I.

Pliocene Rodents of Western North America

Abstract

This thesis embraces a review of Pliocene rodent faunas and their evolution as well as the description of several new Pliocene rodent faunas which contain forms of interest to paleontology. In the course of the work detailed faunal studies were carried on covering rodent faunas from (1) Kern River beds, California; (2) Pliocene beds of Smiths Valley, Nevada; (3) Owyhee Pliocene of Rome, Oregon; (4) Pliocene beds in the Coso Mountains, California; and (5) beds exposed near Grand View and Hagerman, Idaho. Examination, in whole or in part, of the following faunas was also made: (1) Pliocene fauna from Bartlett Mountain near Drewsey, Oregon; (2) Fish Lake Valley fauna, Nevada; (3) Rattlesnake, Oregon; (4) Thousand Creek, Nevada; and (5) Curtis horizon of the San Pedro Valley beds, Arizona. Other Pliocene rodent faunas were studied only through the published accounts of these faunas.

As a result of the studies it was found that Pliocene rodent faunas fall into several major faunal stages distinguished by the general nature of the faunas as well as by the presence of characteristic genera and species. The chief characteristics of these stages are as follows:
II.

I. Lower Pliocene

1. great predominance of sciuromorphs over myomorphs
2. high percentage of extinct genera
3. no strikingly new or introduced types
4. presence of the genus Eucastror

II. Middle Pliocene

1. great predominance of sciuromorphs over myomorphs
2. genera about half extinct and half living
3. introduction of Castor in later faunas
4. first appearance of Microtinae
5. presence of "gigantic" Peromyscine types
6. presence of the genus Dipoides
7. last appearance of the mylagaulid rodents

III. Upper Pliocene

1. sharp faunal break with the middle Pliocene as evidenced in:
   a. decided increase in the myomorph population
   b. decided decrease in the number of extinct genera
   c. first appearance of many modern types
2. no Mylagaulidae
3. presence of the genus Mimomys, as well as the relative abundance of microtines
4. no Dipoides, or at present any representative of the Eucastror-Dipoides line
5. absence of Lepus, except perhaps in final faunal stages
6. first appearance of "typical" Citellus
7. all species probably extinct

The rodent record is still very incomplete and this fact together with the short duration of Pliocene time has served to limit the amount of observable evolution in the Rodentia during this epoch. However, the study has shown, contrary to the usual belief, that in certain groups evolution has proceeded at a fairly rapid rate. Moreover, it appears that post-Pliocene evolution in the rodent group is quite marked, in certain families at least.
III.

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Knowledge concerning the extinct mammal faunas of North America has increased enormously since the beginning of the present century. Certain groups of mammals are known in great detail and fairly secure phylogenetic schemes have been erected. Other groups are not so well known but the general outline of their history has been traced and little remains but to fill in the gaps and to make minor corrections. On the other hand, a few groups have proved more or less refractory, and the order Rodentia is to be regarded as one of the most important of these. Not only are the broader phases of rodent evolution such as the differentiation of modern families from ancestral stocks not at all well known, but it is commonly assumed that rodent types are remarkably stable, the same genus, and even species, having an extremely long range in geologic time as compared to other orders. Hence, the rodents, at present, are regarded by the vast majority of vertebrate paleontologists as an order from which little can be expected from an evolutionary standpoint, and secondly, their stability bars them from any use in detailed stratigraphy and correlation.
The views expressed above are, as has been indicated, those held by most paleontologists. However, they are views for the most part inherited from older workers handicapped by lack of sufficient material and knowledge of the stratigraphic location of that material. Most present-day workers on fossil rodents, although not agreeing among themselves as to the limiting possibilities in rodent research, feel that the older views are not altogether correct.

Before proceeding to a discussion of the scope of the present paper, it seems pertinent to outline briefly the various lines of rodent research, and the attained as well as expectable results of a study of fossil rodents.

The most fundamental line of research is the investigation of the differentiation of modern families from a common rodent stock. At present, extremely little is known, and the most widely diverse views are held as to the time and manner of differentiation. If results are to be attained in this direction it will be particularly through a careful study of middle and upper Eocene rodents. The present possibilities of such research will be discussed later in a more suitable place.

A second direction of research is the establishment of phylogenetic lines within the family. Fossil materials known at the present time are hardly sufficient for detailed phylogenetic studies. They are sufficient in most cases to establish broad lines of evolution, or at least to sug-
gest such lines.

A third field of investigation is concerned primarily with the description of rodent faunas from various horizons. This type of work has value in making our picture of mammalian life more complete, and in furnishing a basis for work on the previously mentioned types of study. At present, even this work is neglected and large collections of undescribed rodents are in existence. Omission of studies of this type has proved a stumbling block for more ambitious projects along other lines. Of course in connection with such work phylogenetic studies should not be neglected.

An outgrowth of faunal studies is the recognition of the time range of various genera and species, and the establishment of important "index fossils." With increasing knowledge of fossil rodents it has become apparent that certain groups of rodents at least, will ultimately furnish important horizon markers. At present, the number of such index fossils are few. However, if the existing rodents, which number more different types than all other mammals combined, have descended, as commonly believed, from a single lower Eocene genus or at most several closely related genera, it is obvious that the amount of evolution occurring in the Tertiary is very great, and consequently the group should furnish many such horizon markers.

The nature of the present paper practically limits the fields of discussion to the latter two mentioned above.
All present day families were established long before the opening of Pliocene time. The short duration of that epoch, as well as the fragmentary nature of the material, sharply limits the observable evolution of the order during that time.

Pliocene rodent remains are not very abundant or complete, but neither are other mammalian remains from the epoch so that any data secured as to stratigraphic position of faunas, ecology, and so forth are relatively more important than in other divisions of the Tertiary. The term Pliocene is here used not only to cover all true Pliocene occurrences but also the doubtful Miocene-Pliocene and Pliocene-Pleistocene faunas. In a general way this covers a period embraced by the European time sequence Pontian to Sicilian. The present paper deals only with Pliocene faunas from western North America but since no Pliocene types have been recorded elsewhere in North America, the study is not actually limited geographically.

In the course of the work detailed faunal studies were carried on embracing faunas from: (1) Kern River beds, California; (2) Pliocene beds in Smiths Valley, Nevada; (3) Owyhee Pliocene of Rome, Oregon; (4) Pliocene beds in the Coso Mountains, California; and (5) beds exposed near Grand View and Hagerman, Idaho. Examination, in whole or in part, of the following faunas was also made: (1) Pliocene fauna from near Bartlett Mountain, Oregon; (2) Fish Lake Valley fauna,
Nevada; and (5) Curtis fauna from San Pedro Valley, Arizona. Other Pliocene rodent faunas are known to the author only through a reading knowledge of their published descriptions.

Previous Studies On North American Fossil Rodents

Early workers in the field of North American fossil rodents were first Joseph Leidy, followed by E. D. Cope, O. C. Marsh, and finally W. D. Matthew. Other paleontologists contributed to be sure but by far the bulk of the work was carried on by these four men. Their work covered a period extending from the first studies of Leidy down to 1910. It was mainly a period of description with little or no attempt made to construct phylogenetic trees. It is true that relationships of various extinct types of rodents to modern forms were recognized, sometimes with surprising accuracy considering the poor material available for study. On the other hand, we find identifications of John Day lagomorphs as Lepus, lower Oligocene ischyromyids as Sciurus, and John Day castorids as Castor. Perhaps it was such identifications that established the belief that rodents were extremely stable forms.

It is difficult to ascertain the relative importance of Leidy, Cope, Marsh, and the early work of Matthew. Leidy, publishing chiefly in the proceedings of the Philadelphia Academy of Natural Sciences and various government reports,
is probably important principally because his work was the starting point for later, more complete work. Cope was probably the dominant figure of the first period of rodent research in this country. His work is summarized in the, "Vertebrata of the Tertiary Formations of the West."[1]

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Marsh's contribution is relatively unimportant compared to the other three paleontologists. His most important work was in connection with building up a large collection of Bridger rodents which have never been completely described or even prepared for study. With Cope's death, Matthew became the leading worker in the field, a position which he held to his own death. Practically all his contributions are to be found in the various publications of the American Museum.

The modern period of fossil rodent research starts with the publication by Matthew, in 1910, of his classic contribution, "On the Osteology and Relationships of Paramys, and the Affinities of the Ischyromyidae."[2] His view that the order of rodents is descended from a Paramys or Paramys-like ancestry is accepted at present by most workers in the field of rodent paleontology. The only exception taken to this view, in this country, was made in 1918 by Miller and Gidley in

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This paper was originally intended to be a preliminary report on an ambitious program of reviewing the entire field of fossil and living rodents. The final report has never been published. The paper contained many new ideas, extremely discouraging to further rodent work if they could be proved. As has been pointed out at various times by several paleontologists, this paper is more an artificial key for the recognition of supragenetic or family groups than a genetic classification. The principal view presented by Miller and Gidley is that all rodent families were completely differentiated at their first appearance in the paleontological record.

A more recent phase of the modern period has been research on family or subfamily groups of rodents. Here, might be mentioned one European work, Schaub's, "Die Hamsterartigen Nagetiere Des Tertiaers", which is probably the first accurately written and accurately figured publication dealing with the evolution of a phylum of rodents. Recent American publications of this type have been, "Evolution and Relationships of the Heteromyid Rodents" by A.E. Wood, and


A review of the literature dealing exclusively with Pliocene rodents is difficult to present. Most of the work accomplished to date has been in connection with descriptions of other mammals. Papers dealing exclusively with Pliocene rodents are very limited. In 1910 Miss Louise Kellogg published a description of a, "Rodent Fauna of the Tertiary Beds at Virgin Valley and Thousand Creek, Nevada." In 1922 J. W. Gidley's, "Preliminary Report on Fossil Vertebrata of the San Pedro Valley, Arizona, with Descriptions of New Species of Rodentia and Lagomorpha" appeared in 1922. Lastly, in 1930, E. Raymond Hall issued a report on the, "Rodents and Lagomorphs from the Later Tertiary of Fish Lake Valley, Nevada."
The Nature of North American Tertiary Rodent Faunas

**Taxonomic Classification**

The taxonomic classification of rodents used in this paper is in no sense original. It perhaps is closest to Simpson's arrangement presented in 1931. Certain changes have been made when such changes seemed suitable to the author or in cases where compromise with several arrangements was most convenient. Since no known classification is very satisfactory the present writer does not feel unduly presumptive for using his own. The following outline omits families not recorded from North America as well as the families Dipodidae and Muridae which have been very dubiously recorded.

Order Rodentia (rodents in a strict sense)

Infraorder Sciuromorpha (squirrel-like rodents)

Superfamily Aplodontoidea

†Family Ischyromyidae
†Family Mylagaulidae
Family Aplodontiidae (mountain-beavers or sewellels)

Superfamily Sciuroidea

Family Sciuridae (squirrels)

Superfamily Castoroidea

Family Castoridae (beavers)

Superfamily Geomyoidea

Family Heteromyidae (pocket-mice and kangaroo-rats)
Family Geomyidae (pocket-gophers)
Infraorder Myomorpha (mouse-like rodents)

Superfamily Myoidea

Family Cricetidae (rats and mice)

Superfamily Dipodoidea

Family Zapodidae (jumping-mice)

Infraorder Hystricomorpha (porcupine-like rodents)

Superfamily Hystricoidea

Family Erethizontidae (North American porcupines)

*Family Caviidae (guinea-pigs)

Order Lagomorpha (rabbits, hares, and pikas)

Family Ochotonidae (pikas)
Family Leporidae (rabbits and hares)

*Not present in Pliocene
†Extinct

The popular term rodent embraces two orders of mammals which may have only a very distant relationship. One order, the Lagomorpha which include the hares, rabbits, and pikas is a rather restricted group which has proved remarkably stable from its first appearance in the fossil record. The second order, that of the Rodentia, or true rodents, is marked by an extreme diversity of types all arising from a central stock, and consequently exhibiting parallelism among themselves to an extraordinary degree. The present study will include both orders since the Lagomorpha are so limited as to make separate treatment not very desirable.

The classification of the Rodentia used here is the
old three-fold division into the Sciuromorpha or squirrel-like rodents, the Myomorpha or mouse-like rodents, and the Hystricomorpha or porcupine-like rodents, based principally on the character of the masseter muscle and its attachment on the skull. This division is not universally accepted nor entirely satisfactory but in the case of North American rodents it is a fairly logical one and very convenient.

The North American sciuromorphs include the mountain-beavers, squirrels, beavers, gophers, pocket-mice, and kangaroo-rats among living forms, and the ischyromyids and mylagaulids among extinct types. These forms are characterized by possessing relatively small infraorbital foramina in which no invasion by the masseter muscle takes place. Moreover, the angle of the ramus appears to originate on the inferior border of the ramus, and not upon the side as in the Hystricomorpha.

Only two families of North American myomorphs have been definitely recorded, namely the Cricetidae, including indigenous rats and mice, and the Zapodidae or jumping-mice. In these forms the infraorbital foramen becomes enlarged and is traversed by a branch of the masseter muscle. The angle of the ramus is similar to that of the Sciuromorpha.

The North American Hystricomorpha include representatives of the Erethizontidae or porcupines, and the Caviidae or guinea-pigs. In these forms the infraorbital foramen is extremely large, and transmits the masseter medialis. The
angle of the ramus appears to originate on the side of the ramus in contrast to the more normal angle of the Sciuro­
morpha and Myomorpha. This group is relatively unimportant among North American rodents. Our only known forms are in-
vaders from South America.

Sciuromorpha Predominance in North America

The Sciuromorpha is the most primitive of the infra-
orders, and probably gave rise to the other two. In North America it is the dominant group of the Tertiary. All sciuro-
morph families are represented excepting the anomoluroids.
The mylagaulids, gophers, and heteromyids are confined to North America, and the aplodontids are represented elsewhere only by a single Pliocene specimen from Asia.

The predominance of sciuromorphs in North America is in contrast with most other continents in which, in the Mio-
cene and Pliocene at least, the higher types of Rodentia are dominant. In Asia the vast majority of the later Tertiary types are myomorphs; in South America the fauna is almost exclusively hystricomorph. For these reasons study in North American rodents is essentially limited to the Sciuro-
morpha. Studies concerning the evolution of the Aplodontiidae, Mylagaulidae, Geomyidae, and Heteromyidae should furnish, and are furnishing important data on the evolution of these families since the groups mentioned are virtually confined to this continent. North American fossil Myomorpha may fur-
nish a limited amount of data on certain members of the Cricetidae and Zapodidae but the seat of higher rodent evo-
olution is certainly elsewhere. The date of appearance of certain hystricomorph types may eventually furnish horizon markers, but their evolution occurred farther to the south.

Review of Evolutionary History of North American Rodentia, with Evidence for Paramys Ancestry

The earliest known form which has been referred to the Rodentia is *Eurymylus* of the Gashato Paleocene of Mongolia. If *Eurymylus* is a rodent it is too unlike other known forms to suggest affinities with them. It may represent an early but highly specialized rodent type. In spite of certain resemblances in the dentition to the Lagomorpha it can not very well be related to them. It is believed by most paleontologists that the Rodentia have been derived from some branch of the insectivores (s.l.). In this connection, it is interesting to note that *Eurymylus* was originally referred to the Menotyphla.

The first undoubted rodent type is *Paramys*. This genus has been reported from the Clark Fork Paleocene but is typically developed in the Eocene. *Paramys* in a strict sense probably does not occur in either the lower or upper Eocene, but types found in these horizons are closely related to the typical Bridger *Paramys*. The genus *Paramys* is charac-
terized as follows: Skull proportioned as in the wood-chuck, but muzzle shorter and basicranial region longer; without post-orbital processes; bullae loosely attached. Zygomatico-teric structure similar to that in mountain-beaver. Cheek-teeth sciurid in pattern but with certain distinctive characters. Coronoid process of ramus relatively larger than in Sciuridae. Angle a vertical plate, not inflected. In the lowermost Eocene (Sand Coulee to Lysite) it is the only rodent so far obtained. From Lost Cabin time on, forms which are quite distinct generically from Paramys begin to make their appearance in the paleontological record. The first of these, Mysops, Sciuravus, and Tillomys are clearly related to Paramys and are usually classed with this genus in the Ischyromyidae. Numerous attempts have been made to trace back various Oligocene families to these rodents but without marked success. This is chiefly due to a lack of adequate upper Eocene faunas. These early forms are all sciuromorphs of a very primitive type in which the area on the skull for attachment of the masseter muscle is limited to the zygomatic arch; and the plane of attachment is inferior to the infraorbital foramen, and moreover, nearly horizontal. Although this type of attachment is not limited to the Ischyromyidae it might conveniently be termed the ischyromyd condition for the purpose of the present paper. By the upper Eocene, some rodents are present which clearly cannot be placed in the Ischyromyidae. At least one myomorph
representative is known and several genera of uncertain affinities. In the Oligocene a number of modern families have appeared, and probably all families which are not later invaders from other regions were in existence.

Very few later Tertiary and Recent families can be traced back into the Eocene. Eocene ancestors of living North American forms can be pointed out in not more than three families, namely the aplodontids, sciurids, and either the c细则ds or zapodids depending on the systematic position of the upper Eocene Simimys. With the exception of the Aplodontiidae even these cases would probably not be accepted by all paleontologists. It should be pointed out that each superfamily has a more or less characteristic development of the masseter muscle on the skull. Cases of transition from one type to another are very rare in the paleontological record. In view of the great extent of parallelism in tooth structure among various rodent groups some authorities feel that before accepting the derivation of modern families from Eocene rodents the transition from the ischyromyid type of zygomatic structure to more modern types must be demonstrated. As a matter of fact, one of the chief drawbacks to any work on the differentiation of modern fam-
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ilies is the absence of skull material from the critical horizons. This fact is probably more apt to account for lack of intermediate types than the alternative view that they do not exist.

A study of all material now available would probably go a long way toward demonstrating the Eocene ancestry of our modern families. However, it is likely that final proof will have to await the finding of more perfect specimens and the acquiring of more extensive upper Eocene rodent faunas. At present a Paramys ancestry can be reasonably demonstrated for the Aplodontiidae as shown by the structural series Paramys-Eohaplomys-Haplomys-Allomys-Liodontia-Aplodontia.

The extinct Mylagaulidae appear to be related to the Aplodontiidae as shown by the milk teeth of Mylagaulus as well as by characters in the skull, etc., and therefore, a Paramys ancestry for this family is also indicated. The same ancestry is shown for the Sciuridae on the basis of the dentition. Such forms as Paramys sciuroides and Prosciurus appear to bridge the gap in tooth structure. It would be rather unusual if the strong resemblance in dental pattern had no genetic affinity. Moreover, A. E. Wood has mentioned that in the genus Tamius certain individuals occur which are very close to members of the Aplodontoidae in zygomasseteric structure. 12


Descent from a Paramys stock has been advocated for the
Castoridae, Geomyidae, and Heteromyidae, chiefly it seems because a hypothetical ancestor for all these groups should look like *Paramys*. Certainly, no annectant forms are definitely known.

In the case of the Myomorpha still less is known concerning their possible *Paramys* ancestry. The early cricetid *Eumys* bears a resemblance in its lower molars to some of the smaller Eocene ischyromyids. Since in later cricetids the resemblance is far less marked this may indicate a real relationship and not be due simply to parallelism. The North American fossil Zapodidae are not known well enough to suggest a relationship to any Eocene form. Early European relatives of this family resemble contemporaneous cricetids to a marked degree. *Simimys* from the Sespe upper Eocene is either the most primitive known cricetid, or zapodid, or ancestral to both. The remains of this myomorph are still too poor to make certain its exact relationship. The second lower molar of *Simimys* resembles to a certain extent the comparable tooth in such forms as *Sciuravus*.

North American hystricomorphs appear too late in the fossil record to suggest ancestry to any other forms than earlier Hystricomorpha. I am not familiar with early Tertiary types but their apparent relationship to late Eocene types in Europe which are in turn close to a *Paramys* ancestry has been noted.

A discussion of the evolution of the post-Eocene rodents
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is beyond the scope of the present paper. However, the accompanying charts show in a general way a series of phylogenetic schemes for various families. The data for these charts have been drawn from various sources, both original and otherwise. They are not to be taken as in any sense final but are suggestive of the present state of our knowledge.
### Phylogeny of the Aplodontiidae and Mylagaulidae

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<td>Liodontia alexandrae</td>
<td>Epigaulus, Ceratogaulus</td>
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<td>Haplomys</td>
<td>Allomys (Meniscomys hippocus)</td>
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<td>Eocene</td>
<td>Echaplomys</td>
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<td>Paramys</td>
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## Phylogeny of the Sciuridae

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<td>Paramys (P. sciuroides)</td>
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<td>Paramys</td>
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### Pliocene
- **Upper**: Palaearctomys, Citellus, Eutamius
- **Middle**: Marmota, Citellus, Sciurus
- **Lower**: ?

### Miocene
- **Upper**: Palaearctomys, Eutamius
- **Middle**: Citellus, Sciurus
- **Lower**: Sciurus, Prosciurus

### Oligocene
- **Upper**: Sciurus, Prosciurus
- **Middle**: Prosciurus
- **Lower**: Prosciurus

### Eocene
- **Upper**: Prosciurus
- **Middle**: Prosciurus
- **Lower**: Paramys (P. sciuroides), Paramys, Paramys
PHYLOGENY OF THE CASTORIDAE

QUATERNARY

UPPER

Castoroides

MIDDLE

Dipoides

LOWER

Eucastor

Castor

Castor?  

PALAEOCENE

UPPER

Monossulax

MIDDLE

Amblycastor

LOWER

Palaeomys (Old World)

EUHAPSIS

Palaeocastor

Fossiliferous

Stratigraphers:

TO OLD WORLD

Eocene

UPPER

Agnotocastor

MIDDLE

LOWER

EOCENE ISCHYROMYIDAE
PHYLOGENY OF THE HETEROMYIDAE

QUATERNARY

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<th>Perognathus</th>
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<td>LOWER</td>
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MIocene

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<th>Perognathus</th>
<th>Cupidinimus?</th>
<th>Perognathoides</th>
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Oligocene

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Eocene

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PHYLOGENY OF THE GEOMYIDAE

| QUATERNARY | UPPER | MIDDLE | LOWER |
|------------+-------+--------+-------|
|            | Thomomys | Plesiethomomys | Geomys | Cratogeomys |
|            | Thomomys   | Geomys       | Cratogeomys |
|            | Heliocomomys | Thomomys  |
|            | Mookomys?  | Proheteromys |
|           | Pleuroicus | Intoptychus |
|           | Heliosomys |
| EOCENE     | Eocene Ischyromyidae |
PHYLOGENY OF THE HYSTRICOMORPHA

CENOSAMPLE

Eocene

Upper
Middle
Lower

Oligocene

THERIDOMYIDAE (Old World)

To _Ischyromyidae_

Miocene

SANTA CRUZ HYSTRICOMORPHA (South America)

Eocene

Pliocene Rodent Faunas

The relative position of most of our various Pliocene faunas is more or less agreed upon. However, there is a wide divergence of views as to just where the Miocene-Pliocene and Pliocene-Pleistocene boundary lines should be drawn. Consequently, unless one makes clear just what is meant by lower Pliocene, for example, considerable confusion may arise. The lower Pliocene of one author may include the Thousand Creek, of another the Fish Lake Valley beds, and so forth. To say that the extinct beaver, *Eucastor*, is characteristic of the lower Pliocene is ambiguous if not accompanied by a qualifying explanation since the characteristic Thousand Creek beaver is *Dipoides*.

In the present paper a three-fold division of the Pliocene into lower, middle, and upper, is used. The lower division includes such faunas as the Fish Lake Valley or Esmeralda which would be considered upper Miocene or perhaps transitional by some authorities. It is roughly equivalent to the so-called Pontian faunas of Europe and Asia. The author has no particular convictions on the subject of placing the faunas assigned to this division, in the lower Pliocene instead of the upper Miocene, but it seems a rather convenient system. As a matter of fact, if the extreme views of some authors were applied regarding the lower and upper boundaries of the Pliocene, Pliocene time would be reduced
almost to the vanishing point. In any case, the placing of boundary lines seems an academic question which geologic time ignores.

The middle Pliocene of this paper includes such faunas as the Thousand Creek, Rattlesnake, and upper Snake Creek. The Pliocene age of these faunas is agreed upon by all American paleontologists. They are roughly comparable to the Plaisancian faunas of Europe.

The division termed upper Pliocene includes faunas from Grand View, Hagerman, the upper Etchegoin, and San Pedro Valley. These faunas correspond in part to the lower Pleistocene of some authors. Their European equivalents are the Norwich Crag and Val d'Arno. There seems some justification for the belief that at least part of the author's upper Pliocene should be termed lower Pleistocene. This will be discussed in some detail in a later, and more convenient place.

The following rodent faunal lists are as complete and accurate as it was possible to make them. Determinations have been brought up to-date whenever possible, and some genera of doubtful presence eliminated. It is extremely difficult to give accurate faunal lists of the Great Plains Pliocene since considerable reworking and indistinct contacts seem to be characteristic of these deposits. Moreover, the exact locality of many types are not known as collecting in this region was inaugurated in the days of Joseph Leidy.
28.

Rodent faunas which are too poorly known, and possess no particular importance are omitted.

LOWER PLIOCENE

Fish Lake Valley Fauna (the Esmeralda of Stirton)

Locality: Fish Lake Valley, Esmeralda Co., Nevada

Rodentia

Family Mylagaulidae
  Mylagaulus, sp. (cf. monodon Cope)
Family Castoridae
  Eucastor dividerus Stirton
Family Heteromyidae
  Perognathoides tertius (Hall)
  Perognathoides quartus (Hall)
Family Geomyidae
  Geomyid, gen. and sp. ?
Family Cricetidae
  Peromyscus dentalis Hall
  Macrognathomys nanus Hall

Lagomorpha

Family Leporidae
  Hypolagus cf. vetus (Kellogg)
  Sylvilagus?, sp.

Burge Fauna (of Stirton), Valentine Formation in Part

Locality: Valentine, Nebraska

Rodentia

Family Mylagaulidae
  Mylagaulus, sp.
Family Castoridae
  Eucastor, sp.
29.

Siestan Formation

Locality: Berkeley Hills, California

Rodentia
Family Castoridae
Eucastor lecontei (Merriam)

Lagomorpha
Family Leporidae
Lepus, sp.

The reference of lagomorph material to Lepus, by J. C. Merriam, is probably incorrect. Since there is no published description of the material the original designation is maintained, but the form represented is probably Hypolagus or some similar type.

Valentine Formation

Locality: Valentine, Nebraska

The Valentine formation was found by Stirton and McGrew to contain three faunal horizons, namely: the Niobrara River fauna (upper Miocene or transitional); the Burge fauna (lower Pliocene); and the Valentine fauna (transitional from lower to middle Pliocene). The usual faunal lists cover all three stages. The Burge fauna has already been listed. At present the Valentine fauna rodents have been determined only as representing the Castoridae. It should be noted that according to Stirton (oral communication) Cupidinimus nebraskensis Wood and ?Diprionomys, sp. nov. indet., heteromyids listed by A. E. Wood as coming from the Valentine, are representatives
of the Niobrara River fauna. A faunal list from the Valentine formation is given below for what it is worth. Part of the fauna is certainly upper Miocene.

Rodentia

Family Mylagaulidae
- Mylagaulus "monodon" Cope
- Epigaulus hatcheri Gidley

Family Castoridae
- Monosaulax, sp.
- Euextend, sp.

Family Heteromyidae
- Cupidinimus nebraskensis Wood
- Diprionomys agrarius Wood (Devil's Gulch beds, Teleoceras level)
- ?Diprionomys, sp. nov. indet. (determination by Wood)
- Heteromyid, n. gen. and sp., related to Microdipodops (Niobrara River fauna)

Lagomorpha
- some remains recorded

MIDDLE PLIOCENE

Bartlett Mountain Fauna

Locality: Bartlett Mountain, near Drewsey, Harney Co., Oregon

Rodentia

Family Mylagaulidae
- Mylagaulus cf. "monodon" Cope

Family Sciuridae
- Citellid, sp.

Family Castoridae
- Dipoides?, sp.

Family Geomyidae
- Geomyid?, sp.

Lagomorpha
- Family Leporidae
  - Leporid, sp.
Rattlesnake Formation

**Locality:** Dayville, Grant Co., Oregon

**Rodentia**
- Family Sciuridae
  - Otospermophilus gidleyi Merriam, Stock and Moody
- Family Castoridae
  - Dipoides, sp.

**Lagomorpha**
- Family Leporidae
  - Hypolagus near vetus (Kellogg)

Kern River Deposits


**Rodentia**
- Family Sciuridae
  - Citellus?, sp.
- Family Cricetidae
  - Peromyscus pliocenicus, n. sp.

**Lagomorpha**
- Family Leporidae
  - Hypolagus near limnetus Gazin
  - Hypolagus, small species

Smiths Valley Fauna

**Locality:** Smiths Valley, Lyon Co., Nevada

**Rodentia**
- Family Aplodontiidae
  - Aplodontid, sp.
- Family Sciuridae
  - Citellus?, sp.
- Family Geomyidae
  - Pliosaccomys dubius Wilson
- Family Cricetidae
  - Peromyscus near antiquus Kellogg
- Family Zapodidae
  - Pliozapus solus Wilson
Lagomorpha
   Family Leporidae
   Leporid, sp.

   Thousand Creek Beds

   Locality: Thousand Creek, Humboldt Co., Nevada

Rodentia
   Family Mylagaulidae
   Mylagaulus cf. monodon Cope
   Family Aplodontiidae
   Liodontia furlongi Gazin
   Family Sciuridae
   Marmota nevadensis (Kellogg)
   Marmota minor (Kellogg)
   Citellus, sp.
   Family Castoridae
   Dipoides, sp.
   Family Heteromyidae
   Diprionomys parvus Kellogg
   Cupidinimus magnus (Kellogg)
   Family Cricetidae
   Peromyscus antiquus Kellogg

Lagomorpha
   Family Leporidae
   Hypolagus vetus (Kellogg)

   Rome Fauna (Owyhee Formation)

   Locality: Rome, Malheur Co., Oregon

Rodentia
   Family Mylagaulidae
   Mylagaulus? cf. monodon Cope
   Family Castoridae
   Dipoides stirtoni Wilson
   Castor?, sp.
   Family Cricetidae
   Goniodontomys disjunctus, n. gen. and sp.

Lagomorpha
   Family Leporidae
   Hypolagus vetus (Kellogg)
   Hypolagus, sp.
There may be some doubt as to the association of the *Castor?* species with the remaining rodent fauna. The occurrence of the specimen in an area isolated from that in which the other rodents were obtained, and the presence of beds of possible upper Pliocene or Pleistocene age in the vicinity raises this question. However, not only the association in the field of *Castor?* with *Plihippus* teeth, but the characters exhibited by the specimen itself obviates this possibility to large extent.

**Upper Snake Creek Beds**

**Locality:** About twenty miles south of Agate, Sioux Co., Nebraska.

**Rodentia**

**Family Mylagaulidae**
- *Mylagaulus "monodon"* Cope
- *Mylagaulus sesquipedalis* Cope

**Family Sciuridae**
- *Sciurus cf. aberti* Woodhouse

**Family Castoridae**
- *Eucastor cf. tortus* Leidy
- *Eucastor, sp.*
- *Dipoides, prob. n. sp.* (according to Stirton)
- *Castor cf. Californicus* Kellogg

**Family Heteromyidae**
- *Perognathus coquorum* Wood

**Family Geomyidae**
- *?Thomomys, sp.*
- *?Geomys, sp.*

Similarly to the Valentine, the upper Snake Creek beds of the Great Plains apparently possesses a mixed fauna. There is some evidence that the upper Snake Creek fauna as usually listed involves faunas from some stage in the Miocene to faunas well up in the Pliocene. The rodent fauna listed above also seems to involve forms coming from several time stages.
Noticeably is this so in the case of the presence of both Eucastor and Dipoides, especially with associated Castor. Among the Geomyidae I have tentatively listed both Geomys and Thomomys. Both genera are sometimes listed as occurring in the upper Snake Creek beds but apparently this is an error. Matthew in 1924 lists only Thomomys, known by a single ramus without teeth. Matthew in an earlier contribution to the Snake Creek faunas has mentioned the presence of Geomys as evidenced by a lower jaw without dentition. Probably, a single specimen has accounted for both determinations, and the later assignment is Matthew's final opinion on the specimen.

While the upper Snake Creek rodent fauna has been listed its apparent composite nature militates against its use in correlation and the fauna is presented only for the sake of completeness.

UPPER PLIOCENE

Upper Etchegoin Formation (San Joaquin Clays)

Locality: Southwestern San Joaquin Valley, California

Rodentia
  Family Castoridae
    Castor californicus Kellogg
  Family Cricetidae
    Thomomys primus (Wilson)
Castor californicus is recorded from the Kettleman Hills, and Mimomys primus from the Buttonwillow gas field some distance away. However, the stratigraphy of the west side of the San Joaquin Valley is rather well known and the specimens apparently belong to approximately the same stage of geologic time.

Coso Mountains Fauna

**Locality:** Coso Mountains, Inyo Co., California

**Rodentia**
- Family Cricetidae
  - Mimomys primus (Wilson)

**Lagomorpha**
- Family Leporidae
  - Hypolagus near limnetus Gazin

Hagerman Lake Beds

**Locality:** Hagerman, Twin Falls Co., Idaho

**Rodentia**
- Family Sciuridae
  - Citellus?, sp.
- Family Castoridae
  - Castor, sp. (On the whole, intermediate between C. californicus and C. canadensis, according to Stirton)
  - Family Geomyidae
    - Thomomys gidleyi Wilson
- Family Cricetidae
  - Mimomys primus (Wilson)
  - Ondatra idahoensis minor Wilson

**Lagomorpha**
- Family Leporidae
  - Hypolagus near vetus (Kellogg)
  - Hypolagus limnetus Gazin
  - Alilepus? vagus Gazin
Grand View Fauna, Idaho Formation (?)  

**Locality:** Near Grand View, Owyhee Co., Idaho

**Rodentia**
- Family Castoridae  
  Castor cf. accessor Hay
- Family Cricetidae  
  Synaptomys vetus Wilson
  Mimomys? parvus Wilson
  Ondatra idahoensis idahoensis Wilson
- Family Erethizontidae  
  Erethizon bathygnathum Wilson

**Lagomorpha**  
- Family Leporidae  
  Hypolagus furlongi Gazin

Both the Grand View and Hagerman faunas come from beds which in the past have been called the Idaho formation. C. L. Gazin in various papers on the Hagerman fauna has referred to the beds near Hagerman as the Hagerman lake beds. The two faunas are probably separated somewhat in time, the Hagerman fauna being slightly the older.

Benson Fauna (San Pedro Valley beds)  

**Locality:** Near Benson, Cochise Co., Arizona

**Rodentia**
- Family Sciuridae  
  Citellus bensoni Gidley
- Family Heteromyidae  
  Dipodomys minor Gidley
  Cupidinimus magnus (Kellogg)
- Family Geomyidae  
  Geomys minor Gidley
  Cratogeomys bensoni Gidley
- Family Cricetidae  
  Peromyscus brachygnathus Gidley
  Peromyscus minimus Gidley
  Eligmodontia arizonae Gidley
  Onychomys bensoni Gidley
  Sigmodon medius Gidley
  Neotoma fossilis Gidley
Lagomorpha
Family Leporidae
Lepus, 2 sp.
Sylvilagus or Brachylagus, sp.

Curtis Fauna (San Pedro Valley beds)

Locality: Near Benson, Cochise Co., Arizona

Rodentia
Family Sciuridae
Citellus cochisei Gidley
Family Heteromyidae
Perognathus, sp.
Dipodomys minor Gidley
Dipodomys gidleyi Wood
Family Geomyidae
Geomyx parvidens Gidley
Family Cricetidae
Onychomys pedroensis Gidley
Sigmodon curtisi Gidley
Sigmodon minor Gidley
Neofiber?, sp.

Lagomorpha
Family Leporidae
Lepus, sp.

The Curtis and Benson mammalian assemblages, exclusive of the rodents, suggest a difference in age. However, both faunas seem to come from approximately the same stratigraphic horizon, in the same formation. While the rodent faunas do not suggest any great difference in age, few species are found to be common to both.

The problem of the San Pedro Valley faunas is also confused by a somewhat anomalous association of Pliocene and Pleistocene types among the larger mammals. The apparent association of Lepus with some of the more primitive types
of larger mammals is also confusing. The problem of these faunas will be discussed in more detail elsewhere.

Pliocene Rodent Genera (by stages)

*Lower Pliocene*

*Mylagaulus*
*M. Eucastror*
*Diprionomys*
*Epigaulus*
*Perognathoides*
*Macrogaphamomys*
*Peromyscus*
*Hypolagus*
*Sylvilagus*

The following genera reported from the Miocene and present subsequent to the lower Pliocene should be added:

?Geomys
?Thomomys
Perognathus
*Cupidinimus*
*Sciurus*
Citellus
*Liodontia*

*Middle Pliocene*

*Mylagaulus*
*Sciurus*
*Eucastor*
*Dipoides*
*Castor*
Perognathus
Thomomys
*Liodontia*
Marmota

Citellus
*Diprionomys*
*Cupidinimus*
*Pliosaccomys*
*Pliozapus*
Peromyscus
*Hypolagus*
Otospermophilus
*Goniodontomys, n. gen.*

The following genera should be added for the same reason given above:

?Sylvilagus
?Geomys
Upper Pliocene

Citellus
Perognathus
Geomys
Dipodomys
Onychomys
Sigmodon
?Neofiber
Cratogeomys
*?Cupidinimus
Peromyscus
Eligmodontia

Genera to be added:

Sciurus
Marmota
Otospermophilus

* genus extinct

Pliocene Rodent Evolution

Family Ischyromyidae

The Ischyromyidae have not been recorded from the Pliocene. Their last appearance may have been in the John Day faunas. The Museum of Paleontology, University of California, possesses an undescribed genus of rodent from the middle Pliocene of the Great Plains. This genus of uncertain affinities, may possibly be related to the ischyromyids, but the probability is not very great.

Family Mylagaulidae

This family of fossorial rodents seems to have become extinct by the end of the middle Pliocene. They have not
been certainly recorded from any upper Pliocene beds.

The evolution of the family is not well known. Even the important question of individual and age variation has not been solved. There probably are two distinct phyla, one horned, the other hornless. The alternative view that the presence of horns is a sex character seems less likely as the absence of horns would place the female at a considerable disadvantage since the horns apparently were used in digging. Moreover, there seems to be a preponderance of hornless types. In the various skulls from the Institute collections none exhibit horns.

Horned mylagaulid types may not occur above the lower Pliocene or even the upper Miocene. Of the two horned specimens which have been described, Ceratogaulus is from the Pawnee Creek beds, and Epigaulus from the Republican River (upper Miocene?).

Two species of mylagaulids have been recognized in the Pliocene, namely, Mylagaulus monodon and M. sesquipedalis. The types of both species are, however, from upper Miocene or questionably lower Pliocene beds. The two are distinguished by the fact that M. sesquipedalis is smaller; possesses fewer lakes; the lakes are less elongate, and more irregularly arranged. M. monodon is the more common type and practically all Pliocene mylagaulids have been referred to this species. It differs from the more typically Miocene forms by its large size, relatively high number of lakes, which tend to
align themselves in rows, and the fact that cement frequently forms an integral part of the wearing surface of the teeth (as in Mesogaulus). According to Matthew, the type of *M. monodon* is probably identical with *Epigaulus hatcheri*. The latter genus and species is horned. Although Gidley states that *E. hatcheri* is from the upper Miocene, it is possible that the type comes from beds of middle Pliocene age. A more complete statement of this possibility is given in the discussion of the Rome mylagaulids in a later section of the thesis.

It is not practical to discuss here more fully the problems associated with the Mylagaulidae. In many ways little is known about the group and present knowledge has been summed up by various authors, principally by Matthew in 1924.  


More specific discussion of a few of the problems will be presented in this paper in the section dealing with the Rome rodent fauna.

**Family Aplodontiidae**

The known history of the Aplodontiidae extends from the upper Eocene to Recent. However, aplodonts are relatively rare as fossils, and the post-John Day forms are limited to the middle Miocene *Liodontia*, middle Pliocene *Liodontia*,
Pleistocene and Recent Aplodontia, and a single specimen from Asia, Aplodontia? asiaticus (lower Pliocene?). In addition, a single upper premolar of an aplodontid is known from the Cedar Mountain region. Stirton has made the most recent determination on this specimen and regards it as representing Meniscomys (Allomys), and middle Miocene in age. It is more probable, however, that the specimen represents a DP4 of Liodontia alexandreae or closely related species as suggested by C. L. Gazin, unless Stirton has obtained additional material from this locality.

The chief changes which took place between the middle Miocene and middle Pliocene were, in Pliocene forms:

1. mesostyles on upper teeth more acute;
2. reduction of ventral protuberance on lower jaws (approaching Aplodontia);
3. changes in the development and position of masseter muscle (strongly developed and slightly farther forward, approaching Aplodontia); and
4. antero-external fold of lower molars more reduced. There was apparently no increase in size.

Liodontia is usually assigned to a position intermediate between Meniscomys hippocus (Allomys) and the Quaternary Aplodontia. The later Tertiary form is distinguished from Aplodontia by the absence of a mesostylid on the lower molars of the former genus, and by an early reduction of the antero-external fold in the lower cheek-teeth. While Liodontia is certainly intermediate between the John Day and Recent aplodontids, it
seems rather doubtful to the author if *Aplodontia* is a
direct descendant of the Tertiary genus.

**Family Sciuridae**

The Miocene has furnished more or less complete skulls
of both *Sciurus* (tree-squirrels) and *Citellus* (ground-squirrels). These forms, especially those recorded in the Skull Spring
middle Miocene fauna, probably do not represent Recent *Sciurus*
and *Citellus* in a strict sense. In a broad way, however,
they do represent a differentiation into tree-squirrel and
ground-squirrel types.

No skulls or even fragments of skulls have been secured
as yet from Pliocene beds. Hence, our whole knowledge of the
family for the Pliocene epoch is based on the dentition. Un-
fortunately, the dentition is extremely stable in the Sciuri-
dae. It is the little modified descendant of the ancestral
*Paramys* type, and in this respect is closer to the ancestral
stock of the Rodentia than any other modern family of rodents.
As a result, Pliocene sciurids offer little help in problems
of correlation. Both tree-squirrels and intermediate types
of ground-squirrels, which are fairly close to Recent types,
are found in Pliocene strata. Some of the more specialized
sciurids, such as *Marmota*, are also recorded. Noteworthy
perhaps is the fact that no typical ground-squirrel of the
genus *Citellus* has been recorded as yet in strata older than
the upper Pliocene. Hence, the appearance of these sciurids may be of value in correlation. However, until more complete phylogenies of the Sciuridae can be established this fact is negative evidence, and should be used with caution.

Family Castoridae

Pliocene beavers appear to be represented only by the genera Eucastor, Dipoides, and Castor. These genera fall into two distinct phyla. Pliocene Castor represents the more primitive ancestor of the existing beaver (Castor), and Eucastor-Dipoides culminates perhaps in the Pleistocene extinct giant beaver, Castoroides.

The earliest appearance of Castor, on this continent, may be in the upper Snake Creek and Rome middle Pliocene faunas. Members of the genus are not abundant, however, until the upper Pliocene. Pliocene Castor is distinctly shorter crowned than Quaternary representatives of the genus, and with more complete material it may be found necessary to distinguish the former, at least in part, under a separate generic name. Somewhat similar forms in the Pliocene of Asia have been made the types of a new genus, Sinocastor, by Young. The direct ancestor of Castor is not found in North America, and Pliocene forms on this continent probably migrated here during this period. However, the lower Miocene Paleocastor, perhaps is ancestral in a broad way to the line terminating in Castor.
Eucastor and Dipoides are successive types of an evolutionary series beginning with Monosaulax of the middle and upper Miocene and possibly leading to Castoroides. Dipoides is restricted apparently to the middle Pliocene of North America. Eucastor is characteristic of the lower Pliocene, although it is recorded also from the upper Snake Creek. Its presence in the middle Pliocene fauna may be the result of reworking or of mixing during collecting. An alternative explanation is that it is a survivor from the lower Pliocene.

Dipoides is distinguished from Eucastor by (1) a lengthening of the tooth crown; (2) simplification of cheek-tooth pattern, and persistency of the simplified pattern (i.e. resistance to the formation of lakes); and (3) increase in size.

Possibly, as has been mentioned above, Dipoides in turn gave rise to Castoroides, since otherwise the Pleistocene genus stands in a strangely isolated position. This view has been advocated by Matthew, and more recently by Stirton. In favor of the above belief is the striking resemblance in cheek-tooth pattern, and continued increase in hypsodonty and size. However, Castoroides has been placed in a distinct family, the Castoroididae, by Hay, Gidley, and others, on the basis of the quite noticeably modified skull. A skull of Dipoides described by Young appears to be fairly close to Castor. It might be added that although Castoroides shows
an increase in size over Dipoides, this increase is tremendous, and a beaver phylum in which the various species have been smaller than other castorids for most of its evolutionary history would have to give rise suddenly to forms which are the largest of all known beavers, and the largest of North American rodents. Unfortunately, no upper Pliocene types are known which are related to either Dipoides or Castoroides so that the descent of Castoroides can not be definitely determined.

Beaver types are known from the Niobrara River fauna (upper Miocene or transitional) which are intermediate between Eucastor and the Miocene Monosaulax. Typical Monosaulax, however, is less progressive than Eucastor with less hypsodonty in the cheek-teeth, more tendency to form isolated lakes, and so forth. Until Stirton's work on the Tertiary beavers, Monosaulax was confused with Palaeocastor but the genus apparently is more closely related to the Old World Steneofiber than to North American palaeocastors.

Family Heteromyidae

All three subfamilies of Heteromyidae were in existence by lower Pliocene, namely the Perognathinae (pocket-mice), Dipodomyinae (kangaroo-rats), and Heteromyinae (spiny pocket-mice). Representatives of the kangaroo-rats are rather poorly known, however, and indicate that this group is not as important a division of the family as the other two. The only
Recent genus of heteromyid in existence by the lower Pliocene is *Perognathus*, the most unspecialized of the modern genera.

In contrast, during the upper Pliocene the only extinct genus so far recorded is *Cupidinimus*. Even the presence of this genus in the upper Pliocene is very doubtful, but the form represented is not referable to any living genus.

Several aberrant lines are indicated by Pliocene heteromyid material. *Cupidinimus magnus*, if heteromyid at all, is an aberrant kangaroo-rat, *Perognathoides* an aberrant pocket-mouse, and *Diprionomys* an aberrant heteromyine. Unfortunately, as is so often the case with fossil rodents, as well as larger mammals, only the approximate ancestors of Recent genera are known. Exception to this statement is seen in the Pliocene *Perognathus*, and possibly an extinct genus (undescribed) from the Niobrara River fauna which is related to the Recent *Microdipodops*. The direct ancestors of the the living spiny pocket-mice, *Heteromys* and *Liomys*, are not known.

The detailed evolution of the Heteromyidae is too involved for discussion in the present paper. For further particulars, A. E. Wood's paper on the Heteromyidae should be consulted.15

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Pliocene heteromyids are represented by the following genera:

(1) Lower Pliocene
   *Cupidinimus, *Perognathoides, *Diprionomys, Perognathus

(2) Middle Pliocene
   *Cupidinimus, *Diprionomys, Perognathus

(3) Upper Pliocene
   *Cupidinimus, Dipodomys, Perognathus

* extinct genera

**Family Geomyidae**

In spite of some determinations to the contrary, Pliocene gophers appear to be restricted to the true gophers of the subfamily Geomyinae. The extinct group of the Entoptychinae have been reported from the Pliocene in two cases. A single tooth from the Fish Lake Valley beds was referred by E. Raymond Hall to Entoptychus? However, Hall pointed out that even reference of the specimen to the Geomyidae is doubtful. Miss Louise Kellogg has referred a specimen from the Thousand Creek to Entoptychus minimus, new species. This species is congeneric with Diprionomys from the same locality, and perhaps specifically identical with D. parvus. In other words, it is heteromyid and not geomyid.

Lower and middle Pliocene gophers are in a state of considerable confusion. Some of these, as for example
Pliosaccomys, are far removed from Recent genera. The Recent forms, Geomys and Thomomys, have been reported from the early Pliocene and even from the Miocene. It must be admitted that it seems highly probable that Thomomys, at least, was present by lower Pliocene time. On the other hand, no adequate description of any gopher material in the lower and middle Pliocene which might be referred to a Recent genus has ever been published. None of the specimens have even been figured.

The first undoubted Recent genera are from the upper Pliocene, and Geomys, Cratogeomys, and Thomomys have been reported from this stage.

The genus Pliosaccomys from the early Pliocene appears to be a true geomyid, although a very primitive form for so late a stage in time. It is highly probable that this genus is aberrant, certainly so if Thomomys is actually present in the lower Pliocene. However, in the absence of any other types which are adequately known, it can be used to suggest the main features of Pliocene evolution in the gophers. The relationships of this form are discussed in a paper by the author on the Smiths Valley rodent fauna. The problem is too involved to be discussed at this point.

Characters in Pliosaccomys together with certain features of the Recent genera, especially the character of the unworn geomyid tooth, suggest that evolution in the Pliocene proceeded toward acquiring of (a) persistent growth of crown;
(b) differentiation of the enamel of the tooth crown into discontinuous bands; and (c) more completely fossorial characters.

**Family Cricetidae**

The evolution of later Tertiary cricetids is very poorly known even for rodents. Only three genera have been recognized in the lower and middle Pliocene and only one of these, the Recent genus *Peromyscus*, has any descendants in the upper Pliocene and Quaternary. Hence, observations on the evolution of the family during the Pliocene are limited to remarks on *Peromyscus* and a few statements concerning the relations of upper Pliocene species to Recent species.

The family Cricetidae may be conveniently divided into two groups, the Cricetinae and the Microtinae. The former group is characterized by rooted molars whose crowns are normally brachydont and tubercular. A gradual transition exists to more flat-topped, prismatic teeth. The teeth are never rootless, however, and the posterior terminations of $\text{M}_1$ and $\text{M}_2$ are never angular. This group comprises the forms usually referred to as rats and mice (deer-mice, cotton-rats, wood-rats, and so forth). The Microtinae are characterized by possessing flat-topped, prismatic teeth, which are usually but not invariably rootless. The posterior terminations of $\text{M}_1$ and $\text{M}_2$ are angular. They are the voles and lemmings.
Cricetinae

Two genera of cricetines are known from the lower Pliocene, Recent *Peromyscus* and *Macrognathomys*. The latter genus is aberrant and need not be considered further. *Peromyscus* is represented by a single species from Fish Lake Valley, *P. dentalis*. Compared to Recent species it is characterized by its low-crowned teeth and relatively unreduced third lower molars. It is much smaller than middle Pliocene members of the genus.

*Peromyscus* is the sole Cricetine genus known from the middle Pliocene. Two species are present. Both differ from the lower Pliocene form in much larger size, and higher crowned teeth. They approach *P. dentalis* in possessing a relatively unreduced M3, and thus differ from upper Pliocene and Quaternary species in which M3 is usually more reduced. The difference in size between middle and lower Pliocene species of *Peromyscus* is of more significance than at first appears. Three different middle Pliocene localities have furnished remains of *Peromyscus*, and the specimens from these localities all agree in large size. Actually, they are much larger than any species of the genus living at present in the confines of the United States. These species are also much larger than any other fossil species in the later Cenozoic with the single exception of *Peromyscus nesodytes* from the Pleistocene of Santa Rosa Island. The difference in size between lower and middle Pliocene forms is perhaps made more convincing by the statement that *Peromyscus* or *Peromyscus*...
like species from the upper Miocene of the Barstow and Tonopah faunas are also much smaller than middle Pliocene forms. Thus it seems likely that the middle Pliocene is characterized by possessing "gigantic" representatives of *Peromyscus*.

In a strict sense, the genus *Peromyscus* probably does not exist previous to the upper Pliocene, and the earlier species should receive separate generic recognition. However, in view of the present state of our knowledge it is convenient to continue to refer these related types to *Peromyscus*.

The known upper Pliocene species of *Peromyscus* are relatively small forms with reduced third lower molars.

Upper Pliocene cricetines, in contrast to the preceding stages, are known by a number of rather diverse genera, all of which are still living. It is worth noting, however, that although the genera are living genera, the species are extinct.

Unfortunately, all of our upper Pliocene cricetines come from the Benson and Curtis faunas of the San Pedro Valley. Thus we not only know nothing of the upper Pliocene cricetines of other parts of western North America, but the nature of the San Pedro Valley occurrence introduces doubt as to the exact age of the fauna from this area. In these faunas we find the earliest record of *Sigmodon* (cotton-rat), *Onychomys* (grasshopper-mouse), and *Neotoma* (wood-rat). Moreover, *Eligmodontia* is likewise recorded from this locality. This genus is of interest since it is now confined to South
America. Whether the Arizonan species was invading or leaving North America is not known. It is not necessary to discuss the detailed characters which separate the upper Pliocene cricetines from their living relatives. The characters are minor ones but apparently distinct.

**Microtinae**

Pliocene microtines are practically confined to the upper stage of the epoch. This statement has world-wide application at present. The earliest record of a microtine may be that of *Poamys* from the lower Snake Creek Miocene. Matthew has suggested the genus as a structural ancestor. The genetic relationship of this genus to the microtines remains to be proved. The only other pre-upper Pliocene record is that of the new genus, *Goniodontomys* occurring in the Rome fauna of middle Pliocene age. Perhaps reference of this genus to the microtines is subject to some doubt but it seems closer to this group than to any other. If it is admitted that the genus is microtine, it points to the fact that the early voles possessed simpler teeth than at present, rather than more complex ones as has been advocated by M.A.C. Hinton. *Goniodontomys*, if a vole, is an aberrant member of the group without descendants.

Certain upper Pliocene localities have yielded abundant, if incomplete remains of Microtinae. They are markedly less advanced than Recent types. In most of them, in comparison
to Recent types, there is a decided difference in tooth pattern, less persistent growth of the teeth, and a lack of cement deposit on the teeth. Some upper Pliocene microtines are even distinct generically from Recent forms. Both voles and lemmings are represented in the faunas. The latter are the only myomorphs with rootless teeth so far discovered in the North American Pliocene.

The microtine group has been used in Europe with marked success in correlation problems. Work on this group in North America also should prove fruitful. As a matter of fact, it appears that if studies on the evolution of any group of mammals in the upper Pliocene-Pleistocene is to bring success in zoning this period of time, it will be in connection with the microtine Rodentia. The group also offers possibilities of inter-continental correlation, especially as regards to the genus *Mimomys.*

The following cicitids have been recorded from the Pliocene:

**Lower Pliocene**
- *Peromyscus, *Macrognathomys*

**Middle Pliocene**

**Upper Pliocene**
- *Onychomys, Sigmodon, Peromyscus, Eligmodontia, Neotama, Neofiber, Synaptomys, Ondatra, *Mimomys*
  - *extinct*

It is evident from the above list that few of the upper
Pliocene genera have any known ancestors in the earlier Pliocene. This point will be discussed later in some detail as it has an important bearing on correlation of rodent faunas.

Family Zapodidae

The only known North American Tertiary representative of the Zapodidae is Pliozapus from the middle Pliocene of Smiths Valley. Strangely enough at first sight, this genus is more closely related to the Recent Asiatic genus Eozapus than it is to either Zapus or Napaeozapus, Quaternary representatives of the family on this continent. In cheek-tooth characters Eozapus is distinctly more primitive than either Zapus or Napaeozapus which explains to some degree its closer approximation to Pliozapus. Pliozapus, as represented by its single species solus, could hardly have given rise to Eozapus as the species is already too specialized. However, in most of its characters it is a good structural ancestor for the Asiatic type. If the Smiths Valley genus is ancestral also to Recent North American types, considerable evolution must have taken place in regard to height of crown, and more particularly in the development of the highly complex tooth patterns of Zapus and Napaeozapus. The ramus of Pliozapus, however, is quite close to that of Recent North American zapodids.

The North American ancestors of Pliozapus, if they are
to be found on this continent, are quite unknown unless the Sespe Eocene Simimys proves to be a zapodid. *Protoptychus* from the Uinta and *Pacculus* from the John Day have both been referred, by Hay, to the Dipodoidea. A. E. Wood has suggested recently that *Pacculus* is a cricetid. *Protoptychus* even if a dipodid can not be even distantly related to *Pliozapus*. Moreover, both *Protoptychus* and *Simimys* are so far removed in time from *Pliozapus* that whatever their true relationships, they can have little real bearing on the problem of later zapodid evolution.

**Family Erethizontidae**

Hystricomorphs are typically developed in South America, and all North American forms are invaders from that continent, or descendants of those invaders. For this reason, no hystricomorphs are found in North America before the later Tertiary union with the southern continent was established.

The first undoubted appearance of the group is seen in the presence of the extinct species *Erethizon bathygnathum* in the upper Pliocene Grand View fauna. The principal differences between this species and living North American porcupines are in the heavier jaw, and slightly different tooth proportions.

The first appearance of hystricomorphs on this continent should furnish an important marker when the date can be established. South American sloths have been found in our fauna as early as the upper Snake Creek and Rattlesnake
so that it is not certain that the upper Pliocene marks
the first appearance of southern rodents in our faunas.
Moreover, *Hystricops* Leidy (upper Miocene?) has been referred
at various times to both the beavers and the porcupines.
Stirton has considered this genus as castercid.

**Family Caviidae**

Guinea-pigs related to the living giant capybara of
South America are found in the Pleistocene faunas of North
America. So far, none of these forms have been recorded from
the Pliocene. An exception to this statement may have to
be made in the case of a single cheek-tooth of *Hydrochoerus?*
from the Rio Virgenes fauna of southern Nuevo Leon, Mexico.
This fauna is either late Pliocene or early Pleistocene.

**Family Ochotonidae**

As has been mentioned previously, the lagomorphs are not
rodents in a strict sense. Since, however, the order Lagomorpha
is so restricted and compact, and they are usually associated
with rodents in a popular sense both groups have been included
in the present paper.

The lagomorph family Ochotonidae or pikas have not been
definitely recorded in the Pliocene. The presence of an aberrant
ochotonid in the Virgin Valley middle Miocene fauna and the
occurrence of *Ochotona* in the Recent fauna indicates their
presence in the Pliocene. Probably, undescribed pikas
are in existence in Pliocene lagomorph collections but have
been confused with the leporids. The Fish Lake Valley lagomorph described by E. Raymond Hall as *Sylvilagus?*, sp. may be such a form. The specimen is very poorly preserved but is suggestive of the pikas in the narrow union of the anterior and posterior columns of the lower cheek-teeth.

**Family Leporidae**

No definitely observable evolution takes place in Pliocene Leporidae. The genera include *Hypolagus, Sylvilagus?*, *Alilepus?*, *Lepus*, and *Sylvilagus* or *Brachylagus*. *Hypolagus* is the most important Pliocene genus, and *Lepus* deserves mention because of stratigraphic problems attached to its first appearance in North America. The other genera are of minor importance and will not be mentioned further.

The generic status of *Hypolagus* has long been a subject of considerable debate. Matthew always held to the view that there was not sufficient evidence to warrant its recognition as a distinct genus. However, more later work, and the general tenure of the evidence suggests that *Hypolagus* is entitled to generic rank. Moreover, distinct or not, the genus is distinguishable from *Lepus*, and there is little evidence to indicate that it ever gave rise to the Recent *Lepus*.

*Hypolagus* and *Lepus* have never been found in association in the Pliocene, and the only fauna in which this occurs is the lower Pleistocene Anita, Arizona assemblage. In this case the species of *Hypolagus* present in the fauna may not be
a typical *Hypolagus*. This is the last appearance of the genus. The earliest record of *Lepus* is in association with the Benson and Curtis faunas of San Pedro Valley, Arizona.

In the opinion of the author, *Lepus* is to be considered an emigrant from Asia and its appearance in North America resulted in the rapid extinction of *Hypolagus*. Moreover, *Lepus* seems to have arrived at about the opening of the Pleistocene as defined in this paper, and faunas in which *Hypolagus* but not *Lepus* is present are older than faunas in which the modern genus is a member. According to this view, the Grand View and Hagerman faunas are older than the San Pedro Valley faunas, if *Lepus* is actually associated with them. As the view that the San Pedro Valley faunas are younger than those from Grand View and Hagerman is probably not held by many or any American paleontologists at present, a more complete discussion will be presented in a later section of the thesis.

Analysis of Pliocene Rodent Faunas

The following lists are in part a repetition of those already given. They are repeated for the sake of clearness in the sections to follow. Most of the doubtful genera have been omitted. Likewise genera which were undoubtedly present (for example *Liodontia* in the lower Pliocene) but have not been recorded are also omitted. The latter omission is made in order to give ratios of myomorphs to sciuromorphs without
including genera which have not actually been found.

**LOWER PLIOcene**

**Order Rodentia**
- *Family Ischyromyidae*
  - none
- Family Aplodontiidae (North America and Asia?)
  - none
- *Family Mylagaulidae (North America)*
  - *Mylagaulus* (one species)
  - *Epigaulus* (one species)
- Family Sciuoridae (practically world-wide distribution)
  - none
- Family Castoridae (Holarctic)
  - *Eucastor* (four species)
- Family Heteromyidae (North America)
  - *Perognathoides* (two species)
  - *Diprionomys* (one species)
- Family Geomyidae (North America)
  - none
- Family Cricetidae (practically world-wide distribution)
  - *Peromyscus* (one species)
  - *Macrognathomys* (one species)
- Family Zapodidae (North America and Eurasia)
  - none
- Family Erethizontidae (North America)
  - none
- Family Caviidae (South America; Pleistocene of North America)
  - none

**Order Lagomorpha**
- Family Leporidae (practically world-wide distribution)
  - *Hypolagus* (one species)

| Lower Pliocene extinct genera | 7 |
| Lower Pliocene living genera | 1 |
| Lower Pliocene sciuromorph genera | 5 |
| Lower Pliocene myomorph genera | 2 |
| Lower Pliocene hystricomorph genera | 0 |

If lower Pliocene genera which are known to be present but have not so far been recorded are added to the above list the predominance of sciuromorphs over myomorphs is increased to five to one. Not enough types are known for this ratio to
mean very much in a mathematical sense, but it is never-the-less true that the sciuromorphs greatly outnumber the myomorphs. Practically all known lower Pliocene rodents represent extinct genera. Even *Peromyscus*, in the above list, is probably generically distinct from the living form. The only living North American genera which very likely extended back without generic change to the lower Pliocene are *Perognathus*, *Sciurus*, *Citellus* (in a broad way), and possibly *Thomomys*.

It should also be noted that there is no decided faunal break between the upper Miocene and lower Pliocene faunas. None of the lower Pliocene genera appear to be introduced types, and the whole fauna evolved from existing North American Miocene forms. Probably, the only very distinctive rodent type for this stage is *Eucastor*.

The lower Pliocene rodent faunas can be characterized as follows:

1. great predominance of sciuromorphs over myomorphs
2. high percentage of extinct genera
3. no strikingly new or introduced types
4. presence of the genus *Eucastor*

**MIDDLE PLIOCENE**

Rodentia
*Family Ischyromyidae*
  none
*Family Mylagaulidae*
  *Mylagaulus* (one species?)
Family Aplodontiidae
  *Liodontia (one species)

Family Sciuridae
  Sciurus (one species)
  Citellus (one species?)
  Marmota (two species)
  Otospermophilus (one species)

Family Castoridae
  *Dipoides (probably two or more species)
  Castor (one species?)

Family Heteromyidae
  *Diprionomys (one species?)
  *Cupidinimus (one species)
  Perognathus (one species)

Family Geomyidae
  *Pliosaccomys (one species)
  Thomomys (one species?)

Family Cricetidae
  *Goniolonotomys (one species)
  Peromyscus (two species)

Family Zapodidae
  *Pliozapus (one species)

Family Erethizontidae
  none

Family Caviidae
  none

Lagomorpha
  Family Ochotonidae
    none
  Family Leporidae
    *Hypolagus (three species?)

Middle Pliocene extinct genera 8
Middle Pliocene living genera 8
Middle Pliocene sciromorph genera 13
Middle Pliocene myomorph genera 3
Middle Pliocene hystricomorph genera 0

Due to the larger number of known middle Pliocene genera the sciromorph predominance over the myomorphs is more convincing. There are relatively fewer extinct genera. The ratio of living to extinct genera during this stage is about one to one. Several introduced or at least distinctly
new types are present, namely; Castor, Goniodontomys, and possibly Pliozapus. The introduction of the true beaver phylum (Castor) from the Old World is fairly well established. Moreover, the only beavers which appear to be related to Castor and are older than middle Pliocene, are Old World types. The microtine genus Goniodontomys may also have an Old World background. It is usually agreed upon that the Old World was the seat of higher myomorph evolution, but it should be pointed out that no microtine older than, or as old as Goniodontomys has ever been found there. If Poamys from the lower Snake Creek can be shown to be approximately ancestral to the Microtinae, this continent may after all be the site of evolution of some of the higher Myomorpha. Pliozapus may also be an introduced type but it seems possible that North America was the place of evolution of the Zapodinae. In this case, the upper Eocene Simimys may be a remote ancestor of the subfamily. The most distinctive middle Pliocene rodent is the beaver genus Dipoides. Dipoides appears to be characteristic for the mid-Pliocene everywhere in North America. It should be noted that the Mylagaulidae become extinct with the close of this stage. It has already been pointed out that large species of Peromyscus are characteristic for the middle Pliocene.

Middle Pliocene rodent faunas can be characterized as follows:

(1) great predominance of sciuromorphs over myomorphs
(2) genera about half extinct and half living
(3) introduction of *Castor* in later faunas
(4) first appearance of Microtinae
(5) presence of "gigantic" *Peromyscus*
(6) presence of the genus *Dipoidea*
(7) last appearance of the mylagaulid rodents

Nothing has been said so far concerning conclusions which may be drawn concerning the ecologic conditions under which the various faunas lived, and of the lower and middle Pliocene in general. Most of our rodent faunas are too incomplete to draw any very definite conclusions. Moreover, although we know a great deal about the ecology of living rodents, the application of this knowledge to fossil forms becomes increasingly uncertain as we go back in geologic time. In all probability forms which at present are restricted to certain types of environment, enjoyed a wider latitude in the past. In addition, many genera of living rodents occupy a wide range of environments even though particular species or races may be sharply restricted. Hence, the presence of a related type in the Pliocene does not very often suggest any definite living conditions. However, in many Pliocene rodents there is an increase in hypsodonty in middle Pliocene forms over those of the lower. The suggestion may be made that this is in response to the increasing aridity of the Pliocene; a response which culminated in the upper Pliocene with the appearance of many of our long-crowned Recent genera.
UPPER PLIOCENE

Rodentia

*Family Ischyromyidae
   none
*Family Mylagaulidae
   none
Family Aplodontiidae
   none
Family Sciuridae
   Citellus (two or more species)
Family Castoridae
   Castor (two species?)
Family Heteromyidae
   *Cupinus? (one species)
   Perognathus (one species)
   Dipodomys (two species)
Family Geomyidae
   Thomomys (one species)
   Geomys (two species)
   Cratogeomys (one species)
Family Cricetidae
   Peromyscus (two species)
   Onychomys (two species)
   Sigmodon (three species)
   Eligmodontia (one species)
   Neotoma (one species)
   Synaptomys (one species)
   Ondatra (one species)
   *Mimomys (two species)
Family Zapodidae
   none
Family Erethizontidae
   Erethizon (one species)
Family Caviidae
   Hydrochoerus? (one species)

Lagomorpha

Family Ochotonidae
   none
Family Leporidae
   *Hypolagus (three species)
   *Alilepus? (one species)
   Lepus (two species)

Upper Pliocene extinct genera 4
Upper Pliocene living genera 17
Upper Pliocene sciuromorph genera 8
Upper Pliocene myomorph genera 3
Upper Pliocene hystricomorph genera 2
For the first time in the Tertiary of North America, myomorphs form an important element in the fauna. The above ratio of one to one is probably in a large measure accidental but that there is a relative increase of myomorph genera can not be doubted. A decrease of sciuromorph genera is also indicated but this is fortuitous. Undoubtedly all Recent genera of Sciuromorpha were in existence by the end of the Pliocene which would double at least the above mentioned number.

An idea of the expansion of the myomorph element can be gained by recalling that all eight of the above genera belong to one family, the Cricetidae. The same family in the middle Pliocene has only two recorded representatives. Not only do the number of myomorph genera increase between the middle and upper Pliocene but the number of recorded specimens increase even more. Four myomorph genera are known from the lower and middle Pliocene. Of these, three are extinct, and one living. The extinct genera are represented by a total of only four specimens. I do not know how many specimens of myomorphs are actually known from the lower and middle Pliocene but from what I have seen an estimate would be less than two dozen, mostly Peromyscus. Specimens in the Institute collections of one upper Pliocene species alone, Mimomys? parvus, would exceed this figure. A specimen of Mimomys has been obtained even in an oil well core. Of course, it must be remembered that most myomorphs are very
tiny mammals, in general smaller than the average sciuromorph. It is only logical to suggest that this fact has influenced collecting. However, a number of small sciuromorphs have been collected, and this would in no way influence the number of specimens of pre-upper Pliocene myomorphs as compared to upper Pliocene and Pleistocene types. In many cases the same collectors are responsible for collections from each of the horizons, and collecting technique was approximately uniform.

If as it seems, therefore, there was a decided expansion of myomorph types in the upper Pliocene, this fact can be made useful in distinguishing upper Pliocene rodent faunas from other Pliocene assemblages. The expansion is probably due to a combination of evolution and of migration from other regions.

The generally high percentage of sciuromorphs in the early Pliocene rodent fauna of North America is in decided contrast to the faunas of the two adjoining continents, South America and Asia. The former continent possesses a large hystricomorph fauna and hence has no particular interest in connection with the subject under discussion. The Asiatic faunas, more particularly those of Northern China and Mongolia, show a decided myomorph predominance. The following rodent list from the upper Miocene and early Pliocene of Mongolia and Northern China is given for comparison with our own early Pliocene faunas. Some of the forms in this list are incorrectly determined but this is relatively unimportant since the
purpose is to show the contrast in the major details of the fauna between Asia and North America. It is also possible that some upper Pliocene genera are included in this list. In many cases it seems that the describers of the material did not know from what horizon the material came. Genera that appear too doubtful have been omitted.

### Asia (upper Miocene and early Pliocene)

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<thead>
<tr>
<th>Rodentia</th>
<th>Sciurromorpha</th>
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<tr>
<td>Aplodontia?</td>
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<td>Tamius?</td>
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<td>Gerbillinae</td>
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### North America (early Pliocene)

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<td>Citellus</td>
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<td>Castor</td>
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<tr>
<td>Perognathus</td>
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<tr>
<td>Perognathoides</td>
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<tr>
<td>Diprionomys</td>
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</tr>
<tr>
<td>Cupidinimus</td>
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<tr>
<td>Thomomys</td>
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<tr>
<td>Pliosaccamys</td>
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<tr>
<td>Myomorpha</td>
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<td>Pliozapus</td>
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<tr>
<td>Peromyscus</td>
<td></td>
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<tr>
<td>Macrognathomys</td>
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<tr>
<td>Goniodontomys</td>
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</tr>
<tr>
<td><strong>Sciurromorph genera</strong></td>
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<tr>
<td><strong>Myomorph genera</strong></td>
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<tr>
<td><strong>Hystricomorph genera</strong></td>
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</table>
A second distinctive feature in the upper Pliocene rodent faunas of North America as compared to the earlier faunas lies in the modernization of the faunas. Very few extinct genera are found, and with the possible exception of Hypolagus, these genera are fairly close to modern types.

A number of upper Pliocene genera have no immediate ancestors in the North American Pliocene. Such genera are: Sigmodon, Neotoma, Erethizon, Lepus, Alilepus?, the microtine genera, and possibly Eligmodontia.

Pliocene Sigmodon, Neotoma, and Eligmodontia are found only in the San Pedro Valley fauna. It should be noted that this fauna has the most southern position of any of the Pliocene rodent assemblages. Moreover, the above genera at present have a pronounced southern distribution. This statement is not true of Neotoma, but the genus is one of a number of genera which have such a distribution, and are sometimes included in a separate subfamily, the Neotominae. Several extinct South American rodents have also been included in this group. It is doubtful whether the Neotominae originated in any very southern locality, since the time available does not seem sufficient for an ancestral stock of the Neotominae to have migrated southward and then returned. However, some such event may in part account for the lack of immediate ancestors of Neotoma in the early Pliocene of North America.

A species of Sigmodon, namely atavus, has been recorded
by Schlosser from Mongolian Pliocene beds. G. S. Miller has stated that this supposed occurrence is false and made Schlosser's species the type of a new genus, Microtodon, without affinities to Sigmodon. This view is more nearly in accord with the distributional facts and Sigmodon is probably to be considered an offshoot from some American Peromyscus-like stock.

The present southern distribution of Eligmodontia has been mentioned. The genus is close enough to Peromyscus to have been derived from this form or its immediate predecessors before migration to South America, but what actually occurred is not known.

Erethizon and the Erethizontidae are undoubted derivatives of a South American stock. The first appearance of the family may be of considerable importance in Pliocene stratigraphy.

Lepus and Alilepus, if the latter is properly referred to the Asiatic genus, were invaders from Asia. It seems likely that Alilepus was an earlier arrival than the modern hare. The first appearance of Lepus, according to the author's views, is very close to the beginning of the Pleistocene as used in this paper.

The earliest appearance of Lepus is in the San Pedro Valley faunas. Lepus can hardly be considered a derivative of Hypolagus, and presumably invaded this continent from the north during the later Cenozoic. The rapid extinction of Hypolagus, consequent upon the arrival of Lepus is evidenced
by the fact that in only one known fauna, the Anita, of lower Pleistocene age, is there any association of the two genera. The Grand View fauna is either latest Pliocene or Pleistocene. Equine remains from this fauna are extremely close to Equus and perhaps could as well be assigned to that genus as to Plesippus. Hypolagus is a member of this fauna but no remains of Lepus are known. Since the fauna occupies a geographic position far to the north of the San Pedro Valley faunas, if Lepus had already arrived on this continent it should have been recorded. It thus seems reasonable to suppose that the San Pedro Valley faunas, on this basis, are younger than that from Grand View.

The San Pedro Valley fauna has been divided into two parts, an earlier fauna, the Benson, and a later one, the Curtis. Lepus is recorded from both. J. W. Gidley has regarded the Benson fauna as of upper Pliocene age and slightly older than the Blanco; the Curtis fauna as slightly younger.\(^\text{16}\)


Unfortunately, the only detailed descriptions of these faunas are of the rodents, lagomorphs, edentates, and proboscideans. Other forms have received only preliminary mention. Gidley records the presence of true Equus, Lama, Cf. Pliauchenia, Cf. Procamelus, Odocoileus, Merycodus, Stegomastodon, and Glyptotherium from the Curtis fauna. The Benson assemblage
includes Pliohippus, Hippotherium, Cf. Pliauchenia, Cf. Pro-
camelus, Platygonus, Merycodus, and Anancus. It should be
recalled that both faunas apparently occupy the same strati-
graphic position in the San Pedro Valley beds. The Curtis
fauna possesses some forms which may well be Pleistocene.
The apparently anomalous presence of Merycodus, and so forth,
suggests a reworking of the materials from this fauna, and
that part of the fauna is indeed Pleistocene, thus agreeing
with the evidence furnished by the presence of Lepus. If
this is true for the Curtis locality, in view of the supposed
agreement in stratigraphic position a similar circumstance
might also account for the presence of Lepus in the Benson
fauna. According to this view, not necessarily held by the
writer, two faunas are present, an upper Pliocene fauna
equivalent or slightly older than the Blanco, and a Pleisto-
cene fauna. I have not examined material from the Benson lo-
cality but that of the Curtis fauna in the Institute collec-
tions is very fragmentary, and is not incompatible with views
of reworking, even of the Curtis fauna. However, the rodent
faunas from the two localities indicate no great separation
in time. Moreover, Gidley's description of the occurrence and
the rather complete preservation in some cases, seemingly
militates against any mixing on a large scale.

In view of their southern position, the San Pedro Valley
faunas may appear slightly older than they actually are. This
suggestion, however, is again inadequate to explain entirely
the stage of evolution presented by some of the forms. The
author of course, is here concerned only with the presence of Lepus in the faunas. The Rodentia could well be upper Pliocene, but not older. Perhaps the hares are not a true member of either fauna and have been introduced, for example by burrowing.

The final solution of the problem of the San Pedro Valley faunas must await detailed descriptions of the remaining elements of the fauna, and perhaps more detailed geologic examination. For the present, these faunas present an obstacle to the view of a Pleistocene age for Lepus. A more complete description of the geologic occurrence is given by J. W. Gidley in Professional Paper 140.

Previous mention has already been made of the fact that the upper Pliocene seems to have marked the first appearance of "typical" members of the genus Citellus. The chief characteristics of the upper Pliocene rodent faunas are as follows:

(1) sharp faunal break with the middle Pliocene as evidenced in:
   (a) decided increase in the myomorph population
   (b) decided decrease in the number of extinct genera
   (c) first appearance of many modern types
(2) no Mylagaulidae
(3) presence of the genus Mimomys, as well as the relative abundance of microtines
(4) no Dipoideae, or at present any representative of the Eucastor-Dipoides line
(5) absence of Lepus, except perhaps in final faunal stages
The Grand View, Hagerman, Benson, and Curtis faunas are the only upper Pliocene rodent faunas complete enough to afford much evidence on ecologic conditions during the upper Pliocene. These faunas fall into two groups both geographically and ecologically. The Grand View and Hagerman faunas suggest the close proximity of fresh water, and of the general prevalence of rather moist conditions with abundant grasses. Moreover, the presence of voles and especially lemmings perhaps indicate a relatively cool climate. Lemmings in general point to a boreal or transition climate. Hence, their presence in the Grand View fauna might suggest the oncoming or actual glaciation of the continents. However, it must be pointed out that Synaptomys is found even in the upper Austral zone, its range extending as far south as North Carolina and Iowa. The Benson and Curtis faunas on the other hand, suggest in the presence of Dipodomys, Onychomys, and Perognathus, that the rodent fauna existed under arid or semi-arid conditions. The presence of Sigmodon and Neofiber suggest that areas of more moist surroundings were also present. On the whole, the Grand View and Hagerman assemblages point to a cool, rather moist climatic condition, and the San Pedro Valley fauna to a warm, drier environment.

During the early Pliocene there was a gradual increase in hypsodonty of the cheek-teeth in many rodent types. This
change seems to have become abruptly accelerated in the upper Pliocene. The oncoming of actual glacial conditions may account for the appearance of such forms as the microtines, and the increasing aridity for the appearance of Dipodomys and similar types.

Correlation of Pliocene Rodent Faunas

It must be admitted that the correlations made in this section are extremely tentative. Many of the rodent faunas are small and incompletely known. However, since this is practically a first attempt, these correlations are made with a view to seeing how far one may go with the evidence at hand, and how well rodent correlation checks with the more generally accepted ones made on the basis of mammalian assemblages as a whole. It would be as surprising to the author as to anyone else if some of the more exact correlations attempted were not in error. Perhaps such correlations as the present one should not be made, but it is presented in the nature of an experiment. In some cases, the larger mammals associated with the rodent faunas have not been studied in detail and the relative position of the faunas is not known. Hence, if the attempted correlations finally are proved correct, it may show that rodent work has already progressed to a stage in which it has value in detailed stratigraphy. If later studies show them to be incorrect then further study is needed in order to use the group successfully, or less likely,
rodents can not be employed in such work.

It seems fairly well established that the known Pliocene rodent faunas fall into three groups corresponding to the lower, middle, and upper stages of this paper. The characteristics of these stages have been listed in the preceding section. A fourth stage, characterized by the presence of *Lepus*, may also be present. If such a stage exists it would best be referred to the lower Pleistocene. Consequently, the chief characteristics of the upper Pliocene-Pleistocene rodent faunas would be as follows:

**upper Pliocene**

1. marked increase in myomorph genera
2. genera mostly living, but all species extinct
3. no mylagaulids
4. typical beaver is *Castor*
5. *Lepus* not present

**lower Pleistocene**

1. *Lepus* present
2. most if not all species extinct, and extinct species readily recognizable

**middle Pleistocene**

1. mixture of living types and those clearly extinct

**upper Pleistocene**

1. only existing species present, or if any extinct they are forms closely allied to living species (exception
to this statement must be made if genus is extinct, as may be the case if the aberrant *Castoroides* is present).

The Pleistocene stages are presented only as suggestions. Not enough recent work has been done on the rodent assemblages to furnish a basis for real faunal stages. The lower Pleistocene would be represented by the Anita, Arizona occurrence, and possibly the San Pedro Valley faunas, more certainly the Curtis fauna. The majority of the Eastern wet cave faunas would correspond to the middle Pleistocene, and the California tar pit assemblages to the upper. The age of the tar pit faunas has been a subject of much discussion. At first, Rancho la Brea was regarded as representative of the Aftonian interglacial stage. Later work has tended to transfer this assemblage to the upper Pleistocene. It is interesting to note that the rodent faunas of this and similar occurrences strongly suggest a late stage of Pleistocene time.

If some or all of the more typical upper Pliocene faunas are eventually placed in the Pleistocene, this will serve only to move up the Pleistocene faunas without changing their relative positions. In this event the appearance of *Lepus* in the faunas would not coincide with the beginning of the Pleistocene but with a later stage.

Certain Pliocene rodent faunas have been omitted from the discussion. These so omitted are either very poorly known or represent supposed mixed faunas. The following faunas are discussed in the present section: Fish Lake Valley,
Siesta, Bartlett Mountain, Kern River, Rattlesnake, Rome, Smiths Valley, Thousand Creek, Coso Mountains, upper Etchegoin, Hagerman, Grand View, Benson, and Curtis. These assemblages fall more or less readily into one or another of the three main faunal stages of this paper.

LOWER PLIOCENE

The Siesta and Fish Lake Valley faunas are characteristic of the lower Pliocene. The Siesta is so poorly known that it would have been omitted except for the fact that the beds have furnished material of Eucastror, one of the most useful of rodent types in correlation work. The species represented is clearly more advanced than that from Fish Lake Valley, and less advanced than Dipoides from the middle Pliocene. For this reason the Siesta is placed above the Fish Lake Valley fauna and below the mid-Pliocene faunas.

The Fish Lake Valley or Esmeralda fauna is clearly the most primitive of the rodent faunas dealt with in the present paper. Not only is it characterized by the most primitive known species of Eucastror, but Peromyscus dentalis, from this fauna, is distinctly more primitive than mid-Pliocene species. Moreover, the Fish Lake Valley heteromyids appear to be closely related to forms from the Barstow. The fauna would be considered Miocene by some paleontologists. The author has no preference for assignment to either the lower Pliocene
or upper Miocene, but the appearance of the genus *Eucastor* is a convenient Pliocene marker for rodent work. The Equidae from the Fish Lake Valley fauna are characterized by the presence of *Hipparion* which is still considered the "signpost" of the Pliocene by most workers.

**MIDDLE PLIOCENE**

The following faunas appear to be of middle Pliocene age: Bartlett Mountain, Rattlesnake, Kern River, Smiths Valley, Thousand Creek, and Rome. The relative position of these faunas in regard to one another is uncertain. The Bartlett Mountain fauna contains a species of beaver which is probably best referred to *Dipoides*. The species represented, if the generic reference is correct, is a primitive one so consequently this fauna has been placed at the base of the middle Pliocene. None of the other recorded forms in this fauna are especially characteristic.

A species of *Dipoides* is also recorded from the Rattlesnake. This species is apparently more advanced than the Bartlett Mountain form, and less advanced than *Dipoides stirtoni* from the Rome fauna. Hence, the Rattlesnake rodent fauna is considered as slightly younger than the Bartlett Mountain, slightly older than the Rome fauna.

No especially diagnostic forms are known from the Kern River. The presence of a large species of *Peromyscus* suggests
a middle Pliocene age. Since the fauna is one of those which I have used in attempting to show that the middle Pliocene was characterized by large species of *Peromyscus*, the line of argument is somewhat circular. However, even if this is true to a great extent, the middle Pliocene age of the Kern River assemblage as a whole is sufficiently well established. As a matter of fact, due to the fragmentary nature of most of the rodent faunas, more or less use must be made of other lines of evidence in arriving at age determinations. If the rodent faunas offer evidence concerning the relative ages of the faunas I have used that in preference to other lines, but in the absence of any conclusive criteria I have fallen back on the more usually accepted testimony of the larger mammals.

The Thousand Creek rodent assemblage is the largest and most complete of the middle Pliocene faunas. Fragmentary *Dipoides* remains are represented in the assemblage which may be identical with *Dipoides stirtoni*. A large species of *Peromyscus* is also recorded. The Thousand Creek rodent fauna is regarded as slightly older than that from Rome. The chief reason for this view is the presence in the latter of *Castor* and a microtine genus, *Goniodontomys*. These forms are more characteristic of the upper than middle Pliocene, and may point to the younger age of the Rome fauna. However, these animals are rare in the Rome collection, and their absence in that from Thousand Creek may be fortuitous or due to
different environmental conditions. The Rome assemblage as a whole may resemble the Rattlesnake more closely than it does the Thousand Creek.

The Smiths Valley fauna is tentatively regarded as approximately contemporaneous with, or slightly older than, the Thousand Creek fauna. Practically identical species of *Peromyscus* are found at both localities. A number of types, more fully known in the Thousand Creek fauna, are suggested by poorly preserved material from Smiths Valley. However, in most cases certain differences are evident which give the impression that the faunas are not exactly equivalent. The co-type of *Cupidinimus magnus* from the Thousand Creek shows certain resemblances to the Smiths Valley *Pliosaccomys*. If specific identity could be established the similarity of the two faunas would be strengthened. However, the relation of these rodent types can not be satisfactorily determined with the existing Thousand Creek material. At present they are even referred to separate families.

**UPPER PLIOCENE**

The upper Pliocene rodent faunas included in this discussion are: upper Etchegoin, Coso Mountains, Hagerman, Grand View, Benson, and Curtis. The latter four are the only faunas of any considerable number of types. The Hagerman-Grand View faunas differ so much in type of fauna from the Benson-Curtis assemblages that comparisons are quite limited.
I have placed the Idaho faunas as slightly older than the Arizonan, chiefly because the latter are characterized by the presence of Lepus, the former by Hypolagus.

The Grand View mammalian assemblage appears to be slightly younger than that from Hagerman. Rodent forms suggesting this difference in age are Mimomys primus, present in the Hagerman fauna, absent in the Grand View, and species of Ondatra. Ondatra from Grand View may be slightly advanced over that from the older locality.

The rodent faunas of the Curtis and Benson are quite close to one another. A slight difference in age may be indicated in certain instances, in which cases the Benson fauna appears to be the older. The only extinct genus recorded from either assemblage is from the Benson. In case a genus is represented in both faunas, the species are usually distinct with some evidence that Benson species may be slightly less advanced. However, there does not seem to be the anomalous association of advanced and primitive types indicated in some of the larger mammals.

The Coso Mountains fauna is tentatively correlated with the Hagerman, since both its rodent types, a vole and a lagomorph, are probably identical with Hagerman species. Similarly to the Coso Mountains fauna, only two rodent forms are known from the upper Etchegoin. This fauna is considered as slightly older than the Hagerman on the evidence
of the beavers. *Castor californicus* from the former assemblage is somewhat more primitive, according to Stirton, than the Hagerman beavers. The other species of rodent, *Mimomys primus*, is found at both localities.

It is quite possible that some of the faunas here referred to the upper Pliocene are actually lower Pleistocene. The possibility of this in connection with the San Pedro Valley faunas has already been mentioned. The Grand View fauna may also be more appropriately placed in the Quaternary. Barbat and Galloway, in a recent paper on the San Joaquin clay\(^{17}\) (upper Etchegoin)

\[^{17}\text{Barbat, W.F., and Galloway, J., Bull. A.A.P.G., Vol. 18, No. 4, pp. 476-499, 2 figs., 1934.}\]

have placed the strata (zone "B") in which *Mimomys primus* occurs, in the lower Pleistocene. *Castor californicus* apparently occurs in their zone "C" which is placed in the lower Pleistocene, or transitional between the Pliocene and Pleistocene. They tentatively correlated zone "C" with the Cromer Forest Bed, and the Las Posas (first interglacial). Zone "B" was correlated with the Mindelian glaciation of Europe, and the Timms Point. If Barbat and Galloway are correct in these views almost all of our upper Pliocene faunas could be placed in the lower Pleistocene. As a matter of fact even these authors have left the first glacial period (San Joaquin clay, zones "D" and "E"; Günz glaciation of Europe) in the upper Pliocene. According to the definition of the Pleistocene used by the United States Geological Survey, this glaciation
should also be placed in the Quaternary. Haug, in Europe, has maintained this viewpoint. Most paleontologists, at any rate, still include the first glaciaation in the Pliocene. However, according to Hay\(^{18}\) there has been some change of feeling, and several modern workers have placed the Norwich Crag, and so forth in the Pleistocene.

The author has no way of judging the correctness or incorrectness of Barbat's and Galloway's views. However, it seems hardly likely that *Mimomys primus* would occur in a faunal stage which could be associated with the Mindelian glaciaation. *M. primus* is closest in characters to *M. pliocoenicus* of Europe. This species is typical of the Norwich Crag and extends no higher than the lower Cromerian. The genus *Mimomys* might extend into the Mindelian, but the various species in the European deposits are relatively short-lived. Since *M. primus* is somewhat more primitive than *M. pliocoenicus* and this form in turn is in many ways the most primitive known European representative of the genus, it is improbable that the assignment of zone "B" to the Mindelian is correct. It also seems that these authors misunderstood a statement of mine as to the geologic range of *Mimomys*. They state that, "this species (*M. primus*) is nearly identical with a form found in Europe ranging from the Norwich Crag to the High Terrace of

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the Thames." The range cited is for the genus, not the species *M. pliocenicus*. Moreover, the American species is not "nearly identical" with *M. pliocenicus* but decidedly more primitive. As a matter of fact, English geologists themselves, apparently feel that attempts to correlate European glaciation with the English deposits have not met with success. If this is the case the whole problem is too hypothetical to deserve further mention here.

Pliocene glaciation may in part account for the marked change in the rodent faunas in the upper Pliocene as noted on previous pages. This change is sharper than any succeeding one, and from this standpoint it might be convenient to place the upper Pliocene rodent faunas in the Pleistocene. However considered, it seems likely that some of the upper Pliocene rodent faunas discussed in the present paper belong to the first glacial and interglacial stages. This point is interesting since O.P. Hay always maintained that Rancho la Brea was Aftonian (first interglacial). Since it is obvious that the faunas under discussion are in no wise equivalent to Rancho la Brea, these faunas furnish an additional reason for believing that Rancho la Brea is upper Pleistocene. In fairness to Hay it must be stated that he considered the San Pedro Valley fauna as possibly Nebraskan. Moreover, the Idaho faunas were very poorly known at the time Hay did most of his Pleistocene

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work.

Wherever the dividing line between Pliocene and Pleistocene may be drawn, the relative positions of the faunas are not altered. For that reason, among others, the author sees no necessity for any immediate change, and the faunas under discussion have been kept where usually placed, in the upper Pliocene.

The following chart is intended to represent in graphic form a tentative correlation of Pliocene rodent faunas. The second chart is presented for convenience in comparing the correlations obtained by a study of Pliocene rodents, and that suggested by the faunas as a whole. Some of the faunas have not been completely described so that doubt as to exact correlation exists in these cases. This chart is compiled, with some modifications, from correlations made recently in papers by Simpson and Stirton.


PLIOGENE RODENT CORRELATION

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<tr>
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<td>Upper Etchegoin</td>
<td>Coso Mountains</td>
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<td>Middle</td>
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<td>Siesta</td>
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The following section is devoted to the faunal studies from which was drawn the material presented in antecedent chapters. Studies which have been published are not repeated here although citations are given.

It is to be noted that the Rome, Kern River, and Coso Mountains assemblages are treated essentially as separate papers. The unavoidable repetition of certain parts consequent upon this method may not be altogether disadvantageous to the reader. However, the usual introduction, comparisons of the fauna as a whole to other faunas, and so forth have been omitted since this would entail too much recapitulation of previous pages.

LOWER PLIOCENE

No original studies of faunas pertaining to this stage were carried on. However, during the course of the work an examination was made of the greater part of the rodent collection from Fish Lake Valley, Nevada, including a study of the type material.
The Mylagaulidae present many problems which need to be solved before a satisfactory understanding of the group is reached. Not only are the various species in considerable confusion, but even the genera are in a rather poor state of definition. The relation of horned to hornless types has not been determined, nor has the limits of individual and age variation been fixed.

It has been suggested that the presence or absence of horns is a sex character. However, as Matthew has pointed out, no other known rodent possesses a like amount of sex distinction, although as he states further this argument is partly vitiated by the fact that no other rodent possesses horns. Such a variation, in a burrowing form in which the horns were presumably used as digging implements, would place the female at a decided disadvantage. Moreover, the Institute collection embraces a number of Miocene and Pliocene mylagaulids complete enough to demonstrate the presence of horns if such were actually the case. None of them do, and it is extremely unlikely that these and similar specimens elsewhere are all females.
Judging from the written descriptions, horned types are everywhere relatively rare.

It can be shown rather satisfactorily that the tooth-pattern undergoes considerable change during the life of the individual. The variation of the skull with age is not known, nor has there been a sufficient answer to the question of individual variation in the premolar pattern. In certain species the individual variation of teeth representing approximately the same stage of wear is not great. However, if the conclusion implied in this statement was used widely, an extremely large number of species in regard to number of known specimens would have to be recorded. Moreover, some of the mylagaulid material in the Institute collections points to considerable individual variation in species from the same horizon and locality. A study of this material suggests that one lake may divide to form two or more lakes, and less certainly, that two lakes may unite to form one. Small, accessory lakes apparently may be present or absent in a single species. Accessory lakes may disappear long before the tooth is worn out.

By means of relatively unworn teeth it is possible to identify in the upper premolar, the lakes with the original basins of the unworn teeth, and moreover, the dentinal areas with the original cusps just as has been done for the cheek-teeth of such forms as Equus. The lower premolar appears susceptible to a similar treatment although more difficult of
application. Use of this method of study leads to a clearer appreciation of the differences or similarities in two distinct species than can be obtained by citing the number of lakes present and their arrangement in a varying number of rows. The author feels that this method of study combined with sectioning of individual teeth might eventually lead to an understanding of the characters exhibited by isolated grinding teeth. Such work would have to be based primarily on a thorough study of species which are known by a considerable amount of material, and in which teeth in all stages of wear were present.

It seems likely that a greater number of species and perhaps genera are in existence than have been described. Burrowing types would seem to have a rather limited geographic range and in consequence a number of distinct species probably were present in each faunal stage. However, with our present understanding of the group the establishment of more types is decidedly not a desirable procedure.

Pliocene mylagaulids are known only by fragmentary material. A possible exception to this statement may be *Epigaulus hatcheri*, the type of which consists of a fairly complete skull and skeleton. Gidley referred the beds (Republican River) from which the type was obtained to the upper Miocene. The type locality is near Long Island, Kansas. Stirton has re-

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cently referred a fauna termed by him the Long Island fauna to
the middle Pliocene. *Mylagaulus monodon* and *M. sesquipedalis*
also have been recorded from Pliocene beds. The type locali-
ties of these two species are in Republican River beds, and
hence the exact age of the specimens are not known although
usually referred to the upper Miocene or lower Pliocene. A
referred specimen of *M. monodon* apparently comes from the same
beds as *E. hatcheri*. Matthew has suggested that *Mylagaulus*
monodon may have to be referred to *Epigaulus*. He states that
*M. Monodon* and *E. hatcheri* are probably identical.  
Matthew in describing the type of *M. monodon* states that F4
has no cement outside the external enamel ring. The type of
*E. hatcheri* was described by Gidley as possessing premolars
with an investment of cement which formed a functional part of
the teeth. This discrepancy can be removed only by assuming:
(1) cement was present originally on the type of *M. monodon*
but has sloughed away; or (2) the type was incorrectly des-
cribed (not probable); or (3) the presence or absence of cement
is not a distinctive character. Perhaps (1) is the most likely
explanation. *M. sesquipedalis* is distinguished from *M. monodon*
by its smaller size, fewer, less elongate lakes, and the more
irregular arrangement of the lakes.
Mylagaulus? cf. monodon Cope

Pliocene mylagaulids from the Great Basin have hitherto been known only by two isolated grinders. A P4 has been recorded by Miss Kellogg24 from Thousand Creek, Nevada, and E. Raymond Hall has described a lower premolar from the Fish Lake Valley beds of Nevada.25 As a consequence, mylagaulid material from Rome is relatively abundant. The most perfectly preserved specimen is an almost complete lower jaw, C.I.T. No. 72 (Pl. 1, figs. 8, 8a, 8b). The extreme tip of the coronoid is missing as is the posterior portion of the angle but the dentition is complete including all three molars. A second ramus, No. 1951, was also obtained although not as complete as No. 72. The dentition in this specimen lacks M1. Isolated premolars, Nos. 1952-1958 (Pl. 1, figs. 1-7), both upper and lower, and various fragmentary limb elements are present also in the Rome collection. Some of these limb bones are not easily distinguished from those of Dipoides stirtoni from the same locality. The two rami represent young individuals in which practically none of the enamel inflections have become isolated thus making comparisons with other specimens difficult. All the specimens have been considered as representing a


single species although this is a doubtful procedure in one or two cases.

The Rome species is characterized by possessing premolar teeth which become elongate with wear. The enamel lakes are numerous, elongate, and tend to arrange themselves in rows. The teeth possess an external investment of cement which in some cases at least is a functional part of the tooth. The ramus is very heavy and deep, thick transversely below the premolar. P4 possesses from six to usually nine lakes. The single specimen exhibiting six lakes, No. 1954 (Pl. 1, fig. 2) is relatively unworn and indicates an increase in the number of lakes with further wear. The lower premolars possess a minimum of eight lakes in a well worn tooth, and a maximum of nine although this figure might be increased to ten. The teeth are larger than those of Mylagaulus laevis but smaller than the type of Epigaulus hatcheri. A mylagaulid humerus is distinctly smaller than the comparable element in E. hatcheri.

The Rome species does not agree exactly with any described species, but may be closest to Mylagaulus monodon. Compared to the type of M. monodon, the Rome species possesses a larger ramus which is deeper and more distinctly bulged by the premolar. P4 is narrower transversely and possesses a higher number of lakes with somewhat different arrangement. A P4 referred by Cope to M. monodon agrees in size and shape with the Oregon type but the occlusal pattern appears to be distinct. If both the type and referred specimen of M. monodon
actually are conspecific the Rome specimens are rather close to them. However, cement forms a functional part of the wearing surface of the premolar which differs from the condition in *M. monodon* as described by Matthew.

*Epigaulus hatcheri* Gidley,²⁶ although with larger P4/4,


is comparable with our form in possessing cheek-teeth with an external coat of cement. The ramus of the Rome species apparently possesses slightly different proportions but is thick and deep below P4, a character of *E. hatcheri*. The tooth row is slightly shorter in the Oregon form, and P4/4 differ somewhat in pattern in the two species. If *E. hatcheri* and *M. monodon* are conspecific the Rome species would be close to that species. However, the upper premolars of the Rome type show a close agreement with those of a species of mylagaulid from Bartlett Mountain, Oregon (Pliocene). A very well preserved skull of the latter is without bony horn cores, a point of distinct disagreement with *Epigaulus*.

*Mylagaulus*, sp. from Fish Lake Valley, Nevada is represented by a single isolated P4. This species is smaller than the Rome type with somewhat different occlusal pattern. Unfortunately, the dimensions of the figure given by Hall do not check with his measurements. In any case the species is
probably distinct from our form.

The only other Pliocene mylagaulid on record from the Great Basin is an unworn P4 from the Thousand Creek beds described by Miss Kellogg. This specimen is referred to *Mylagaulus monodon*. Although Miss Kellogg compared this tooth directly with figures of the type of *M. laevis* in the belief that it was still referred to *M. monodon*, the Thousand Creek form is probably closer to the latter than to *M. laevis*. However, in the case of the Virgin Valley specimen referred by her to *M. monodon*, the figure shows a tooth more closely resembling *M*.* laevis* from Skull Spring than *M. monodon*. U.C. No. 12580, a P4 referred to *M. pristinus*, may also represent the Skull Spring species. Virgin Valley mylagaulids in the Institute collection indicate the presence of a species distinct from the Skull Spring type. Whether this second species is referable to *M. pristinus* was not determined. An isolated P4 in the Institute collection from Thousand Creek appears to be distinct from the Rome species.

The fragmentary limb material from Rome is too incomplete to add anything to our knowledge of the skeletal structure of the Mylagaulidae.

It is quite possible that *Mylagaulus?* cf. *monodon* from Rome represents an undescribed species of rodent. In view of our very incomplete knowledge of the Mylagaulidae nothing would be gained by establishing a new species.
Measurements (in millimeters)

<table>
<thead>
<tr>
<th></th>
<th>No. 72</th>
<th>No. 1951</th>
</tr>
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<tbody>
<tr>
<td>$P_4^-M_3^-$, alveolar length</td>
<td>19.1</td>
<td>17.8</td>
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<tr>
<td>Length of diastema, $I^-P_4$</td>
<td>10.6</td>
<td>----</td>
</tr>
<tr>
<td>Depth of ramus beneath $P_4$</td>
<td>18.9</td>
<td>----</td>
</tr>
<tr>
<td>Depth of ramus beneath diastema</td>
<td>12.6</td>
<td>----</td>
</tr>
<tr>
<td>Thickness (transverse) of ramus beneath $P_4$</td>
<td>11.8</td>
<td>----</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Maximum</th>
<th>Minimum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Several isolated $P_4$'s</td>
<td></td>
<td></td>
</tr>
<tr>
<td>greatest antero-post. diam.</td>
<td>12.0</td>
<td>11.0</td>
</tr>
<tr>
<td>greatest transverse diam.</td>
<td>6.4</td>
<td>5.6</td>
</tr>
<tr>
<td>Several isolated $P_4$'s</td>
<td></td>
<td></td>
</tr>
<tr>
<td>greatest antero-post. diam.</td>
<td>13.3</td>
<td>10.4</td>
</tr>
<tr>
<td>greatest transverse diam.</td>
<td>6.0</td>
<td>5.2</td>
</tr>
</tbody>
</table>

**Castoridae**

**Dipoides stirtoni Wilson**

Remains of this species of aberrant beaver are very common in the Rome fauna. A detailed account of the fossil material has already been published.\(^{27}\)

Castor, species

The true beaver is represented only by a single isolated $M_3$. This specimen, No. 1961 (Pl. 1, figs. 9, 9a), represented an individual about comparable in size to existing *Castor canadensis*. The base of the tooth is somewhat damaged but practically the full height of the cheek-tooth seems to be preserved. Three internal and one external lateral grooves are present as is normal for *Castor*. The external groove extends to the base of the portion preserved, while the three internal inflections extend somewhat less than half the distance to the base of the tooth. In a measure, the extent of the internal grooves is a function of the amount of wear that the tooth has undergone, but undoubtedly the grooves are much less persistent than in Recent species. The posterior groove (metastrid) is slightly longer than the other two (mesostriid and parastriid) which are equal in length. The occlusal pattern is that of a normal *Castor* except for the presence of an enamel lake in the anterior enamel loop. Such a lake is present in the first molar of a ramus of the Asiatic *Castor andersonii*, as figured by Schlosser. However, in this species $M_1$ and $M_2$

28 Schlosser, M., Palae. Sin., Ser. C, Vol. 1, Fasc. 1, Pl. 2, Fig. 43, 1924.

are shorter transversely than in the Rome molar, although $M_3$ has the same antero-posterior diameter, and $M_1$ only a slightly greater measurement. *Castor andersonii*, together with the Asiatic species *zdanskyi* and *broilii* have been placed by
Young in a new genus, *Sinocastor*. The author has not observed the above mentioned lake in any other specimens of *Castor*.

There may be some doubt as to the association of the Rome *Castor* with the rest of the rodent fauna. The occurrence of the specimen in an area isolated from that in which the other rodents were obtained, and the presence of beds of possible upper Pliocene or Pleistocene age in the vicinity raises this question. However, not only the association in the field of *Castor* with *Pliohippus* teeth, but the characters exhibited by the specimen itself obviates this possibility to a large extent.

True beavers from North America are extremely rare in beds older than the upper Pliocene. Two teeth from the upper Snake Creek (P4 and P4) and the present one are all that have been so far recorded. The geologic range of *Castor* is not accurately determined but the genus or closely allied types are known from the early Pliocene of Europe and Asia.

**Measurements* (in millimeters)**

M3?, antero-posterior diameter 8.2
M3?, transverse diameter 7.1

* measured at occlusal surface
107.

Microtinae?

Goniodontomys disjunotus, n. gen. and sp.

**Geological Horizon and Locality:** Middle Pliocene beds exposed along the Crooked Creek drainage, tributary to the Owyhee River, five miles southwest of Rome, Malheur County, Oregon. **Genotype:** No. 1959, C.I.T. Coll. Vert. Pale., an incomplete left ramus bearing $M_1-M_3$ (Pl. 2, figs. 2, 2a, 2b). **Referred Specimen:** No. 1960, C.I.T. Coll. Vert. Pale., a small fragment of ramus with left $M_3$ in place. **Generic and Specific Characters:** Mandibular incisor passing from lingual to buccal side of tooth row, and probably extending well up into the ascending ramus. Cheek-teeth, hypsodont, prismatic and flat-crowned, rooted and without cement. Re-entrant angles of cheek-teeth generally opposed. Re-entrant angles from opposite sides normally in contact. Enamel not differentiated into thick and thin tracts. $M_1$ with posterior loop, three triangles, and complex anterior loop. Second salient angle of $M_1$ opposite third internal salient angle. Ramus heavy and apparently shortened. Length of tooth-row approximately as in *Mimomys primus*.

**Description**

**Inferior Dentition:** The mandibular incisor crosses from lingual to buccal side of the tooth row under (?) $M_3$, and probably extends well up into the ascending ramus. The first molar
(Pl. 2, fig. 2) is composed of a posterior loop, three triangles, the anterior two opposed to form a somewhat tetragonal loop of enamel, and a complex anterior loop. The anterior loop is complicated by a pronounced inflection on the internal side, a similar but less pronounced inflection buccally, and an antero-median inflection in front. A very shallow fold of enamel is also present on the buccal side and just anterior to the main external fold mentioned above. The posterior triangle communicates broadly with the posterior loop, but the commisures connecting the median pair of triangles with the anterior and posterior portions of the tooth are narrow. $M_2$ is a less complex tooth which may be characterized as possessing three loops of enamel connected by narrow commisures. The median loop is apparently analogous to the two posterior alternating triangles in normal voles. A second, less worn specimen of Goniodontomys, No. 1960, possesses slightly more triangular salient angles, and in addition some slight angulation of the anterior loop suggestive of the two more or less alternating triangles which replace this loop in the normal vole dentition. $M_2$ is distinctly shorter than $M_1$.

Ramus: The ramus (Pl. 2, figs. 2a, 2b) is rather deep and apparently shortened. The juncture of ascending and alveolar portions of the ramus occurs opposite the posterior root of $M_1$ as in voles, rather than opposite the posterior root of $M_2$ as in Neotoma. The ridge for attachment of the masseter muscle
terminates anteriorly about opposite the posterior surface of the anterior root of $\text{M}_1$. The masseter medialis scar is slightly less developed than the preserved portion of the masseter lateralis scar. The mental foramen is situated close to the superior surface of the ramus, and almost directly beneath the anterior tip of $\text{M}_1$. A second small foramen is found just above the tip of the ridge for the attachment of the masseter muscle. The area for symphyseal attachment extends back well under the posterior portion of $\text{M}_1$. In this character our genus resembles *Microtus* and differs from *Neotoma*. In the latter genus the symphyseal area is much more limited posteriorly.

Relationships: Although the systematic position of *Goniodontomys* is not entirely clear, it has been assigned to the Microtinae. The genus is known by such fragmentary material that it is difficult to eliminate from consideration some other groups of rodents with hypsodont teeth. *Goniodontomys* is widely separated from most microtines by the more or less complete opposition of the usually alternating prisms of the cheek-teeth. The second molar has an occlusal pattern somewhat like that exhibited by some species of *Hyperacrius* and *Eothenomys*. The first molar, however, is quite unlike the usual microtine $\text{M}_1$, especially in the nearly opposite second external and third internal salient angles. In more normal voles when the triangles are opposite one another, the second
external triangle or salient angle is opposed by the second internal triangle. An approach to the pattern of $M_2$ in the Oregon genus is made in a specimen of *Prometheomys scheaposchikowii*, figured by Hinton, but the resemblance is remote.

Moreover, the anterior termination of $M_2$ in *Gonio4ontomys* is not angular as is usually the case in Microtinae. No. 1960, the dentition of which is somewhat less worn than the type, suggests this angular termination, and some Recent voles possess second molars with a more or less rounded appearance.

Relationship to the microtines is suggested in *Gonio4ontomys* by the thin enamel of the cheek-teeth, the triangular shape of the salient angles, the relatively large number of elements composing $M_1$, and various characters in the ramus. A relatively large area of exposed osteodentine in the occlusal surfaces of the cheek-teeth in our genus is also suggestive of microtine affinities. Owen has stated that the water-voile molar has osteodentine in greater proportion than has, "been demonstrated in any other tooth." The author has not made a sufficient study of the subject to confirm this statement, but the condition found in *Gonio4ontomys* is perhaps suggestive of affinities with the Microtinae. If the intermediate-external
triangle of $M_2$, and the internal triangles of $M_1$ of Goniodontomys were shifted anteriorly, an occlusal pattern would result quite close to many microtines.

If Goniodontomys is to be assigned to the Microtinae, the genus is a vole and not a lemming. Enough of the mandibular incisor is preserved in the type specimen to demonstrate this conclusion.

Reference of Goniodontomys to some group of rodents other than the microtines seems less likely than the present assignment. A number of rodent families possess members with hypsodont teeth, but most of them are quite removed structurally as well as geographically from the Oregon genus. Neotoma and its relatives suggest a relationship with Goniodontomys in certain features of the dentition. However, the dentition of Neotoma has relatively thick enamel borders, the salient angles are less triangular, the ramus is slimmer, and the ascending ramus rises from the horizontal ramus farther back than in Goniodontomys. Moreover, not only does Goniodontomys possess a more complicated $M_1$ but it is hardly likely that any Neotoma-like form from the middle Pliocene would be so high-crowned as is the case in the former genus. The second lower molar of Neotoma is strikingly like Goniodontomys in the general aspect of the pattern. On the other hand, in our genus the second external salient angle and the third internal salient of $M_1$ form a loop directed forward and inward. The correspond-
ing loop in Neotoma is more transverse or if oblique, is directed slightly forward and outward. Relatives of Neotoma found in Central and South America, some as fossils, were not examined except by means of figures. It appears that most of these are shorter crowned than the Oregon genus. A fossil species of Oxymycterus, impexus Ameghino from the Pampean, resembles Goniodontomys more closely in pattern of $M_1$ than does Neotoma. However, $M_2$ is quite different and the resemblance is probably superficial.\footnote{Ameghino, F., Contr. al Conocimiento de los Mam. Fos., de la Republ. Argent., Actos Acad. Nac. de Ciencias Republ. Argent. en Cordoba, Atlat, Pl. 4, fig. 3b, 1889.}

The cape-rats possess extremely hypsodont teeth with occlusal patterns quite similar to that of microtines. However, the group has never been recorded from North America and their dental pattern is less close to Goniodontomys than that of some voles. Moreover, early Pliocene forms are known from Asia, and these are no closer to our genus in occlusal pattern than are existing types. The early Pliocene Asiatic fossil specimens show a pronounced tendency to isolate the re-entrant folds of enamel as lakes. In this respect Goniodontomys is closer to normal microtines in which such a condition is limited to extreme wear.

Other groups of rodents with hypsodont teeth have decidedly less resemblance to Goniodontomys than those mentioned above. Such forms as Sigmodon, the jerboas, and the Gerbillinae
differ in one or more characters. *Sigmodon* is not advanced enough even at present. For example, the height of crown is less than in the Pliocene genus. The jerboa tooth-pattern has no special resemblance to that of our genus, and Recent Gerbillinae teeth are too simple in construction.

If *Goniodontomys* is a vole it is the oldest so far recorded. Unfortunately, it is not very close to existing forms, and apparently represents an aberrant type. It is surprising that the Microtinae are not more common in the Tertiary as the subfamily must have a considerable geologic range. *Poamys* Matthew from the lower Snake Creek was regarded by Matthew as possibly a structural ancestor of the Microtinae. The truth of this hypothesis can not be determined on the available evidence. However, the presence of *Goniodontomys* and *Poamys* in beds older than the upper Pliocene suggest the possible presence of other microtine-like forms in the late Miocene and early Pliocene.

Since *Goniodontomys* is an aberrant type it does not furnish much evidence as to the evolution of the Microtinae. Such evidence as it does give, suggests that the vole dentition is becoming progressively more complicated not less so as believed by Hinton. The opposition of the triangles in *Goniodontomys* does not necessarily demonstrate that this is the primitive microtine condition, although the perfect alternation of prisms

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seen in many voles is probably a specialized and advanced state.

Measurements (in millimeters)

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Goniodontomys disjunctus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of crown, M1-M2</td>
<td>5.5</td>
</tr>
<tr>
<td>M1, antero-posterior diam.</td>
<td>3.0</td>
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<tr>
<td>M1, transverse diam.</td>
<td>1.5+</td>
</tr>
<tr>
<td>M2, antero-posterior diam.</td>
<td>2.2</td>
</tr>
<tr>
<td>M2, transverse diam.</td>
<td>1.5</td>
</tr>
<tr>
<td>Depth of ramus beneath M1</td>
<td>6.3</td>
</tr>
</tbody>
</table>

Lagomorpha
Leporidae

Hypolagus vetus (Kellogg)

Several fragmentary lower jaws and a number of isolated teeth, both lowers and uppers, appear to be referable to *Hypolagus vetus* (Kellogg). The Rome specimens are approximately the same size as topotype material of *H. vetus* from Thousand Creek. Characters exhibited by P3 agree with those of the

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latter material except that this tooth in the Rome form may be slightly broader on the average, with flatter or more gently rounded anterior face thus serving to widen this portion of the tooth. Some topotype specimens exhibit these characters but the average specimen is probably somewhat different. The lower molariform teeth as seen in No. 1962 (Pl. 2, figs. 3, 3a), fragmentary left ramus with P3-M1, and No. 1963, fragmentary left ramus with P3-M1, C.I.T. Coll. Vert. Pale. from Rome may be slightly larger than comparable material from Thousand Creek.

A single isolated P3 is present in our collections. If this tooth is referable to the same species as the rami it differs from Thousand Creek H. vetus in lengthening of the tooth transversely. However, the specimen shows a deep antero-internal fold and a shallower antero-external fold as in H. vetus. The upper molariform teeth do not seem to show such heavy external ribs as in the Nevadan species.

C. L. Gazin has referred a large species of Hypolagus from Hagerman to Hypolagus near vetus. In shape of P3, and size of some specimens at least, the Rome material is close to that from Hagerman. If the Rome fauna is actually advanced over that from Thousand Creek as suggested by the rodents,

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the Thousand Creek, Rome, and Hagerman specimens may form a progressive series. However, it is doubtful if the Rome fauna
as a whole is more advanced than that from Thousand Creek.

Compared to other known species of *Hypolagus* the Rome specimens are readily distinguished by their large size as well as characters in the dentition and so forth.

A large series of topotype material of *Hypolagus vetus* was available for comparisons. It should be noted that this material shows decided variation in the characters of P₃ as well as some variation in most of the other characters which have been used to establish species of *Hypolagus*. The Rome material is too scanty to establish whether characters seen in the specimens average somewhat differently than those from Thousand Creek, although study of the collection suggests this to a certain extent. However, since certain specimens from Thousand Creek are closely comparable to individuals from the Oregon locality, the specific designation is justified.

### Measurements (in millimeters)

<table>
<thead>
<tr>
<th></th>
<th>No. 1962</th>
<th>No. 1963</th>
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<tbody>
<tr>
<td>P₃-M₁, occlusal length</td>
<td>9.1</td>
<td>9.3</td>
</tr>
<tr>
<td>Depth of ramus below M₁, measured on inside</td>
<td>12.7</td>
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</table>

Hypolagus, species

A left ramus of *Hypolagus* with P₄-M₃, No. 1964 (Pl. 2, figs. 1, 1a), appears to represent a species distinct from *Hypolagus vetus*. This specimen is characterized by a much lighter dentition than is present in *H. vetus* although the
ramus is as deep and apparently as robust. The lower molariform teeth have convex postero-internal ribs, most noticeably developed in P4 and M1. This surface is flattened in typical H. vetus. H. vetus from Rome may be intermediate in this respect. Several additional specimens representing individuals smaller than those of H. vetus in the collection, have also been referred tentatively to this type. One isolated P3 is present which is smaller than the comparable tooth of H. vetus. Aside from difference in size the tooth is close to the vetus type.

Comparison of the Rome species with small species of Hypolagus is handicapped by lack of suitable material. However, the robust jaw of the Rome form would seem to distinguish this species from others in which the dentition is similar in size.

It should be stated that sufficient material does not exist to make certain that this second species of Hypolagus does not represent merely a young or immature phase of H. vetus. Comparisons, as stated above, are based mostly on a single ramus. A second jaw apparently possesses a larger dentition, but still distinctly smaller than H. vetus from Rome. Until more material becomes available it seems desirable to recognize two types from the Rome locality.

Measurements (in millimeters) No. 1964
P4-M3, occlusal length 8.4
Depth of ramus below M3, measured on inside 12.9
118.

A Pliocene Rodent Fauna from the Kern River Series, California

Description

Sciuridae

Citellus?, species

Sciurid remains from the Kern River beds are limited to a right ramus with $P_4$-$M_2$ and alveolus for $M_3$, No. 1965 (Pl. 3, figs. 1, 1a); a second right ramus without dentition; and fragments of an upper and a lower incisor which may be referable also to this family. Specimen No. 1965 is the basis for the doubtful generic determination given above.

The dentition of No. 1965 is extremely worn and part of the first molar is missing. As a consequence, comparisons are difficult to make. No. 1965 is relatively small, agreeing in size with Recent specimens of Callospermophilus lateralis certus. The molars do not show the pronounced fore-and-aft compression and the high trigonids characteristic of typical Citellus, and the specimen certainly does not represent the genus in a restricted sense. $P_4$ is rather triangular in outline and the anterior two cusps were probably closely appressed in their originally unworn condition. The mandibular incisor is relatively broad and lacks pronounced furrows. Thus, No. 1965 appears to represent the genus Citellus in a broad way, and to be related to such genera or subgenera as Callospermophilus...
and *Otospermophilus* which occupy a position intermediate between typical *Citellus* and typical *Sciurus*.

No. 1965 seems to be more closely related to *Otospermophilus gidleyi* (Rattlesnake), *Citellus*, sp. (Thousand Creek), and *Citellus?*, sp. (Smiths Valley) than to any other Pliocene sciurid. It is about the size of these species and moreover agrees in general character of the dentition, at least in-so-far as may be observed in the well worn dentition of the Kern River specimen.

*Otospermophilus gidleyi* Merriam, Stock and Moody from the

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Rattlesnake formation of eastern Oregon approximates the Kern River species in length of tooth-row, but the ramus of the former is deeper. The talonid rim in M2 of No. 1965 may be more angulate than in the Oregon species. Degree of angulation in No. 1965 is difficult to determine because of breaking away of the inner margins of the molars in the specimen.

*Citellus?*, species from Smiths Valley, central Nevada, also

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approaches No. 1965 in size, although the tooth-row in the Smiths Valley species may be slightly longer. M2 of the former is slightly larger than the comparable tooth in the latter and may be somewhat more compressed antero-posteriorly. In addi-
tion, the mandibular incisor of the Nevadan species is heavier and perhaps slightly more compressed although degree of compression is difficult to determine accurately with the present material. *Citellus*, species from the Thousand Creek beds of northern Nevada is too inadequately known for comparisons. No. 1965 agrees with the Thousand Creek specimen in size. Other Pliocene Sciuridae appear to be clearly distinguishable from the Kern River species.

For purposes of comparison it may be stated that the alveolar length, $P_4-M_3$, in No. 1965 is 8.4 millimeters.

**Cricetidae**

*Peromyscus pliccoenicus*, n. sp.

**Type:** Fragmentary right ramus with $M_1-M_3$, No. 1966, C.I.T. Coll. Vert. Pale. (Pl. 3, figs. 2, 2a).

**Paratypes:** Fragmentary left ramus with $M_1-M_3$ and alveolus for $M_3$, No. 1967 (Pl. 3, fig. 6); fragment of right maxillary with $M_1$ and incomplete $M_2$, No. 1968 (Pl. 3, fig. 3); C.I.T. Coll. Vert. Pale.

**Geological Horizon and Locality:** Middle Pliocene Kern River beds, Kern County, California. C.I.T. Locality No. 49.

**Specific Characters:** Cheek-teeth hypsodont, but crowns showing...
tendency to wear to flat surfaces; without accessory folds although intermediate tubercles may be present or absent. $M^1$ with divided antero-median cusp; tip of antero-internal re-entrant angle becomes isolated with wear leaving a broad, shallow re-entrant. $M^3$ relatively unreduced. Pit or foramen in maxillary bone lateral to anterior root of $M^1$. Size large, exceeding slightly any known fossil species but approximating that in *Peromyscus nesodytes*.

**Discussion**

*Peromyscus pliocoenicus* is distinguished from all other fossil species of the genus, except *P. antiquus* and *P. nesodytes*, by its large size. Even these two species are somewhat smaller, in length of tooth-row, than the Kern River type. Compared to *Peromyscus antiquus* Kellogg from the Thousand Creek beds of northern Nevada, *P. pliocoenicus* is not only larger but is distinguished by the following selected differences: (1) antero-median cusp of $M^1$ divided, resulting in an external cusp rather than a narrow sloping ridge as in the Nevadan species; (2) $M^1$ relatively longer; (3) antero-posterior ridge of $M^3$ may be slightly less well developed; and (4) intermediate tubercles are variably developed whereas they are entirely absent in *P. antiquus*. Relatively large intermediate
tubercles are present on the type of *P. pliocoenicus* (Pl. 3, figs. 2, 2a) but are absent on paratype No. 1967. Rudimentary intermediate tubercles also are present in the upper cheek-teeth as demonstrated in the paratype specimen, No. 1968.

**Peromyscus nesodytes** Wilson, from the Santa Rosa Island

Wilson, R.W., Jour. Mamm., 1 fig., description in press.

Pleistocene, approaches *P. pliocoenicus* more closely in size than does *P. antiquus*. The Kern River species differs from the island form in the following characters: (1) more hypsodont; (2) internal cusps of cheek-teeth may be narrower; (3) intermediate tubercles are variably developed whereas in *P. nesodytes* they appear to be absent; (4) M̄₂, although possessing approximately the same antero-posterior diameter is perhaps less triangular in outline; the tip of the antero-internal re-entrant angle shows a tendency to become isolated, the remainder becoming very shallow and open in contrast to the more permanently V-shaped notch in *P. nesodytes*. In the relatively unworn M̄₂, the antero-external re-entrant angle is very deep extending almost to the anterior margin of the tooth. With wear the tip of this re-entrant also becomes isolated. In *P. nesodytes* this re-entrant angle apparently never was so deep, although wear may have obliterated any enamel islet resulting from such a condition; and (5) judging from the alveolus, M̄₃ is less reduced.

Other fossil forms are either much smaller or are closely
related to living representatives of the genus.

The Kern River species is clearly separable from Recent species of the genus. It is sharply marked off by its large size from all but members of the subgenera Megadontomys, Peromyscus, and Haplomyomys. Some members of the subgenus Megadontomys apparently exceed Peromyscus plioceneus in size. However in the former, supplementary enamel loops and tubercles are highly developed, whereas in our species the accessory tubercles between the primary cusps are apparently not always present, and most important, no accessory loops or folds of enamel enter into the cheek-tooth patterns of either the superior or inferior dentitions. Megadontomys is an inhabitant of southern Mexico and central America.

Many of the southern species of the subgenus Peromyscus are characterized by relatively large size. These species are all smaller than the Californian type, and moreover, possess upper cheek-teeth with supplementary tubercles at the buccal margin which wear to form accessory enamel folds in the cheek-teeth. These supplementary folds may be small but are apparently always present. No. 1968, a maxillary fragment of P. plioceneus, exhibits rudimentary tubercles. However, these cuspules do not enter into the cheek-tooth pattern.

Members of the subgenus Haplomyomys possess cheek-teeth without supplementary tubercles or with such tubercles in a rudimentary condition. The largest species of the subgenus, P. californicus, is distinctly smaller than is P. plioceneus.
Moreover, the accessory tubercles in the dentition of No. 1966 exceed those of any specimen of Haplomyelomys.

It is not to be assumed, on the basis of the brief and by no means complete comparisons given above, that Peromyscus pliocoenicus bears a close relationship to any Recent subgenus. As a matter of fact, it is highly improbable that any of the modern subgenera were differentiated as early as the middle Pliocene. Limited comparisons with Recent subgenera are given merely as the simplest means of eliminating from consideration the large number of Recent species. However, it is worth noting that large species were common in the middle Pliocene of the United States, whereas now, except for P. californicus, the large Peromyscine forms are all southern in distribution. This fact may indicate a general southward movement of many of the Pliocene forms with, of course, considerable evolutionary change with the passing of geologic time.

### Comparative Measurements (in millimeters)

<table>
<thead>
<tr>
<th></th>
<th>P. pliocoenicus</th>
<th>P. pliocoenicus</th>
<th>P. antiquus</th>
<th>P. nesodytes</th>
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<tbody>
<tr>
<td></td>
<td>Kern River beds</td>
<td>Kern River beds</td>
<td>Thousand</td>
<td>No. 1780</td>
</tr>
<tr>
<td></td>
<td>No. 1966, C.I.T.</td>
<td>No. 1967, C.I.T.</td>
<td>Type</td>
<td>Santa Rosa I</td>
</tr>
<tr>
<td></td>
<td>Type</td>
<td>Paratype</td>
<td>U.C. Type</td>
<td>Pleistocene</td>
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<td>6.1</td>
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<td>5.8</td>
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<tr>
<td>M1-M2, alveolar length</td>
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<td>4.3</td>
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<td>---</td>
</tr>
<tr>
<td>M1-M2, occlusal length</td>
<td>4.4</td>
<td>4.4</td>
<td>3.9</td>
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</table>
Peromyscus plocoenicus
Kern River beds
No. 1968, C.I.T., Paratype

M1, antero-posterior diameter ................. 2.3
M1, transverse diameter ...................... 1.5

Hypolagus near limnetus Gazin

Lagomorpha
Leporidae

Leporid remains are rather abundant in the Kern River collection. These remains include fragmentary rami and maxillae as well as isolated teeth and skeletal parts. Two species appear to be present, the larger of which is near Hypolagus limnetus of the Hagerman fauna. The more complete material

representing this form include No. 1969 (Pl. 3, fig. 5), a specimen with the palatal portion of the maxillae preserved with P3-M2 present on both sides; a left maxillary with P2-M2, No. 1970 (Pl. 3, fig. 4); a right ramus with P3-M3, No. 1972 (Pl. 2, fig. 5); a left ramus with P3-M2, No. 1973 (Pl. 2, fig. 4); and a second left ramus with P4-M2, No. 1974. Although our form is from an older horizon it agrees with H. limnetus in approximate size and in the shape of P3, as well as in depth of re-entrant folds in this tooth. P3 is rather broad with the antero-internal border rounded (Pl. 2, fig. 4). The antero-external fold is relatively deep, a point of resemblance to the Hagerman type. The character of the plications on the median re-entrant fold of the upper molariform teeth is apparently similar to that in H. limnetus. The fold may be slightly less deep and complex on the average but there seems to be variation in this regard in the Kern River form.

Hypolagus furlongi Gazin from Grand View is closely re-


related to H. limnetus. However, our form is apparently distinguished by a less triangular P3 with deeper antero-external fold. Moreover, in P2 of H. furlongi the antero-internal fold is deep and crenulated. P2 in our form is more like that of H. limnetus and is not crenulated.

Other species of Hypolagus do not appear to be closely
related to the Kern River type. *H. vetus*, although from an approximately equivalent horizon is larger and possesses a $P^3$ in which the antero-external fold is shallower and the outline of the tooth somewhat narrower anteriorly.

42  
*Hypolagus edensis* Frick from the middle (?) Pliocene Eden beds is smaller than *H. near limnetus*; the inner borders of the lower molariform teeth are rounded, not angulate as in our form; and the antero-external fold in $P^3$ is more anterior in position.

43  
*Hypolagus? apachensis* Gazin compared to *H. near limnetus* is from an older horizon. It is a smaller form with the median fold of the upper molariform teeth less complexly plicated. In addition, $P^3$ is relatively longer and the antero-external fold in that tooth is shallow.

44  
Lastly, *Hypolagus browni* (Hay) appears to be more advanced in character of the postero-external fold of $P^3$ than is that tooth in the Kern River species. However, the antero-external
fold is relatively less deep than in *Hypolagus near limnetus*. This species is smaller and from a distinctly later horizon (early Pleistocene).

*Hypolagus near limnetus* more nearly agrees in characters with *H. limnetus* from Hagerman than with any other species of the genus. However, it comes from an earlier horizon and may represent a distinct species. Since six or seven species of *Hypolagus*, representing a wide variety of types, are already known nothing is gained by separating the Kern River species as a distinct type.

**Measurements (in millimeters)**

<table>
<thead>
<tr>
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<tbody>
<tr>
<td><strong>P₂-M₃</strong>, alveolar length</td>
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<td>---</td>
<td>13.1</td>
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<tr>
<td><strong>P₂-M₂</strong>, oclusal length</td>
<td>---</td>
<td>9.3+</td>
<td>---</td>
</tr>
<tr>
<td><strong>P₂-M₂</strong>, alveolar length</td>
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<td>11.9</td>
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</tr>
<tr>
<td><strong>P₃-M₂</strong>, oclusal length</td>
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<td>8.4</td>
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<tr>
<td>Greatest width across antero-ventral prominence of zygomatic arches</td>
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<tr>
<td>Least antero-posterior length of bony palate</td>
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<tr>
<td><strong>P₃-M₃</strong>, alveolar length</td>
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<td>---</td>
<td>14.1 (a)</td>
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<tr>
<td><strong>P₃-M₂</strong>, oclusal length</td>
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<td>10.8-</td>
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</tr>
<tr>
<td>Depth of ramus beneath <strong>M₁</strong>, measured on outside</td>
<td>10.6</td>
<td>---</td>
<td>10.4</td>
</tr>
</tbody>
</table>

(a) approximate
Hypolagus, small species

Several of the Hypolagus specimens from the Kern River beds appear to represent a second, smaller species of the genus. The species is represented by No. 1975, a fragment of left ramus with P3–M1, and several isolated teeth. In contrast to the larger Kern River species, P3 in this type is somewhat elongate and triangular. Only three third lower premolars in the collection appear referable to the species of Hypolagus under discussion. All these teeth are somewhat different, including one, No. 1976, with a postero-internal groove on the side of the tooth reflected as a slight fold on the occlusal surface of the tooth. The antero-external fold in P3 is fairly deep but shows a tendency to be quite wide. In one specimen, No. 1975, the anterior limb of the fold is parallel to the axis of the tooth. The lower molariform teeth compared to H. near limnetus may be relatively a little longer antero-posteriorly but the limited remains available make this character doubtful. The upper molariform teeth, represented by isolated teeth, may possess median re-entrant folds which are less complexly plicated than in the larger species. This statement is also doubtful in view of uncertainty as to the position of the teeth in the maxillary and since individual variation is seen in this character when large series of teeth are available for comparison. Moreover, if these teeth are viewed from below they appear to be more complexly folded.
Remains of this species are not complete enough to warrant a specific designation. As a matter of fact, the specimens may represent young individuals, and difference in tooth-pattern between this form and *H. near limnetus* from the same locality may be due to age. Comparisons with known small species of *Hypolagus* were made, but because of the limited material available, proved inadequate to reveal any real relationships. A statement of these comparisons would not add anything, and have been omitted.

Measurements (in millimeters

No. 1975

P3-P4, antero-posterior length 5.2

A Pliocene Rodent Fauna from Smiths Valley, Nevada

The Smiths Valley rodent assemblage has been described recently by the author in a publication entitled, "A Pliocene Rodent Fauna from Smiths Valley, Nevada."


A Pliocene Rodent Fauna from Bartlett Mountain, Southeastern Oregon

Due to insufficient time, work on this assemblage was limited to determining the provisional rodent fauna given in
an earlier section. Such notes as might be given at this
time are covered essentially in other parts of the thesis.

Thousand Creek Rodent Fauna

During the course of the work this fauna was examined
in part. A revised faunal list has been presented in another
place. Other results of the examination are contained in
comparisons of rodent types made in other parts of the thesis.

Rattlesnake Rodent Fauna

The only Rattlesnake rodents which I have examined per-
sonally are specimens of Dipoides. A brief note on the
Rattlesnake Dipoides is contained in the author's paper on
Dipoides stirtoni from Rome, Oregon.

Wilson, R.W., Carnegie Inst. Wash., Publ. No. 453, Part 3,
p. 28, 1934.

UPPER PLIOCENE

A Late Pliocene Rodent Fauna from the Coso Mountains, California

Description

Rodentia

Cricetidae

Mimomys primus (Wilson)

This rodent was described in a paper entitled, "Cosomys,
A New Genus of Vole from the Pliocene of California. 47


Additional observations on the type are to be found in a later paper on the late Pliocene rodents of southwestern Idaho. 48


It may be noted that it is still uncertain whether or not Cosomys is generically distinct from Mimomys. Fragments of the bony palate of a rodent type in the Hagerman collection, which may be referable to M. primus, suggests a generic separation, as well as characters which were pointed out in the two papers cited. However, without additional material of undoubted association it is deemed best to follow the opinion of so eminent an authority as M.A.C. Hinton and refer Cosomys primus to the European genus Mimomys.

Lagomorpha

Leporidae

Hypolagus near limnetus Gazin

Several lagomorph specimens are represented in the Coso Mountains collection. The material consists of a right ramus, No. 1978 (Pl. 3, figs. 7, 7a), complete except for the ascend-
ing ramus; a fragment of left ramus with M₂-M₃, No. 1979; a fragment of maxillary with left M₂-M₃, No. 1980; and a few skeletal elements. The fossil remains appear to represent a species near Hypolagus limnetus.

The Coso Mountains leporid although occurring in beds of approximately the same age as those at Hagerman yielding Hypolagus limnetus remains is somewhat smaller than the type of the latter species. The ramus in No. 1978 (Pl. 3, fig. 7a) is actually not so deep, but may be relatively, as in typical H. limnetus. On the other hand, the diastema between I and P₃ is very slightly longer. The actual depth of ramus corresponds more closely to that in Hypolagus furlongi, a closely related type from Grand View. P₃ (Pl. 3, fig. 7) in the Coso Mountains form is quite close in characters to that of H. limnetus. The antero-external fold in the tooth is relatively deep thus agreeing with the third premolar of the Hagerman species. However, the tooth may be slightly more narrow anteriorly, and the postero-external fold possesses a small plication on the anterior enamel face, a feature not recorded in the description of H. limnetus. The presence of a similar plication in a specimen of Hypolagus vetus in which species it is normally absent indicates that in the above case no particular reliance can be placed on a single plication. The lower molariform

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teeth of *H. near limnetus* appear to be similar to those in the Hagerman type. In No. 1980 the enamel infold of M2 is rather complexly plicated probably agreeing more closely in this regard with *H. limnetus*, than do specimens from the Kern River beds referred to *H. near limnetus*. Without actual specimens from Hagerman, certain other characters which have been cited for *H. limnetus* are difficult to check in our specimens.

See section under description of the Kern River rodents.

Hypolagus furlongi Gazin from Grand View, although perhaps slightly larger than the Coso Mountains form apparently is closer to it in size than the latter is to *H. limnetus*. However, in character of P3, the Californian form is less triangular, more as in the Hagerman type, and the antero-external fold is deeper, again a character which is closer to that shown in *H. limnetus*. Moreover, the diastema between I and P3 is distinctly shorter in the Grand View species. On the whole, the Coso Mountains leporid is closer to *H. limnetus* than to *H. furlongi*, and especially in regard to character of P3. The slightly better agreement in size between No. 1978 and *H. furlongi* is probably of no great importance since size must be a variable character to a certain extent, and the Coso Mountains material is limited in amount.
Hypolagus browni (Hay) compared to H. near limnetus is recorded from a somewhat younger horizon, namely early Pleistocene. The species is smaller than our form. A certain amount of variation in $P_3$ is seen in the Pleistocene type. However, this tooth appears to be more advanced in character of the posteroexternal fold than in our species. The antero-external fold is shallower. $M_2$ appears to be less complexly plicated than in H. near limnetus.

Hypolagus vetus (Kellogg) is not at all close to the Coso Mountains species. It is much larger, and differs as well in several characters in the dentition.

Hypolagus edensis Frick is readily distinguished from our form. The rounded internal borders of the lower molariform teeth, and perhaps the pronounced anterior position of the antero-external fold in $P_3$ as well, are characters which appear to be quite pe-
culiar to *H. edensis* if the type is correctly figured.

The Coso Mountains species is somewhat smaller than average *Hypolagus* near *limnetus* from the Kern River beds, although only slightly smaller than some specimens. The important third lower premolar is similar to that in the Kern River species but in the latter the average $P_3$ is a little more rounded anteriorly, and the widest part of the tooth slightly farther forward than in No. 1978. The only upper molariform tooth available for comparison is $M_2$. The anterior border of the median re-entrant fold of this tooth appears to be slightly more complexly plicated in the Coso Mountains type.

It is doubtful if *Hypolagus* near *limnetus* from the Kern River beds is conspecific with *Hypolagus* near *limnetus* from the Coso Mountains, but either is probably closer to typical *H. limnetus* than to any other species of *Hypolagus*. It may be that the Kern River form represents a distinct species. Probably, the Coso Mountains species is merely a small individual of typical *H. limnetus*. In any case, in view of the number of species of *Hypolagus* already distinguished, nothing is gained by a further separation of types.

Measurements (in millimeters)

<table>
<thead>
<tr>
<th>No. 1978</th>
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<tbody>
<tr>
<td>$P_3-M_3$, alveolar length</td>
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<tr>
<td>$P_3-M_3$, occlusal length</td>
<td>10.7</td>
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<tr>
<td>Depth of ramus beneath $M_1$, measured from inside</td>
<td>10.9</td>
</tr>
<tr>
<td>Length of diastema between $I$ and $P_3$</td>
<td>13.4</td>
</tr>
</tbody>
</table>
A Late Pliocene Rodent Fauna from the Hagerman Lake Beds, Southwestern Idaho

The Hagerman rodent fauna was described by the author in a paper entitled, "A Rodent Fauna from Later Cenozoic Beds of Southwestern Idaho. Lagomorphs from this locality were described by C. L. Gazin under the heading, "Fossil Hares from the Late Pliocene of Southern Idaho."

A Late Pliocene Rodent Fauna from Near Grand View, Idaho

The Grand View rodent assemblage was described by the author in the Carnegie Institution of Washington publication just cited. A second paper, "A New Species of Porcupine from the Later Cenozoic of Idaho," is also a contribution on this fauna. The lagomorph fauna was treated by Gazin in the National Museum publication cited under the Hagerman note.

Curtis Fauna, San Pedro Valley Beds, Arizona

An Institute collection of rodent and lagomorph remains
from the Curtis fauna of the San Pedro Valley was briefly studied by the author. This study was undertaken to gain an idea of the value of the characters distinguishing the various species of this fauna from Recent types.
Plate 1

Mylagaulus? cf. monodon Cope

Figs. 1, 4, 5. Isolated right P4's; Nos. 1955, 1952, and 1953; X3.

Fig. 2. Isolated left P4; No. 1954; X3.

Fig. 3. Isolated left P4; No. 1956; X3.

Fig. 6. Isolated right P4; No. 1958; X3.

Fig. 7. Isolated P4; No. 1957; X3.

Figs. 8, 8a, 8b. Left rami with P4-M3 inclusive; No. 72.

Fig. 8, occlusal view, X3; fig. 8a, intero-lateral view, X1; and fig. 8b, extero-lateral view, X1.

Castor?, species

Figs. 9, 9a. Isolated left M2?; No. 1961; X3. Fig. 9, occlusal view; fig. 9a, intero-lateral view.

Plate 3

Goniodontomys disjunctus, n. gen. and sp.
Figs. 2, 2a, 2b. Fragmentary left ramus with M1-M3, genotype specimen; No. 1959. Fig. 2, occlusal view, X12; fig. 2a, intero-lateral view, X6; fig. 2b, extero-lateral view, X8. Middle Pliocene, Rome, Oregon.

Hypolagus vetus (Kellogg)
Figs. 3, 3a. Incomplete left ramus with P3-M1; No. 1962. Fig. 3, occlusal view, X3; fig. 3a, lateral view, X2. Middle Pliocene, Rome, Oregon.

Hypolagus, species
Figs. 1, 1a. Incomplete left ramus with P4-M3; No. 1964. Fig. 1, occlusal view, X3; fig. 1a, lateral view, X2. Middle Pliocene, Rome, Oregon.

Hypolagus near limnetus Gazin
Fig. 4. Incomplete left ramus with P3-M2; No. 1973; X3; occlusal view.

Fig. 5. Right ramus with P3-M3; No. 1972; X2; lateral view.

Middle Pliocene, Kern River Beds, California.

Plate 3

Citellus?, species

Figs. 1, 1a. Right ramus with P4-M2; No. 1965; X4.
Fig. 1, occlusal view; fig. 1a, lateral view.
Middle Pliocene, Kern River Beds, California.

Peromyscus pliocoenicus, n. sp.

Figs. 2, 2a. Incomplete right ramus with M1-M2, type specimen;
No. 1966. Fig. 2, occlusal view, X9; fig. 2a, lateral view, X6.

Fig. 3. Fragment of right maxillary with M1 and incomplete M2,
paratype specimen; No. 1968; X9.

Fig. 6. Left ramus with M1-M2, paratype specimen; No. 1967; X9.
Middle Pliocene, Kern River Beds, California.

Hypolagus near limnetus Gazin

Fig. 4. Fragmentary left maxillary with P2-M2; No. 1970; X3.

Fig. 5. Incomplete maxillae with right P3-M2 and left P3-M2;
No. 1969; X2.

Middle Pliocene, Kern River Beds, California.

Hypolagus near limnetus Gazin

Figs. 7, 7a. Right ramus with P3-M3; No. 1978.
Fig. 7, occlusal view, X3; fig. 7a, lateral view, X2.
Upper Pliocene, Coso Mts., California.
