular shape of P₃, *A. acaricolus* resembles certain later species of *Hypolagus*, and *A. acaricolus* and the species closely related to it, *Archaeolagus* sp. and *A. primigenius*, may be near the line that gave rise to *Hypolagus*.

TABLE 8.—Measurements in millimeters of *Archaeolagus acaricolus*

	C.I.T. No. 5173	C.I.T. No. 5174
P ² anteroposterior	1.1	0.9
width	2.2	2.1
P ³ anteroposterior	1.6	1.7
width anteroloph	3.0	ca. 2.5
width posteroloph	3.4	ca. 3.2
P ⁴ anteroposterior	1.6	1.7
width anteroloph	3.5	3.6
width posteroloph	3.5	3.6
M ¹ anteroposterior	1.7	1.7
width anteroloph	3.3	3.3
width posteroloph	3.1	3.0
M ² anteroposterior	1.6	1.6
width anteroloph	2.9	3.0
width posteroloph	2.5	2.5
M ³ anteroposterior	0.6	0.7
width	1.3	1.3
length P ² -M ³	8.7	ca. 8.9
length P ³ -M ²	7.0	ca. 7.4
dorsoventral depth, anterior root of zygoma	ca. 5.3	

	C.I.T. No. 5171	C.I.T. No. 5172	C.I.T. No. 5176 (immature)
P ₃ anteroposterior	2.0	2.1	1.7
width trigonid	1.8	ca. 1.8	1.3
width talonid	2.0	ca. 1.9	1.7
P ₄ anteroposterior	2.2	2.2	
width trigonid	2.5	2.4	1.8
width talonid	1.9	2.2	
M ₁ anteroposterior	2.1	2.2	2.0
width trigonid	2.4	2.4	ca. 2.0
width talonid	1.9	1.8	ca. 1.7
M ₂ anteroposterior	2.2	2.1	1.8
width trigonid	2.3	2.4	1.7
width talonid	1.8	1.9	1.5
M ₃ anteroposterior	1.2	1.3	
width trigonid	1.3	1.3	
width talonid	0.9	0.8	
length P ₃ -M ₃	9.6	9.8	
length P ₄ -M ₃	6.3	6.4	

Archaeolagus primigenius (Matthew)

Lepus primigenius MATTHEW, Amer. Mus. Nat. Hist., Bull., v. 23, art. 9, p. 216, March 14, 1907.
Archaeolagus primigenius, MATTHEW, Amer. Mus. Nat. Hist., Bull., v. 50, art. 2, p. 87, July 3, 1924.

Type specimen.—Partial right lower jaw having P_3 - M_1 , A.M.N.H. No. 12911, upper Rosebud beds, Porcupine Creek, South Dakota.

Geologic age and distribution.—Early Hemingfordian (early middle Miocene) of South Dakota.

Specific characters.—Size larger and anteroexternal groove on trigonid of P_3 deeper than in *A. acaricolus*. P_3 proportionately shorter anteroposteriorly and anteroexternal groove faces more anteriorly than in *A. ennisianus* and *A. macrocephalus*.

Archaeolagus ennisianus (Cope)

Figure 22

Lepus ennisianus COPE, U. S. Geol. and Geog. Surv. Terr., Bull., v. 6, no. 2, art. 15, p. 385, September 19, 1881.
Archaeolagus ennisianus, DICE, Univ. California Pub., Bull. Dept. Geol., v. 10, no. 12, p. 180, March 23, 1917.

Type specimen.—Nearly complete skull and lower jaws, atlas and fragmentary axis, A.M.N.H. No. 7190, John Day formation, north fork of John Day River, Oregon.

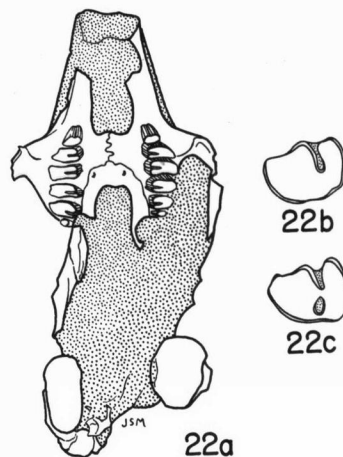
Geologic age and distribution.—Arikareean (early Miocene) of Oregon (middle and upper John Day formation).

Specific characters.—Size of skull near that in *Palaeolagus intermedius*. Pattern on moderately worn upper cheek-teeth consists of single anterior fold on P^2 and essentially straight-walled internal hypostria on each of P^3 - M^2 ; hypostriae tend to be shortened on premolars at earlier stage of wear than on molars. Lower incisor dorsoventrally flattened, usually extends posteriorly to below anterior or middle of P_3 . P_3 anteroposteriorly elongate and having two persistent external reentrants: anteroexternal reentrant wide and shallow, usually lacking cement; posteroexternal reentrant cement filled and crossing approximately half the occlusal surface. Compared to known Oligocene species of *Palaeolagus* and *Megalagus*, *A. ennisianus* has larger angle between basicranial and palatal axes of skull, palatine component of palate shorter, and anterior root of zygomatic arch situated more anteriorly and extending outward more abruptly.

Description.—*Archaeolagus ennisianus* is the common fossil leporid in the John Day formation of Oregon. The following description consolidates the previous descriptions of COPE (1884, p. 886-887), MATTHEW (1902, p. 306-307), and DICE (1917, p. 180-181; 1928) and supplements them. Additions to the previous descriptions are made on the basis of study of specimens in the collections of the American Museum of Natural History, Yale Peabody Museum, and the California Institute of Technology, including three skulls, A.M.N.H. Nos. 7190 (type specimen) and 7191, and C.I.T. No. 5181.

Dentition. The shafts of the hypsodont upper cheek-teeth extend into a well-developed maxillary tuberosity, which reaches farther dorsally than the dorsal rim of the

zygoma. Upper cheek-teeth in an adult present the following patterns: on P^2 a single, shallow, anterior fold occurs; each of the next four teeth, P^3 - M^2 , has an internal, straight-walled hypostria; on M^1 and M^2 the hypostria extends transversely across slightly more than one-third of the occlusal surface; the hypostriae tend to become shortened at an earlier stage of wear on the premolars than on the molars; M^3 is a cylindrical tooth lacking folds. Enamel is present on the walls of P^2 ; on P^3 - M^2 enamel is well developed anteriorly and lingually, reduced posteriorly, and usually absent buccally. Cement fills the hypostriae on P^3 - M^2 but is thin or absent in the fold on P^2 . At an earlier stage of wear, P^2 has an additional anterior fold, which is buccal to the persistent fold; isolated lakes, seemingly remnants of a fold between central and lingual lobes, may occur on P^3 and P^4 . Corresponding lakes have not been observed on the molars but would possibly be present in specimens of young individuals. DICE (1917, p. 180, fig. 1; 1928, p. 239) described and figured on P^3 - M^2 "enamel crescents" that are external to the hypostriae and sometimes connect to the external wall of the tooth. Such enamel crescents have not been observed in connection with the present study, although several specimens of *A. ennisianus* have darkened areas in the dentine that correspond in shape and position to the

FIGURE 22. *Archaeolagus ennisianus*.

22a, Ventral view of skull (C.I.T. No. 5181), $\times 1$; 22b, occlusal view of right P_3 (C.I.T. No. 5181), $\times 4$; 22c, occlusal view of right P_3 having isolated postero-internal lake (C.I.T. specimen lacking catalogue number, locality 3), $\times 4$.

"crescents" of DICE. In A.M.N.H. No. 7210, such darkened areas occur on P^3 and P^4 that have also the enamel-lined lakes described above. It seems likely that the "crescents" described by DICE correspond to the darkened areas in the dentine. True enamel-lined lakes do appear to be present during early stages of wear in *A. ennisianus*, but these lakes are similar in general to those in *Palaeolagus intermedius* and do not have a connection to the external wall of the tooth.

In cross section the lower incisor is longer transversely than dorsoventrally and is more flattened dorsoventrally than in *Palaeolagus* and *Megalagus*. On the medial surface of the jaw the posterior end of the swelling

over the incisor is anterior to or approximately in line with the trigonid of P_3 , and its dorsal border is at mid-depth of the jaw. The swelling is lower and longer in *Palaeolagus* and *Megalagus* but higher on the jaw in *Hypolagus*. In one specimen of *A. ennisianus*, A.M.N.H. No. 7199, the swelling over the incisor is low, as in *Palaeolagus*, and extends posteriorly to a line between P_3 and P_4 , thus suggesting that the incisor might have been somewhat variable. In occlusal view, moderately worn P_3 (Fig. 22b) is elongate anteroposteriorly and has two external reentrants; the anterior of these reentrants is wide, shallow, and seems to lack a coating of cement; the posteroexternal reentrant is situated between trigonid and talonid, crosses approximately half of the occlusal surface, and is filled with cement. Some specimens of *A. ennisianus*, seemingly having less wear on P_3 , have an isolated posterointernal, enamel-lined lake that is probably a remnant of an internal reentrant between trigonid and talonid (Fig. 22c). This lake is absent in most known specimens of *A. ennisianus*; it seems to be a transient indication of age and possibly individual variation, and suggests the affinities of *Archaeolagus* with the palaeolagines. On each of the following teeth, P_4 - M_3 , the trigonid and talonid are united, after the tooth is worn, by a lingual bridge of enamel and dentine; cement fills the remaining space between trigonid and talonid. On the lower cheek-teeth enamel tends to be thicker buccally and thinner or absent lingually, as in most other leporids.

Skull. The angle between basicranial and palatal axes of the skull is greater in *A. ennisianus* than in *Palaeolagus haydeni*, *P. intermedius*, and *Megalagus turgidus*. The dorsal surface of the nasal bone is pitted along its lateral margins, and pitting is also present on the frontals and parietals. The nasals are proportionately wider posteriorly than in *P. haydeni*. The supraorbital process in *A. ennisianus* has a well-developed posterior extension. The frontoparietal suture is in a line slightly posterior to the posterior surface of the zygomatic process of the squamosal; a small process of the parietal extends into the posterior wall of the orbit. In *P. haydeni* the frontals reach less far posteriorly, and the process of the parietal in the orbit is larger; *P. intermedius* is approximately intermediate between *A. ennisianus* and *P. haydeni* in the structure of frontal and parietal.

The zygomatic arches essentially parallel the long axis of the skull. The anterior root of the zygoma extends abruptly outward from the rostrum approximately in line with the middle of P^2 . A ridge proceeds ventrally from the thickened anteroventral rim of the zygoma to intersect the alveolar border posterior to P^3 . In *Palaeolagus haydeni*, *P. intermedius*, and *Megalagus turgidus*, the anterior root of the zygoma extends outward more gradually, is slightly more posterior in position, and is closer to the alveolar border. In *A. acaricolus* that root is slightly more posteriorly situated, and the maxilla anterior to the root is more concave than in *A. ennisianus*. The lateral surface of the zygoma in *A. ennisianus* is concave.

On the palate (Fig. 22a) the bony bridge is between the posterior ends of the incisive foramina, approximately in line with the middle of P^2 , and the internal nares, in line with the anteroloph of M^1 . The maxillopalatine su-

ture crosses the palate essentially transversely in line with the middle of P^4 . Thus, the part of the palatal bridge formed by the palatine is proportionately shorter than in *Palaeolagus* and *Megalagus*. The maxillopalatine suture and the suture between the maxillae on the palate are wavy, and the palatine foramina appear to be slightly posterior to the maxillopalatine suture. The internal nares are proportionately wider than in *P. haydeni*.

The auditory bullae are proportionately smaller than in *P. haydeni* but larger than in *M. turgidus*. The mastoid has a rugose and pitted surface. A posterolateral ridge on the mastoid extends from the dorsal border of that bone ventrally onto the mastoid process. The mastoid curves onto the occipital surface more gradually than in *P. haydeni* and *M. turgidus*. The dorsal portion of the mastoid extends farther medially onto the occipital surface than does the ventral portion, due to lateral expansion of the more ventral part of the exoccipital. The occipital condyle seems to be more nearly vertical than in *P. haydeni* and *M. turgidus*. The pitting on the mastoid, the shape of that bone, and the orientation of the occipital condyles are features in which *A. ennisianus* is more advanced toward Recent leporids than are *Palaeolagus* and *Megalagus*.

Lower jaw. In general shape the lower jaw is similar to those in *Palaeolagus* and *Megalagus*. On the lateral surface of the horizontal ramus one mental foramen occurs below the diastema, and a second may be present below P_3 or P_4 . In some cases the region below P_3 and P_4 is heavily pitted, and no single larger foramen can be differentiated. The postalveolar foramen is tiny or has been reported to be absent (DICE, 1928, p. 238). The masseteric fossa is shallow, and the ridge marking its anterior border is variable, being rounded or V-shaped anteriorly and extending to below M_3 or the talonid of M_2 .

Summary.—In over-all level of development of teeth and skull, *Archaeolagus ennisianus* stands between typical Oligocene members of the genus *Palaeolagus* and the later leporid, *Hypolagus*. Most traces of the primitive leporid pattern in the upper cheek-teeth are worn away rapidly in *A. ennisianus*, leaving simple hypostriae on P^3 - M^2 . In the skull, the following are among the features suggesting advance over *Palaeolagus*: larger angle between the basicranial and palatal axes; more posterior position of the frontoparietal suture; shorter proportion of the palatine on the palate; shape of the mastoid and orientation of the occipital condyle. More rapid shortening of the hypostriae on the upper premolars than on the molars suggests that the premolars are less molariform relative to the molars than in *Hypolagus*, and the shallow anteroexternal fold on P_3 and the simple hypostriae on the upper cheek-teeth indicate that although a definite archaeolagine, *A. ennisianus* is a primitive member of the subfamily. The structure of the anterior zygomatic root may indicate that *A. ennisianus* is not on the line of development leading toward *Hypolagus*.

In structure of P_3 , *A. ennisianus* resembles *A. macrocephalus* of the upper Rosebud more closely than the other known species of *Archaeolagus*. The John Day leporid seems to be closely allied to and may be near the ancestry of *A. macrocephalus*. Incomplete material of the latter does not permit a more definite statement of relationships.

TABLE 9.—Measurements in millimeters of *Archaeolagus ennisianus*

	C.I.T. No. 5181	A.M.N.H. No. 7190	A.M.N.H. No. 7191	A.M.N.H. No. 7208
P ² anteroposterior	1.7			
width	2.4			
P ³ anteroposterior	1.7			
width anteroloph	2.8			
width posteroloph	3.5			
P ⁴ anteroposterior	1.7			
width anteroloph	3.5			
width posteroloph	3.3			
M ¹ anteroposterior	1.8			
width anteroloph	3.1			
width posteroloph	3.1			
M ² anteroposterior	1.6			
width anteroloph	2.8			
width posteroloph	2.6			
M ³ anteroposterior	0.8			
width	1.0			
length P ² -M ²	11.1	12.2	10.8	
length P ³ -M ²	8.5	9.1	8.5	8.6
width across anterior roots of zygomata	ca. 26.7		28.8	
width nasals posteriorly				
width palate between P ⁴	ca. 8.9			
length palate	6.5			6.3
length palatine on palate	2.2			2.6
length maxilla on palate	4.3			3.8
width internal nares	ca. 3.8			
dorsoventral depth, anterior root of zygoma	4.2	5.0	ca. 4.2	
length zygoma from anterior wall to posterior wall of squamosal process		23.2	22.2	
	C.I.T. No. 5181	Y.P.M. (unnumbered)	C.I.T. (locality 3)	
P ₃ anteroposterior	2.7	2.6	2.5	
width trigonid	2.0	2.2	1.9	
width talonid	2.0	2.5	2.1	
P ₄ anteroposterior	2.4	2.5	2.4	
width trigonid	2.4	2.8	2.5	
width talonid	1.9	2.4	2.0	
M ₁ anteroposterior	2.4	2.5	2.4	
width trigonid	2.2	2.6	2.4	
width talonid	1.8	2.2	2.0	
M ₂ anteroposterior		2.7		
width trigonid		2.6		
width talonid		2.3		
M ₃ anteroposterior		1.8		
width trigonid		1.5		
width talonid		1.4		
length P ₃ -M ₃		12.1		
length P ₄ -M ₂		7.8		
inside depth of jaw below M ₁	10.6	11.0	11.2	

Archaeolagus macrocephalus (Matthew)

Lepus macrocephalus MATTHEW, Amer. Mus. Nat. Hist., Bull., v. 23, art. 9, p. 214, March 14, 1907.
Archaeolagus macrocephalus, MATTHEW, Amer. Mus. Nat. Hist., Bull., v. 50, art. 2, p. 87, July 3, 1924.

Type specimen.—Incomplete left lower jaw having P₃-M₃; parts of two hind feet, distal end of tibiofibula, metacarpals, A.M.N.H. No. 12910, upper Rosebud beds, Porcupine Creek, South Dakota.

Geologic age and distribution.—Early Hemingfordian (early middle Miocene) of South Dakota.

Specific characters.—Size larger than other known species of *Archaeolagus*. P₃ elongate anteroposteriorly, having on trigonid shallow anteroexternal groove that

seems to lack cement and faces mostly externally. On medial surface of jaw, posterior end of swelling over incisor is situated in a line below middle of P₃ and slightly above mid-depth of jaw.

Genus HYPOLAGUS Dice, 1917

Hypolagus DICE, Univ. California Pub., Bull. Dept. Geol., v. 10, no. 12, p. 181, March 23, 1917. Type, *Lepus vetus* KELLOGG.

Geologic age and distribution.—Hemingfordian (middle Miocene) to early Pleistocene of western North America; middle Pliocene? of Asia; Villafranchian of Asia and Europe.

Generic characters.—On anterior surface of P² one well-developed reentrant and shallower, more external groove; internal hypostria on P³-M² crenulated at some stage of wear, crenulations usually more pronounced and persistent on premolars than on molars. Anteroexternal fold on P₃ deeper than in *Archaeolagus*, usually cement filled.

Hypolagus is in a more advanced level of evolutionary development than its probable ancestor, *Archaeolagus*; typical species of each genus are well differentiated from one another, but it may be difficult to distinguish advanced species of *Archaeolagus* from primitive species of *Hypolagus*, especially when dealing with incomplete material. Leporids of Hemingfordian age, which seems to be the time of transition between the two genera, are not well known. On the basis of lower jaws, *Archaeolagus primigenius* and *A. macrocephalus* from upper Rosebud deposits, which are approximately early Hemingfordian in age, seem to be referable to *Archaeolagus*, but the affinities of certain leporids from other deposits that are near the upper Rosebud in age are more problematical. C.N.-H.M. No. P27076, a left lower jaw having P₃-M₃, from the Marsland formation, Marsland, Dawes County, Nebraska, is more advanced than *Archaeolagus macrocephalus* and *A. primigenius* in having on P₃ a deeper anteroexternal groove that has a thin filling of cement; in general shape, P₃ resembles those in *A. primigenius* and the lower Pliocene species of *Hypolagus* named below on page 48. The lower jaw is more primitive than in the latter species. In C.N.H.M. No. P27210, an incomplete maxilla having P³-P⁴, from Marsland deposits, the hypostria on P³ and P⁴ is straight-sided and crosses approximately half the occlusal surface; the teeth are relatively narrow transversely. Whether No. P27210 represents the same species of leporid as does the lower jaw, No. P27076, is not known; if associated, the Marsland leporid would seem to combine characteristics of *Archaeolagus* and *Hypolagus*, resembling the former in the upper cheek-teeth and the latter in the lower. At any rate, these Marsland specimens seem to represent an undescribed leporid or leporids, perhaps intermediate between more typical species of *Archaeolagus* and *Hypolagus*. Additional middle Miocene leporid specimens are known from University of Kansas Quarry A, Martin Canyon, northeastern Colorado, approximately equivalent in age to Marsland deposits (GALBREATH, 1953, p. 36); of four isolated upper cheek-teeth, which are near one another in size but wider transversely than those in No. P27210, two have a crenulated hypostria that persists the length of the tooth, and

two have a shorter, straight-walled hypostria, also persistent. Whether these teeth represent one species that has considerable age and individual variation or one primitive and one advanced species cannot be determined on the basis of these few specimens. Here again, *Archaeolagus* and/or *Hypolagus* could be represented. Definite taxonomic assignment of these middle Miocene leporids should await more complete and associated specimens; regardless of generic assignment, the important point is the seemingly intermediate or transitional character of these leporids between *Archaeolagus* and *Hypolagus*.

Although descent of *Hypolagus* from *Archaeolagus* seems to be established, determination of more precise lines between the genera is difficult. Evidence from C.N.H.M. No. P27076 indicates descent of *Hypolagus* from the line of *Archaeolagus* having an anteroposteriorly short P_3 ; this descent could lead from *A. primigenius* through the Marsland leporid, No. P27076, to the species of *Hypolagus* named below on page 48. On the other hand, other leporids having characteristics that seemingly differentiate them as primitive species of *Hypolagus* have a more elongate P_3 that could be derived from the line of *Archaeolagus* having a somewhat similarly elongate P_3 . Possibly the level of development here recognized as characteristic of the genus *Hypolagus* has been attained more than once by parallel lines of *Archaeolagus*.

Exact lines of descent from Miocene to Pliocene species of *Hypolagus* are not known, but within the Pliocene two main lines of *Hypolagus*, probably phylogenetic, can be traced—a line of larger leporids including *H. vetus* and *H. regalis*, and a line of smaller leporids including the lower Pliocene species named below on page 48, *H. near limnetus*, and *H. limnetus*. In addition to these lines, other species of more uncertain relationships indicate diversity within the genus: in this category are *H. apachensis*, which seems to have had some primitive characteristics at a time when other species were more advanced, *H. oregonensis*, in which there is a tendency toward increased complexity of P_3 by the addition of anterior folds, and *H. edensis*, a small leporid having a distinctive, deep anteroexternal reentrant on P_3 . *Hypolagus* ranged through the Pliocene and is represented in Blancan faunas from Coso Mountains, Hagerman and Grand View, Benson, Cita Canyon, Blanco, and Meade County, Kansas (Rexroad). The latest appearance of *Hypolagus* in North America is not precisely known, but *Hypolagus* has been listed from the early Pleistocene Broadwater (SCHULTZ, *et al.*, 1951, table 1) and Deer Park (HIBBARD, 1956, p. 177) faunas. Leporids from the Borchers fauna, which is approximately middle Pleistocene in age, listed as *Hypolagus* (HIBBARD, 1941a, p. 216), K.U. Nos. 5735H and 5735L, are probably young individuals of the genus *Lepus*.

Hypolagus parviplicatus,⁶ n. sp.

Figure 23

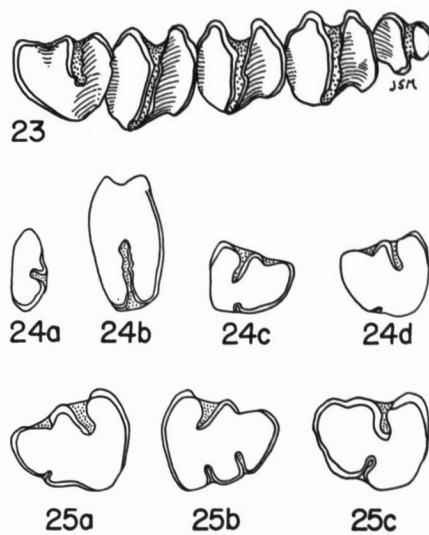
Type specimen.—Incomplete right lower jaw having P_3 - M_3 , U.C.M.P. No. 11571, upper middle Miocene or

⁶ From Latin, *parvus*, little, and *plicatus*, fold, referring to the shallow anteroexternal fold on P_3 .

lower upper Miocene, U.C. locality 1065, Virgin Valley, Humboldt County, Nevada.

Geologic age and distribution.—Late Hemingfordian (late middle Miocene) or early Barstovian (early late Miocene) of Nevada.

Specific characters.— P_3 having anteroexternal fold deeper than in *Archaeolagus* but shallower and facing more directly laterally than in *Hypolagus vetus*; trigonid anterior to anteroexternal fold extended farther laterally than in *H. vetus*.



FIGURES 23-25. Species of *Hypolagus*.

23. *Hypolagus parviplicatus*, type specimen (U.C.M.P. No. 11571), occlusal view of right P_3 - M_3 , $\times 4$.—24. Occlusal views of cheek teeth of *Hypolagus* near *parviplicatus*; 24a-c, right P_3 , right upper molariform tooth, and left P_3 (C.I.T. No. 5179), $\times 4$; 24d, right P_3 (C.I.T. No. 5180), $\times 4$.—25. *Hypolagus apachensis*, occlusal views of P_3 showing variation in pattern, $\times 6.7$; 25a, right P_3 (C.I.T. No. 38); 25b, left P_3 (C.I.T. No. 5183); 25c, right P_3 (A.E.W. No. 35-50-18) (from Wood, 1937, fig. 21).

Description.—The type specimen of *Hypolagus parviplicatus* (Fig. 23), U.C.M.P. No. 11571 from Virgin Valley beds, was designated the "cotype" of *Lepus vetus* by KELLOGG (1910, p. 436). Later DICE (1917, p. 181-182) retained this specimen in *Hypolagus vetus* but mentioned that it might be a different species, although material was too incomplete to allow a definite statement. Topotype material now known of *H. vetus* permits an estimation of the dental variation within that species; this material shows that although P_3 does vary in shape, none of the variants are close to P_3 in U.C.M.P. No. 11571. P_3 in *H. parviplicatus* differs from that in *H. vetus* as follows: proportionately more elongate anteroposteriorly; anteroexternal reentrant shallower, and the cement in the reentrant, although possibly eroded away in part, is thin and probably was naturally thinner than in *H. vetus*; the lobe of the trigonid anterior to the anteroexternal reentrant extends farther laterally, and the reentrant faces more directly laterally and less anteriorly. The posteroexternal reentrant on P_3 , which is filled with cement, crosses approximately half the occlusal surface and has a wavy posterior wall. In general the more posterior cheek-teeth

resemble those in *H. vetus*. The swelling over the incisor on the medial surface of the jaw terminates below the trigonid of P_3 , in a position nearly the same as in *H. vetus*. On the lateral surface of the jaw there is light pitting below P_3 and the trigonid of P_4 , and the anterior border of the masseteric fossa is marked by a low ridge, convex anteriorly, that extends to below the trigonid of M_3 .

Discussion.—Assignment of this species to *Hypolagus* is somewhat questionable due to absence of upper cheek-teeth, which would be useful in establishing affinities, and to the seemingly primitive P_3 , which is elongate and has a shallow anteroexternal fold. Downs (1956, p. 214) referred to upper and lower cheek-teeth, the latter having a crenulated hypostria characteristic of *Hypolagus*, from the Mascall fauna of Oregon as *Hypolagus* cf. *vetus* but suggested that the specimens may show closer affinity to the Virgin Valley leporid than to *H. vetus* from Thousand Creek. The Mascall specimens have not been examined in connection with this study, but if the above suggestion of affinities is correct, assignment of the Virgin Valley species to the genus *Hypolagus* is strengthened.

Hypolagus near *parviplicatus*

Figure 24

Specimens.—Incomplete left lower jaw having P_3 - M_3 , right diastemal region of lower jaw and incisor, isolated upper cheek-teeth, C.I.T. No. 5179; isolated lower cheek-teeth, C.I.T. No. 5180. Late Barstovian (latest Miocene), Quarry C, C.I.T. locality 172, approximately 9 miles north of Tonopah, Nevada.

Description.—The Tonopah leporid, which is from a stratigraphically higher horizon than No. 11571, was first described by WILSON (in HENSHAW, 1942, p. 104-105), who listed the specimens as *Hypolagus* sp. and mentioned that a new species was probably represented. The lower cheek-teeth in No. 5179 are smaller than in No. 5180, but the differences are of a magnitude that might be due to age and individual variation (the largest coefficient of variation necessary to account for the size difference is 7), and the specimens seem to represent the same species. In No. 5179 P_3 (Fig. 24c) is longer anteroposteriorly than transversely. As in *Hypolagus parviplicatus* the anteroexternal fold on P_3 is shallow and faces mostly laterally; the lobe of the trigonid anterior to the anteroexternal fold, although extending approximately as far laterally, is more rounded than in the Virgin Valley specimen. A small posterointernal reentrant, which persists approximately 1.4 mm. down the tooth, occurs on P_3 in a position seemingly between the trigonid and talonid. Cement fills the internal reentrant, both external reentrants, and covers most of the external surface of P_3 . In No. 5180 P_3 (Fig. 24d) is proportionately shorter anteroposteriorly than in No. 5179 and *H. parviplicatus* but has a similarly shaped trigonid and anteroexternal groove. A tiny internal reentrant, which would be removed following little wear, is present on P_3 . This reentrant, which is relatively more anteriorly situated than the internal reentrant in No. 5179, could be comparable to the reentrant between trigonid and talonid or to a more anterior internal reentrant such as is occasionally found in *H. apach-*

ensis; the former seems more probable. The presence of these ephemeral internal reentrants may indicate that Nos. 5179 and 5180 are slightly immature individuals and may account in part for the smaller size than in *H. parviplicatus*. The more posterior cheek-teeth, P_4 - M_3 , resemble those in *H. parviplicatus* in shape; those of No. 5179 are smaller and those of No. 5180 are approximately the same size as in the Virgin Valley specimen. In the jaw of No. 5179 the swelling over the posterior end of the incisor is situated approximately in line with the anterior wall of P_3 and slightly above mid-depth of the jaw. A post-alveolar foramen is present. The upper cheek-teeth seemingly associated with the lower jaw in No. 5179 include P^2 and molariform teeth. P^2 (Fig. 24a) has a single anterior, cement-filled reentrant; a much more shallow concavity occurs external to the reentrant. On the molariform teeth (Fig. 24b), the internal hypostria crosses half or slightly more of the occlusal surface. The walls of the hypostriae may have pronounced crenulations, especially on the anterior wall, or the walls may be only slightly wavy. In *H. vetus* similar variation in the walls of the hypostriae may occur between teeth in a single individual and seem to reflect differences between individual teeth in a series and between stages of wear. However, in none of the upper cheek-teeth of No. 5179 are the crenulations so well developed as in some specimens of *H. vetus*.

Discussion.—The Tonopah leporid is close to *H. parviplicatus* of the Virgin Valley in general level of development and character of P_3 ; the size differences between specimens from the two localities could be found within a single species. However, the Tonopah leporid is tentatively referred to as *Hypolagus* near *parviplicatus*, in view of inadequate comparative material and differences

TABLE 10.—Measurements in millimeters of *Hypolagus parviplicatus* and *H. near parviplicatus*

	U.C.M.P. No. 11571	C.I.T. No. 5179	C.I.T. No. 5180	
P_3 anteroposterior	3.1	2.7	2.9	
width trigonid	2.4	2.1	2.5	
width talonid	2.7	2.3	2.8	
P_4 anteroposterior	2.7	2.4		
width trigonid	3.0	2.6		
width talonid	2.7	2.1		
M_1 anteroposterior	2.9	2.5		
width trigonid	3.0	2.7		
width talonid	2.6	2.1		
M_2 anteroposterior	2.8	2.5		
width trigonid	2.9	2.5		
width talonid	2.5	2.1		
M_3 anteroposterior	2.0	1.7		
width trigonid	2.0	1.4		
width talonid	1.1	1.0		
lower molariform teeth				
anteroposterior			2.8	2.8
width trigonid			3.0	3.1
width talonid			2.5	2.7
length P_3 - M_3	13.1	11.9		
length P_4 - M_2	8.4	7.7		
inside depth of jaw be-				
low M_1	ca. 12.0			
		left	right	
P^2 anteroposterior		1.2	1.2	
transverse		2.8	2.7	
upper molariform teeth				
anteroposterior		2.0	2.3	
transverse		4.1	4.3	

from the Virgin Valley specimen, as well as different geologic ages. If *H.* near *parviplicatus* is closely allied to *H. parviplicatus*, the presence of crenulations in the hypostriae on the upper cheek-teeth in the former would add to the evidence supporting reference of the Virgin Valley leporid to *Hypolagus*. Considered jointly, *H. parviplicatus* and *H.* near *parviplicatus* represent a level of development in which P_3 has a shallow anteroexternal groove and somewhat elongate proportions. This structure of P_3 suggests possible derivation from the line of *Archaeolagus* having an elongate P_3 .

Hypolagus apachensis Gazin

Figure 25

Hypolagus? apachensis GAZIN, Carnegie Inst. Washington Pub. 404, pt. 6, p. 67, August, 1930.

Hypolagus apachensis, Wood, Amer. Jour. Sci., v. 33, p. 33, January, 1937.

Type specimen.—Incomplete left lower jaw having P_3 - M_2 , C.I.T. No. 36, Apache Canyon, C.I.T. locality 64, Ventura County, California.

Geologic age and distribution.—Barstovian? (late Miocene?) of Quatal Canyon, Clarendonian? (early Pliocene?) of Apache Canyon, and Clarendonian of Mint Canyon formation, southern California.

Specific characters.—Internal hypostriae on P^3 - M^2 crosses one-half to three-fourths of the occlusal surface; enamel walls of hypostriae vary with wear from crenulated to straight, crenulations tend to be worn away at earlier stage of wear on molars than on premolars. P_3 anteroposteriorly elongate, having usually wide and shallow anteroexternal reentrant. Smaller than *H. limnetus*.

Specimens of *Hypolagus apachensis* from C.I.T. localities 64 and 48 have been described by GAZIN (1930, p. 67-69) and WOOD (1937, p. 33-40): dental characteristics are relatively completely known, but the skull and postcranial skeleton are less well known. The leporid from Mint Canyon deposits, which is represented by isolated teeth and an incomplete lower jaw and is cited by MAXSON (1930, p. 88) as *Hypolagus? cf. apachensis*, seems to be *H. apachensis*.

In the dentition, *H. apachensis* is more primitive than *H. vetus* in the shallower anteroexternal groove on P_3 , and in loss, following wear, of crenulations in internal hypostriae of the cheek-teeth. There is a tendency toward greater anteroposterior elongation and a less triangular shape of P_3 than in *H. vetus*. Among topotypes of *H. apachensis*, P_3 exhibits variation in pattern of reentrants and in shape (GAZIN, 1930, p. 68; WOOD, 1937, p. 35-36 and figs. 13-15, 21). A wide, shallow concavity often occurs on the inner side of that tooth, and enamel folds additional to the anteroexternal and posterointernal reentrants may be present: in C.I.T. No. 38 (Fig. 25a) the inner surface has the shallow concavity approximately between the trigonid and talonid and a short anteroexternal reentrant that is lined with enamel, which is thicker on the posterior wall, filled with cement, and persists down the shaft of the tooth at least to the alveolar level; in C.I.T. No. 5183 (Fig. 25b) there are two internal reentrants that persist down the shaft—one is comparable in structure and position to the anteroexternal reentrant in No. 38 and the second is approximately between the trigonid and talonid. Another specimen of P_3 (Fig. 25c),

A.E.W. No. 35-50-18, has a single internal reentrant situated similarly to the posterointernal reentrant in C.I.T. No. 5183; the anteroexternal reentrant in No. 35-50-18 is shallow but is within the range of variation observed in *H. apachensis*. WOOD (1937, p. 40 and fig. 21) cited No. 35-50-18 as an indeterminate palaeolagine, but more probably it is a specimen of *H. apachensis* showing another variant in pattern on P_3 . Unworn P_3 in *H. apachensis* has three transverse lophs or crests (WOOD, 1937, p. 34-35 and fig. 11), and the internal reentrants that occur as variants in adult specimens may be remnants of folds present in an unworn tooth. Thus, the anteroexternal reentrant of the adult may represent the internal fold between anterior and central lophs in an unworn tooth, and the posterointernal reentrant may correspond to the internal fold between the central loph and the posterior loph or talonid. The condition of P_3 in which variable internal reentrants are present occurs less frequently in *H. apachensis* than does a condition in which internal reentrants are absent. Possibly it may be argued that the internal reentrants on P_3 mark *H. apachensis* as a palaeolagine or leporine. However, the more common condition in P_3 , in which internal reentrants are lacking, suggests that *H. apachensis* is an archaeolagine: usually the immature pattern is worn away early, but the medial side of P_3 seems to be subject to considerable individual variation with the result that folds, reminiscent of the immature pattern, persist in aberrant individuals.

The postcranial skeleton in *H. apachensis* is known only from incomplete material, consisting mostly of proximal and distal ends of bones. The proximal end of the humerus differs from those in *H. vetus* and the Recent leporids as follows: the head is proportionately narrower transversely, more elongate anteroposteriorly, less flattened, and less extended medially; the greater tuberosity is lower relative to the head of the humerus. In orientation of the greater and lesser tuberosities, *H. apachensis* is approximately intermediate between *Megalagus turgidus* and *Romerolagus*. On the distal end of the humerus the keels are slightly smaller and the medial condyle proportionately a little larger than in *H. vetus*, *Sylvilagus*, and *Lepus*. In total the humerus seems to be slightly more primitive than in *Romerolagus* and distinctly more primitive than in *H. vetus*, *Sylvilagus*, and *Lepus*; probably in *H. apachensis* a moderately wide range of movement at the shoulder was possible, but in the lower forelimb pronation and supination were limited. In the pelvic girdle the low iliac tubercle is relatively closer to the acetabulum than in *Palaeolagus haydeni*, *H. vetus*, and the Recent leporids. There seems to be no facet or tubercle between the iliac tubercle and the acetabulum comparable to that in *Palaeolagus*, *Megalagus*, and *Litolagus*. On the proximal end of the femur the third trochanter is more proximal than in *Palaeolagus* (WOOD, 1937, p. 37). The proximal end of the tibiofibula resembles that in *H. vetus* in general shape, but the tibial tuberosity may be proportionately a little lower in *H. apachensis*. In *Romerolagus* the proximal end of the tibiofibula is proportionately shorter anteroposteriorly and the tibial tuberosity is lower than in *H. apachensis*; this Recent leporid may have a shorter swing at the knee and less advantageous leverage by the extensors of the shank than in *H. apach-*

ensis. The astragalus and calcaneum in *H. apachensis* are similar in general to those in *H. vetus* except that the facets for articulation between those bones are slightly less distinct in *H. apachensis*, possibly indicating less firm contact between astragalus and calcaneum. Comparisons between functional levels of postcranial development in *H. apachensis* and *H. vetus* are difficult due to incomplete material of the former and to size differences between the two species. However, the available material suggests that in *H. apachensis* there was a greater latitude of movement at the shoulder and less specialization for anteroposterior action; the two species are more nearly alike in the known parts of the hind limb, but *H. apachensis* may have been slightly less modified cursorially.

Hypolagus apachensis is a primitive species of the genus. In some specimens of *H. apachensis* P_3 has a shallow anteroexternal reentrant reminiscent of that in *H. parviplicatus*, but other specimens have a deeper reentrant. The upper cheek-teeth in *H. apachensis* seem to be more primitive than are the upper cheek-teeth in specimens of *H. near parviplicatus*. *H. apachensis* does not seem to be ancestral to known later species of the genus but structurally suggests a stage of archaolagine development from which the genus *Notolagus*, an archaolagine having a persistent anterointernal reentrant on P_3 , could have been derived.

Hypolagus fontinalis,⁷ n. sp.

Figure 26

Type specimen.—Incomplete left lower jaw having P_3 - M_2 , U.C.M.P. No. 33425, lower Pliocene, U.C. locality V3322, Big Spring Canyon, Bennett County, South Dakota.

Referred specimens.—Incomplete lower jaws: U.C.M.P. No. 29540, C.N.H.M. Nos. P15812, P15813, P15814, lower Pliocene, Big Spring Canyon, Bennett County, South Dakota; S.D.S.M. No. 5549, lower Pliocene, Todd County, South Dakota; C.N.H.M. Nos. P26938, P26939, P26940, lower Pliocene, basal Ash Hollow formation, Quinn Canyon, Brown County, Nebraska. Incomplete right and left lower jaws, anterior upper incisor, U.C.M.P. No. 29630, lower Pliocene, U.C. locality V2804, Esmeralda formation, Esmeralda County, Nevada.

Geologic age and distribution.—Clarendonian (early Pliocene) of South Dakota, Nebraska, Nevada.

Specific characters.—Differs from *H. limnetus* as follows: on P_3 anteroexternal fold longer anteroposteriorly and slightly shallower transversely, lingual side less rounded. Near *H. limnetus* in size.

Description.—Only lower teeth and lower jaws of *Hypolagus fontinalis* are known, except for a grooved anterior upper incisor of No. 29630. The known specimens vary in size, No. 29630 from Nevada being smaller than the specimens from South Dakota and Nebraska, and vary in shape of the teeth, but all variants seem to be within the limits of a species. On P_3 the anteroexternal fold, which is deeper than in *H. parviplicatus*, faces anterolaterally. The lingual side of P_3 tends to be flattened or slightly concave. Cement fills the anteroexternal

and posteroexternal folds on P_3 and covers most of the external surface. The more posterior cheek-teeth seem to resemble those in *H. limnetus*: the columns of each tooth are joined by a lingual bridge, and cement is well developed.

On the lateral surface of the lower jaw a mental foramen occurs below the posterior half of the diastema, and variable pitting is present below P_3 and P_4 . The anterior border of the masseteric fossa extends forward to a line below the talonid of M_2 , and the ventral and anteroventral edges of the fossa form a laterally protruding ridge. On the medial surface of the jaw the swelling over the incisor extends posteriorly to below P_3 . Along the ventromedial edge of the jaw in a line slightly anterior to P_3 there is a facet that marks the posterior end of a contact with the opposite half of the jaw. A postalveolar foramen is present.

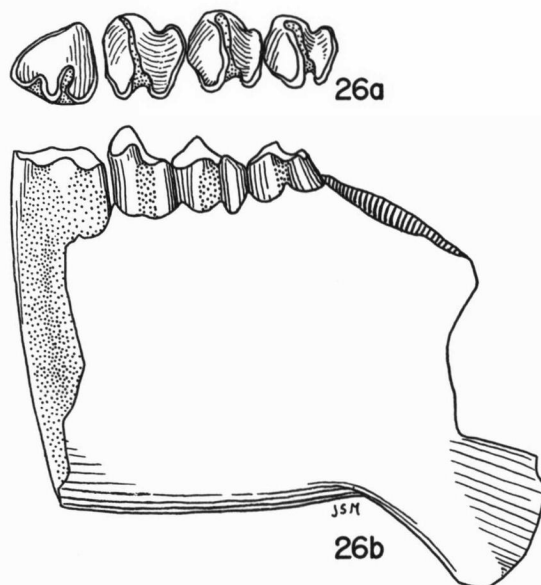


FIGURE 26. *Hypolagus fontinalis*, type specimen (U.C.M.P. No. 33425).

26a, Occlusal view of left P_3 - M_2 , $\times 4$; 26b, lateral view of left lower jaw, $\times 4$.

Relationships.—U.C.M.P. No. 29630 from the lower Pliocene Esmeralda formation of Nevada was referred to by HALL (1930a, p. 308-310, figs. 23, 24) as *Hypolagus cf. vetus*; later GREGORY (1942, p. 337-338) noted the resemblance of U.C.M.P. Nos. 29540 and 33425 from the lower Pliocene of Big Spring Canyon, South Dakota, and No. 29630 to *H. limnetus* and referred to these lower Pliocene specimens as *Hypolagus near limnetus*. These specimens and the others referred above to *Hypolagus fontinalis* represent a leporid that is close to *H. limnetus* but is seemingly more primitive in the structure of P_3 , which has a longer, shallower anteroexternal fold and a more flattened or concave lingual surface than in *H. limnetus*. Unfortunately upper teeth and cranial material of *H. fontinalis*, which could be expected to yield evidence on the relationships of that species to *H. limnetus*, are unknown. However, on the basis of the known

⁷ Latin, *fontinalis*, of a spring, referring to Big Spring Canyon, the type locality.

specimens, *Hypolagus fontinalis* seems to be more primitive than *H. limnetus* but is probably closely related to and near the ancestry of that species.

Although possibly not referable to this species, several known specimens seem to represent a leporid near *H. fontinalis*. C.I.T. No. 2506, a specimen of P_3 from the early Pliocene Avawatz fauna of southern California (WILSON, 1939, p. 38), is smaller than P_3 in *H. vetus* and larger than in *H. fontinalis* but in general shape is much like P_3 in the latter. In U.C.M.P. No. 29628, which includes broken fragments and isolated teeth of a leporid from the lower Pliocene Esmeralda formation of Nevada (HALL, 1930a, p. 308), P_3 resembles that of C.I.T. No. 2506. Upper cheek-teeth of No. 29628 have crenulated hypostriae: the hypostriae tend to be relatively longer anteroposteriorly and shorter transversely than in *H. vetus* and are as strongly crenulated as in some worn specimens but do not exhibit such pronounced folding as in less worn specimens of the latter. Nos. 2506 and 29628 may represent either large individuals of *H. fontinalis* or an undescribed species. More complete material is required in order to determine the affinities of these larger leporids, and Nos. 2506 and 29628 are tentatively recorded as representing a leporid near *Hypolagus fontinalis*.

TABLE 11.—Measurements in millimeters of *Hypolagus fontinalis*

	U.C.M.P. No. 33425	C.N.H.M. No. P26939	U.C.M.P. No. 29630
P_3 anteroposterior	2.6	2.6	2.6
width trigonid	2.0	2.0	2.0
width talonid	2.5	2.4	2.3
P_4 anteroposterior	2.4	2.4	2.3
width trigonid	2.5	2.4	2.4
width talonid	2.3	2.2	2.3
M_1 anteroposterior	2.5	2.6	2.4
width trigonid	2.5	2.4	2.5
width talonid	2.1	2.1	2.1
M_2 anteroposterior	2.5	2.4	2.3
width trigonid	2.4	2.4	2.3
width talonid	2.2	2.0	2.2
length P_4 - M_2	7.2	7.4	7.0
inside depth of jaw below			
M_1	11.1	12.1	11.2
depth jaw below diastema at			
mental foramen		6.2	7.4

Hypolagus near *limnetus* Gazin

Certain leporids from the middle Pliocene Kern River local fauna (WILSON, 1937a, p. 17-18) and from the Coso Mountains local fauna of Blancan age (WILSON, in SCHULTZ, 1937, p. 106-108) are similar to *H. limnetus*. The internal hypostria on the upper molars in the Kern River leporid may tend to have slightly simpler crenulations than in *H. limnetus* and the Coso Mountain leporid. The Kern River leporid may represent a different species, but the leporid from the Coso Mountains is probably a small individual of *H. limnetus* (WILSON, in SCHULTZ, 1937, p. 108). It may be necessary to have more nearly complete specimens that show individual and age variation before the affinities of these leporids are more precisely determined. The specimens from the Kern River fauna that were referred to as *Hypolagus* small species (WILSON, 1937a, p. 19) are probably young individuals of the Kern River *H. near limnetus*, although they may represent a different species.

Hypolagus limnetus Gazin

Hypolagus limnetus GAZIN, U. S. Natl. Mus., Proc., v. 83, no. 2976, p. 114, 1934.

Type specimen.—Skull, right lower jaw, and atlas, U.S.N.M. No. 12619, Hagerman lake beds, T. 7 S., R. 13 E., Twin Falls County, about 2 miles south of Plesipus quarry, near Hagerman, Idaho.

Geologic age and distribution.—Blancan (early Pleistocene?) of Idaho.

Specific characters.—Two unequal, uncrenulated anterior folds on P^2 ; internal hypostria on upper molariform teeth long transversely and having well-crenulated walls. Anteroexternal fold on P_3 deep transversely and narrow anteroposteriorly, facing mostly externally; anterior column on P_3 extends farther externally than in *H. vetus*. In skull, rostrum relatively short, cranial part elongate; bulla relatively large. Smaller than *H. vetus* (GAZIN, 1934, p. 114-116).

Hypolagus furlongi Gazin

Hypolagus furlongi GAZIN, U. S. Natl. Mus., Proc., v. 83, no. 2976, p. 118, 1934.

Type specimen.—Partial right lower jaw having incisor and P_3 - M_2 , C.I.T. No. 1321, Idaho formation?, near Grand View, Idaho.

Geologic age and distribution.—Blancan (early Pleistocene) of Idaho.

Specific characters.—Differs from *H. limnetus* as follows: lower jaw shallower dorsoventrally and diastema between incisor and P_3 shorter; crenulations present in main anterior reentrant on P^2 ; P_3 more nearly triangular in outline and having shallower anteroexternal fold. Near *H. limnetus* in size (GAZIN, 1934, p. 118).

Hypolagus furlongi seems to be closely allied to *H. limnetus*. In addition to the differences from *H. limnetus* mentioned above, P_3 in some specimens of *H. furlongi* has a slight anterior groove, seemingly absent in *H. limnetus*. The deposits in which *H. furlongi* was found may be slightly younger than those in which *H. limnetus* has been found (GAZIN, 1934, p. 119).

Hypolagus vetus (Kellogg)

Figures 27-35

Lepus vetus KELLOGG, Univ. California Pub., Bull. Dept. Geol., v. 5, no. 29, p. 436, July 13, 1910.

Hypolagus vetus, DICKE, Univ. California Pub., Bull. Dept. Geol., v. 10, no. 12, p. 181, March 23, 1917.

Type specimen.—Incomplete left lower jaw having incisor and P_3 - M_2 , U.C.M.P. No. 12565, middle Pliocene, U.C. locality No. 1100, Thousand Creek formation, Humboldt County, Nevada.

Geologic age and distribution.—Hemphillian (middle Pliocene) of Great Basin; possibly Barstovian (late Miocene) and Clarendonian (early Pliocene) of Nebraska and Blancan (early Pleistocene?) of Idaho.

Specific characters.—Enamel fold and more external shallower groove on anterior surface of P^2 ; hypostria on upper molariform teeth crenulated; crenulations persist as distinct folds on premolars longer than on molars. Anteroexternal fold on P_3 faces anteroexternally, shorter transversely than posteroexternal fold, deeper transversely

than in *H. parviplicatus* and *H. apachensis*, longer antero-posteriorly than in *H. limnetus*. Larger than *H. limnetus*.

Although definite records of *Hypolagus vetus* seem to be limited to the middle Pliocene, leporids near and possibly referable to the species are known from earlier deposits: a large leporid close to *H. vetus* has been recorded from the latest Miocene Niobrara River fauna (GREGORY, 1942, p. 338); C.N.H.M. No. P14739 from the lower Pliocene of the Valentine formation of Nebraska may be near *H. vetus*, although near the upper size limit of that species. Whether or not directly referable to *H. vetus*, these specimens seem to establish the presence of this line of leporid earlier than the middle Pliocene. *H.* near *vetus* from the Blancan Hagerman fauna (GAZIN, 1934, p. 112-114), while possibly referable here, may be more closely allied to *H. regalis*.

Description.—Previous descriptions of *Hypolagus vetus*, the type species of the genus, have been based mostly on the lower cheek-teeth (KELLOGG, 1910, p. 435-436, fig. 20; DICE, 1917, p. 181-182, figs. 4, 5), although some upper cheek-teeth have been described and figured. In the collections of the California Institute of Technology from C.I.T. locality 63, Thousand Creek, Nevada, there are numerous topotypes of *Hypolagus vetus* which permit a more complete description of some dental and postcranial characteristics of the species. Specimens of *H. vetus* have been important as a standard of comparison for other species of the genus, and the listing of leporid remains, often fragmentary, as *Hypolagus cf. vetus* or *Hypolagus near vetus* has been common. The following description adds to the understanding of the morphology and level of evolutionary development of *H. vetus* and of the relationships of this species to other Pliocene leporids.

Included in the C.I.T. collection of topotypes are at least thirty-five individuals of *Hypolagus vetus* from one relatively small site: these specimens were found in place, and the fossil remains in the site were probably completely collected; the specimens with matrix attached filled a ten-gallon gasoline case (from the field notes of C. L. GAZIN, July 31 and August 1, 1929). The specimens from this deposit all represent *Hypolagus vetus* and consist of teeth, fragments of skulls and jaws, broken ends of long bones, and other postcranial material. Nearly all postcranial parts are represented, although usually broken. The specimens do not seem to be water worn. Some speculation may be warranted regarding the method of accumulation of this "population" of leporids. The pieces of bone are relatively uniform in size; the edges of the pieces tend to be sharp, and the shafts of the long bones are frequently split; vertebrae are usually single or attached in twos or threes; skeletal elements from different parts of the body tend to be "plastered" together, such as a phalanx associated with a lumbar vertebra and a piece of ilium associated with a lower jaw. All the specimens seem to represent adults. In general, the specimens closely resemble bony remains of *Sylvilagus floridanus* found in pellets of *Bubo virginianus*, the great horned owl. Bone fragments somewhat like those fossil specimens may be found in the fecal material of carnivores, such as some canids. The accumulation of bones in the Thousand Creek site consists entirely of the remains of *H. vetus*, whereas bones from owl pellets or from fecal material of

other carnivores usually represent several species, but perhaps remains from only one prey species would be found in pellets or fecal material during a condition of great abundance of that prey. Thus, the evidence seems to suggest that this Thousand Creek "population" of leporids results from the accumulation under a perch or nest of pellets from a bird of prey or that some other carnivore was responsible for the remains, although some entirely different mode of accumulation may have occurred.

The specimens of *H. vetus* in the topotype "population" make possible an estimation of variation within the species, despite the fragmentary nature of the material. In the classification of fossil leporids, considerable weight is placed on the shape of P_3 ; specimens in the "population" illustrate the range of variation in shape of that tooth in one species and thus can be used as a standard in an approximation of the variation in P_3 that might be expected in other leporids. Size is also used taxonomically, and an estimation of the variation in size among the relatively homogeneous topotype "population" may be helpful in recognition of the limits of a species of leporid. In tables 12 and 13 statistical data for the cheek-teeth, which are most commonly preserved, are given, based on measurements in millimeters of the "population" of *H. vetus*. The following statistics are given:

- N—number of specimens measured
- O.R.—observed range
- S.R.—standard range (span), an estimation of mean sample range for a sample size of 1000 (SIMPSON, 1941)
- M—mean
- s—standard deviation
- V'—coefficient of variation corrected for small size of sample. $V' = (1 + \frac{1}{4N}) \times \text{true coefficient of variation}$ (HALDANE, 1955)

Standard errors are given for the mean, standard deviation, and corrected coefficient of variation.

If the "population" sample does represent the remains of the prey of a carnivore, as suggested above, selection has been effected, which may result in a smaller coefficient of variation than in a random sample. Other factors may cause the coefficient of variation in the "population" sample to be lower than in the species as a whole: all the specimens come from one small locality and probably represent a single subspecies; measurements of both sides of the dentition have been included, so one individual may have been measured twice. The specimens seem to represent adults; the variation in size would naturally be greater in a sample including younger individuals. However, as long as the limitations of the material measured are recognized, the coefficient of variation from this sample may be useful in estimating the size variation that might be expected within a species of leporid. Probably some of the variation is accounted for by peculiarities of wear on the hypsodont teeth that characterize the later leporids, and thus these coefficients of variation are not necessarily applicable to other mammalian groups.

The following description of *Hypolagus* is based largely on the topotype "population". In addition, the type specimen and other C.I.T. specimens from Thousand Creek, some of which are more complete than the broken

TABLE 12.—Statistical data on upper cheek-teeth of population of *Hypolagus vetus*

	N	O.R.	S.R.	M	s	V'
P ² anteroposterior	10	1.5-1.8	.84	1.65±.038	.13±.029	8.0±1.79
transverse	10	2.6-3.5	1.56	3.05±.076	.24±.054	8.1±1.81
P ³ anteroposterior	19	2.2-2.7	.98	2.39±.034	.15±.024	6.4±1.04
width anteroloph	16	3.4-4.2	1.65	3.68±.064	.25±.045	7.0±1.24
width posteroloph	14	4.2-5.6	2.43	4.81±.100	.38±.071	7.9±1.50
P ⁴ anteroposterior	17	2.4-3.0	1.12	2.65±.042	.17±.030	6.6±1.14
width anteroloph	16	4.0-5.0	1.76	4.36±.068	.27±.048	6.3±1.11
width posteroloph	15	4.3-5.2	1.81	4.73±.072	.28±.051	6.0±1.09
M ¹ anteroposterior	15	2.3-2.7	.88	2.48±.035	.14±.025	5.6±1.02
width anteroloph	13	3.8-4.8	1.78	4.25±.076	.28±.054	6.6±1.29
width posteroloph	13	3.8-4.8	1.84	4.29±.079	.28±.056	6.7±1.32
M ² anteroposterior	11	1.9-2.5	1.14	2.19±.053	.18±.038	8.2±1.75
width anteroloph	10	3.4-4.2	1.77	3.85±.086	.27±.061	7.3±1.62
width posteroloph	11	3.0-4.1	2.42	3.51±.112	.37±.079	10.9±2.31
M ³ anteroposterior	6	1.0-1.3	.82	1.10±.052	.13±.037	12.0±3.46
transverse	6	1.6-2.2	1.39	1.95±.088	.21±.062	11.5±3.31

TABLE 13.—Statistical data on lower cheek-teeth of population of *Hypolagus vetus*

	N	U.C.M.P. No. 12565 (type)*	O.R.	S.R.	M	s	V'
P ₃ anteroposterior	25	3.0	2.8-3.3	.91	3.08±.028	.14±.020	4.6±.66
width trigonid	24	2.2	2.2-2.8	1.02	2.48±.032	.16±.023	6.4±.92
width talonid	24	2.9	2.6-3.2	1.13	2.90±.036	.17±.025	6.1±.88
P ₄ anteroposterior	24	2.7	2.7-3.3	.97	2.99±.030	.15±.022	5.0±.72
width trigonid	20	3.1	3.0-3.5	1.0	3.20±.034	.15±.024	4.9±.77
width talonid	23	2.9	2.5-3.0	.98	2.80±.031	.15±.022	5.4±.80
M ₁ anteroposterior	20	2.7	2.8-3.4	.90	3.04±.031	.14±.022	4.6±.74
width trigonid	15	3.0	2.9-3.6	1.22	3.18±.048	.19±.034	6.0±1.10
width talonid	18	2.6	2.4-2.8	.89	2.60±.032	.14±.023	5.3±.89
M ₂ anteroposterior	10	2.7	2.8-3.2	.71	2.99±.035	.11±.025	3.8±.84
width trigonid	9	2.8	2.9-3.4	1.05	3.11±.054	.16±.038	5.3±1.26
width talonid	8	2.4	2.4-2.9	1.07	2.59±.058	.16±.041	2.1±.53
M ₃ anteroposterior	7		1.8-2.2	.91	2.00±.054	.14±.038	7.3±1.96
width trigonid	7		1.9-2.2	.74	2.00±.043	.11±.030	5.9±1.58
width talonid	6		1.2-1.4	.65	1.33±.041	.10±.029	7.8±2.26

*Not included in calculation of statistical data.

pieces from the "population", have been utilized. *Hypolagus vetus* is approximately intermediate between *Lepus californicus* and *Sylvilagus floridanus* in size; measurements from the topotype "population" indicate that in most measurements *L. californicus* ranges from approximately 11 to 33 per cent larger and *S. floridanus* from approximately 12 to 35 per cent smaller than *H. vetus*.

Dentition (Fig. 27). On the anterior face of the anterior upper incisor slightly medial to the midline of the tooth, there is a groove, which is shallow, lacks a cement filling, and in general resembles that in *Sylvilagus floridanus*. In *Brachylagus*, *Romerolagus*, and *Lepus* the groove on the incisor is proportionately deeper and in the latter is filled with cement and may be branched. The posterior upper incisors are simple, peglike teeth and resemble those in *Sylvilagus* and *Lepus*. The row of upper cheek-teeth is widest transversely either at the posteroloph of P³ or at P⁴, and the molariform premolars tend to be larger, especially transversely, than the molars. The upper cheek-teeth are a little narrower transversely relative to anteroposterior length than in *Lepus*. P² has a median, anterior fold; external to this fold there is a shallow groove. On moderately worn teeth the internal hypostria on P³-M² crosses one-half or usually a little more of the occlusal surface. Enamel is usually heavier on the anterior than on the posterior wall of each hypostria; the crenulations in the enamel lining the hypostriae tend to

be more pronounced on the anterior wall and seem to be better developed and more persistent on P³ and P⁴ than on M¹ and M². The external walls of P⁴, M¹, and M² are concave. M³ is a simple cylindrical tooth and is longer transversely than anteroposteriorly. Cement is well developed: on P² cement covers the anterior surface, fills the fold, and extends onto the lingual surface; on P³-M² cement fills the hypostria and covers a large part of the lingual wall. The enamel is most pronounced on the anterior and lingual walls of the upper cheek-teeth, as in most leporids.

In cross section the lower incisor has the shape of a trapezoid having rounded corners; the posterior, or dorsal, surface is slightly narrower transversely than the anterior, or ventral, surface. The swelling over the shaft of the incisor extends posteriorly to a level approximately below the middle of P₃ and at its posterior end is slightly above mid-depth of the jaw. On P₃ the anteroexternal reentrant is long anteroposteriorly and faces anteroexternally; the posteroexternal reentrant crosses approximately half of the occlusal surface. P₃ varies considerably in shape (Figs. 27c-e). Often that tooth is essentially three-sided: one side faces posteriorly, a second anteroexternally, and the third side, which may be slightly convex, faces anterolingually. In some specimens from the topotype "population" the third side has two parts, the anterior part slightly convex and facing anterolingually and the pos-

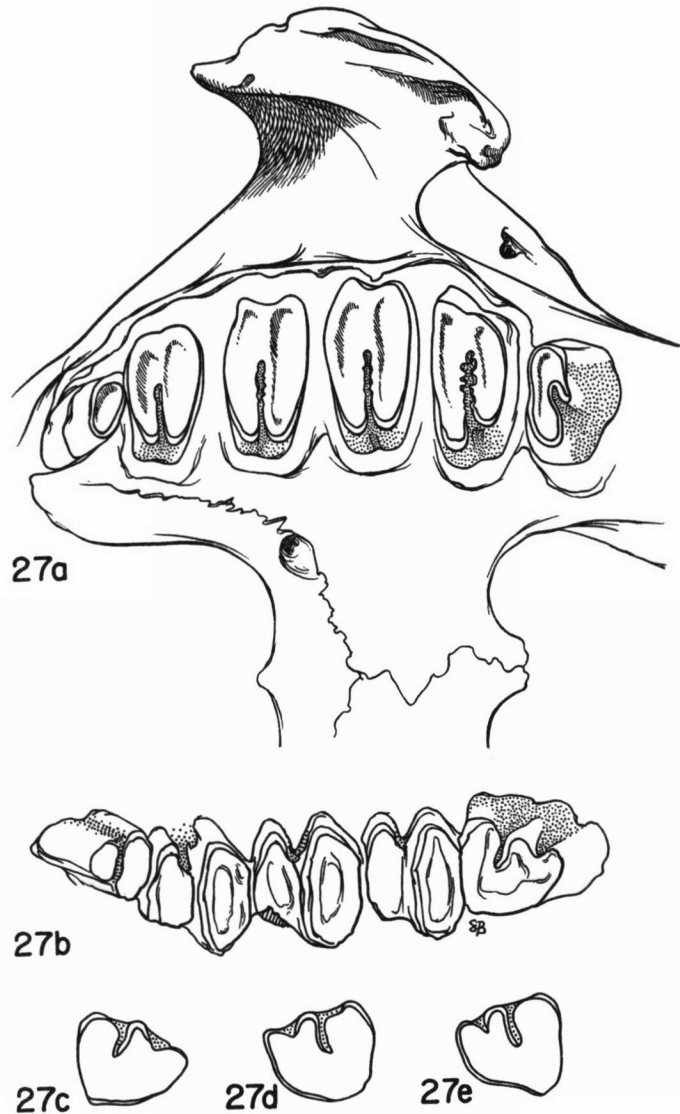


FIGURE 27. *Hypolagus vetus* (C.I.T. Locality 63).

27a, Ventral view of skull fragment having right P^2 - M^2 (composite), $\times 4.5$; 27b, occlusal view of left P_3 - M_3 (composite), $\times 4.5$;

27c-e, occlusal views of P_3 showing variation (27c, left, 27d,e, right), $\times 4.5$.

terior part flattened or slightly concave and facing more directly lingually. The shape of P_3 in the type specimen, U.C.M.P. No. 12565, is not "typical" of the topotype sample but does fit within the variation observed in that sample. P_3 seems to be a little smaller relative to the more posterior cheek-teeth than in *Lepus*. On P_4 , M_1 , and M_2 trigonid and talonid are joined lingually by a bridge of dentine and enamel. The trigonids are wider transversely than the corresponding talonids. In most specimens of M_3 the trigonid and talonid are united only by cement, but one specimen has a narrow bridge of dentine and enamel between the columns. On P_3 cement fills the reëntrants and covers the outer wall; on P_4 - M_3 cement is present between the trigonid and talonid. The development of enamel resembles that in most leporids: on P_3 enamel is thick buccally, thinner anteriorly and anterolingually, and

reduced or absent posteriorly and posterolingually; on P_4 - M_3 enamel is thick buccally on both columns and posteriorly on the trigonid, and thinner or absent lingually, anteriorly, and posteriorly on the talonid. In *H. vetus* the anteroposterior length of P_4 - M_2 is greater relative to the depth of the mandible than in *Lepus*, and the lower cheek-teeth, like the uppers, tend to be narrower transversely relative to anteroposteriorly than in *Lepus*. In the type specimen the lower cheek-teeth are smaller than the mean for the population: the measurements of the type are within the observed range for the population except for anteroposterior lengths of M_1 and M_2 and width of the trigonid of M_2 , which are within M-3s for the population. Thus, the type specimen could fit as a small individual within the range of variation in the relatively homogeneous topotype population. However, per-

haps the type specimen represents an individual from a population having a different mean size for the teeth than in the topotype population.

Skull. Remains of the skull in the topotype collection are fragmentary but furnish limited information on its structure. The anterior root of the zygoma resembles in general those in *Sylvilagus* and *Lepus* but is situated proportionately closer to the alveolar border. The anteroventral edge of the zygoma forms a thickened ridge nearly like that in *Lepus*; the anterior-most edge of the ridge is usually approximately in line with the anteroloph of P³. A variably-developed ridge, ranging from clearly marked to almost absent, extends from below the anterior zygomatic root to the alveolar border approximately between P³ and P⁴. As in *Lepus* a pit enters the lateral surface of the anterior zygomatic root. The zygomatic process of the squamosal resembles that in *Sylvilagus* in general. In *H. vetus* and *Sylvilagus* the dorsal surface of the process forms part of the temporal fossa; in *Lepus* most of the fossa is more medially situated. The supraorbital process of the frontal is incomplete in all available specimens, but the parts preserved show that the process has a well-developed posterior projection; the posterior end of the process probably ended freely as in *Brachylagus* and *Romerolagus* rather than in contact with the skull roof as in *Sylvilagus* and *Lepus*.

On the palate the anterior borders of the incisive foramina are posterior to the posterior incisors as in *Sylvilagus* and *Lepus*; in *Palaeolagus* and *Megalagus* the incisive foramina extend anteriorly to between the posterior incisors. The incisive foramina extend posteriorly approximately to a level with the posterior wall of P². The internal nares reach forward to a level between P⁴ and M¹ and are proportionately a little narrower transversely than in *Sylvilagus* and *Lepus*. The maxillopalatine suture crosses the bony palatal bridge approximately in line with the middle of P⁴ and is slightly convex anteriorly. In *H. vetus*, *Sylvilagus*, and *Lepus* the palatine forms relatively less of the palatal bridge than in *Palaeolagus*, *Megalagus*, and *Archaeolagus*.

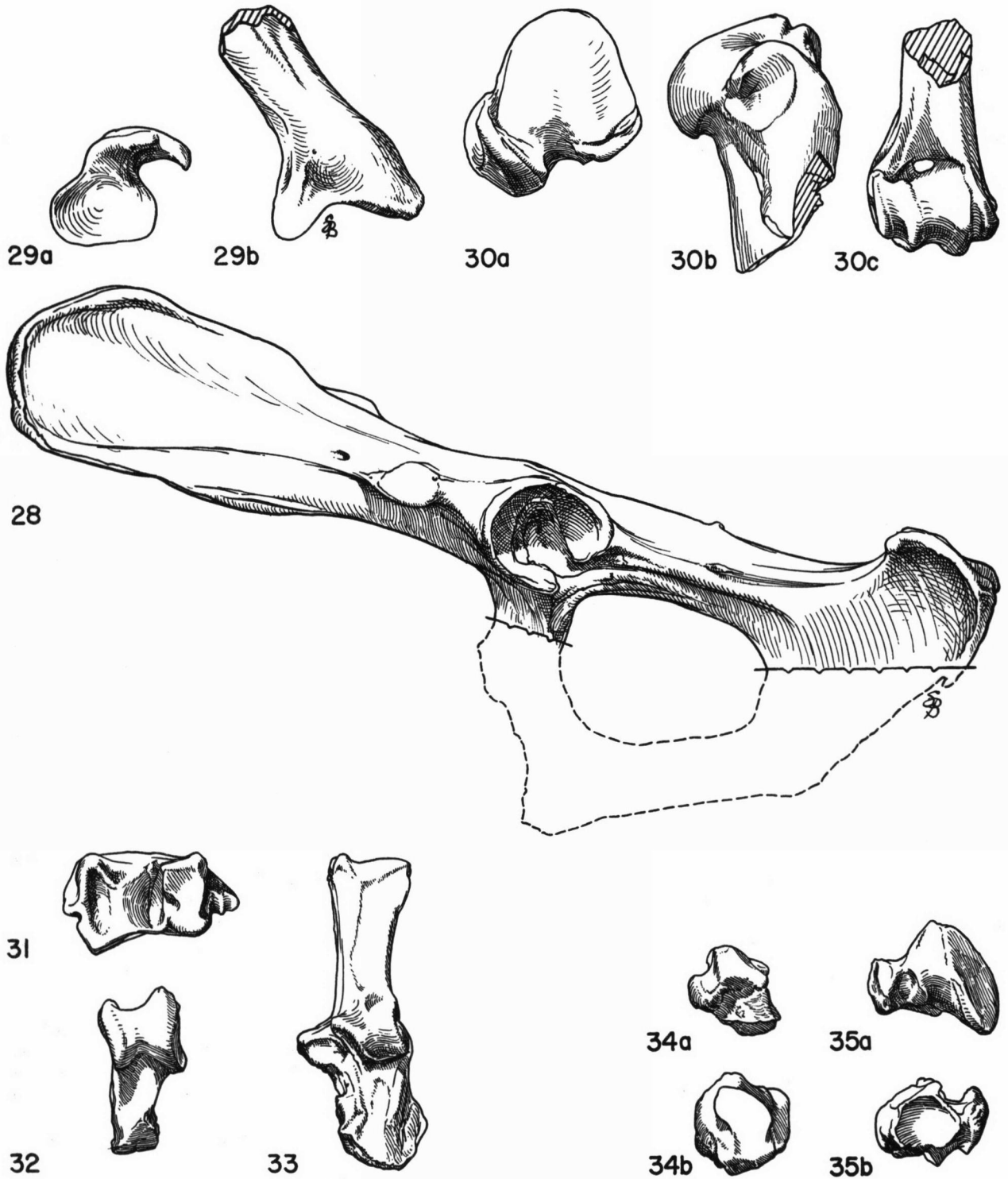
Lower jaw. In general the horizontal ramus resembles those in *Sylvilagus* and *Lepus*. There is a mental foramen on the dorsolateral surface of the jaw in the region below the posterior half of the diastema. Variable pits, one of which usually exceeds the others in size, occur on the lateral surface of the jaw anterior to and below P₃. The masseteric and pterygoid fossae seem to resemble those in *Sylvilagus* and *Lepus*. Dental and postalveolar foramina are present. The angle between horizontal and ascending rami cannot be determined in the available specimens. The condyle is rounded anteriorly and tapered posteriorly as in other leporids. The anterior part of the articular surface of the condyle is proportionately longer dorsoventrally and overlaps the neck less than in *Lepus* and *Sylvilagus*; the condyle in *Alilepus* (BOHLIN, 1942b, p. 124, fig. 4G) seems to be somewhat like that in *H. vetus*.

Postcranial skeleton. Although the processes are usually broken from vertebrae in the topotype sample, known parts show that the vertebrae resemble those in *Sylvilagus* and *Lepus* in general and in such characteristics as presence of anapophyses on some thoracic and lumbar vertebrae. On the sixth cervical vertebra the in-

ferior lamella of the transverse process terminates posteriorly on a level approximately below the postzygapophysis; in the Recent leporids the anterior part of the inferior lamella has a more pronounced outward flare, and the lamella extends proportionately farther posteriorly. The transverse process of the first thoracic vertebra terminates in a cup-shaped socket that faces mostly ventrally as in *Sylvilagus* and *Romerolagus*. In *Lepus* the socket is more concave and faces anteroventrally. In the sacral region the transverse processes that articulate with the pelvic girdle expand outward anteriorly approximately as in *Sylvilagus* but less than in *Lepus*. The auricular surface is variable in *H. vetus* but generally its two arms intersect at an angle nearly similar to, or slightly greater than, that in *Sylvilagus* but smaller than that in *Lepus*. In *H. vetus*, *Sylvilagus*, and *Lepus* the auricular surface faces dorsolaterally but is more nearly vertical in *H. vetus* and *Sylvilagus* than in *Lepus*. These characteristics of the sacral region indicate that the contact between the sacral vertebrae and the pelvic girdle was slightly weaker and less adapted to withstanding strong thrusts from the hind limbs in *H. vetus* and *Sylvilagus* than in *Lepus*.

The blade of the scapula in *H. vetus* resembles those in the Recent leporids in shape: the supraspinous fossa is smaller than the infraspinous; the scapular neck is long and narrow; a definite ridge sets off the axillary border from the subscapular fossa; the latter fossa is somewhat concave. In *H. vetus* and *Sylvilagus* the scapular spine merges with the blade proportionately closer to the glenoid fossa than in *Lepus*. Viewed laterally the anteroposterior concavity of the glenoid fossa (Fig. 29b) is slightly greater than in *Megalagus* and *Palaeolagus* and more nearly like that in the Recent leporids. Transversely the posterior part of the glenoid fossa (Fig. 29a) is proportionately more elongate and more concave than in *Megalagus turgidus* and *Romerolagus*; the transverse elongation is proportionately nearly the same and the transverse concavity is nearly the same or slightly greater than in *Sylvilagus*. In *Lepus* the elongated part, in addition to having greater transverse elongation and concavity, seems to form a slightly greater proportion of the anteroposterior length of the glenoid fossa.

The head of the humerus (Figs. 30a-b) in *H. vetus* resembles that in *Lepus* in general shape. As in *Sylvilagus* and *Lepus* the head protrudes medially and is somewhat flattened, and an extension of the bicipital groove partially divides the head into medial and lateral parts. In *Megalagus turgidus* the head is not elongated medially, is more rounded and less flattened, and the bicipital groove continues less far posteriorly than in *H. vetus* and the Recent leporids. The greater tuberosity, as in *Sylvilagus*, is slightly higher than the head but is proportionately lower than in *Lepus*. The greater and lesser tuberosities are oriented essentially as in *Sylvilagus*. *Romerolagus* is approximately intermediate between *M. turgidus* and *H. vetus* or *Sylvilagus* in orientation of the tuberosities. *Lepus* is a little more advanced in orientation of the tuberosities than *H. vetus* and *Sylvilagus*: the lesser tuberosity is more anteriorly situated, and the axis of the greater tuberosity is directed more anteroposteriorly. The knoblike eminence on the lateral side of the greater tuberosity is less elevated in *H. vetus* and *Sylvilagus* than



FIGURES 28-35. *Hypolagus vetus* (C.I.T. Locality 63).

28. Lateral view of left innominate bone (composite), $\times 2$.
 —29. Apex of scapula, $\times 2$; 29a, articular surface; 29b, lateral view.
 —30. Right humerus, $\times 2$; 30a, articular surface of proximal end; 30b, lateral view of proximal end; 30c, anterior view of distal end.
 —31. Distal end of left tibiofibula, articular view, $\times 2$.
 —32. Dorsal view of left astragalus, $\times 2$.
 —33. Dorsal view of left calcaneum, $\times 2$.
 —34. Left cuboid, $\times 2$; 34a, medial view; 34b, proximal view.
 —35. Left navicular, $\times 2$; 35a, lateral view; 35b, proximal view.

in *Lepus*. The distal end of the humerus (Fig. 30c) resembles those in the Recent leporids in the development of a pulleylike shape with distinct keels; the keels seem to be proportionately larger than in *Romerolagus*. In *H. vetus* and *Romerolagus* the medial condyle is slightly larger in proportion to the width of the distal end and a little more distinctly notched for muscle attachment than in *Lepus*. In *Megalagus* and *Palaeolagus* the medial condyle is proportionately larger than in *H. vetus* and the Recent leporids. The flexors and pronators of the lower forelimb, which originate on the medial condyle of the humerus, were probably better developed in these Oligocene leporids than in *H. vetus* and the Recent leporids. More evidence of this primitive development of the medial condyle seems to be retained in *H. vetus* and *Romerolagus* than in *Lepus*.

On the ulna in *H. vetus* the olecranon resembles that in *Sylvilagus* in general. The semilunar notch is less deeply concave than in *Lepus* and slightly less than in *Sylvilagus*. No complete ulnar shafts are present in the topotype sample, but some estimation of the development of the shaft can be made from available parts. Below the semilunar notch the shaft of the ulna has three surfaces: one, slightly concave transversely, faces anterolaterally, the second posterolaterally, and the third posteromedially. The two posterior surfaces are at an acute angle with one another; the junction between the surfaces is rounded. More distally the two surfaces merge into a single curved one. The posterior surfaces of the shaft in *Sylvilagus* resemble those in *H. vetus* in general, but in *Lepus* the intersection of the posterolateral and posteromedial surfaces forms a sharper ridge, which seems to persist along a proportionately greater length of the shaft. The anterolateral surface is more concave transversely in *Sylvilagus* and *Lepus* than in *H. vetus*. A short distance above its distal end the ulnar shaft seems to be proportionately a little thicker anteroposteriorly than in *Sylvilagus* and larger both anteroposteriorly and transversely than in *Lepus*. In general, the ulnar shaft in *H. vetus* is relatively better developed than in *Lepus* and more nearly like that in *Sylvilagus*, although proportionately a little larger than in the latter; the shaft is not so robust as in *Megalagus turgidus*. Above the distal end of the ulna a swelling, similar to that in some adults of Recent leporids, represents the place of fusion of the distal epiphysis to the shaft. The styloid process forms more than half the distal surface of the ulna; anteromedial to this process there is a facet that does not extend so far distally. In *Sylvilagus* the distal end of the ulna has a styloid process that forms a similar proportion of the distal end, but in *Romerolagus* the process is proportionately smaller and in *Lepus* that process forms almost the entire distal end of the ulna. In both *Sylvilagus* and *Lepus* the styloid process forms a more compact knob, which is proportionately less elongated anteromedially to posterolaterally, than in *H. vetus*. On the medial surface above the distal end *H. vetus* has a raised process for contact with the radius; this process seems to be less elevated in *Sylvilagus* and *Lepus*.

On the proximal end of the radius in *H. vetus* the grooves for articulation with the humerus are approximately comparable in development to those in *Sylvilagus* but proportionately deeper than in *Romerolagus* and

slightly shallower than in *Lepus*. No complete radial shafts are preserved, but broken parts show that the shaft resembles those in the Recent leporids in general: the shaft is wide transversely and narrow anteroposteriorly; in cross section the posterior surface is flattened or slightly concave and the anterior surface gently convex; viewed laterally the shaft is slightly convex anteriorly. A ridge on the posterior surface of the radius indicates that the length of contact with the ulna along this ridge was proportionately about as long as in *Lepus* and *Sylvilagus* but longer than in *Romerolagus*. The shape of the distal articular surface for the carpus resembles that in *Lepus* in general.

Of the carpal elements, lunar and cuneiform are represented in the topotype collection. In most characteristics of shape the lunar resembles that in *Sylvilagus*. However, medially the anterior part of the lunar does not extend proportionately so far distally as in *Sylvilagus* and *Lepus*. Possibly the centrale, which has a position distad of the medial part of the lunar, was proportionately larger in *H. vetus* than in *Sylvilagus* and *Lepus*; in *H. vetus* the anterior face of the centrale may have exceeded that of the magnum in size as in *Romerolagus* and *Litolagus*, which is the reverse of the size relationship between these two carpals in *Sylvilagus* and *Lepus*. The cuneiform in *H. vetus* differs from that in *Lepus* as follows: shorter proximodistally; the posterior process, which curves distally, forms a larger angle with the anterior part of the bone; on the proximal surface the socket for reception of the styloid process of the ulna is shallower and more elongate, and the anteromedial process for contact with the anteromedial facet on the distal end of the ulna is more prominent. *Sylvilagus* seems to be near *H. vetus* in the characteristics of the cuneiform but is slightly more advanced toward the condition found in *Lepus*. In *Romerolagus* the cuneiform is proportionately shorter proximodistally, the posterior curved process forms a wider angle with the dorsal part, and the bone seems to be more primitive in general than in *H. vetus*.

All metacarpals except the first are represented and resemble those in the Recent leporids in general. The metacarpals in *H. vetus* seem to be shorter in proportion to the over-all size of the forelimb than in *Sylvilagus* and *Lepus*.

Broken pieces of most of the innominate bone (Fig. 28) are represented except for the ventral parts of the pubis and ischium. A low, convex crest, which parallels the long axis of the ilium, separates the iliac blade into superior and inferior fossae. The more primitive ilium in *Palaeolagus* is characterized by a more distinct crest and by fossae that are set at a greater angle with one another. In *Sylvilagus* the ilium is more advanced than in *H. vetus* in having a crest that is less elevated, especially anteriorly, and more nearly coplanar fossae. *Lepus* is still more advanced in the structure of the ilium: the crest is indistinct, the fossae are nearly coplanar, and the inferior part flares laterally more than in *H. vetus* and *Sylvilagus*. Thus, in *Lepus* the ilium furnishes a larger and more continuous surface for attachment of the gluteal group of muscles. The iliac tubercle resembles those in *Sylvilagus* and *Lepus* in general shape and proportionate distance from the acetabulum but is less elevated from the

surface of the ilium than in *Sylvilagus* and more elevated than in *Lepus*. The auricular surface in *H. vetus* is varied, but the two arms tend to be set at an angle nearly the same as in *Sylvilagus* and more acute than in *Lepus*. The ischial tuberosity seems to be slightly more primitive than in *Sylvilagus*: the tuberosity is less thickened, and the lateral process is more elongated than in *Sylvilagus*. The ischial tuberosity in *Lepus* is still more compact and thicker than in *H. vetus* and *Sylvilagus*. In *Romerolagus*, on the other hand, the ischial tuberosity has an elongate lateral process somewhat like that in *H. vetus* but is less thickened than in *H. vetus*, *Sylvilagus*, and *Lepus*.

The proximal end of the femur forms a transversely widened plate of bone similar in general to those in *Sylvilagus* and *Lepus*. The greater trochanter is slightly less elevated above the head than in *Lepus*. In *Romerolagus* the long axis of the greater trochanter is nearly anteroposterior as in *Palaeolagus*, whereas in *H. vetus*, *Sylvilagus*, and *Lepus* the axis is anterolateral to posteromedial. In lateral view the shaft is convex anteriorly approximately as in *Sylvilagus* and *Lepus*; in *Romerolagus*, *Palaeolagus*, and *Megalagus* the shafts are straighter. On the posterior surface of the femur above the distal condyles there is a lateral roughened area for the origin of part of the gastrocnemius muscle. This roughened area reaches medially from the lateral edge past the midline of the bone in *H. vetus*, *Sylvilagus*, and *Lepus*, whereas in *Romerolagus*, *Palaeolagus*, and *Megalagus* the roughened area does not quite reach the mid-line and indicates a weaker origin for part of the gastrocnemius.

The tibiofibula is similar in general development to that in *Sylvilagus*. In *Lepus* the proximal end is proportionately longer anteroposteriorly, the tibial tuberosity is more elevated, the distal third of the shaft tends to be proportionately thicker anteroposteriorly and narrower transversely, and the grooves on the distal end (Fig. 31) are proportionately deeper, suggesting a firmer tarsal contact. The tibiofibula in *Romerolagus* is more primitive than those in *H. vetus*, *Sylvilagus*, and *Lepus* in having a proportionately shorter proximal end, less elevated tibial tuberosity, a shaft that is more convex medially in anterior view, and shallower grooves on the distal end.

In *H. vetus* the tarsal elements tend to be less elongated proximodistally and seem to have contacted one another less firmly than in *Sylvilagus* and *Lepus*. The calcaneum (Fig. 33) extends farther distally than the astragalus and contacts the navicular as in the Recent leporids. In the more primitive tarsus in *Megalagus* there seems to be no calcaneonavicular contact. On the knoblike process of the calcaneum that contacts astragalus and tibiofibula, the medial facet for the astragalus is divided into two distinct surfaces by a ridge similar to that in *Sylvilagus*. In *Lepus* the two surfaces are separated by a sharper ridge, but in *Romerolagus* the ridge is more rounded. The astragalus (Fig. 32) resembles that in *Sylvilagus* in general. In *Lepus* the trochlear keels form proportionately larger ridges, which are closer together and extend farther onto the plantar surface than in *H. vetus* and *Sylvilagus*. *Romerolagus* is more primitive than *H. vetus* in having smaller keels on the astragalus. The navicular (Fig. 35) and cuboid (Fig. 34) in *H. vetus* are proportionately shorter proximodistally than in *Sylvilagus* and

Lepus. On the lateral surface of the navicular the notch for contact with the cuboid is incised into a larger proportion of the proximodistal length than in *Sylvilagus* and *Lepus* but seems to be proportionately a little shorter than in *Romerolagus*. The facet on the navicular for contact with the calcaneum is proportionately shorter than in *Sylvilagus* and *Lepus*. Thus, in *H. vetus* interlocking of the proximal tarsals with the navicular and cuboid seems to have been weaker than in *Sylvilagus* and *Lepus* although possibly a little stronger than in *Romerolagus*. On the medial surface of the navicular the knoblike process for contact with metatarsal II faces slightly more medially than in *Sylvilagus* and *Lepus* and suggests that the pes in *H. vetus* may have been capable of more movement in a medial direction. On the navicular in *Megalagus* this process faces still more medially than in *H. vetus*.

The proximal ends of the metatarsals are represented. The proximal articular surface of metatarsal II extends slightly farther proximad than in *Sylvilagus* and *Lepus*, probably in correlation with the medial knoblike process on the navicular. The proximal ends of the other metatarsals resemble those in the Recent leporids. Unfortunately, no metatarsals are complete; therefore, their proportions relative to the remainder of the hind limb cannot be determined.

Summary. Within the Archaeolaginae, *Hypolagus vetus* is advanced in general structure of the teeth, although probably no more than might be expected in a middle Pliocene archaeolagine. Compared to the cheek-teeth in *Lepus*, however, those in *H. vetus* are somewhat more primitive in being longer anteroposteriorly relative to transversely; in addition, P² and P₃ are less complex in *H. vetus* and may have formed a somewhat less effective mechanism for grinding food. Little is known of the skull in *H. vetus*, but the palate is modernized in general, although the internal nares are narrower than in *Sylvilagus* and *Lepus*. The zygomatic arch resembles that in *Sylvilagus* and *Lepus* in general but is situated closer to the alveolar border, a primitive character. *H. vetus* resembles *Sylvilagus* in many characteristics of the postcranial skeleton but is more primitive in the following: the ulnar shaft is slightly heavier; the styloid process on the distal end of the ulna is more elongated, and the cuneiform is correspondingly modified; the metacarpals seem to be proportionately shorter; the ilium has more distinctly separated fossae and thus furnishes a less continuous surface for attachment of the gluteal muscles, which may have been weaker; the ischial tuberosity is less compact and thickened, suggesting that the hamstring muscles may have been less well developed; the tarsal elements tend to be proportionately shorter proximodistally and to interlock less firmly. Thus, the forelimb of *H. vetus* may have been somewhat heavier distally, the limbs less elongate distally, and some of the muscles in the pelvic girdle and hind limb weaker than in *Sylvilagus*; the hind limb in *H. vetus* may tend to lag in level of evolutionary development more than does the forelimb. Unfortunately, the proportions of the limbs, which are an important factor in locomotive development, are unknown in *H. vetus*, but taken together, the known features suggest that *H. vetus* was less cursorially adapted than *Sylvilagus* but probably had a somewhat similar

bounding mode of locomotion. *H. vetus* was probably closer to *Sylvilagus* in locomotive adaptation than to *Romerolagus*, which is more primitive than *H. vetus* in the postcranial skeleton; the mode of locomotion in *Romerolagus* somewhat resembles that in *Microtus* (NELSON, 1909, p. 280). The typical leporid half-bound or leaping gallop seems to reach its best development in *Lepus*, in which the postcranial skeleton is correspondingly more advanced than in *H. vetus* and *Sylvilagus*.

TABLE 14.—Measurements in millimeters of *Hypolagus vetus* (based on mean of three or more measurements)

Topotype sample, C.I.T. locality 63	
anterior root of zygoma, dorsoventral depth	6.2
length palate	6.0
length palatine on palate	1.7
length maxilla on palate	4.4
P ₁ -M ₂	9.0
inside depth of jaw below M ₁	14.3
scapula	
anteroposterior length glenoid fossa	9.4
transverse width glenoid fossa	8.6
humerus	
anteroposterior length proximal end	14.3
transverse width proximal end	12.9
transverse width distal end	9.0
radius	
transverse width proximal end	6.4
metacarpals	
length II	20.9
length III	21.6
length IV	17.8
length V	11.8
femur	
transverse width distal end	14.9
tibiofibula	
transverse width proximal end	15.9
transverse width distal end	12.4
calcaneum	
proximodistal length	23.6
astragalus	
proximodistal length	12.1
transverse width body	5.8

Hypolagus regalis Hibbard

Hypolagus regalis HIBBARD, Amer. Mid. Nat., v. 21, no. 2, p. 510, May 19, 1939.

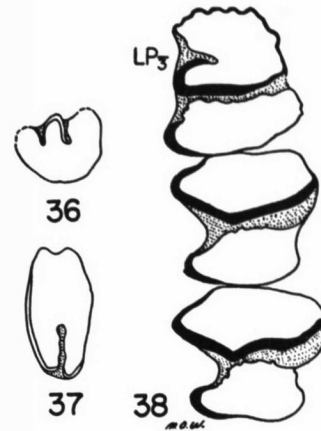
Type specimen.—Incomplete left lower jaw having incisor and P₃-M₂, K.U. No. 4572, locality No. 3, Rexroad fauna, Meade County, Kansas.

Geologic age and distribution.—Blancan (early Pleistocene?) of Kansas, possibly Texas.

Specific characters.—On P₃ anterior column relatively wider transversely than in *H. vetus*, anteroexternal reentrant faces mostly externally, lingual surface flattened. Lower molariform teeth tend to be relatively wider transversely and jaw tends to be dorsoventrally deeper than in *H. vetus*.

Crenulations are present in the walls of the anteroexternal and posteroexternal reentrants on P₃ in the type specimen of *Hypolagus regalis*, but are lacking in one of the paratypes, K.U. No. 4571; the presence or absence of crenulations may reflect different stages of wear. Some specimens of *H. vetus* from a topotype sample, C.I.T. locality 63, have characteristics in P₃ suggestive of those in the Blancan species, and *H. regalis* may be closely allied to *H. vetus*.

Material from the Cita Canyon, Texas, fauna of



FIGURES 36-38. *Hypolagus*, ?Archaeolaginae, and ?Pratilepus.

36. *Hypolagus edensis*, type specimen (U.C.M.P. No. 23376), occlusal view of right P₃, ×4.5.—37. Occlusal view of left upper molariform tooth of form doubtfully assigned to Archaeolaginae (C.I.T. No. 2507), ×3.—38. ?*Pratilepus progressus*, (U.M.M.P. No. 31080), occlusal view of left P₃-M₁, showing separation of trigonid and talonid on P₃, ×6.

Blancan age, not examined in connection with this study, has been listed as *Hypolagus* cf. *regalis* (JOHNSTON & SAVAGE, 1955, p. 39). The Hagerman leporid referred to as *Hypolagus* near *vetus* is known from incomplete material but seems to vary from middle Pliocene specimens of *H. vetus* in the same direction as does *H. regalis* in that P₃ is relatively wider anteriorly and the jaw is more robust (GAZIN, 1934, p. 112-113). Possibly the Hagerman leporid is allied to *H. regalis*.

Hypolagus edensis Frick

Figure 36

Hypolagus edensis FRICK, Univ. California Pub., Bull. Dept. Geol., v. 12, no. 5, p. 348, December 28, 1921.

Type specimen.—Fragmentary right lower jaw having P₃-M₁, U.C.M.P. No. 23376, middle Pliocene of Mount Eden formation, U.C. locality 3269, Riverside County, California.

Geologic age and distribution.—Hemphillian (middle Pliocene) of California.

Specific characters.—On P₃ anteroexternal reentrant deep transversely, extending across approximately half the width of the tooth, and narrow anteroposteriorly. Size near that in *H. apachensis*.

The anteroexternal groove on P₃ shown in the original figure of the type specimen of *Hypolagus edensis* (FRICK, 1921, fig. 52) is more widely open than in the specimen itself. Figure 36 shows the outline of P₃ more nearly as it is.

Hypolagus oregonensis Shotwell

Hypolagus oregonensis SHOTWELL (misspelled *oregonensis*), Geol. Soc. Amer., Bull., v. 67, p. 727, June, 1956.

Type specimen.—Left lower jaw having P₃-M₃, U.O.M.N.H. No. F-4094, middle Pliocene, east bank of McKay Reservoir, 5 miles south of Pendleton, north-eastern Oregon.

Geologic age and distribution.—Hemphillian (middle Pliocene) of Oregon.

Specific characters.—Anterior surface of P_3 has variable grooves and striations (SHOTWELL, 1956, p. 727). Size near *H. vetus*.

Hypolagus spp.

Leporids from various upper Miocene and Pliocene localities, often incomplete specimens, have been recorded as *Hypolagus* sp. or *Hypolagus* cf. *vetus*, and other previously unreported specimens seem to represent this genus. Some of these specimens will be mentioned because of distinctive morphologic or stratigraphic features.

A.M.N.H. No. 22395, recorded as coming from the Sheep Creek formation, channel beds, Ashbrook pasture, western Nebraska, includes an incomplete skull and right lower jaw and represents a leporid that is slightly smaller than *H. vetus*. In this specimen the walls of the hypostria on P^3-M^2 are lightly crenulated, and the anteroexternal reentrant on P_3 is shallow and seems to have only a thin filling of cement. The bony palatal bridge in No. 22395 is more primitive than in *H. vetus* in having a proportionately longer palatine component. This leporid seems to represent a primitive species of *Hypolagus*. Pending further study this leporid is listed here as *Hypolagus* sp.

U.C.M.P. No. 28524 from the upper Miocene Barstow beds, San Bernardino County, California, which was cited as *Hypolagus* cf. *vetus* (HALL, 1930b, p. 318), is smaller than *H. vetus* and more nearly like C.I.T. No. 5179, *Hypolagus* near *parviplicatus*, and *H. fontinalis* in size. P_3 seems to be approximately intermediate in shape between that in *H. near parviplicatus* and in *H. fontinalis*; the anteroexternal fold tends to be deeper than in the former and smaller than in the latter. Whether No. 28524 is referable to either of those species or represents a different species cannot be determined on the basis of the known specimens. U.C.M.P. No. 28526 from the Barstow beds, listed as *Hypolagus* sp. (HALL, 1930b, p. 318) is fragmentary but probably represents the same species as No. 28524.

A right maxilla having P^2-M^2 , U.C.M.P. No. 32907, from the middle Pliocene Mulholland fauna, U.C. locality V3611, of the San Francisco Bay region, California (STIRTON, 1939, p. 367) represents a species of *Hypolagus* having upper cheek-teeth that are near in size to those in *H. limnetus* or the Kern River *H. near limnetus*. *H. fontinalis* is known from lower cheek-teeth only but probably had upper cheek-teeth near those of No. 32907 in size. The Mulholland leporid seems to be closer to the line of leporids represented by *H. fontinalis* and *H. limnetus* than to *H. vetus*.

In the middle Pliocene Rome fauna of Malheur County, Oregon, two species of leporid seem to be present, *Hypolagus vetus* and *Hypolagus* sp. In C.I.T. No. 1964, *Hypolagus* sp., the lower cheek-teeth are near in size to those in specimens of *H. fontinalis* from South Dakota and smaller than those in *H. vetus*, whereas the lower jaw is nearly as deep dorsoventrally as in *H. vetus*; thus, the lower cheek-teeth are smaller relative to the depth of the jaw than in *H. vetus*. Available comparative material of the Rome *Hypolagus* sp. is inadequate, and No. 1964

may represent a young individual of *H. vetus* but more probably is a different species (WILSON, 1937a, p. 12-13).

A specimen of *Hypolagus*, K.U. No. 3747, from the middle Pliocene Feldt Ranch fauna (HESSE, 1935, p. 83) is larger than *H. vetus* and *H. regalis*. A.M.N.H. No. 20476 from the upper Snake Creek, Pliohippus draw, western Nebraska, and C.N.H.M. No. P27073 from upper Snake Creek beds, Mitchell, Scotts Bluff County, Nebraska, are leporids near No. 3747 in size. The leporid listed as *Hypolagus* cf. *vetus* from the middle Pliocene Optima fauna, O.M.P. No. 29-4-S52 (SAVAGE, 1941, p. 704-705) also is larger than *H. vetus*. These specimens establish the presence in the middle Pliocene of the Great Plains of a line of leporids that is probably closely allied to but larger than *H. vetus*; whether these specimens are referable to the same species may be difficult or impossible to determine on the basis of the known incomplete material.

The small species of *Hypolagus* from the Coso Mountains local fauna of Blancan age is smaller than other known species of *Hypolagus* and has a flattened lingual wall and shallow anteroexternal fold on P_3 . M_3 consists of a single column having a posteroexternal fold. The known specimens suggest that this leporid is distinct from other known species of *Hypolagus*, and if more complete specimens show that the distinctions are constant, this leporid probably represents an unnamed species (WILSON, in SCHULTZ, 1937, p. 108-109).

Genus NOTOLAGUS Wilson, 1938

Notolagus WILSON, Southern California Acad. Sci., Bull., v. 36, pt. 3, p. 98, January 25, 1938. Type, *Notolagus velox*.
DICEA HIBBARD, Amer. Mid. Nat., v. 21, no. 2, p. 509, May 19, 1939.

Geologic age and distribution.—Late Hemphillian (late middle Pliocene) of Chihuahua, Mexico; Blancan (early Pleistocene?) of Kansas.

Generic characters.—Two or three anterior reentrants on P^2 ; internal hypostria on P^3-M^2 crenulated, crosses two-thirds or slightly less of occlusal surface. P_3 tends to be elongate anteroposteriorly: on that tooth posteroexternal reentrant usually crosses less than half the width of occlusal surface; anteroexternal reentrant deep, enamel walls usually crenulated and thicker posteriorly than anteriorly.

Greater complexity of the enamel folds on P^2 and P_3 in *Notolagus* is one of the characteristics differentiating this genus from other archaeolagines. In adult specimens of *Archaeolagus* P^2 has a single anterior reentrant and in *Hypolagus* there is one well-developed reentrant plus a more external shallow groove. In *Notolagus* two of the reentrants probably correspond to the reentrant and groove in *Hypolagus*, whereas the third fold, which occurs in one species of *Notolagus*, is not present in P^2 of known adult specimens of *Hypolagus*. The folds on P_3 , which are anteroexternal, posteroexternal, and anteroexternal in position, are more complex than in *Archaeolagus* and *Hypolagus* but are probably all represented in some specimens of at least one other archaeolagine, *Hypolagus apachensis* (WILSON, 1949b, p. 137). In the latter, P_3 tends to be anteroposteriorly elongated and has in some adult specimens an anteroexternal reentrant that is a variant from the more usual condition in that species in

which that fold is absent; the anterointernal fold may represent a persistent remnant of a groove present between cusps in an unworn tooth. In *H. apachensis* the anterointernal fold, where present, is short and simple, whereas in *Notolagus* the fold is deep and complex and may unite with the anteroexternal fold. Thus, the anterointernal fold on P_3 in *Notolagus* is not unique among the archaeolagines. P_3 in *Notolagus* could be derived from a stage such as that found in some specimens of *H. apachensis*, although intermediates between the two levels of development are not known. *H. apachensis* does not seem to foreshadow *Notolagus* in characters other than in the pattern of P_3 , although no characters would bar *H. apachensis* from the ancestry of *Notolagus*; whether or not a phylogenetic connection occurred, *H. apachensis* does suggest a structural stage within the genus *Hypolagus* from which *Notolagus* may have been derived.

Notolagus velox Wilson

Notolagus velox WILSON, Southern California Acad. Sci., Bull., v. 36, pt. 3, p. 98, January 25, 1938.

Type specimen.—Incomplete left lower jaw having incisor and P_3 - M_2 , C.I.T. No. 2133, middle Pliocene beds near Rincon, Chihuahua, Mexico.

Geologic age and distribution.—Late Hemphillian (late middle Pliocene) of Mexico.

Specific characters.—Two anterior folds on P^2 . Anterointernal fold on P_3 deep transversely, usually unites with anteroexternal fold, resulting in isolation of anterior column of tooth from more posterior part. Near *Hypolagus limnetus* in size.

In some specimens of *Notolagus velox* the anterior column of P_3 is connected to the more posterior part of the tooth by a bridge of dentine and enamel between anteroexternal and anterointernal reentrants, but the more usual condition of union of anteroexternal and anterointernal reentrants results in isolation of the anterior column, which is then connected to the posterior part of the tooth only by cement. Variation with age and between individuals seems to account for these differences (WILSON, 1937b, p. 99-100). The anterior surface of the anterior zygomatic root seems to be less concave than in *N. lepusculus*.

Notolagus lepusculus (Hibbard)

Dicella lepuscula HIBBARD, Amer. Mid. Nat., v. 21, no. 2, p. 509, May 19, 1939. *Notolagus lepusculus*, HIBBARD & RIGGS, Geol. Soc. Amer., Bull., v. 60, p. 841, May, 1949.

Type specimen.—Incomplete right lower jaw having incisor and P_3 - M_3 , K.U. No. 4583, locality No. 3, Rexroad fauna, Meade County, Kansas.

Geologic age and distribution.—Blancan (early Pleistocene?) of Meade County, Kansas.

Specific characters.—Three anterior folds on P^2 . On P_3 wide, shallow anteroexternal reentrant and deep anterointernal reentrant separated by bridge of enamel and dentine. Near *Hypolagus apachensis* in size.

Notolagus lepusculus seems to be more advanced than *N. velox* in having an added anterior fold on P^2 . Upper cheek-teeth of the two species of *Notolagus* are known

only from one individual each; the crenulations in the walls of the internal hypostria on P^3 - M^2 are more complexly folded in the known specimen of *N. lepusculus* than in *N. velox*. This difference may be due to different stages of wear on the teeth in the known specimens, but if constant with wear, is probably an advanced character in *N. lepusculus*. P_3 seems to be of approximately equal complexity in the two species, but none of the known specimens of *N. lepusculus* exhibit the isolation of an anterior column that seems to be characteristic of *N. velox*.

Subfamily ARCHAEOLAGINAE?

Genus PANOLAX Cope, 1874

Panolax COPE, Acad. Nat. Sci. Philadelphia, Proc., 1874, p. 151, October 20, 1874. Type, *Panolax sanctaefidei*.

Geologic age and distribution.—Barstovian (late Miocene) or Clarendonian (early Pliocene) of Santa Fe formation, north-central New Mexico; possibly southern California.

Generic characters.—Single anterior reentrant on P^2 ; on upper molariform teeth internal reentrant straight walled, cement filled, and crossing half or less of occlusal surface.

Panolax sanctaefidei Cope

Panolax sanctaefidei COPE, Acad. Nat. Sci. Philadelphia, Proc., 1874, p. 151, October 20, 1874.

Type specimen.—Isolated upper cheek-teeth and M_3 , U.S.N.M. No. 1095, "Loup Fork formation", New Mexico.

Geologic age and distribution.—As for genus.

Specific characters.—Only species of genus as defined above. Somewhat larger than *Hypolagus vetus*.

Panolax is incompletely known: the parts represented include P^2 , isolated upper molariform teeth, M_3 , and a few postcranial fragments. As mentioned by DICE (1923, p. 191), the upper molariform teeth, which have a simple internal hypostria, resemble those in *Archaeolagus* more than those in *Hypolagus*. The available material permits little to be said of the affinities of this leporid: a precise subfamilial allocation cannot be made, although the general character and stratigraphic position of this leporid suggest that it is an archaeolagine; it seems to be more closely allied to *Archaeolagus* than to *Hypolagus* and may represent a late survivor of a primitive stock.

WILSON (1939, p. 38) described C.I.T. No. 2507 (Fig. 37), an upper left cheek-tooth, possibly P^4 , from the lower Pliocene Avawatz deposits, C.I.T. locality 267, of

TABLE 15.—Measurements in millimeters of *P. sanctaefidei*

	U.S.N.M. No. 1095	C.I.T. No. 2507
P^2 anteroposterior	1.6	
transverse width	3.4	
upper molariform tooth		
anteroposterior	2.5	2.8
transverse width	6.0	5.5
M_3 anteroposterior	2.2	
transverse width	1.9	

southern California. This tooth is near in size to upper molariform teeth in *P. sanctaefidei*; a straight-walled, cement-filled internal hypostria crosses less than half the occlusal surface. The general character of this tooth and its stratigraphic position suggest that this specimen represents a leporid near *Panolax sanctaefidei*.

Subfamily LEPORINAE Trouessart, 1880

The subfamily Leporinae ranges in time from early Pliocene or Pontian to Recent. Included in the subfamily are the extinct genera *Alilepus*, *Pratilepus*, and possibly *Pliolagus*⁸ and *Serengetilagus*, and all living genera of leporids, which are *Romerolagus*, *Pronolagus*, *Pentalagus*, *Brachylagus*, *Nesolagus*, *Caprolagus*, *Oryctolagus*, *Sylvilagus*, and *Lepus*. Leporines are more advanced than palaeolagines in general structure of the skull and lower jaw, as indicated by such features as a short palatine component on the palate, a well-defined anterior zygomatic root, and a prominent ventral border of the masseteric fossa in the lower jaw. The cheek-teeth are hypsodont. The enamel walls in the hypostriae and reëtrants on upper and lower cheek-teeth vary from simple and essentially unfolded as in *Nesolagus* to complexly folded as in *Pentalagus*. A distinguishing character of the leporines is the basic pattern of P_3 : in that tooth an anteroexternal and a posteroexternal reëtrant occur as in archaeolagines, and, in addition, a posterointernal reëtrant or structure derived from that reëtrant forms a usually persistent and often prominent part of the occlusal pattern. In the archaeolagines the posterointernal reëtrant is usually absent in adults. The posterointernal fold occurs variably in the leporines as follows: as a fold connected to the lingual wall and separated from the posteroexternal reëtrant; as an isolated lake that may or may not be worn away in late stages of wear; as a lake that unites with the posteroexternal reëtrant to form a fold crossing the occlusal surface nearly to the lingual wall; as a fold that unites with the posteroexternal reëtrant to form a fold across the entire occlusal surface.

The oldest known leporine is *Alilepus*, which first appears in the Pontian of Europe and Asia. Structurally and temporally *Alilepus* could be near the ancestry of later leporines and suggests an Old World origin for the subfamily. Whether the leporines originated directly from palaeolagines or from a primitive archaeolagine is not definitely known; in either case, the Miocene history of the leporines seems to be unknown. The first record of *Lepus* in the Old World is Villafranchian (SCHREUDER, 1936, p. 229). The earliest known North American leporines occur in the Hagerman and Rexroad faunas of Blancan age. Records of *Lepus* and *Sylvilagus* before the early Pleistocene in North America are questionable. *Sylvilagus?* sp. from the lower Pliocene of Fish Lake Valley (HALL, 1930a, p. 311) is probably an ochotonid. *Sylvilagus? bensonensis* from beds of Blancan age near Benson, Arizona, may be generically distinct from *Sylvilagus*, as discussed below. *Lepus* and *Sylvilagus* are known from the early Pleistocene Curtis fauna (GAZIN, 1942, p. 511). Pleistocene leporids will not be treated in detail here; several extinct species have been reported from the North American Pleistocene including *Lepus benjamini*

(HAY, 1921, p. 628), *Lepus giganteus* (BROWN, 1908, p. 199), *Sylvilagus palustrellus* (GAZIN, 1950, p. 399), and *Sylvilagus leonensis* (CUSHING, 1945, p. 183).

Genus PRATILEPUS Hibbard, 1939

Pratilepus HIBBARD, Amer. Mid. Nat., v. 21, no. 2, p. 506, May 19, 1939. Type, *Pratilepus kansasensis*.

Pediolagus HIBBARD, Amer. Mid. Nat., v. 21, no. 2, p. 512, May 19, 1939 (not *Pediolagus* MARELLI, Mem. Jardin zool. La Plata, v. 3, p. 5, August 12, 1927).

Nekrolagus HIBBARD, Amer. Mid. Nat., v. 21, no. 3, table of contents, June 7, 1939.

Geologic age and distribution.—Blancan (early Pleistocene?), Rexroad fauna, Meade County, Kansas.

Generic characters.—Posterior end of lower incisor terminates above mid-depth of jaw approximately in line with trigonid of P_3 . On P_3 posterointernal reëtrant, which has thicker enamel anteriorly than posteriorly, not united with posteroexternal reëtrant, opens lingually in early stages of wear, later loses lingual connection and forms persistent isolated lake.

In the original descriptions of the two species referred here, *Pratilepus kansasensis* and *P. progressus*, one of the characteristics of the former was a posterointernal fold on P_3 and of the latter, considered to be a distinct genus, *Pediolagus* (later *Nekrolagus*), a posterointernal isolated lake (HIBBARD, 1939, p. 506, 512). More complete series of specimens, which were found later, show that in both species there is a posterointernal fold on P_3 in early stages of wear that forms an isolated posterointernal lake in more worn teeth (HIBBARD, 1941b, p. 293-295, 298-299). This basic similarity between the two species suggests that their common ancestor was not long antecedent and that a single genus is represented.

Pratilepus is definitely known only from the Rexroad fauna, although further study may reveal that *Alilepus? vagus* from the Blancan of Hagerman is referable to this genus. The specimen referred to *Nekrolagus*, K.U. No. 6155, from the Borchers fauna of approximately middle Pleistocene age (HIBBARD, 1941a, p. 216) probably represents an immature individual having a somewhat aberrant and perhaps atavistic occlusal pattern but referable to the genus *Lepus*.

Pratilepus kansasensis Hibbard

Pratilepus kansasensis HIBBARD, Amer. Mid. Nat., v. 21, no. 2, p. 507, May 19, 1939.

Type specimen.—Incomplete right lower jaw having P_3 - M_2 , K.U. No. 4582, locality No. 3, Rexroad fauna, Meade County, Kansas.

Geologic age and distribution.—Blancan (early Pleistocene?), Rexroad fauna, Meade County, Kansas.

Specific characters.—Three anterior folds, of which middle fold is deepest, on P^2 ; internal hypostria on P^3 - M^2 crenulated, crosses two-thirds to three-fourths of occlusal surface. On P_3 anteroexternal reëtrant usually deeper than in *P. progressus*; anteroexternal fold present in early stages of wear; posterointernal fold opens lingually, or in later stages of wear forms isolated lake; crenulations usually present in walls of anteroexternal and posteroexternal reëtrants, may or may not occur in posterointernal

⁸ See note, page 73.

fold or lake. Crenulations usually present in anterior wall of talonid on P_4-M_2 , although may be reduced with wear. Near *Sylvilagus floridanus* in size.

Pratilepus progressus (Hibbard)

Pediolagus progressus HIBBARD, Amer. Mid. Nat., v. 21, no. 2, p. 512, May 19, 1939.

Nekrolagus progressus, HIBBARD, Amer. Mid. Nat., v. 21, no. 3, table of contents, June 7, 1939.

Type specimen.—Incomplete right lower jaw having broken incisor and P_3-M_1 , K.U. No. 4570, locality No. 3, Rexroad fauna, Meade County, Kansas.

Geologic age and distribution.—Blancan (early Pleistocene?), Rexroad fauna, Meade County, Kansas.

Specific characters.—On P_3 anterior fold usually present; anteroexternal fold usually shallower and having less complexly folded walls than in *P. kansasensis*; walls of posteroexternal and posterointernal folds may be crenulated. Anterior wall of talonid on P_4-M_2 may be slightly folded, although less than in *P. kansasensis*, or straight. Jaw between incisor and P_3 shorter relative to depth of jaw than in *Lepus californicus*. Near *Lepus californicus* in size.

In U.M.M.P. No. 31080 (Fig. 38), an incomplete left lower jaw having the incisor and P_3-M_1 from locality 3, Rexroad fauna, P_3 has three small anterior folds, an anteroexternal reentrant, and a trigonid that is united to the talonid by cement only for the entire length of the tooth. This specimen resembles *P. progressus* in size and general structure and may represent an aberrant individual of *P. progressus* in which the posteroexternal and posterointernal folds have united. The Recent genus *Brachylagus* has a similar separation of trigonid and talonid at some stages of wear, possibly attained structurally as in U.M.M.P. No. 31080 but not necessarily implying a phylogenetic connection between *P. progressus* and *Brachylagus*.

Sylvilagus? bensonensis Gazin

Sylvilagus? bensonensis GAZIN, U. S. Natl. Mus., Proc., v. 92, no. 3155, p. 492, 1942.

Type specimen.—Incomplete left lower jaw having P_3-M_1 , U.S.N.M. No. 16595, about two miles south of Benson, Arizona, not from quarry worked by GIDLEY and BRYAN (GAZIN, 1942, p. 492).

Geologic age and distribution.—Blancan (early Pleistocene?) of Arizona.

Specific characters.— P_3 has deep, crenulated anteroexternal reentrant and crenulated posteroexternal fold crossing nearly entire occlusal surface, and lacks anterior reentrant. Jaw robust. Slightly smaller than *Pratilepus kansasensis*.

Differences of *Sylvilagus? bensonensis* from the genus *Sylvilagus* are especially marked in P_3 , in which the anteroexternal reentrant is deeper and more complexly folded than in *Sylvilagus* and the anterior fold, present in *Sylvilagus*, is lacking, and suggest that this leporid is generically distinct from *Sylvilagus* (GAZIN, 1942, p. 492-493). Further, there is a striking resemblance between the single known specimen of *Sylvilagus? bensonensis* and *Pratilepus kansasensis* in most characters, except that on P_3 the posteroexternal fold nearly crosses the occlusal sur-

face in the former whereas in the latter the posteroexternal reentrant and posterointernal fold or lake are separated from one another by a bridge of enamel and dentine. The bridge varies in width in *P. kansasensis* and in at least one specimen, K.U. No. 4574, is unusually thin. The wearing away of this bridge would result in a tooth essentially similar to that in *Sylvilagus? bensonensis*. Possibly No. 16595 is an aberrant individual from a population of *P. kansasensis*, but if more complete material indicates that the erosion of the bridge between posteroexternal and posterointernal folds is a constant feature in adults of *Sylvilagus? bensonensis*, this leporid is probably closely allied to *P. kansasensis* but slightly advanced toward the level of development in *Sylvilagus*. More definite generic assignment should await more complete material.

Genus *ALILEPUS* Dice, 1931

Alilepus DICE, Jour. Mammalogy, v. 12, no. 2, p. 159, May 14, 1931. Type, *Lepus annexens* SCHLOSSER.

Allolagus DICE, Jour. Mammalogy, v. 10, no. 4, p. 342, November 11, 1929 (not *Allolagus* OGNEV, Zool. Anz., v. 84, p. 71, August 1, 1929).

Geologic age and distribution.—Pontian and middle Pliocene of Europe and Asia; tentatively referred, Blancan (early Pleistocene?) of North America.

Generic characters.—Skull and lower jaw modernized. Single reentrant and shallower, more external groove on anterior surface of P^2 ; internal hypostria on upper molariform teeth crosses approximately half the occlusal surface, has walls crenulated in early stages of wear but nearly smooth in more worn teeth. On P_3 posterointernal reentrant as deep as posteroexternal reentrant or shallower (BOHLIN, 1942b, p. 132).

Alilepus? vagus Gazin

Alilepus? vagus GAZIN, U. S. Natl. Mus., Proc., v. 83, no. 2976, p. 119, 1934.

Type specimen.—Anterior part of right lower jaw having P_3 , U.S.N.M. No. 12622, Hagerman lake beds, T. 7 S., R. 13 E., Twin Falls County, Plesippus quarry, near Hagerman, Idaho.

Geologic age and distribution.—Blancan (early Pleistocene?), Twin Falls County, Idaho.

Specific characters.— P_3 lacking reentrants on anterior wall, having shallow anteroexternal fold, posteroexternal reentrant that crosses approximately half of the occlusal surface, and posterointernal reentrant or isolated lake separated from posteroexternal reentrant by narrow bridge of enamel and dentine. Jaw robust, proportionately shorter between incisor and P_3 than in *Hypolagus vetus*. Near *Pratilepus progressus* in size.

When first described, *Alilepus? vagus* was known only from the type specimen, in which P_3 has posteroexternal, posteroexternal, and anteroexternal reentrants, thus resembling that tooth in *Alilepus annexens*. Additional specimens of the Hagerman leporine now in the collections of the United States National Museum show that on P_3 the posterointernal reentrant loses its lingual connection and forms an isolated lake at a later stage of wear than that present in the type specimen. Thus, P_3 in *Alilepus? vagus* resembles that in *Pratilepus* in formation of an isolated lake following wear, whereas the posteroexternal reentrant on P_3 in Old World species of *Alilepus*

seems to retain its lingual connection. Further study of the additional specimens of *Alilepus? vagus* may reveal that the Hagerman leporine is more closely allied to *Pratilepus* than to *Alilepus*.

Hypolagus? browni (Hay)

Brachylagus browni HAY, U. S. Natl. Mus., Proc., v. 59, no. 2391, p. 630, 1921.
Hypolagus browni, DICE, Jour. Mammalogy, v. 10, no. 4, p. 343, November 11, 1929.

Type specimen.—Skull fragment including palate, incomplete maxillae and zygomata, right P³-M¹ and left P³-M², U.S.N.M. No. 10196, lower Pleistocene, Anita, Coconino County, Arizona.

Geologic age and distribution.—Early Pleistocene, Arizona.

Specific characters.—Crenulated hypostria on P³-M² crosses more than half of the occlusal surface. On P₃ anteroexternal fold shallow; posterior fold or folds variable as follows: in worn teeth posteroexternal fold crosses slightly more than half of the occlusal surface, postero-

internal fold lacking; at seemingly earlier stages of wear trigonid and talonid may be united at occlusal surface by cement only, probably due to union of posteroexternal and posteroexternal reentrants, or posteroexternal reentrant may form isolated lake. Size near *Hypolagus apacheensis*.

Reference of this species to *Hypolagus* is probably misleading with regard to the affinities of *Hypolagus? browni*, which is here considered to be a leporine. However, the evidence for these affinities is not conclusive, so a new generic assignment, which would only add to taxonomic confusion and not to phylogenetic clarification at this time, is not made. Known specimens of *Hypolagus? browni* show that on P₃ a posteroexternal fold or lake occurs in earlier stages of wear and is later worn away but seems to be more prominent and persistent than in the archaeolagines. *Serengetilagus* from the early Pleistocene of East Africa (DIETRICH, 1942, p. 56-57) seems to go through stages of isolation and loss of the posteroexternal fold somewhat like those in *Hypolagus? browni*.

MORPHOLOGIC HISTORY

In the following discussion primary emphasis is placed on the North American leporids. The major trends of morphological evolution can be traced from a primitive level in the palaeolagines to a more advanced level in archaeolagines and leporines; the last two subfamilies seem to have undergone parallel development in several dental and skeletal characters. At any one time there have been leporids in varying stages of development, such as *Palaeolagus* and *Megalagus* in the middle Oligocene, *P. hypsodontus* and *P. philoi* in the early Miocene, and *Romerolagus* and *Lepus* in Recent faunas. For this reason, known leporids from certain stratigraphic levels may not represent the stage of development typical of that level due to incompleteness of the fossil record, but the trends described here probably indicate the over-all changes in the family. For the most part the intermediate stages, between *Palaeolagus* and *Lepus*, discussed below could have been anticipated from WOOD'S (1940) discussion of the fundamental characteristics of Oligocene and Recent leporids.

Dentition. Several general changes have affected the upper and lower cheek-teeth of leporids. Starting from a late Eocene condition in which cement is essentially absent, cement becomes progressively better developed—the teeth in early Oligocene species usually have less cement than in middle Oligocene species, in early and middle Miocene *Archaeolagus* there is a moderate amount of cement, and in Pliocene species of *Hypolagus*, cement reaches an essentially modern condition. The cheek-teeth in late Eocene leporids are slightly hypsodont but rooted, in most early Oligocene and some later leporids are more hypsodont but still rooted, and seem to have an essentially complete development of hypsodonty in some later Oligocene and most early Miocene and later leporids. The cheek-teeth have become progressively shorter anteroposteriorly relative to their transverse width, and the length of the row of lower cheek-teeth has become shorter relative to the depth of the jaw. In late

Eocene leporids, in which the greatest transverse width of the tooth-rows occurs at M¹ and M₂, the molars including M³ and M₃ are larger relative to the premolars than in later leporids. By Oligocene times the premolars have become relatively wider and the last molars are reduced; the row of upper cheek-teeth is usually widest at P³ or P⁴ in Oligocene and later leporids. The proportions of P₄, M₁ and M₂ are more nearly equivalent in Oligocene and later leporids than in the late Eocene genus *Mytonolagus*. P₂ and P₃ are larger relative to the size of the more posterior cheek-teeth in later leporids than in those of the Oligocene.

The upper incisors of Oligocene and later leporids seem to be similar in general structure. In most leporids the anterior groove is without cement and simple but in *Lepus* is filled with cement and may be branched. P₂ is not molariform in leporids. In *Mytonolagus* P₂ consists of three lobes, of which the buccal lobe is proportionately larger than in *Palaeolagus*; in the latter, P₂ is three-lobed in young individuals but becomes two-lobed in older individuals through the union of buccal and central lobes (WOOD, 1940, p. 290). P₂ retains this essentially two-lobed condition in *Archaeolagus*, *Hypolagus*, and *Alilepus* but becomes more complex through the addition of anterior folds in *Notolagus*, *Pratilepus*, and some Recent leporids. In the upper cheek-teeth, other trends as recognized by MATTHEW (1903, p. 218) are related to replacement of the type of pattern found in *Palaeolagus* by a pattern similar to that found in *Lepus* and to molarization of P³ and P⁴. The more primitive pattern of P³-M² in the earlier leporids consists of an internal hypostria, the buccal end of which may become isolated to form a lake, and crescents that are variably connected to the buccal wall of the tooth or isolated as lakes. The process of reduction of the crescents and emphasis on the hypostria occurs at variable rates: in some Oligocene leporids the crescents are retained; in some the crescents are absent in adults; in

others the crescents on the molars are lost, but are retained on P^3 , or P^3 and P^4 . Adults of *Archaeolagus* lack the crescents and have on P^3 - M^2 a straight-walled internal hypostria; crescents occur on P^3 and P^4 in early stages of wear in *Archaeolagus ennisianus*. Modernization of pattern on P^3 - M^2 continues in *Hypolagus* and most later leporids, in which crescents are absent in adults and the hypostriae become relatively longer and develop crenulated walls. Even in Recent leporids persistent remnants of the primitive pattern persist, as shown by the presence of crescents on unworn P^3 - M^2 in *Sylvilagus* (DICE & DICE, 1941, p. 224). Molarization of P^3 and P^4 occurs as follows: in *Mytonolagus* and most Oligocene species the internal hypostria is less persistent on P^3 and P^4 than on M^1 and M^2 , and in most specimens crescents are retained on the premolars longer than on the molars; P^3 and P^4 seem to be nearly as molariform as M^1 and M^2 in *Archaeolagus*, although more rapid shortening of the hypostria and traces of the crescent in early stages of wear on P^3 and P^4 indicate that molarization of the premolars is not complete; the internal hypostria forms the persistent pattern, and the premolars seem to be fully molariform in *Hypolagus*. The walls of the internal hypostriae are essentially straight in Oligocene leporids and *Archaeolagus* but are crenulated in *Hypolagus*. These crenulations in *Hypolagus*, especially in earlier species, are more pronounced and persistent on the premolars than on the molars, resulting in a condition in which P^3 and P^4 seem to be "more molariform" than M^1 and M^2 . In later species of *Hypolagus* and most Recent leporids, crenulations persist in the hypostriae on premolars and molars. P^3 and P^4 tend to be longer anteroposteriorly than M^1 and M^2 in Oligocene leporids; in *Archaeolagus* of the early and middle Miocene and the later leporids the anteroposterior lengths of premolars and molars are more nearly equivalent.

The lower incisor in *Mytonolagus* extends posteriorly along the ventrolingual side of the jaw and terminates below M^2 . The posterior end of this tooth in later leporids does not extend so far posteriorly and moves dorsad on the lingual side of the jaw: in *Archaeolagus ennisianus* and *Hypolagus* the incisor terminates in a line in front of or below P^3 ; in the former the posterior end of the incisor is slightly below mid-depth and in *Hypolagus* usually slightly above mid-depth of the jaw. The incisor in Recent leporids usually terminates in a position similar to that in *Hypolagus* or still more anteriorly below the diastema. P^3 , a phylogenetically important tooth, has evolved not only through the addition of new structures but also through differential emphasis on parts represented in the primitive tooth: the posteroexternal fold is a constant feature; the posterointernal fold is present primitively but may be lost, as in *Mytonolagus*, at an early stage of wear, and in the later Palaeolaginae there are trends toward a retention or an early loss of the fold; in the later subfamilies, loss of the posterointernal fold characterizes the archaeolaginae, and retention of the fold, of a lake derived from the fold, or of a remnant of the fold that unites with the posteroexternal fold, characterizes the leporines. The more primitive leporids lack persistent folds on the trigonid of P^3 , but in later leporids an anteroexternal fold develops in more than one line. In the archaeolaginae this new fold appears in unworn teeth as a groove in the buccal cusp of the

trigonid. Another mechanism may account for the shallow anteroexternal fold in *Palaeolagus hypsodus*: some specimens of *P. hypsodus* suggest that the fold between buccal and lingual cusps of the unworn tooth has moved buccally to form the anteroexternal fold of the adult. Proof of such movement must await the discovery of unworn lower teeth in *P. hypsodus*. The method of development of the anteroexternal fold in leporines is not definitely known but may resemble that in archaeolaginae. On the trigonid of P^3 , the anterointernal fold that occurs as a variant in *Hypolagus apachensis* and persistently in *Notolagus* probably represents a deepening of the groove between buccal and lingual cusps of the unworn tooth; *Caprolagus* has a similarly situated and possibly equivalent fold (WILSON, 1949b, p. 137). Anterior folds on the trigonid of P^3 appear in some later species of *Hypolagus* and in some later fossil and Recent leporines. The more posterior lower cheek-teeth, P^4 - M^3 , have been relatively conservative. Lingual union of trigonid and talonid on P^4 , M^1 , and M^2 occurred at a relatively late stage of wear in *Mytonolagus*. The tendency, which developed in several lines of Oligocene leporids, for earlier lingual union of the columns persisted in archaeolaginae and leporines. *Palaeolagus burkei* and *P. hypsodus*, however, have a somewhat ochotonid-like tendency for the columns to remain separate. Usually the columns of M^3 become joined by a dentine bridge in the earlier leporids but are joined only by cement in *Hypolagus* and Recent leporids.

Some evolutionary tendencies can be traced in unworn lower cheek-teeth, which are known in Oligocene leporids (WOOD, 1940), in the Miocene leporids *Palaeolagus philoi* and *Archaeolagus acaricolus*, and in the early Pliocene leporid *Hypolagus apachensis* (WOOD, 1937, p. 34-35). The following changes occur on P^3 : the buccal lobe, or protoconid, of the trigonid becomes proportionately larger, resulting in lingual migration of the groove between protoconid and the lingual cusp, or metaconid, until that groove, which faced anteriorly primitively, is essentially lingual in position in *H. apachensis*; the protoconid is undivided in *Megalagus* and *Palaeolagus* but has a shallow anteroexternal groove in *A. acaricolus* and a deeper groove in *H. apachensis*, persisting in both cases to form the anteroexternal groove on the trigonid of the adult; the lingual groove between trigonid and talonid seems to become less persistent; the posterolophid, present in *Palaeolagus*, is essentially absent in *A. acaricolus* and *H. apachensis*. The posterolophids on P^4 - M^2 are relatively less prominent in *P. philoi* than in *P. haydeni* and still more reduced in *A. acaricolus* and *H. apachensis*. This reduction of the posterolophid is evident in *Sylvilagus*, in which the posterolophids are ephemeral and occur only on P^4 and M^1 (DICE & DICE, 1941, p. 227-228). The post-Oligocene fossil leporids represented by unworn cheek-teeth are on a line in which the posterointernal reentrant on P^3 is suppressed; consequently some of the tendencies mentioned above, particularly those of P^3 , probably do not characterize leporids in general.

Skull. Relatively complete cranial material of the following leporids is known: from the middle Oligocene, *Palaeolagus haydeni*, *P. burkei*, *P. intermedius*, *Megalagus turgidus*, and *Litolagus molidens*; from the early Miocene, *P. hypsodus* and *Archaeolagus ennisianus*; from the

late Pliocene, *Hypolagus limnetus*. Cranial components of other leporids are less completely known, although parts of the maxilla and palatine are frequently preserved with upper cheek-teeth.

Several of the long range trends affecting the skull and lower jaw of leporids seem to be correlated with changing posture and locomotor habits: the more primitive leporids probably held the head more nearly as a continuation of the axis of the vertebral column than in Recent leporids and had a scampering gait or one consisting of short, quick hops as in the pika (Wood, 1940, p. 279, 315); the head is held at a greater angle with the vertebral column in the later leporids, the posture is more erect, and the gait has been variably described as quadrupedal saltation or the half-bound. The angle between basicranial and palatal axes of the skull has become larger in later leporids. Therefore the facial region is bent downward relative to the basicranial region, probably in correlation with the more erect posture. The angle mentioned is smaller in *Palaeolagus* and *Megalagus*, resulting in a more nearly flat skull, than in *Archaeolagus ennisianus* and smaller in the latter than in *Sylvilagus*; the angle seems to be less in *Hypolagus limnetus* than in *Sylvilagus nuttalli* (GAZIN, 1934, p. 114) although greater than in *Romerolagus*. Also in the occipital region, changes seem to be related to the bending of the skull and changing posture. Changes of this kind that are on the morphological line leading toward the Recent leporids are as follows: occiput becoming relatively higher dorsoventrally and facing more posteroventrally, less directly posteriorly than in *Palaeolagus haydeni*, *P. hypsodus*, and *Megalagus turgidus*; parietal and squamosal, which extend nearly to the posterior end of the skull roof in the Oligocene leporids, terminating anterior to the posterior end of the skull, and supraoccipital and mastoid having greater dorsal exposure in later leporids; mastoid becoming more restricted ventrally on occiput, the first suggestion of which is seen in *Archaeolagus ennisianus*; foramen magnum becoming relatively longer dorsoventrally, and occipital condyles becoming more nearly vertical, again suggested in *A. ennisianus*. A prominent external occipital protuberance, lacking in Oligocene species, is developed on the supraoccipital in later leporids, suggesting strengthening of the neck muscles to hold the head up and steady. The surface of the supraoccipital and mastoid, which is rugose or has small pits in Oligocene leporids, becomes more fenestrated in later species.

Some other trends affecting the leporid skull are less directly related to the changing posture and locomotion than those mentioned above. The orbit is smaller, suggesting more diurnal habits, in Oligocene than in Recent leporids (Wood, 1940, p. 279). The supraorbital process, where known in Oligocene and early Miocene leporids, is small, having a short posterior process; in general, the process becomes larger in later leporids and in some of

them has an anterior projection. The maxillary tuberosity is low in Oligocene leporids but becomes higher and extends prominently into the orbit in those early Miocene and later leporids having more hypsodont cheek-teeth. Perhaps part of the increased height of the orbit in later leporids is due to upgrowth of the maxillary tuberosity (Wood, 1940, p. 283). Fenestration of the lateral maxillary surface is more pronounced in Recent than in Oligocene leporids. The parietal sends a process between frontal and squamosal into the orbit in *P. haydeni*; the process is still present but smaller in *Archaeolagus*. The parietal lacks the process, and the frontal and squamosal contact one another superficially in Recent leporids. The anterior root of the zygoma extends gradually outward approximately in line with P⁴ and is close to the alveolar border in *Mytonolagus*; the root is more nearly in line with P³ and farther from the alveolar border in *Palaeolagus* and *Megalagus*. The tendencies toward anterior movement and elevation of the root continue in *Archaeolagus*, and, in addition, the zygoma juts outward more abruptly: the anterior zygomatic root in *A. ennisianus* extends outward opposite P² and essentially lacks an anterior concavity; in *A. acaricolus* the concave anterior surface of the root is approximately in a line between P² and P³. The latter condition in *Archaeolagus* seems closer to that in *Hypolagus* than the former. The anterior root in *Hypolagus* and later leporids usually extends out opposite P² or P³ and is concave anteriorly but is variable in exact position and amount of concavity. The anteroventral edge of the zygoma tends to become slightly thicker in later leporids than in those of the Oligocene, but perhaps more important is the more anterior and lateral protrusion of the edge. The combination of dorsal and anterior movement of the root and lateral protrusion of the ventral edge probably indicates some strengthening of the attachments and a more advantageous angle of action of parts of the masseter muscle in the later leporids. The nasals extend relatively farther anteriorly, and the muzzle is proportionately shorter and wider in Oligocene than in Recent leporids. The main changes leading toward modernization of the palate can be described serially as follows: in most Oligocene leporids the palatine forms a longer part of the palatal bridge than the maxilla, the maxillopalatine suture is arched anteriorly, and more than one palatine foramen occurs on each side of the palatine posterior to the suture; in the Oligocene genus *Litolagus* and in early Miocene species of *Palaeolagus* and *Archaeolagus* the palatine forms a shorter part of the bony palatal bridge than the maxilla, and the maxillopalatine suture crosses the palate transversely in a straighter line. Pliocene species of *Hypolagus* have essentially modernized palates in which the palatal bridge and palatine component are short, the maxillopalatine suture is nearly straight, as in most Recent leporids, and the single palatine foramen on each side of the palate is situated at the

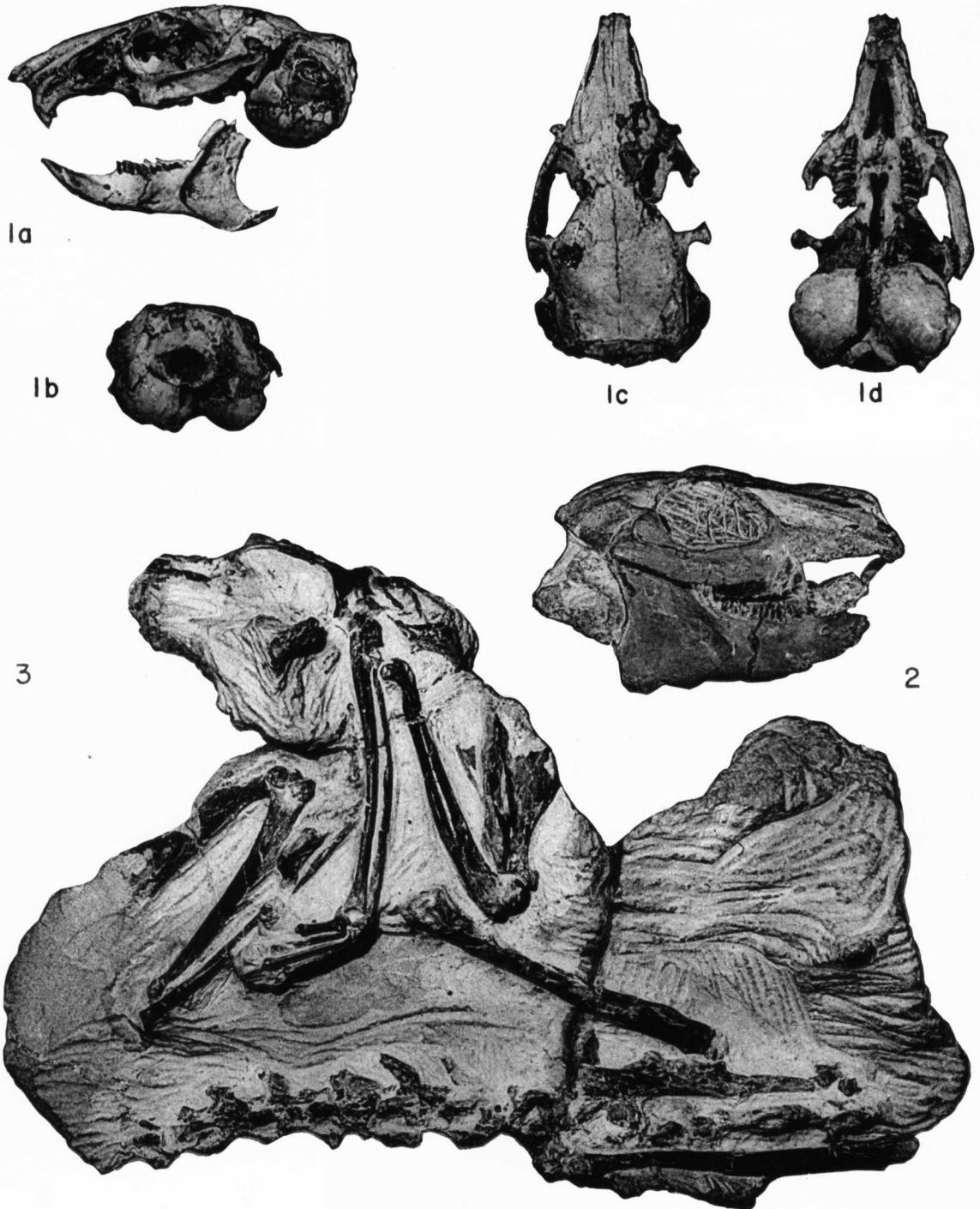
EXPLANATION OF PLATE 1

Megalagus turgidus

Specimen (C.I.T. No. 1563) showing right side of skull and lower jaw, $\times 1$ (Fig. 1), and partial postcranial skeleton in matrix, $\times 1$ (Fig. 2).



DAWSON — Later Tertiary Leporidae



DAWSON — Later Tertiary Leporidae

maxillopalatine suture. The decrease in relative length of the palatine occurs through anterior shortening of the bone and forward movement of the internal nares; the palatine foramina, multiple in the earlier leporids but later reduced to one on each side, seem to have maintained essentially the same position but are situated closer to the maxillopalatine suture in later leporids due to posterior movement of that suture. The anterior ends of the incisive foramina are situated between the posterior incisors in *Palaeolagus* and *Megalagus* but do not reach the posterior incisors in *Hypolagus* and Recent leporids.

Lower jaw. The shape of the horizontal ramus of the lower jaw has been fairly constant with a few exceptions: in *Mytonolagus* the premolar region of the jaw is relatively lighter ventrally and narrower transversely than in *Palaeolagus* (BURKE, 1934, p. 409-410); the ramus tends to be deeper below the cheek-teeth relative to depth below the diastema in some species of *Hypolagus*, in *Sylvilagus* and in *Lepus* than in *Palaeolagus* and *Megalagus*. Possibly both of these changes in proportions are related to increased hypsodonty of the cheek-teeth in later leporids. Two mental foramina, one each below the diastema and below P_4 or M_1 , usually occur on the lateral surface of the horizontal ramus in the Oligocene leporids. The anterior foramen persists in all later leporids. A single posterior foramen may occur in early Miocene species but usually numerous foramina are present below P_3 and P_4 . The latter condition seems to persist in later leporids, in which numerous nutritive foramina, of which one may be most prominent, occur below P_3 and P_4 . A small postalveolar foramen is present in *Megalagus brachyodon* and *Palaeolagus temnodon*, both early Oligocene species; in later species of *Megalagus* and *Palaeolagus* and in *A. ennisianus* the foramen is represented by tiny perforations or may be absent. A small foramen is present in *Archaeolagus acaricolus*, and the foramen is present in all later leporids in which the region is known. This foramen in Recent leporids conducts an anastomotic branch that connects the deep facial vein with the inferior alveolar vein and "provides an outlet through the latter vein for the blood from the former when its passage is obstructed by the pressure of the contracting masseter and internal pterygoid muscles" (BENSLEY, 1945, p. 279). The presence of a distinct foramen in some early Oligocene leporids, reduction of the foramen in later Oligocene and some Miocene leporids, and enlargement of the foramen in other Miocene and later leporids is a puzzling feature, the meaning of which is not clear.

In ventral view, the size of the angle between the horizontal rami in Oligocene species of *Palaeolagus* and *Megalagus* is near that in *Ochotona*. The angle becomes slightly larger in *P. philoi* and *Archaeolagus* and still more so in *Hypolagus fontinalis*. The size of the angle between the rami in *H. vetus* seems to be near that in *Romerolagus*.

Accompanying these changes, the symphyseal region of the jaw shows the following trend: the contact of the rami at the symphysis in Oligocene species of *Palaeolagus* and *Megalagus* resembles that in *Ochotona* except that a short ventral contact has been added posterior to the main part of the symphysis; this posterior contact is slightly better developed in *P. philoi* and *Archaeolagus ennisianus*; in the early Pliocene leporids *Hypolagus apachensis* and *H. fontinalis*, the ventral contact extends farther posteriorly, and its posterior end forms a distinct facet; the facet is more prominent in *H. near limnetus* of WILSON (1937a, p. 17) and is essentially on a modern level in *H. vetus*. The ascending ramus in Oligocene leporids rises more steeply, forming a smaller angle with the horizontal ramus, than in Recent leporids. The differences between Oligocene and Recent leporids in angulation of the rami and in symphyseal contact are similar to differences between Recent ochotonids and leporids that have been shown to be correlated with increased angulation between basicranial and palatal axes of the skull that accompanies the development of more erect posture in the latter (DUBRUL & SICHER, 1954, p. 65-72). Possibly the strengthening of the symphysis in later leporids is due in part to better development and stronger pull in a medial direction of the external pterygoid muscles than in earlier leporids.

Several suggestions have been advanced to account for the shortening and dorsad movement of the lower incisor, the extent of which is usually marked by a swelling on the lingual surface of the jaw, in later leporids. WOOD (1940, p. 298) suggested that "the growth of the prisms of the lower cheek-teeth interfered with the functioning of the enamel organ of the lower incisor" and that forward migration of the incisor resulted. BOHLIN (1942a, p. 63-69) attributed the shortening of the incisor in large part to stress caused by depression of the face, especially depression of the incisors relative to the cheek-teeth. Neither explanation alone seems completely to account for the shortening of the incisor, although the factors discussed by WOOD and BOHLIN have probably been of some influence. That the former explanation is not entirely adequate is suggested by the situation in *Megalagus*, in which the incisor is shorter but the cheek-teeth less hypsodont than in *Palaeolagus*; the situation in *Megalagus* also suggests that the latter explanation does not completely account for the shortening, because the incisor is shorter but the face and the incisors are not more depressed than in *Palaeolagus*. The incisor in *Archaeolagus ennisianus* is shorter and lower than would be expected on the basis of BOHLIN's explanation. Relative lengthening of the diastema, thus "pulling" the incisor anteriorly, in the later leporids has been mentioned as another factor possibly involved in the more anterior termination of the incisor relative to the cheek-teeth (BOHLIN, 1942a, p. 69-70). Possibly a few factors related to the trends in jaw develop-

EXPLANATION OF PLATE 2

Palaeolagus hypsodus and *Litolagus molidens*

FIGURE

1. *Palaeolagus hypsodus* (M.C.Z. No. 3720), $\times 1$; *1a*, left side of skull and lower jaw; *1b*, occipital view of skull; *1c*, dorsal view of skull; *1d*, ventral view of skull.
- 2, 3. *Litolagus molidens*, $\times 1$ —2. Right side of skull and lower

jaw (F.H. No. 10283).—3. Type specimen (C.I.T. No. 1568), parts of skull and postcranial skeleton in matrix, the skull (lacking most of the roof) seen in dorsal view in the upper left part of the figure.

ment discussed above should be considered. A long incisor would tend to be curved outward in leporids that develop greater angulation between the rami; however, the leporid incisor seems to have been straight primitively, and the tendency to remain straight was seemingly stronger than the tendency to remain long. Thus, perhaps in response to stress that could lead toward outward bending or toward shortening, the incisor has followed the latter path. The increased length of the ventral contact between the rami in the later leporids may have been a factor leading to dorsal movement of the incisor; a more ventrally placed incisor would tend to interfere with the contact between the rami. Probably a combination of factors, including those mentioned above and possibly others, are necessary to account for the shortening of the incisor in the evolution of the leporids.

Ventrally the masseteric fossa in *Palaeolagus* curves more gradually and lacks the shelflike rim of the Recent leporids, suggesting weaker insertion for the masseter muscles in the former. The masseteric fossa in *Hypolagus vetus* and *H. limnetus* seems to be essentially like that in Recent leporids. The temporalis muscle may have been better developed in more primitive leporids as suggested by a larger coronoid process on the ascending ramus in *Palaeolagus* (WOOD, 1940, p. 288) and *Archaeolagus* (DICE, 1928, p. 237) than in Recent leporids.

In summary of the evolutionary trends known to affect dentition, skull, and lower jaw, the basic structure and pattern of the cheek-teeth that is characteristic of later leporids is essentially established by the early Miocene. Since that time the main changes have been increased complication of P² and P₃, deepening and folding of the hypostriae on P³-M², and changing proportions such that the teeth become relatively wider transversely. Trends in skull and lower jaw correlated with an increasingly erect posture, including greater bending of the skull and outward angulation of the rami, seem to have proceeded gradually along with changes in posture and locomotion. The zygomatic and palatal structures in early or middle Miocene species of *Archaeolagus* seem to be fundamentally like those in later leporids, and most additional changes have been refinements such as further shortening of the palatine on the palate and increase in the anterior concavity and lateral protrusion of the anterior zygomatic root. Changing development of the muscles of mastication seems to lead toward decrease in the temporalis muscle and some increase in the masseter and pterygoid muscles.

Postcranial skeleton. The skeletons of Oligocene leporids, especially *Palaeolagus haydeni*, *Litolagus*, and *Megalagus turgidus*, are relatively completely known. These leporids differ from one another in some details of postcranial morphology, which indicate corresponding functional differences, but from them and from *P. hypsodus* of the early Miocene an over-all impression of the Oligocene to early Miocene level of evolutionary development in the leporids may be obtained. Postcranial remains of middle Miocene to early Pliocene leporids are known but not completely enough to give an adequate picture of the changing level of postcranial development. Not until the middle Pliocene with *Hypolagus vetus* does the known record of postcranial remains become adequate again,

and an essentially modern condition in many features has already been attained in this leporid. Finally, among the Recent leporids several levels of postcranial development are present: of the Recent leporids considered here the series *Romerolagus*—*Sylvilagus*—*Lepus* shows progressive specialization for a cursorial mode of life. At any one time there seem to have been leporids in varying stages of cursorial development, such as these Recent leporids or *Palaeolagus haydeni* and *Megalagus turgidus* in the Oligocene.

Specimens of vertebrae are limited, but comparisons can be made between Oligocene and Recent leporids in the characters of lumbar and sacral vertebrae. On the lumbar vertebrae *Palaeolagus haydeni* and *Litolagus* have transverse processes that are proportionately shorter transversely and broader anteroposteriorly than in *Sylvilagus* and *Lepus*. The transverse processes in those Oligocene leporids resemble those in *Romerolagus*. The lumbar region in *Lepus* is long, possibly correlated with the well-developed lumbar musculature (HOWELL, 1944, p. 124). The tendency in later leporids toward lengthening of the lumbar transverse processes may also be correlated with strengthening of the lumbar musculature, such as the sacrospinalis muscle, for straightening the back.

The sacral vertebrae in the Oligocene leporids differ from those in the Pliocene and Recent leporids in the following features: the transverse processes of the first two sacral vertebrae are less expanded transversely and extend slightly farther posteriorly; the auricular surface of the sacrum is more nearly vertical and the arms of that surface are at a more acute angle with one another. In the later leporids the contact between ilium and sacrum seems to have become more firm as indicated by: greater outward expansion of the transverse processes, especially anteriorly; more oblique position of the auricular surface, which has its ventral portion extending farther laterally; greater angulation between the arms of that surface. The sacral vertebrae seem to have become adapted to withstand the stronger thrusts that would accompany a bounding type of locomotion. Posterior elongation of the transverse processes in the Oligocene leporids seems to be a primitive lagomorph feature and is more pronounced in ochotonids than in leporids. Probably the tail was short even in Oligocene leporids, but the slight tapering of the posterior sacral vertebrae in *P. haydeni* suggests that the tail was larger and stronger than in Recent leporids (WOOD, 1940, p. 305-306).

Modification in the pectoral girdle and forelimb can be traced in the series from *Palaeolagus* to *Lepus*. From the Oligocene leporids to *Hypolagus vetus* of the middle Pliocene and the Recent leporids the following trends in the scapular blade and spine are distinguishable: the neck and main portion of the blade become longer and narrower, and the vertebral border tends to be elongated posteriorly; beginning in an Oligocene stage in which the supraspinous and infraspinous fossae are subequal, the supraspinous fossa becomes reduced; the distance from the glenoid cavity to the origin of the scapular spine is increased, a change possibly correlated with elongation of the scapular neck; the acromion process becomes smaller. Muscles originating on an elongate, narrow scapula, which is characteristic of many cursorial mam-

mals, are able "to produce a larger angular movement of the humerus at high speed" (SMITH & SAVAGE, 1956, p. 609). Thus, the action resulting from muscles originating on the relatively short, wide scapula of the Oligocene leporids and inserting on the humerus would be expected to have been powerful but slow, whereas the action resulting from elongated muscles on the longer scapula of the later leporids would be expected to be relatively quick and would take place through a larger arc. The infraspinous fossa is larger than the supraspinous in many cursorial mammals (HOWELL, 1944, p. 143; SMITH & SAVAGE, 1956, p. 607), and perhaps this character in the later leporids represents a cursorial specialization. As suggested by WOOD (1940, p. 306), perhaps the larger supraspinous fossa in *P. haydeni* than in the Recent leporids indicates a more muscular forearm in *P. haydeni*. The smaller acromion in the later leporids would seem to indicate weaker action of the acromiodeltoid muscle. If the bone identified as a clavicle in *P. haydeni* is a clavicle, that element is more reduced in later leporids. Reduction of the acromion and of the clavicle have been interpreted as cursorial modifications (HOWELL, 1944, p. 142).

The modifications in the glenoid cavity and head of the humerus are such that increasing restriction of movement to a sagittal plane is suggested. Starting at the Oligocene level of development with a glenoid cavity that is not expanded transversely, there is a trend toward increased expansion and greater transverse concavity of the posterior part of the cavity. Correlated with these changes the head of the humerus shows proportionate anteroposterior shortening, medial extension with flattening of the articular surface, and increase in length of bicipital groove. Restriction to fore-and-aft movements of the forelimb seems to be a function of the character of the ligaments and joints more than of the muscles (HOWELL, 1944, p. 94). In the leporids much of this restriction seems to have occurred at the shoulder, where the features mentioned of glenoid cavity and humeral head restrict lateral movement, especially when the humerus is protracted. The head of the humerus overlaps the shaft posteriorly to a greater extent in the later leporids, which suggests an increased angle of anteroposterior movement for the humerus. The greater tuberosity becomes higher relative to the humeral head, its long axis becomes more nearly anteroposterior, and the areas of insertion of the infraspinatus and teres minor muscles become more distinct. Perhaps the change in orientation of the greater tuberosity is related to attachment of the supraspinatus muscle: orientation of that tuberosity in the Oligocene leporids would seem to have facilitated abduction by that muscle; in the later leporids action would seem to be primarily anteroposterior. The lesser tuberosity moves anteriorly relative to its primitive position and its long axis becomes more nearly transverse, possibly in connection with an increasingly anterior insertion for the subscapularis muscle, which seems to act primarily as a protractor of the limb in the later leporids, whereas primitively that muscle may have functioned more as an adductor. The supraspinatus and subscapularis muscles tend to reduce their rotatory action in cursorial mammals in general (HOWELL, 1944, p. 87, 95). An additional trend in the proximal end of the humerus is toward a shortening of

the deltoid crest distally and resultant concentration proximally, modifications seemingly related to distal lightening of the segment and to more rapid movement of the humerus.

The distal end of the humerus tends to be wider transversely relative to the length of that bone in the Oligocene leporids than in *H. vetus* of the middle Pliocene and the Recent leporids. The medial condyle is proportionately larger in the Oligocene leporids, and the supinator crest is more prominent; the flexors and extensors of the manus, which originate on the distal end of the humerus, may have been stronger in the more primitive leporids, and the position of muscles originating on the well-developed supinator crest probably facilitated supination. Keels, which are more distinct posteriorly than anteriorly, are present on the distal end of the humerus in the Oligocene leporids but are lower and produce a less pulleylike appearance than in *H. vetus* and the Recent leporids. Thus, the main trends in the distal end of the humerus seem to be toward transverse narrowing and development of more prominent keels. An entepicondylar foramen, a primitive feature, occurs in *Mytonolagus*, *Palaeolagus*, and *Litolagus* but is not definitely known in *Megalagus* and is absent in later leporids in which the humerus is known. The supratrochlear fossa is perforate in the known Oligocene leporids and in *H. vetus*, *Sylvilagus*, and *Lepus* but is imperforate in certain post-Oligocene leporids such as *H. apachensis* and *Brachylagus*. In the Oligocene leporids the articulation of the radius and ulna with the humerus was probably somewhat looser than in most later leporids: the semilunar notch was moderately shallow and the head of the radius only slightly grooved. In the later leporids there have been tendencies toward deepening of the notch in the ulna and of the grooves in the radius, proportionate transverse narrowing of the radial head, and development of a more distinct facet on the radius for articulation with the capitulum of the humerus. The structure of the elbow-joint would seem to indicate that, even in the Oligocene, pronation and supination were somewhat restricted; by Pliocene times these actions were probably almost absent; among the known leporids the culmination in restriction of lateral movement and specialization for anteroposterior movement at the elbow-joint seems to be present in *Lepus*, in which it is difficult to remove the humerus from the deep notch formed by the radius and ulna without breaking the bone or disarticulating the radius and ulna (WOOD, 1940, p. 307). Thus in the elbow-joint as well as in the shoulder the later leporids show specialization for restricted sagittal movement and more efficient anteroposterior action.

Additional trends in the forelimb are toward increasingly close contact of the radius and ulna and reduction of the more distal portion of the ulnar shaft. Primitively the radius and ulna were probably more freely movable relative to one another than in the Recent leporids. Contact between these bones has become closer, and in *Lepus* the contact has been described as fused, although the bones do maintain their distinctness (LYON, 1904, p. 376). Reduction of the ulnar shaft accompanied changes in the distal articular surfaces of that bone: in the Oligocene species the anteromedial facet on the distal end is well

developed and the globular styloid process forms less than half the ulnar articular surface for the carpus; the trend has been toward the condition seen in *Lepus* in which the styloid process forms almost the entire articular surface. Reduction of the ulnar shaft seems to have lagged somewhat behind changes in the distal articular surface; in *H. vetus* the articular surface is in essentially the same level of development as in *Sylvilagus*, but the shaft is less reduced in the former. Decreased mobility of the radius and ulna relative to one another and reduction of the ulnar shaft are both cursorial modifications. The distal articular facet of the radius has become proportionately wider transversely in the later leporids. The ratios of length of ulna to length of humerus in some leporids are as follows: *Lepus*, 1.28; *Sylvilagus*, 1.12; *Romerolagus*, 1.04; *Megalagus turgidus*, 1.08; *Palaeolagus haydeni*, 1.07. Changes in proportions from Oligocene to Recent leporids do not seem to be great, except for pronounced distal elongation in *Lepus*.

Among the Oligocene species the carpus is known only in *Litolagus*. Intermediates are unknown between this level of development and those in *Romerolagus* and *Hypolagus*—*Sylvilagus*. In the more primitive carpus in *Litolagus*, anteroposterior hinge action seems to have been restricted and there was a greater propensity for sideward movements of the manus. Increasing emphasis has been placed on the more medial parts of the carpus and manus in the later leporids, seemingly in correlation with the reduction of the ulnar shaft.

In the pelvic girdle of the Oligocene leporids the ilium is divided into two fossae by a prominent rounded crest; the origin of the gluteal muscles on the ilium was probably largely limited to the superior fossa. In the later leporids the ilium has a less distinct crest and is flared anteriorly, thus providing a larger surface for attachment of the muscles of the gluteal group. The gluteal muscles are retractors of the thigh and are important in providing speed at the end of a stroke (SMITH & SAVAGE, 1956, p. 613). The ilium has tended to become shorter, relative to the total length of the innominate bone in the later leporids; thus, the tensor fasciae latae and rectus femoris anterior pull at a sharper angle and the speed of protraction of the femur is increased (CAMP & BORELL, 1937, p. 318; WOOD, 1940, p. 310). On the medial side of the ilium there is a larger angle between the arms of the auricular surface in the later leporids; this change and the modifications of the sacral vertebrae discussed above result in a stronger contact between the vertebral column and girdle. On the ilium in the Oligocene leporids the raised process that was termed the tubercle of the ilium by WOOD (1940, p. 309) has a small tip for muscle attachment, and a low facet or distinct knob is present posterior to the tubercle. In Pliocene and later leporids the iliac tubercle (inferior anterior spine of BENSLEY) is less raised, and the more posterior facet or knob is absent. The exact function of the posterior facet or knob is not known: it may represent the place of origin of a muscle, present in *Sylvilagus* and originating below the iliac tubercle, seemingly similar to that described in the opossum by COUES (1872, p. 125) as the iliofemoralis; however, perhaps a second head of the rectus femoris, having origin on this facet, was present in the Oligocene leporids. The occurrence of a tubercle plus the above-mentioned low

posterior facet in *P. haydeni* and *P. hypsodus*, the presence of a tubercle plus a more distinct posterior knob in *Megalagus* and *Litolagus*, and of a tubercle plus a ridge in *Ochotona*, raises a question as to what the primitive lagomorph condition was with regard to the facet or ridge. If the elongate ridge in *Ochotona* and low posterior facet in *Palaeolagus* are closer to the primitive condition, the leporids seem to have developed in two directions—on the one hand toward decrease in the posterior ridge or facet, as in the more advanced leporids, and on the other toward a more distinct posterior knob as in *Megalagus* and *Litolagus*. However, if the structure in *Megalagus* and *Litolagus* is primitive, *P. haydeni* and *P. hypsodus*, in which the facet is lower and closer to the tubercle, seem to be leading toward the condition in the later leporids; the structure in *Ochotona* could be attained by elongation and decrease in height of the facet. The present record allows only speculation about the primitive lagomorph condition, which will probably become known only when the innominate bones of older lagomorphs are found. The ischial spine, marking the anterior limit of the surface over which the tendon of the obturator internus muscle passes to its insertion in the trochanteric fossa, is relatively farther forward in the Oligocene and early Miocene leporids and in the Recent *Romerolagus* than in the Recent genera *Sylvilagus* and *Lepus*. In the more primitive leporids the obturator internus probably acted largely as a rotator of the thigh, due to the angle at which the tendon would have pulled on the femur, whereas the angle of pull in *Sylvilagus* and *Lepus* would result in more anteroposterior action. In the Oligocene leporids the ischial tuberosity is weak, and the ischium is little, if at all, expanded posterior to the obturator fenestra. In *Palaeolagus hypsodus* of the early Miocene there is greater flare in the region. In *Hypolagus*, *Sylvilagus*, and *Lepus* the ischial tuberosity is stronger and higher, and the ischium is expanded posterior to the obturator fenestra. These changes seem to indicate increased development of the hamstring muscles that originate on the ischium and better leverage for these muscles. The hamstring muscles are retractors of the thigh and are important in slow, powerful movement at the beginning of a stroke (SMITH & SAVAGE, 1956, p. 613).

The main changes in the femur affect the proximal end, which is characterized in the Oligocene leporids by a relatively low greater trochanter that has an essentially anteroposterior long axis, a well-developed lesser trochanter, and a third trochanter that is distad of the lesser trochanter. In the later leporids the proximal end of the femur is relatively wider and more flattened and provides a larger area for muscle attachment; the greater trochanter is higher, suggesting greater leverage for the gluteal group of muscles inserted there. The more oblique axis of the greater trochanter in the later leporids leads to a more complete enclosure of the trochanteric fossa; possibly the tendons of the muscles inserted in the fossa have become stronger (WOOD, 1940, p. 311). In the later leporids the third trochanter has moved proximad of its primitive position, a shift that would promote more rapid action of the gluteus maximus and quadratus femoris muscles inserted there (WOOD, 1940, p. 311). The distal end of the femur seems to have changed less than the proximal end. However, facets on its posterior surface indicate that the

origin of the gastrocnemius muscle was weaker in the Oligocene leporids than in the later cursorial leporids, *Hypolagus vetus*, *Sylvilagus*, and *Lepus*, although not much different from that in the Recent *Romerolagus*.

The tibia and fibula are fused in all known leporids (BURKE, 1934, p. 414; WOOD, 1940, p. 312). The curvature of the tibiofibula that seems to characterize Oligocene leporids is evident in *Romerolagus* but is less pronounced in *Sylvilagus* and *Lepus*. The proximal end of the tibiofibula is proportionately shorter anteroposteriorly in the Oligocene than in later leporids; anteroposterior elongation of the proximal condyles in the later leporids suggests specialization at the knee for a longer stride and more efficient hinge action in a sagittal plane. The tibial tuberosity has become more prominent in the later leporids, possibly indicating progressive increase in development of the lever on which the extensors of the shank insert.

In the tarsal bones the progressive trend toward a firmer interlocking of the bones leads to a decrease in sideward movement and an emphasis on fore-and-aft movement of the foot. In *Palaeolagus haydeni*, *P. hypsodus*, and *Megalagus turgidus*, the astragalus and calcaneum reach approximately the same distance distally, and a naviculocalcaneal contact is lacking. Improved interlocking of the tarsals occurs in *Hypolagus*, in which the calcaneum extends distad of the astragalus and a well-developed naviculocalcaneal contact is present. This condition is retained in the Recent leporids. The neck of the astragalus has become straighter in the later leporids, probably in connection with lessened lateral and improved fore-and-aft movement. Another tendency in the tarsus is elongation of the individual tarsal elements in later genera, resulting in some elongation of the foot. In the calcaneum, elongation of the tuber calcis and deepening of its groove in the later leporids suggest that the leverage of the gastrocnemius is more advantageous.

In summary, the main trends in evolution of the leporid postcranial skeleton seem to have been toward cursorial specialization. Beginning stages in some cursorial trends can be detected in the Oligocene, as exemplified by some differences between *Palaeolagus haydeni* and *Megalagus turgidus*. In the pectoral girdle and forelimb, leporids have changed from a more generalized condition, in which a greater latitude of movement was possible and the forelimb was more muscular and probably usually acted more powerfully and slowly, toward a specialized, cursorial, condition in which movement in a fore-and-aft plane is prominent and muscle attachments are developed that favor quick action. The hind limb of Oligocene leporids was probably moderately strong. In the later leporids modifications of the pelvic girdle and hind limb suggest that the articulation of the pelvic girdle with the sacrum has become strengthened to withstand thrusts from the hind limbs, that certain muscles have become stronger as an adaptation for the typical half-bound or leaping gallop of the leporids, and that others have become modified to promote rapid action. In the Oligocene leporids the hind limb was probably not especially flexible, and sideward movements at the tarsus were probably limited, but in later leporids the articulations at the knee and tarsus suggest still more restriction to, and adaptation for, efficient anteroposterior movement.

In general, the leporids seem to have been conservative throughout most of their history and have followed for the most part the trends discussed above. Nevertheless, there has been some diversification from the main line of development. *Palaeolagus burkei* and *P. hypsodus*, for example, have some ochotonidlike features in the cheek-teeth, including retention of a crescent on P⁸, relatively long hypostriae, and the lack of a lingual union of the trigonid and talonid on P₄-M₂. The flat skull in *P. hypsodus* is ochotonidlike, but the greatly enlarged bullae in that species are not matched in other known lagomorphs. In a few characters some later leporids seemingly parallel the ochotonids: *Notolagus velox* of the middle Pliocene has an isolated anterior column on P₃ in some stages of wear, thus resembling the corresponding tooth in some Tertiary ochotonids: in pattern of enamel on the cheek-teeth and possibly in method of mastication the Recent genera *Pronolagus* and *Romerolagus* resemble ochotonids (BOHLIN, 1942b, p. 139-140). These leporids parallel ochotonids only in the features mentioned and otherwise are leporidlike; the fact that leporids showing diversity come to resemble ochotonids seems to emphasize a basic similarity in some structural characters between the two living families of lagomorphs. As an interesting complement to ochotonidlike features in some leporids, *Kenyalagomys*, an early Miocene African ochotonid, is somewhat leporidlike in the structure of the skull (MACINNIS, 1953, p. 20).

Two main size categories of leporids seem to be present throughout most of the history of the family as in Recent faunas. One of the differences between the living large and small leporids is in the rate of development of the young; in North America the hare *Lepus*, the larger leporid, has precocial young, and the rabbit *Sylvilagus*, the smaller, altricial young. An interesting problem, not investigated in this study, is whether a similar difference in rate of development characterized the larger and smaller Tertiary leporids. Possibly series of immature and adult individuals, such as are known from some Oligocene localities, would produce evidence related to the development of precocity in leporids.

Little needs to be added to WOOD's (1940, p. 315-316) summary of the changing habits and habitat of leporids through the Tertiary. Oligocene leporids are abundant in many localities in the White River badlands of the Great Plains and seem to have been a successful part of the fauna and well adapted for scampering or hopping among clumps of trees and bushes, which were probably abundant in Oligocene times in the region; the moderately hypsodont cheek-teeth were probably able to deal with some harsh and abrasive food. Accompanying the development of the plains, which became more arid and open in the later Tertiary, leporids became more cursorial in general, probably in line with the necessity of quickly covering increasingly greater distances between places of refuge. Recent leporids occur throughout North America but are most abundant in the western United States and on the tableland of Mexico. Leporids seem to be rather generalized in requirements: the success of the leporids, seemingly through generalization and adaptation to many niches, makes an interesting comparison to the success of the rodents, seemingly through diversification and adaptation to specific niches.

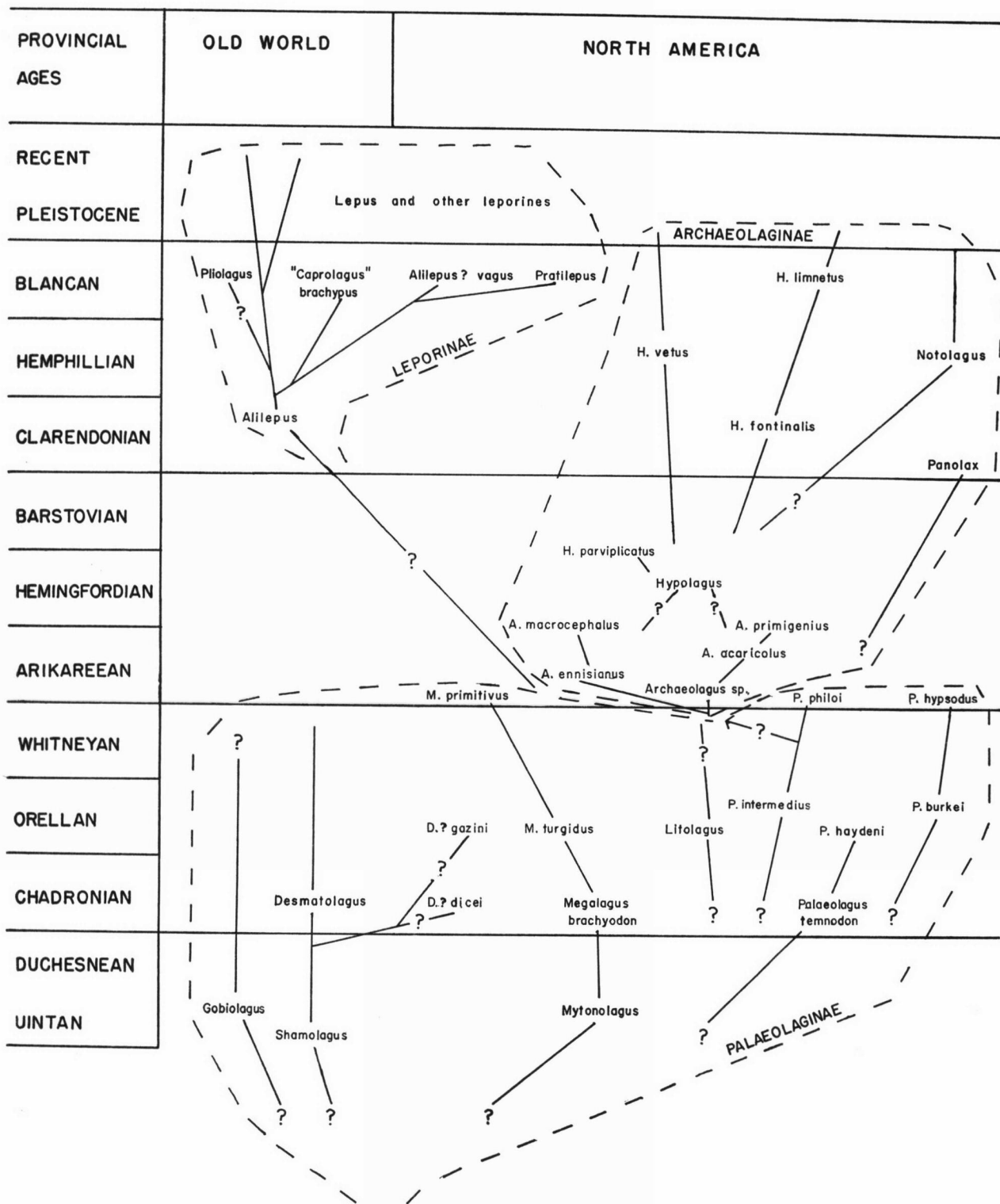


FIGURE 39. Suggested phylogeny of the Leporidae.

Not all genera and species are included, but the main phylogenetic lines are indicated. The record of *Hypolagus* in the Old World is not shown. If one of two possible lines of descent is more probable than the other, the more probable is indicated by an arrow.

PHYLOGENETIC HISTORY

Of the three subfamilies recognized here of the family Leporidae, the Palaeolaginae, a primitive group, form the horizontal base of the family, and the two advanced subfamilies, Archaeolaginae and Leporinae, seem to form distinct lines of descent during the later Tertiary. All subfamilies have had representatives in North America, the Archaeolaginae underwent their main development on this continent, and the Leporinae are represented in Recent North American faunas. Figure 39 illustrates diagrammatically the phylogenetic development of the main lines of North American and Old World leporids as interpreted here.

In the history of leporids the Miocene is a critical time during which the advanced subfamilies seem to have developed. Unfortunately, the fossil record of Miocene leporids is less well documented than that of the Oligocene or Pliocene. Nevertheless, the available fossil record is adequate to suggest phylogenetic lines within the family, although gaps in the fossil record may have influenced the classification. Due to the general lack of morphological diversity among leporids, there seem to be few morphological characteristics that can be used to indicate phylogenetic relationships. The basic leporid pattern of the cheek-teeth seems to have been established by Miocene times, and separate lines of leporids probably have developed parallel dental characters. P^2 and P_3 have been more variable than the more posterior cheek-teeth: the changes in P^2 seem usually to be related to level of evolutionary development, but the structure of P_3 seems to reflect line of descent and has been utilized as the main basis of classification in several, perhaps most, previous studies. Many phylogenetic differences in the structure of P_3 seem to result from differential emphasis on one part or another of the basic structures represented in an unworn tooth. P_3 , however, must be used with some caution: changes with wear in the pattern of the tooth must be recognized lest different stages of wear be mistaken for taxonomic differences; individual variation in shape of the tooth must be considered. P_3 alone may not be adequate to indicate generic affinities, as in the case of certain incompletely known middle Miocene leporids that could represent either *Archaeolagus* or *Hypolagus*. The limitations of P_3 as a phylogenetic character are recognized here, but the structure of P_3 is regarded as a valid indication of relationships, especially on the level of the subfamily. Other morphological characters in addition to P_3 have been considered where possible, and the evidence of geologic and geographic distribution has been utilized in conjunction with morphology in determining relationships.

The Palaeolaginae is the primitive, broad basal subfamily. An external fold is lacking on the trigonid of P_3 in most palaeolagines. The "hour-glass-shape", resulting from opposed posteroexternal and posterointernal folds, that was used by DICE (1929, p. 340-341) to characterize the subfamily is not regarded here as a diagnostic character of the palaeolagines. In the development of the subfamily there are trends toward either retention or reduction and early loss of the posterointernal fold; only the former trend would result in the "hour-glass-shape".

Within the subfamily Palaeolaginae, *Shamolagus*, *Gobiolagus*, *Mytonolagus*, *Desmatolagus*, and *Megalagus* form a group having a more primitive dental pattern and less hypsodont cheek-teeth than the more progressive group composed of *Palaeolagus* and *Litolagus*. Despite the divergent tendencies in these less and more progressive lines, the Palaeolaginae seems to include closely related leporids; Burke's division of the genera here recognized as palaeolagines into four subfamilies seems to obscure these relationships. However, the more primitive palaeolagines might ultimately be differentiated as a subfamily Mytonolaginae. Part of the hesitation in separating primitive palaeolagines from *Palaeolagus* and *Litolagus*, the more progressive members of the subfamily, results from the lack of definite knowledge of the Eocene ancestors of the progressive genera; if these ancestors should prove to be distinct from the more primitive group, subfamilial separation of primitive and progressive palaeolagines may be warranted. Another factor causing hesitation is uncertainty regarding the relationships of some of the late Eocene genera to ochotonids; the classification of these genera might be affected, were ochotonid-leporid relationships to become better known.

The development of the subfamily Archaeolaginae from palaeolagines seems to be documented in the North American fossil record. The ancestry of the archaeolagines would be expected to be found among palaeolagines in which the posterointernal fold on P_3 was suppressed early; this suppression occurs in *Megalagus*, in the *Palaeolagus intermedius* group, and in *Litolagus*. The relatively short crowns and primitive pattern of the cheek-teeth in *Megalagus* suggest that this genus is not ancestral to the archaeolagines. Descent of the archaeolagines from the *P. intermedius*—*P. philoi* line or from *Litolagus* is more probable. *P. intermedius* and *P. philoi* are less advanced in the structure of the upper cheek-teeth than *Litolagus* but more nearly resemble the archaeolagines in the structure of the zygomatic arch than does *Litolagus*. *Litolagus* has upper cheek-teeth that seem to be more advanced in development of the internal hypostriae than are those in the early archaeolagines and has a zygomatic arch that shows little resemblance to that in *Archaeolagus*. This evidence suggests that the archaeolagines descended from the *P. intermedius* group or a group closely similar.

The external fold on the trigonid of P_3 that characterizes the Archaeolaginae and the Leporinae occurs also in the palaeolagine *Palaeolagus hypsodus*, which probably is not on a line leading toward either of the advanced subfamilies. The presence of an external fold on the trigonid of P_3 in this species indicates that a fold in that position, seemingly an advantageous structural modification, has been attained more than once from a more primitive condition in which the fold was lacking: the North American fossil record shows this development twice—once in *P. hypsodus* and again in the archaeolagines. The fold may have developed again independently in the leporines.

The subfamily Archaeolaginae was proposed with some hesitation (DICE, 1929, p. 343), and its taxonomic validity has been in some question ever since. WILSON

(1949b, p. 136-138) has mentioned that whether or not the archaeolagines are a distinct subfamily, they do constitute the bulk of North American leporids in Miocene and Pliocene times and, further, has suggested that in line with a revision of the definition and content of the subfamilies of leporids, the Archaeolaginae could be recognized as a subfamily. The present work is in agreement with this suggestion: morphologically and as a phylogenetic line the archaeolagines are considered to be a distinct subfamily that is differentiated from the palaeolagines by characters approximately comparable in magnitude to those differentiating the leporines from the palaeolagines. Much of the uncertainty as to the validity of the subfamily Archaeolaginae resulted from the impossibility of differentiating archaeolagines and palaeolagines on the basis of the character used by DICE (1929, p. 343) to diagnose the archaeolagines, the lack of a posterointernal fold on P_3 . However, the combination on P_3 of an external fold on the trigonid and the absence of a persistent posterointernal fold or structure derived from such a fold distinguishes the archaeolagines as a line separate from other leporids. The fact that some advanced palaeolagines show tendencies leading toward the archaeolagines in certain characteristics does not invalidate the separation of the two; evolutionary links between ancestor and descendant are to be expected as a result of increasing completeness of the fossil record. The Archaeolaginae is a distinct line that emphasizes one trend in palaeolagine development.

Within the Archaeolaginae, *Archaeolagus* and *Hypolagus* are separated mainly as levels of evolutionary development; *Notolagus* is more distinct. The status of *Hypolagus apachensis* is somewhat difficult to determine: in this leporid the presence in relatively few individuals of a posterointernal fold on P_3 could be regarded as indicative of palaeolagine or leporine affinities, but the more usual condition of absence of such a fold suggests that *H. apachensis* is an archaeolagine; variation on the lingual side of P_3 from this usual condition seems to be due to retention in aberrant individuals of part of the pattern characteristic of unworn teeth.

Archaeolagines experienced their major development in North America but also reached the Old World: *Hypolagus* is recorded from the middle and late Pliocene of Asia (TEILHARD DE CHARDIN, 1940, p. 37) and the Villafranchian of Europe (KORMOS, 1934, p. 74-75). In North America archaeolagines seem to have been present through the late Pliocene but to have become extinct in the early Pleistocene. In the Old World *Hypolagus* was abundant in the earlier part of the Villafranchian but later became less abundant (KORMOS, 1934, p. 74-76) and probably did not survive past the end of the Villafranchian. The causes of the extinction of the Archaeolaginae are not clear. Known morphological evidence does not satisfactorily indicate why archaeolagines failed. Possibly archaeolagines were unable to adapt physiologically to climatic cooling in the late Pliocene and Pleistocene. However, inability to adapt to climatic cooling does not explain the failure of the archaeolagines to survive in regions that were relatively unaffected by cooling, and this explanation of extinction is further weakened by evidence that archaeolagines reached the Old World in the later

Pliocene, presumably via a cool northerly land connection. Perhaps the extinction of the Archaeolaginae was due in part to competition with the second advanced leporid subfamily, the Leporinae (KORMOS, 1934, p. 76).

The Leporinae as here recognized are first known from the Pontian—in faunas probably approximately equivalent to those of Clarendonian age—in Asia and Europe. The subfamily, which seems to have radiated out in the later Pliocene and Pleistocene, first appears in North America in the Blancan. The oldest known leporine is *Alilepus*, a Pontian genus having a persistent posterointernal fold on P_3 . In "*Caprolagus*" *brachypus* from the Villafranchian of Asia, the structure of P_3 seems to resemble that in *Alilepus*, although in at least one specimen the posterointernal reentrant has lost its lingual connection and forms an isolated lake (BOHLIN, 1942b, p. 133). *Pratilepus* and *Alilepus? vagus* of the North American Blancan have on P_3 a posterointernal fold in early stages of wear and an isolated lake in later stages of wear. HUBBARD (1944) has shown that in *Lepus* a posterointernal lake comparable to that in *Pratilepus* occurs as a variant and suggested that the long posteroexternal fold on P_3 in *Lepus* results from the union of a shorter posteroexternal fold with a posterointernal lake. The stratigraphic sequence suggests that the main course of evolution of the posterior folds on P_3 in leporines occurred as follows: presence of posteroexternal and posterointernal folds, both persistent; posteroexternal fold persistent, posterointernal fold connected to lingual wall in early stages of wear but isolated as a lake following greater wear; formation, in the advanced leporines, of a long posterior fold by union of the shorter posteroexternal fold with the posterointernal lake. The Recent genera *Pentalagus*, *Pronolagus*, and *Romerolagus*, regarded by DICE as palaeolagines, are considered here to be primitive leporines that retain a pattern of folds on P_3 similar to that in *Alilepus*. The remaining Recent leporines have a long posterior fold on P_3 .

The subfamilial status of several late Pliocene and Pleistocene leporids is somewhat problematical: in *Pliolagus* from the Villafranchian of Europe, P_3 resembles that in *Alilepus* in early stages of wear but lacks a posterointernal fold or lake in a more worn stage; to KORMOS (1934, p. 73) the structure of P_3 in *Pliolagus* indicated that palaeolagines and archaeolagines could not be separated. In *Serengetilagus* of the early Pleistocene of Africa a posterointernal fold on P_3 is usually absent but is present in some individuals (DIETRICH, 1942, p. 56-57). *Hypolagus? browni* of the early Pleistocene of North America has a posterointernal isolated lake on P_3 , probably a remnant of the posterointernal fold, at an early stage of wear but later lacks any trace of the posterointernal fold. Possibly the leporids mentioned above are archaeolagines in which there was a tendency toward retention of the posterointernal fold. However, these leporids all appear rather late in the history of archaeolagines, at a time when suppression of the posterointernal fold in archaeolagines seems to have been well established. Reversal of this suppression would not be expected in the later archaeolagines. The evidence is not entirely adequate for a definite statement, but tentatively it is suggested that these are not archaeolagines tending toward retention

of a posterointernal fold but are leporines tending toward loss of that fold. As mentioned above, several leporines seem to have been in a stage of isolation of the posterointernal fold on P_3 during the Blancan; perhaps in the Blancan and Pleistocene, in the leporids considered here, isolation of the fold was followed by its eradication. The time ranges of *Pliolagus*, *Serengetilagus*, and *Hypolagus? browni* would seem to substantiate this interpretation, and their wide geographic distribution may have resulted from a leporine radiation.

The ancestry of the leporines is also problematical. In the Pontian genus *Alilepus* the structure of P_3 , in which a persistent posterointernal fold is present, would seem to indicate that the ancestry of the leporines must be sought among the palaeolagines, but between the early Miocene disappearance of palaeolagines and the Pontian appearance of leporines, no leporids having a persistent posterointernal fold on P_3 are known. No leporids of definite reference to the family are known from the Miocene of the Old World. Possibly a line of palaeolagines that had a persistent posterointernal fold on P_3 reached the Old World and, paralleling the archaeolagines in many progressive features, gave rise to the leporines. Although not necessary to account for an Old World distribution, perhaps in late Oligocene or early Miocene times leporids having a persistent posterointernal fold on P_3 were less well adapted than, and were peripheral in distribution to, the line of North American leporids lacking that fold; perhaps the Old World became the refuge for the peripheral line. When the two lines, Leporinae and Archaeolaginae, came in contact again in the later Pliocene, the leporines seem to have been more successful. These suggestions are highly speculative, especially in the absence of a record of Miocene Old World leporids, but seem to result in the most probable explanation of leporine de-

velopment. However, phylogenetic development of leporines may have followed a different course. Leporines could have descended from near the base of the Archaeolaginae and then developed in the Old World, an alternative differing little from the above. The leporine line may have descended from late Miocene or early Pliocene archaeolagines through a modification leading toward reversal of the archaeolagine trend of suppression of the posterointernal fold on P_3 . The fossil record of the leporines would seem to counter this suggestion. Were leporines descended from archaeolagines, it might be expected that the earliest leporines would show early isolation and loss of the posterointernal fold on P_3 . This is not the case. The oldest known leporines possess a persistent posterointernal fold on P_3 , and the isolation of the fold does not occur until later in the leporine fossil record.

In summary, three subfamilies of Leporidae, a primitive basal group and two advanced lines, are here recognized. The Palaeolaginae, primarily an Oligocene group of relatively primitive, closely related leporids that form the horizontal base of the family, occurred in Eurasia and North America but were seemingly more progressive in North America. Each of the two advanced groups seems to emphasize a different trend in development of P_3 : the posterointernal fold is suppressed in the Archaeolaginae and retained in the Leporinae. The Archaeolaginae, descended from palaeolagines, were the main North American leporids in the later Tertiary. The ancestry of the Leporinae is not definitely known but probably should be sought among the palaeolagines. Leporines are known to have been established in Asia and Europe by the Pontian; Blancan leporines are known from North America. The archaeolagines seem to have failed in competition with leporines and became extinct; all Recent leporids are leporines.

NOTE.—A study of *Pliolagus* by NIKOLAUS KRETZOI (1941, *Die unterpleistozäne Säugetierfauna von Betfia bei Nagyvarad: Földtani Közlöny*, v. 71, p. 308-335, fig. 1-7) was called to my attention while this paper by me was in press. KRETZOI restudied KORMOS' original specimens of *Pliolagus* and concluded that the pattern of P_3 in *Pliolagus* is that of an archaeolagine: on P_3 a posterointernal fold is lacking at the occlusal surface as well as at the base of the tooth. KRETZOI considered KORMOS' description of a posterointernal fold on P_3 in *Pliolagus* to be based on an error of observation (op. cit., p. 322-323). Thus, *Pliolagus* seems to be neither an intermediate between palaeolagines and leporines nor a leporine but a typical archaeolagine that made its appearance in Europe in the Villafranchian along with the archaeolagine *Hypolagus*. The added evidence removes *Pliolagus* from a position with the questionable leporines mentioned above. Whether *Pliolagus* is generically distinguishable from *Hypolagus* must be determined by additional study of European specimens.

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