NOTES ON NORTH AMERICAN
FOSSIL LAGOMORPHS

by

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B. S., K. S. T. C. Hays, 1927
Educ.

Submitted to the Department
of Zoology
and the Faculty of the Graduate
school of the University of Kansas in partial fulfillment of the
requirements for the degree of
Master of Arts.

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(Date) Aug. 15, 1931.

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For some unknown reason vertebrate paleontologists have seemed to consider fossil Rodents and especially fossil Lagomorphs a rather unimportant and unfruitful field for study. Perhaps one reason for this attitude has been the fact that as yet few complete or nearly complete skulls and lower jaws, or skeletons have been available for study.

It has now been shown conclusively that fossil Lagomorph remains are extremely abundant in certain localities, and also that fossil Lagomorphs have existed in great numbers in certain restricted localities. During the past year there has been discovered a very choice locality for obtaining a variety of fossil mammals and reptiles in the Lower Oligocene of central Wyoming. The most outstanding thing concerning the vertebrate fauna from this restricted locality is the abundance of certain hitherto uncommon groups and species of terrestrial and arboreal animals of the Lower Oligocene. This locality has yielded an exceedingly interesting assemblage of Camels and Rodents, not to mention the great variety of small Carnivores and Insectivores, large Carnivores, and Oreodonts, Horses and Rhinoceroses.

In this locality an abundance of Lagomorph material was obtained. As far as can be determined, three weeks collecting in this locality gave the following list of specimens:-- Approximately 20 complete skulls and lower jaws; 25 or more skulls without lower jaws, some of which are only slightly damaged; 10 or 15 specimens of skeletal material; and some 75 or more fragments of lower jaws and skulls which contain either a partial or a complete dentition.

Problem: With this amount of recently collected material at hand, it seemed advisable to attempt a thorough study of the dentition of fossil Lagomorphs, with the hope of finding definite clues to the relationships of these early rabbits. The drawings of the teeth have been made with the aid of a camera lucida, and the crown pattern of each tooth has been drawn separately, from a point of view parallel to the length of the tooth.

All the specimens studied are in the collections of two museums. Collection number I is from the private collection of Mr. Geo. F. Sternberg, Fort Hays Kansas State College Museum, Hays, Kansas. Collection number II is from the University of Kansas Museum, Lawrence, Kansas. Thanks are due Dr. H. H. Lane for advice and criticism during the progress of the work, and for the privilege of using the collection in the University of Kansas Museum. To Mr. Geo. F. Sternberg, of the Fort Hays Kansas State College Museum, thanks are due for the

loan of many interesting specimens, which represent a small part of the material that has been obtained during the four collecting seasons from 1927-30.

The literature available concerning the descriptions of fossil Lagomorphs, is rather limited. The early publications of Leidy on "Palaeolagus"[1] and the descriptions of Cope on "Miocene Rodentia and Lagomorphs"[2] are of course necessary for reference. The publications by Matthew on "A horned rodent from the Colorado Miocene, with a revision of the Mylagauli, Beavers, and Hares of the American Tertiary";[4] also, "The fauna of the Titanotherium beds at Pipestone Springs, Montana",[5] and "A lower Miocene fauna from South Dakota",[6] are valuable for their descriptions and plates. The publications by Douglass on "Fossil Mammalia of the White River beds of Montana",[7] and "New vertebrates from the Montana Tertiary"[8] are helpful references. The descriptions by Troxell of "Palaeolagus, and extinct Hare"[9] give valuable information concerning the milk dentition of this species. The recent work along this line by Dice on "Systematic position of several American Tertiary Lagomorphs",[10] and "The Phylogeny of the Leporidae, with descriptions of a new genus",[11] in which the author reviews the known diagnostic characters of fossil Lagomorphs based on the manner of the enamel folding on P3, has aided considerably in this work.

DESCRIPTION OF MATERIAL

Characters used in Revision of Family Leporidae.

After a critical study of the teeth of fossil rabbits, it seems possible to distinguish at least five distinct groups or divisions, based on the character of the enamel folding on the lower P$\overline{3}$.

This tooth seems to show an interesting series of variations which are remarkably distinct in each group. Although there are variations of importance in other teeth, such as in M$\overline{3}$ in the lower jaw, and in P$\underline{2}$ and M$\underline{3}$ in the upper jaw, the molar teeth as a whole show very few variations, and seemingly have changed little since the first known true rabbits from the lower Oligocene. On the basis of the character of the enamel folding on P$\overline{3}$, I have divided all of the Leporidae into five divisions. The variations, and the distribution of the types give strong support for the decision to assign each to the rank of a sub-family. It is confidently expected that future research will confirm this conclusion.

ORDER LAGOMORPHA

Resembling the Rodentia but upper incisors four in number; a large functional pair with enamel extending to posterior face of tooth (as Contrasted to enamel restricted to anterior face of tooth in the Rodentia), and a small pair without cutting edges directly behind them; upper and lower jaws opposing each other only one side at a time and motion of mastication lateral in consequence.

FAMILY LEPORIDAE

Size medium to large for the Order Lagomorpha, Dentition: I 2/1; C 0/0; P 3/2; M 3/3. Superior incisors sulcate, inferior incisors not sulcate. Last superior molar usually simple. First inferior molar of one more or less tranversely divided column; other inferior molars usually consisting of two columns in antero-posterior relation.

SUBFAMILY PROTOLAGINAE nobis

This subfamily is based on the character of the enamel folding on $P\overline{3}$. As observed, $P\overline{3}$ differs from that in all other of the subfamilies in having two internal re-entrant angles or enamel folds. The major internal re-entrant angle separates the tooth into two columns and apparently meets the single external re-entrant angle. A narrow bridge connects the two columns. The second internal re-entrant angle is only faintly developed, and is very narrow, but extends nearly half way across the posterior column of $P\overline{3}$. It is probable that this second internal re-entrant angle would be missing in worn teeth, thus reducing them to the condition observed in *Palaeolagus*. However, a number of very young individuals of *Palaeolagus* have been examined, and they do not show this character. This is further proof of the significance of this character in *Protolagus*. The anterior column of $P\overline{3}$ is smaller than the posterior column and somewhat separated from it. (See Plate I)

PROTOLAGUS gen. nov.

The type of this genus is a fairly complete skull with lower jaws in place (Specimen No. 26, Collection No. I) and to it is referred one additional imperfect skull which has the complete upper dentition present. (Specimen No. 260, Collection No. I).

Besides the character used in designating this sub-family, that is, the enamel folding of $P\overline{3}$, with one external and two internal re-entrant angles, there are four other teeth, which further distinguish and characterize this genus. These may be described as follows:-- $M\overline{2}$ is composed of two columns, entirely separated, the anterior column oval in cross section, while the posterior column is more cylindrical, but with a shallow internal re-entrant enamel fold. This small internal re-entrant angle on the posterior column of $M\overline{2}$ is quite different in form from the "third lobe" which appears on very young Palaeolagus teeth, and with which it need not be confused, since in the latter when this second internal angle is strongly developed, there is also a corresponding external angle opposite to it, which forms the "third lobe". $M\overline{3}$ is composed of two columns connected only by a this bridge of two enamel bands which appear only in old teeth, the young teeth showing two entirely separated columns, the anterior oval, and the posterior more cylindrical in cross section. The posterior column is not more than half as wide (transversely) as the anterior column, and touches the latter column only along its internal posterior edge.

P2 is a simple tooth, oval in cross section and directed transversely across the maxillary; it has a single median anterior re-entrant angle or enamel fold extending at least half way across the crown and directed slightly outward, which gives something of a U-shape to this tooth.

M3 although smaller than P2 is of the same general shape in the worn teeth, but with the re-entrant angle on the median posterior face of the tooth and directed outward. The young or unwarn condition of this tooth is most interesting, the enamel folding being more complex than observed in any other Lagomorphs teeth. (See Plate I).

<u>Protolagus affinus</u> sp. nov.

The type of this species is a fairly complete skull with lower jaws in place. (Specimen No. 26, Collection No.I). The upper incisors 1 are broken off, but upper incisors 2 are present and are the longest observed in any of the specimens of fossil Lagomorphs. Besides the shallow enamel fold on the internal side of P3, there is also a crescentic enamel fold originating on the anterior external side, extending to the center of the crown and then turning and extending over half way toward the posterior external side. This would probably wear into the crescent of enamel usually observed in the corresponding tooth of <u>Palaeolagus</u>.

The posterior enamel fold on M3 is indeed very interesting and along with the other characters mentioned, seems to designate this genus as the most primitive type of fossil rabbit known. The presence of the second internal re-entrant angle on P3 appears to be a "hang over" from the manner of enamel folding in the milk dentition, and indicates a primitive condition. Also the presence of the enamel fold on the posterior face of $M\underline{3}$ may indicate the steps by which it has changed to the simple oval column observed in the same tooth in other Lagomorphs.

In size Protolagus affinus appears to be about the same as Palaeolagus haydeni, and no outstanding difference can be detected in the skull except for the variations in the teeth. The two specimens of Protolagus affinus are from the lower Nodular layer of the Oredon Beds in the Oligocene of central Wyoming.

The measurements of the dentition of Protolagus affinus are as follows:--

Incisors $\underline{2}$ (exposed length)----------------------------2 mm

Incisor $\underline{2}$ to $P\underline{2}$ -------------------------------------9 mm

$P\underline{2}$ (ant. alveolus) to $M\underline{3}$ (post. alveolus)--------------9 mm

$P\underline{2}$ width (transverse)-----------------------------------1 mm

$P\underline{2}$ length (antero-posteriorly)--------------------------.75 mm

$M\underline{1}$ widest tooth, width (transverse)--------------------2.5 mm

Incisor $\overline{1}$ to $P\overline{3}$ -------------------------------------7 mm

$P\overline{3}$ (ant. alveolus) to $M\overline{3}$ (Post. alveolus)--------------9 mm

$P\overline{3}$ anterior column width (transverse)------------------1 mm

$P\overline{3}$ posterior column width (transverse)-----------------1.5 mm

Depth of ramus at $M\overline{1}$ ---------------------------------6 mm

SUBFAMILY PALAEOLAGINAE Dice

This subfamily is distinguished by the character and number of the re-entrant angles or enamel folds on $P\bar{3}$. In this subfamily $P\bar{3}$ has a single external and a single internal re-entrant angle. The two re-entrant angles nearly meet in the center and although separating the tooth into an anterior and a posterior column, the two columns are connected by a narrow bridge composed of two ridges of enamel. The tooth in transverse section has thus something of an "hour-glass" figure. The anterior column is only slightly smaller than the posterior.

Type genus.--Palaeolagus Leidy

This genus which is abundantly represented in the White River Oligocene, and which contains several species, has been described and figured by several writers, Leidy, Cope, Matthew, Douglass, Troxell, and others, yet it seems advisable to review the characters of Palaeolagus for comparative purposes in this paper.

Besides the character of the enamel folds on $P\bar{3}$ with one internal and one external re-entrant angle, together forming an "hour-glass" figure, this genus is further distinguished by the following:-- $M\bar{2}$ is composed of two separate columns in antero-posterior position in all unworn teeth. In worn teeth they appear to be connected along the internal side. The anterior column is oval in cross section, while the posterior column is more nearly cylindrical. $M\bar{3}$ is here composed of two columns connected in the middle by a narrow bridge. The anterior column is somewhat oval and the posterior cylindrical in cross section. These two columns again form more or less of an "hour-glass" figure. (See Plate I)

P2 is quite characteristic, being oval in outline with a main anterior re-entrant angle and a minor anterior re-entrant angle on the face of the tooth. The major angle is nearer the internal side and the minor one nearer the external side. The major anterior angle or fold extends fully half way across the crown of P2. It is very narrow and angular, and directed slightly outward. M3 is a very simple cylindrical column but occasionally with a slight indentation on the posterior, internal side.

The following number of Palaeolagus specimens have been available for study:--

Collection I. Geo. F. Sternberg Private Collection.

Skulls with lower jaws.----------------8 specimens

Skulls only.---------------------------8 specimens

Upper dentition only.------------------30 specimens

Lower jaws (dentition)-----------------75 specimens

Collection II. University of Kansas Museum.

Upper dentition only.------------------6 specimens

Lower jaws (dentition)-----------------38 specimens

A number of variations may be observed in the teeth of this genus. The unworn condition presents a pattern which is sometimes quite different from the worn pattern. However when a large number are arranged in a series these variations seem to be natural conditions of wear, and until a great number of specimens of all ages are available for study, the number of species of this genus is more or less of a question.

<u>SUBFAMILY MEGALAGINAE</u> nobis

In this subfamily P$\overline{3}$ has varied considerably from the conditions characteristic of the preceeding subfamilies, and has only a single external re-entrant angle or enamel fold, there being no evidence of an internal re-entrant angle. The single external re-entrant angle extends to the center of the tooth. This tooth now has the form of a cylinder with the external side somewhat compressed and with its external re-entrant angle again dividing the tooth into two columns of nearly the same size, although the anterior column may be slightly larger than the posterior one.

<u>Megalagus</u> gen. nov.

Type species Palaeolagus turgidus Cope

It appears that the following characters justify the establishment of a new subfamily for this genus, which was formerly included in the subfamily Palaeolaginae.

P$\overline{3}$ is quite distinct, and as described above, is cylindrical with the external side somewhat compressed, and having only a single external re-entrant angle which does not extend more than half way across the crown. M$\overline{2}$ in all unworn teeth is composed of two separate columns, both appearing oval in cross section. M$\overline{3}$ is composed of two separate columns, not connected in the center by enamel. The anterior column is oval while the posterior is circular in cross section.

$P\underline{2}$ is characteristic of this genus, being oval in outline, with two anterior re-entrant angles, separated by a median ridge. Both appear to be of nearly the same depth and do not extend as far as half way across the crown. $M\underline{3}$ is a simple cylindrical tooth.

This genus is by far the largest of all Oligocene fossil rabbits, being nearly twice as large as either Protolagus affinus or Palaeolagus haydeni. The size of the dentition is about the same as the present day plains rabbit, Lepus californicus melanotis, however the lower jaw does not seem to be as deep or as heavy as in the present form. These facts seems to indicate that it should be placed in a separate subfamily.

SUBFAMILY ARCHAEOLAGINAE Dice

This subfamily has characters approaching the modern Leporinae in the folding of the enamel on $P\overline{3}$. In the subfamily Archaeolaginae, $P\overline{3}$ is characterized by the presence of two external re-entrant angles, but no internal re-entrant angle. The main external re-entrant angle is posterior, and does not extend more than half way across the crown. The anterior re-entrant angle is very shallow, being only a slight indentation with a faint ridge on either side. The main external re-entrant angle divides the tooth into two columns of which the posterior is slightly smaller than the anterior one.

Type genus and species: *Archaeolagus ennisianus* (Cope)

This genus has characters approaching the modern *Leporinae*. In *Archaeolagus* $P\overline{3}$ is characterized by having two external re-entrant angles but no internal re-entrant angle. The main external re-entrant angle is posterior, and does not extend more than half way across the crown. The anterior re-entrant angle is very shallow, being only a slight indentation with a faint ridge on either side.

$M\overline{2}$ is composed of two columns, incompletely divided by a deep external re-entrant angle which extends more than half way across the tooth. There is no internal re-entrant angle, or rarely a shallow notch. $M\overline{3}$ is a simple column, somewhat oval in cross section, with a slight indentation on the internal side.

$P\underline{2}$ is nearly cylindrical, compressed slightly on the anterior face, and with a major anterior internal enamel fold and a minor anterior external fold. The folds are shallow and do not extend to the center of the crown. $M\underline{3}$ is a simple, cylindrical, circular column.

This genus is represented in the material at hand by a single specimen, a fairly complete skull with lower jaws in place. (Specimen No. 27, Collection No. I) However, this specimen appears to differ enough from *Archaeolagus ennisianus* to be described as a new species. I therefore propose for this species the name:--

Archaeolagus striatus sp. nov.

Diagnosis of species:-- This species is considerably smaller than _Archaeolagus ennisianus_, being of nearly the same size as _Palaeolagus haydeni_. As in _Archaeolagus ennisianus_, the masseteric fossa is posterior to the tooth row, or barely extending to below $\overline{M3}$. It appears proportionately deeper, and the ridge anterior to it higher, than in _Archaeolagus ennisianus_. $\overline{P3}$ has the characteristic two external re-entrant angles, the posterior the deeper. In this species $\overline{P3}$ has the slight indentation or second anterior enamel fold, but on each side of it there is a minute fold and ridge, which appear very distinct, resembling lines or _striae_, hence the name _Archaeolagus striatus_. $\overline{M3}$ in this specimen has the form of an oval, cylindrical tooth, which is directed antero-posteriorly, with the anterior end turned slightly outward. This tooth in the specimen at hand appears worn and on the verge of being shed. This individual shows the teeth well worn, and is evidently an adult, which represents a new species and not the immature condition of _Archaeolagus ennisianus_. Since _Archaeolagus ennisianus_ if known only from the Upper Oligocene John Day beds of Oregan, it appears interesting to find this genus also represented in the Middle Oligocene beds of central Wyoming. Whether or not _Archaeolagus striatus_ may be considered as ancestral to _Archaeolagus ennisianus_ can not be determined at present.

The measurements of the dentition of _Archaeolagus striatus_ are as follows:--

Incisor $\underline{2}$ (exposed length)	1 mm
Incisor $\underline{2}$ to P$\underline{2}$	9 mm
P$\underline{2}$ (ant. alveolus) to M$\underline{3}$ (post. alveolus)	8.5 mm
P$\underline{2}$ width (transverse)	1.5 mm
P$\underline{2}$ width (antero-posteriorly)	1 mm
P$\underline{4}$ widest tooth, width transverse	2.75 mm
Incisor $\overline{1}$ to P$\overline{3}$	5.5 mm
P$\overline{3}$ (ant. alveolus) to M$\overline{3}$ (post. alveolus)	9 mm
P$\overline{3}$ anterior column length (antero-posteriorly)	1 mm
P$\overline{3}$ Posterior column length (antero-posteriorly)	.5 mm
Depth of ramus at M$\overline{1}$	6.5 mm

SUBFAMILY LEPORINAE Dice

This subfamily, which includes most of our modern hares and rabbits, is again characterized by the enamel folding on P$\overline{3}$. In this subfamily P$\overline{3}$ has two external but no internal re-entrant angles. The main external re-entrant angle, which is posterior, reaches entirely across the tooth, and is in contact with the internal side of the crown. The anterior external re-entrant angle is shallow, not extending to the center of the tooth. The tooth now consists of three columns, the posterior one almost completely separated from the two incomplete anterior columns. The posterior column is considerably smaller (antero-posteriorly), than the two combined incomplete anterior columns. The anterior external re-entrant angle shows a number of interesting variations in the different genera of this subfamily. The anterior face of this tooth is also somewhat compressed, and has a shallow median, re-entrant enamel fold. This further distinguishes the Leporinae from all other of the subfamilies, since they all have the anterior face of P$\overline{3}$ rounded and without any trace of the above mentioned re-entrant angle.

Type genus *Lepus* Linn.

This genus includes most of our larger Lagomorphs. In this genus P$\overline{3}$ has two external but no internal re-entrant angles. The main external re-entrant angle, which is posterior, apparently reaches entirely across the tooth, and is in contact with the internal side of the crown. The anterior external re-entrant angle is shallow, not extending to the center of the tooth. The anterior face of this tooth is also somewhat compressed, and has a shallow median, re-entrant enamel fold. M$\overline{2}$ is composed of two columns incompletely divided by a deep external re-entrant angle which is nearly in contact with the internal edge. The anterior column is at least twice as large as the posterior column. M$\overline{3}$ is a simple cylindrical tooth with a shallow external and a deeper internal re-entrant angle.

P$\underline{2}$ is a slightly compressed oval with three re-entrant folds on its anterior face. The two main folds are median and do not extend half way across the crown. The minor third fold is on the interior, anterior face of P$\underline{2}$. M$\underline{3}$ is a simple cylinder, usually oval in outline. (See Plate I).

SUMMARY

If we may assume that the character of the enamel folding on $P^{\overline{3}}$ is indicative of the relationship of the Leporidae, then the subfamilies may be briefly characterized as follows:-

Subfamily Protolaginae: $P^{\overline{3}}$ with one external and two internal re-entrant angles, the main internal re-entrant angle nearly meeting the external re-entrant angle and dividing the tooth into two columns; the anterior column smaller than the posterior; the second, internal re-entrant angle, which is on the posterior column, is evidently a "hang over" from the milk dentition.

Subfamily Palaeolaginae: $P^{\overline{3}}$ with one external and one internal re-entrant angle, the angles nearly meeting, thus dividing the tooth into two columns, both of which are nearly the same size; the crown pattern of this tooth has thus something of an "hour-glass" figure.

Subfamily Megalaginae: $P^{\overline{3}}$ with one external but no internal re-entrant angle; the internal re-entrant angle of Palaeolagus has apparently been lost. The external re-entrant angle, which does not extend more than half way across the crown of the tooth, divides the tooth into two columns the anterior of which begins to be slightly larger than the posterior.

Subfamily Archaeolaginae: $P^{\overline{3}}$ with two external re-entrant angles but no internal re-entrant angle. The main external angle posterior, and the new external re-entrant angle anterior, and very shallow. The main external re-entrant angle again divides the tooth into two columns, the anterior of which is now considerably larger than the posterior. The main external re-entrant angle not extending past the center of the crown of the tooth.

Subfamily Leporinae: P^3 with two external re-entrant angles, but the main external angle is posterior and reaches entirely across the crown of the tooth and nearly fuses with the internal edge of the crown. The anterior re-entrant angle does not extend past the center of the anterior column. The tooth is made up of three columns in antero-posterior position; the two combined anterior columns which are incompletely divided by the anterior re-entrant angle, are fully twice as large as the nearly completely cut off posterior column.

If we may assume that the character of the enamel folding on P^3 is indicative of the relationship of the Leporidae, then the changes observed in this tooth show that it has developed into its present form by the following steps:- (1) the loss of the internal re-entrant angle of the early forms; (2) the increase in size of the anterior column over the posterior column; (3) the addition of a second anterior external re-entrant angle; (4) finally, a general lengthening of the anterior column of the tooth (antero-posteriorly).

CONCLUSION

This study of the teeth of Fossil Lagomorphs shows clearly how little the teeth have varied during the evolution of the group. If there has been any great change in the structure of Lagomorphs since early Oligocene time, it has effected other parts of the skeleton, namely, length of limbs and size and manner of carrying the head, rather than any profound changes in the dentition. The type of dentition acquired by the early Oligocene Lagomorphs, has been adequate to fit rabbits for nearly every type of food habitat that they have been subjected to since that time. It is clear that the teeth have remained largely in the early primitive condition, while the feet have had to carry the burden and solve the problem of maintenance.

From the amount of material that has been collected in the last few years, it is evident that Lagomorphs were very abundant during Oligocene time. Hundreds of jaws and fragments of skulls may be collected from the washes in the badlands. The choice localities, which seem to be associated with the Nodular layers in the Oreodon beds, may show that the Lagomorphs had already preferred the open, possibly arid conditions, of which these Nodular layers seem to be indicative.[12]

FAMILY LEPORINAE

SUBFAMILY