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Early Tertiary Rodents of North America

ROBERT W. WILSON

With thirteen text figures

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# Early Tertiary Rodents of North America

## INTRODUCTION

The gnawing mammals of the present day exist in the greatest of profusion and diversity. In sheer population they exceed all other mammals combined, and this is nearly as true of number of species and genera. In the higher taxonomic categories below the rank of suborder, their great diversity is shown by the much greater number of families and subfamilies than in any other order of mammals. Almost all these gnawing animals are classified in a single order, the Rodentia (rodents). Those that are not, the Lagomorpha (hares, rabbits, pikas), though existing in considerable numbers, are among the most homogeneous of orders. They are at best only distantly related to the rodents. The following remarks apply only to the Rodentia.

The great number of categories necessary for classifying existing rodents testifies to the tremendous evolutionary development which has taken place within the order. A second outstanding feature of the order is the astonishing amount of parallelism in tooth pattern between forms placed in different major groups. The same pattern in some instances is reproduced several times over. The repeated parallel developments in both living and fossil rodents suggest that all these animals have descended from a common ancestor which lived in the not too remote past. It is generally agreed that the greater the parallelism, the greater the genetic relationship, and this tenet applies not only to duplication of pattern, but necessarily also in some measure to the number of such duplications. Similar needs acting on distantly related groups should not be so effective in producing parallelisms as are those which act on closely related stocks.

All modern American authorities are agreed that the Recent rodents have descended from a common ancestor very much like the typical paramyines of the Eocene, if not actually from this group of primitive rodents. Further, they all are agreed, in practice at least, as to the key characters to be used in classifying this diverse host. In rodents, the heavy gnawing work performed by the incisors, and the contrasting grinding or bruising action of the cheek teeth, have necessitated the development of an elaborate jaw musculature, and modification of the jaws and the anterior part of the skull for its attachment. Different rodents have developed different modifications, and herein lies the clue to existing rodent classification. All modern classifications thus use as basic characters the features of the zygomaseteric structure, that is, the combined features of the masseter muscles, anterior zygoma and rostrum, and mandible. It is assumed that a particular type develops only once.

Some rodents, even among those still living, have comparatively simple zygomaseteric structures, approaching the condition found in other mammals. In other groups, the structure is complex and departs considerably from that of any nonrodent. It is obvious that the zygomaseteric structures have evolved

just as other structures have evolved, and that the more primitive zygomaseteric type represents the ancestral rodent condition. A decided difference of opinion exists, however, as to the time of differentiation of the higher types of structure. Because the simplest structure is the almost universal Eocene condition, followed by appearance of more complex structures in the Oligocene, and marked decline thereafter of the primitive type, some, particularly W. D. Matthew (1910), have felt that zygomaseteric evolution has taken place within the limits of the known record of rodents (late Paleocene to Recent). Miller and Gidley (1918), however, have argued that within the known record, the various kinds of zygomaseteric structures are distinct, and none has evolved from another. Thus, according to their belief, all major evolution must have occurred in pre-Eocene times. In either case, differentiation of major groups was complete in North American rodents by early Miocene (Arikarean) time.

The present paper is concerned in part with a review of the present evidence bearing on the problem of rodent differentiation. Partly for this reason, but largely for its own sake, a summary of the stratigraphic development of early Tertiary rodent faunas is presented. This paper is concerned also with the evolution of rodents within major groups. Following the section on stratigraphic development, summaries for each major group (families, subfamilies) are given in so far as the present state of our knowledge permits. The stratigraphic development is then analyzed with reference to the two theories mentioned above. Finally, several features of rodent evolution are set forth in the light of the known stratigraphic occurrence, and the evolutionary history of the various groups. In many instances the record is defective, and suggestions as to development are indicated which are frankly theoretical and subjective. Because members of the order Lagomorpha are rodents in a popular sense, and because the group is not a large one, a brief statement on the early Tertiary lagomorphs is also given.

#### ACKNOWLEDGMENTS

This paper has been prepared during the author's tenure as National Research Council Fellow in paleontology, 1946-1947. I wish to thank the National Research Fellowship Board in the Natural Sciences for making this work possible. Also my thanks are due to the Division of the Geological Sciences, California Institute of Technology, for research facilities, and particularly to Dr. Chester Stock, of the California Institute, for sponsoring the project through a number of years, and for a critical reading of the manuscript.

Because this work is based on a program of study and systematic description over a number of years, it is appropriate at this time to express my thanks again to Yale University for appointment as Sterling Research Fellow, 1936-1937; and to Mr. Childs Frick for financial assistance during the period 1937-1939, at which time I was Research Fellow in paleontology at the California Institute of Technology.

The text figures have been prepared by Mr. David P. Willoughby, scientific illustrator, Division of the Geological Sciences, California Institute of Technology.

## PREVIOUS STUDIES

The present paper attempts to draw together much of the scattered information dealing with the sequence of early Tertiary North American rodent faunas, and to summarize the histories of the groups making up this record. Needless to say, there is much information which is not yet available, so that this paper must be regarded at best as a summary of existing information, and of the author's tentative conclusions regarding the significance of this information. That such a subject as this can be undertaken at all is the result of the researches of many men over a period of nearly one hundred years. To many of these men, collectors, stratigraphers, and vertebrate paleontologists alike, the goal has been far from that of the author, but by their collecting and their contributions to general stratigraphic and faunal knowledge, they made possible the more specific study of fossil rodents. The men who have contributed more directly are recognized by means of the bibliography. Mention should be made, however, of W. D. Matthew, whose views coincide most nearly with those of the writer. His most significant contribution from the standpoint of the present study is "On the osteology and relationships of *Paramys*, and the affinities of the *Ischyromyidae*" (1910). Mention should also be made of Miller and Gidley, who in their classification of 1918 present a divergent point of view. Lastly, special acknowledgment should be made to the writer's colleagues who are primarily interested in rodent paleontology. Mr. J. J. Burke has made important contributions to knowledge of the late Eocene and Oligocene rodent and lagomorph faunas. Dr. A. E. Wood has published monographs on the White River fauna of both these orders. Although the work of Dr. Samuel Schaub does not bear directly on North American faunas, his contributions to knowledge of Old World cricetids, sicutids, and dipodids have been of prime importance. The present writer's own background for this review is the result of systematic work on Bridger rodents exclusive of the paramyines, and of description of recently acquired faunas of the Sespe and Poway formations of southern California. In addition, most of the Uinta types, a large number of the typical *Paramys* of the Bridger, and some of the Wasatchian specimens have been examined. Many of the White River species of Wyoming, Nebraska, and Colorado have been available for study, though these were chiefly from the middle and upper Oligocene. Lastly, a small collection of John Day rodents was available. Although the systematic study and description of the Californian types was begun as far back as 1934, most of the work was done in the period 1936-1939. Seven years intervened before completion of the studies was possible, during 1946-1947.

STRATIGRAPHIC DEVELOPMENT OF EARLY CONTINENTAL  
CENOZOIC

As is well known, the chief accumulation of continental Paleocene and particularly Eocene deposits occurs as fill in the various structural basins of the Rocky Mountains formed as a result of the Laramide Revolution. No one

basin has a complete section, but a composite of the records of several basins yields a nearly complete sequence. Sediments are chiefly of flood-plain type, reach a thickness of many thousands of feet, and contain in the upper parts a remarkable amount of volcanic debris. Because of a certain degree of contemporaneity of sedimentation in the several basins, unconformities are largely bridged over. Correlation of the stratal units is based on faunal identity or at least close similarity, the geological conditions not permitting the tracing of beds from one basin to another. In turn, because the section is essentially complete, and the associated faunas are in known sequence, the faunal succession in this area is the standard for North America, and more isolated occurrences are correlated in respect to it.

The site of record shifts in the Oligocene from the intermontane basins of the Rockies to the adjacent High Plains to the east. Sedimentation here furnishes an almost complete record for the Oligocene, which is the accepted standard for correlation purposes. Uplift along the Rocky Mountain axis at the close of Oligocene time interrupted deposition so that an unconformity exists between the youngest Oligocene (upper Brule) and the earliest Miocene (Gering), but the faunal break is not very great. Faunally a much greater break exists between the latest Eocene or earliest Oligocene (Duchesne River) and the early Oligocene (Chadron), although this may be in part the result of a shift in facies rather than a lost interval of time.

Although true Eocene sediments are largely confined to the Rocky Mountain basins, significant development in respect to mammalian faunas of late Eocene age is also found in southern California, where the Poway and lower and middle Sespe formations were deposited during that time. Rocks of early and middle Oligocene age are more or less restricted to the Great Plains area, although they may exist as scattered remnants of once extensive formations in the mountain basins to the west. During late Oligocene or early Miocene or both, however, important fossiliferous sediments accumulated in east-central Oregon as the John Day formation. In addition, less noteworthy sedimentation went on in California (upper Sespe). The latter gains in importance from its association, at least in part, with marine rocks of comparable or immediately younger age (Vaqueros).

The principal rock units dealt with in this paper, and their time relations, are given in the accompanying correlation chart (fig. 1). Stage names are those proposed in 1941 by a committee of the Paleontological Society headed by Dr. H. E. Wood 2d (see bibliography, Wood, H. E., 1941). They have become standard terms in the literature of vertebrate paleontology. The localities of the principal mammal-bearing formations of the early Tertiary are shown in the accompanying map (fig. 2).

#### SYSTEM OF CLASSIFICATION EMPLOYED

The present classification most nearly resembles that of Simpson (1945; see bibliography), and represents a departure from that used by the author in papers on some of the Eocene Sespe rodents—not in major features perhaps, but in





FIG. 2. Locality map of principal mammal-bearing formations of the early Tertiary

1. Poway formation. Early Uintan
2. Sespe formation. Late Uintan, Duchesnean, Whitneyan?, and Arikarean
3. John Day formation. Arikarean
4. San Juan Basin. Puerco formation, Torrejon formation, and part of the Canyon Largo group (middle and late Wasatchian)
5. Canyon Largo group. Type area of Tiffanian
6. Huerfano formation. Late Wasatchian and early Bridgerian
7. North Horn "formation." Dragonian
8. Uinta Basin. Uinta formation and Duchesne River formation
9. Bridger formation
10. Washakie formation. Late Bridgerian and early Uintan
11. Wind River formation. Middle and late Wasatchian
12. Willwood formation. Clarkforkian and Wasatchian
13. Polecat Bench formation. Puercan to Clarkforkian inclusive
14. Oligocene, Miocene, and Pliocene formations of the Great Plains

the size of taxonomic units employed for the primitive rodents. Simpson's groupings express more nearly the relationships as they seem to the writer than do others of recent date. The only important change from Simpson is the shifting of the Eomyidae from the Aplodontoidea into the advanced Sciuromorpha as advocated by Wood (1937a), and the placing of this family in a superfamily, Geomyoidea, rather than leaving it *incertae sedis*. The genus *Prosciurus* is made the type for a new subfamily, Prosciurinae, chiefly because it does not seem possible to place it in any other group except as an expedient. The present classification is undoubtedly defective as are all existing classifications, and is presented for the purposes of this paper rather than as a taxonomic proposal. Some of the difficulties are pointed out on subsequent pages.

## ORDER RODENTIA BOWDICH, 1821

- Suborder Sciuromorpha Brandt, 1855
  - Superfamily Aplodontoidea Matthew, 1910
    - Family Ischyromyidae Alston, 1876
      - Subfamily Paramyinae Simpson, 1945
      - Subfamily Prosciurinae, new, but see comment above
      - Subfamily Cylindrodontinae Simpson, 1945
      - Subfamily Sciuravinae Simpson, 1945
      - Subfamily Ischyromyinae Schlosser, 1911
    - Family Protoptychidae Wood, 1937a
    - Family Aplodontidae Trouessart, 1897
    - Family Mylagaulidae Cope, 1881
  - Superfamily Sciuroidae Gill, 1872
    - Family Sciuridae Gray, 1821
  - Superfamily Castoroidea Gill, 1872
    - Family Eutypomyidae Miller and Gidley, 1918
    - Family Castoridae Gray, 1821
  - Superfamily Geomyoidea Weber, 1904
    - Family Eomyidae Depéret and Douxami, 1902
    - Family Heteromyidae Allen and Chapman, 1893
    - Family Geomyidae Gill, 1872
  - ?Sciuromorpha *incertae sedis*
    - Superfamily ?Anomaluroidea Gill, 1872
- Suborder Myomorpha Brandt, 1855
  - Superfamily Gliroidea Simpson, 1945
  - Superfamily Muroidea Miller and Gidley, 1918
    - Family Cricetidae Rochebrune, 1883
    - Family Muridae Gray, 1821
  - Superfamily Dipodoidea Weber, 1904
    - Family Zapodidae Coues, 1875
    - Family Dipodidae Waterhouse, 1842
- Suborder Hystricomorpha Brandt, 1855

## ORDER LAGOMORPHA BRANDT, 1855

- Family Eurymylidae Matthew, Granger, and Simpson, 1929
- Family Ochotonidae Thomas, 1897
- Family Leporidae Gray, 1821

## STRATIGRAPHIC SEQUENCE OF EARLY TERTIARY RODENT FAUNAS

### LATE PALEOCENE

The earliest rodent record is from the Tiffanian stage (late Paleocene) of the Fort Union deposits. Likewise, the first lagomorph, if *Eurymylus* is one, is recorded from beds of comparable age in Mongolia. Paleocene rodents, however, are very scarce elements of the fauna, actually unrecorded until recently, and it is not until early Eocene times that rodents become almost ubiquitous in mammalian faunas. The known record is as follows:

TIFFANIAN of Bear Creek local fauna, Fort Union Series:

*"Paramys" atavus*

CLARKFORKIAN of Polecat Bench formation:

*"Paramys" sp. indet.*

*"Paramys"* (family Ischyromyidae) of the Paleocene probably does not represent the genus *sensu stricto*, but is a closely related type. It is the only rodent genus so far reported from the Paleocene.

### EOCENE

#### WASATCHIAN (EARLY EOCENE)

Genera: *"Paramys," "Sciuravus depressus"* (presumably not this genus), *"Mysops kalicola"* (presumably not this genus).

The Wasatchian provincial stage may be divided into Gray Bull, Lysite, and Lost Cabin faunas, ascending in that order.

#### *Gray Bull*

Apparently known only from the lower part (Gray Bull beds) of the Willwood formation.

Ischyromyidae

Paramyinae

*"Paramys"*

*murinus*

*copei*

*atwateri*

*major major*

*buccatus* (provisional reference)

*excavatus* (provisional reference)

Only *"Paramys"* is known from this faunal zone.

*Lysite*

	Willwood	Lysite	Almagre
Ischyromyidae			
Paramyinae			
"Paramys".....	x	x	x
buccatus.....	prov.	x	?
excavatus.....	x	x	...
copei.....	...	x	x
major major.....	x	x	...
major quadratus.....	?	x	...
Sciuravinae?			
"Sciuravus depressus".....	...	x	...

Only "*Paramys*" and "*Sciuravus depressus*" are known from this faunal stage. "*Sciuravus depressus*" apparently cannot be referred to the genus *Sciuravus* (Troxell, 1923c, p. 385), but perhaps may be tentatively included in the Sciuravinae.

*Lost Cabin*

	Willwood	Lost Cabin	Largo	Huerfano A
Ischyromyidae				
Paramyinae				
"Paramys".....	x	x	x	x
buccatus.....	...	x	?	...
copei.....	...	x	...	cf.
major major.....	...	x	x	...
major quadratus.....	x	x	...	...
excavatus.....	...	prov.	...	...
atwateri.....	...	prov.	...	...
murinus.....	...	?	...	...
" <i>Mysops kalicola</i> ".....	...	x	...	...

Only "*Paramys*" and "*Mysops kalicola*" have been recorded. "*Mysops kalicola*" is not a member of the genus *Mysops*, but apparently represents an undescribed genus, probably paramyine, but with certain features suggesting *Mysops* and *Sciuravus*.

## BRIDGERIAN (MIDDLE EOCENE)

Genera: "*Paramys*," *Paramys*, *Pseudotomus*, *Reithroparamys*, *Mysops*, *Pauromys*, *Sciuravus*, *Tillomys*, *Taxymys*.

Faunally, the type Bridger may be divided into the Black's Fork (Bridger A, B) and Twin Buttes (C, D) zones. The exact stratigraphic levels are not known for several types, and these are placed in a separate column. *Sciuravus eucristadens* is from the early Bridgerian (Green River formation) of the Uinta Basin. *Pauromys* is of uncertain systematic position, combining features of the Paramyinae and Sciuravinae. It is tentatively assigned to the latter group.

	Black's Fork	Twin Buttes	Bridger level?	Green River, Uinta Basin
Ischyromyidae				
Paramyinae				
"Paramys" minutus.....	...	...	x	...
Paramys.....	x	x	...	...
delicatus.....	x	x	...	...
delicatur.....	x	x	...	...
Pseudotomus.....	x	x	...	x
hians.....	x	x	...	...
robustus.....	x	x	...	...
Pseudotomus? superbus.....	x	x	...	...
Reithroparamys delicatissimus....	x	x	...	...
Cylindrodontinae				
Mysops.....	x	x	...	...
minimus.....	x	...	...	...
parvus parvus.....	x	x	...	...
parvus plicatus.....	...	...	x	...
fraternus.....	...	...	x	...
Sciuravinae				
Pauromys perditus.....	...	x	...	...
Sciuravus.....	x	x	...	...
nitidus.....	x	x	...	...
bridgeri.....	x	...	...	...
eucristadens.....	...	...	...	x
Sciuravus? rarus.....	...	...	x*	...
Tillomys senex.....	...	x	...	...
Tillomys? parvidens.....	x	...	...	...
Taxymys lucaris.....	...	x	...	...
Taxymys? progressus.....	...	...	x	...

\*Probably upper Bridger.

### UINTAN (LATE EOCENE)

Genera: "*Paramys*," *Ischyrotomus*, *Leptotomus*, *Rapamys*, *Pareumys*, *Sciuravus*, *Protoptychus*, *Eohaplomys*, *Griphomys*, *Simimys*, *Mytonolagus*.

The type Uinta may be divided into the Wagonhound member (Uinta A, B) and the Myton member (Uinta C). Washakie B of the neighboring Washakie Basin is the equivalent of the Wagonhound. The Poway and the Tapo Ranch fauna of the middle Sespe seem to be approximate Californian equivalents of the Wagonhound and Myton respectively.

### *Wagonhound and Equivalents*

	Wagonhound	Washakie B	Poway
Ischyromyidae			
Paramyinae			
"Paramys" uintensis.....	x	...	...
Ischyrotomus.....	x	...	x
petersoni.....	x	...	...
californicus.....	...	...	x
Ischyrotomus(?) littoralis.....	...	...	x

	Wagonhound	Washakie B	Poway
Leptotomus.....	...	x	x?
grangeri.....	...	x	...
leptodus.....	...	x	...
Leptotomus(?) caryophilus.....	...	...	x
Cylindrodontinae			
Pareumys.....	x	...	x
grangeri.....	x	...	...
near grangeri.....	...	...	x
Pareumys(?) troxelli.....	x	...	...
Sciuravinae			
Sciuravus.....	x	...	x
altidens.....	x	...	...
powayensis.....	...	...	x
Protoptychidae			
Protoptychus hatcheri.....	x	...	...
Protoptychus? smithi.....	...	x?	...
Leporidae			
Mytonolagus.....	x	...	...

The type of *Protoptychus hatcheri* is recorded by Matthew as from the Myton (1910, p. 72), but the Princeton specimen label reads "Gray clays of upper B, Uinta Eocene." The age of *Protoptychus? smithi* is doubtful, for it is not certain that the type of this species is from the Washakie B.

### *Myton and Tapo Ranch*

	Myton	Tapo Ranch stage, Sespe
Ischyromyidae		
Paramyinae		
"Paramys".....	x	x
sciuroides.....	x	...
medius.....	x	...
cf. minutus.....	...	x
Ischyrotomus.....	x	?
eugeni.....	x	...
gidleyi.....	x	...
compressidens.....	x	...
Ischyrotomus(?) tapensis.....	...	x
Leptotomus.....	x	x
grangeri.....	x	...
burkei.....	...	x
near burkei.....	...	x
Leptotomus(?) robustus.....	x	...
Rapamys fricki.....	...	x
Cylindrodontinae		
Pareumys milleri.....	x	...
Pareumys sp.....	...	x
Pareumys(?) sp.....	...	x
Aplodontidae		
Eohoplomys.....	...	x
serus.....	...	x
matutinus.....	...	x
tradux.....	...	x

	Myton	Tapo Ranch stage, Sespe
Geomyoidea(?).....	...	x
Griphomys.....	...	x
alecer.....	...	x
near alecer.....	...	x
Muroidea(?).....	...	x
Simimys.....	...	x
vetus.....	...	x
cf. vetus.....	...	x
Simimys(?) murinus.....	...	x
Leporidae.....	x	...
Mytonolagus petersoni.....	x	...

The paramyine species *gidleyi* and *compressidens* have been referred to the genus *Ischyrotomus* by Peterson and Hay. They are not typical representatives. In fact, *Ischyrotomus compressidens* and *Paramys medius* may possibly be conspecific (Wilson, 1940a, pp. 70-71). The type of *Leptotomus grangeri* is from the top of the "Telmatherium beds." This species should occur also in the Wagonhound member of the Uinta formation, but nowhere in the literature can the writer find an unequivocal record of this.

#### DUCHESNEAN (LATEST EOCENE)

Genera: "*Paramys*," *Leptotomus*, *Pareumys*, *Presbymys*, *Sciuravus*(?),<sup>1</sup> *Protad-jidaumo*, *Griphomys*, *Simimys*, *Mytonolagus*.

Three stratigraphic levels are recognized in the Duchesne River series: the Randlett, Halfway, and Lapoint. The Pearson Ranch stage of the middle Sespe may be tentatively correlated with the Randlett. No rodent remains have been recorded from the Halfway member.

	Duchesne River		Pearson Ranch
	Randlett	Lapoint	stage, Sespe
Ischyromyidae			
Paramyinae			
"Paramys" tricus.....	...	...	x
Leptotomus kayi.....	x	...	...
Cylindrodontinae			
Pareumys near milleri.....	...	...	x
Pareumys(?) sp.....	x	...	...
Cylindrodontinae(?)			
Presbymys lophatus.....	...	...	x
Sciuravinae			
Sciuravus(?) sp.....	x	...	...
Geomyoidea(?).....	...	...	x
Griphomys near alecer.....	...	...	x

<sup>1</sup> Based on a note by Burke (1934a, p. 391): "... scattered teeth recovered in the same beds show that species of the *Sciuravus* and *Tillomys* type persisted to the base of the Duchesne River." If this be true, Burke's reference to *Tillomys* probably means *Mysops* as now defined, and suggests the presence of the genus *Pareumys*.

	Duchesne River		Pearson Ranch stage, Sespe
	Randlett	Lapoint	
Eomyidae.....	...	x	...
Protadjidaumo typus.....	...	x	...
Muroidea(?).....	...	...	x
Simimys simplex.....	...	...	x
Leporidae.....	x	...	...
Mytonolagus sp.....	x	...	...

## POST-DUCHESNEAN—PRE-CHADRONIAN

Whatever rodents occur in the interval between the Duchesnean and the Chadronian (including Pipestone and Thompson's Springs) are fragmentary, and not listed here. It might be worth recording, however, that the Titus Canyon fauna apparently includes a large paramyine.

## OLIGOCENE

The rodents and lagomorphs of the Chadronian-Arikarean stages are listed only by genera, not by species, except for the few types found in the upper Sespe. Lists of White River species arranged according to localities may be found in A. E. Wood's monographs on the White River fauna (1937a, p. 262; 1940, p. 359).

## CHADRONIAN (EARLY OLIGOCENE) GENERA

## Ischyromyidae

Prosciurinae: *Prosciurus*Cylindrodontinae: *Pseudocylindrodon*, *Cylindrodon*, *Ardynomys*Ischyromyinae: *Titanotheriomys*, *Ischyromys*Eutyromyidae: *Eutyromys*Castoridae: *Agnotocastor*(?)Eomyidae: *Adjidaumo*, *Paradjidaumo*Heteromyidae: *Heliscomys*Leporidae: *Palaeolagus*, *Megalagus*, *Desmatolagus*

## ORELLAN (MIDDLE OLIGOCENE) GENERA

## Ischyromyidae

Paramyinae: *Manitsha*, ?*Cedromus*Prosciurinae: *Prosciurus*Ischyromyinae: *Ischyromys*, *Titanotheriomys*(?)\*Eutyromyidae: *Eutyromys*Castoridae: *Agnotocastor*Eomyidae: *Adjidaumo*, *Paradjidaumo*Heteromyidae: *Heliscomys*Geomyoidea(?): *Diplolophus*Cricetidae: *Eumys*, *Cricetodon*, *Leidymys*Leporidae: *Palaeolagus*, *Megalagus*, *Desmatolagus*

\*According to A. E. Wood, 1937a, pp. 194, 262.

## WHITNEYAN (LATE OLIGOCENE) GENERA

To this stage the classic late Oligocene White River genera are referred, and as an expedient the Kew Quarry genera of the upper Sespe. All the John Day genera are excluded.

## Ischyromyidae

Prosciurinae: *Prosciurus*, ?*Sespemys thurstoni*,\* ?cf. *Sespemys*Ischyromyinae: *Ischyromys*

Sciuridae: Sciurid sp.\*

Castoridae: *Agnotocastor*Eomyidae: *Adjidaumo*

## Heteromyidae

Perognathinae: *Mookomys*(?) *bodei*†Heteromyinae: *Proheteromys*Cricetidae: *Eumys*, *Scottimus*, Cricetid sp.\*Leporidae: *Palaeolagus*, ?*Desmatolagus* sp.,\* ?*Megalagus*, ?*Archaeolagus*‡

\*Kew Quarry fauna of the Las Posas Hills upper Sespe.

† *Leptauchenia*(?) zone of the South Mountain upper Sespe.

‡ Recognition of this genus in the White River is probably an error in identification.

## EARLY MIOCENE

## ARIKAREEAN GENERA

This includes all of the John Day as well as the standard early Miocene of the Great Plains.

Aplodontidae: *Allomys*, *Meniscomys*, *Haplomys*Mylagaulidae: *Mesogaulus*, *Promylagaulus*, *Mylagaulodon*Sciuridae: *Sciurus*Castoridae: *Palaeocastor*, *Euhapsis*

## Heteromyidae

Perognathinae: *Mookomys*Heteromyinae: *Proheteromys*Florentiamyinae: *Florentiamys**Incertae sedis*: *Heliscomys*

## Geomyidae

Entoptychinae: *Pleurolicus*, *Grangerimus*, *Gregorymys*, *Entoptychus*Geomyinae: *Dikkomys*Cricetidae: *Leidymys*, *Pacculus*, *Schaubeumys*Muridae?: *Palustrimus*\*Leporidae: *Archaeolagus*

\*A record of the Muridae seems inherently improbable. *Palustrimus* is placed here on Wood's authority. Further comment is made in a more appropriate place.

The very highest Sespe has yielded the following two species:

Entoptychinae: *Grangerimus* or *Gregorymys* sp.Leporidae: *Archaeolagus*(?) sp.EARLY TERTIARY HISTORY OF NORTH AMERICAN  
RODENT GROUPS

The preceding section summarizes the stratigraphic development of the rodents. An analysis of these data suggests several important conclusions regarding early Tertiary rodent history. Before proceeding to this, however, it is necessary to outline at least what is known, inferred, or even guessed concerning the forms whose names appear in these lists, and their evolutionary history.

This section also is a convenient place for drawing together scattered information not dealing necessarily with the more important problems of rodent evolution. Hence, each family or subfamily will be treated in turn, following in order the classification previously outlined. Although this is essentially a review of North American groups, some mention will be made of Old World Eocene forms not represented on this continent.

#### ORDER RODENTIA

The consistent development of the gnawing habit among rodents has resulted in such characteristic structures that almost any individual specimen with which any tooth or skull material is associated, however fragmentary, can be almost immediately included in or excluded from the order. For over a hundred years practically the only problem has been the position of the hares, rabbits, and pikas in the classification. At present, almost everyone who has studied the fossil evidence, even casually, is convinced of the necessity for two separate orders, and the problem has now changed to that of evaluating the degree of relationship of these two orders. Regarding this point, Simpson (1945, p. 196) says:

It is still a moot point whether the Lagomorpha and Rodentia should be placed in a superorder or cohort Glires. Increasing evidence of their distinctness has naturally given many or most students the feeling that they have nothing at all to do with each other aside from being eutherian mammals (see, e.g., Wood, 1940). Their union on any lower level, once accepted as an "obvious" fact, is now only a hypothesis without much evidence, perhaps with no really clear evidence, although the resemblances formerly used to unite them were not, after all, imaginary. . . . The frankly hypothetical union in one cohort is yet warranted on that basis. It has practical and pedagogical advantages and, I think, no disadvantages when accompanied by a statement that it is permitted by our ignorance rather than sustained by our knowledge.

For a statement of the evidence for the ordinal separation, reference may be made to Gidley (1912) and Wood (1940).

As regards the major divisions of the order Rodentia, the classic division into three suborders, recently maintained by Simpson, is here followed. As before mentioned, it is undoubtedly defective, but has the advantage of being familiar, and is hardly less adequate than the more modern arrangements. Not only are these divisions based on zoological criteria, but the stratigraphic record suggests something similar. The real objection may lie not so much in these divisions as in the manner in which lesser groups are allocated to them. In any case, any alternative which would better satisfy the present writer would not correspond so closely to other existing classifications, and would be too personal and too premature to satisfy other students.

Consultation of stratigraphic lists reveals that fossil rodent species, or names at least, and specimens are relatively common from the base of the true Eocene upward. Most of the material is fragmentary, however, and the more complete specimens are restricted to certain groups and, particularly in respect to the

critical early Tertiary, to certain stratigraphic levels. Although the point is open to considerable debate, it may be suggested that a fair cross section of North American rodent groups of family or subfamily size is on record. The record with regard to genera is admittedly incomplete, although locally probably representative. Simpson (1945, pp. 34-35) lists only four orders in which living genera exceed in number extinct genera—Monotremata, Chiroptera, Rodentia, and Tubulidentata—and the reasons for the scarcity of the others do not apply in the case of the rodents. Even for genera, however, the record is somewhat more complete for the early Tertiary than might be inferred, for the rodents have apparently undergone a decided post-Miocene expansion.

For North America, at least, the deficiencies of the supergeneric record seem to be more the result of fragmentary condition of specimens than of nonappearance. More specifically, for the considerable and important span of time from late Paleocene to early Oligocene, only the Bridger furnishes much more than dentitions, rami, and scant skeletal fragments. Even in the Bridger few good specimens other than those of paramyines are available. The Oligocene White River and overlying Arikarean have produced a wealth of material, but good specimens are still not available for several critical types, and the John Day has furnished little postcranial skeletal material despite the presence of numerous rodent skulls.

Identifiable specimens, without regard to quality, are fairly common in the Wasatchian, abundant in the Bridger, relatively rare in the Uinta and Duchesne River but not in the Poway and Sespe, extraordinarily abundant in many parts of the White River, and, finally, common enough in the Arikaree and John Day. It is probably conservative to estimate that considerably more than half the material has been collected, if not adequately described, of all we shall ever possess from these critical stages. Hence, although a good deal of careful study of existing material remains to be made, it seems profitable to summarize existing information.

#### SUBORDER SCIUROMORPHA

Living North American members of the Sciuromorpha include the mountain beaver, squirrels, beaver, pocket mice, and pocket gophers. Extinct members include the most primitive known rodents and also the geologically most ancient. They are the dominant rodent types in North America for most of the Tertiary. Not until late Pliocene (Blancan) times did the Myomorpha assume their present importance on this continent.

The various members of the suborder are united by the fact that the infra-orbital canal does not transmit any part of the masseter medialis, or at least that the canal is not modified for transmission of the muscle. The dental formula is  $1/1, 0/0, 2-1/1, 3/3$  except in a few exceptional cases, and the fourth premolars are usually large and important teeth. Otherwise, the group as now constituted is so diverse that there is little to bind it together.

Two quite different types of zygomaseteric structure are found within the Sciuromorpha. The first is decidedly more primitive in that the masseter origin

is wholly beneath the infraorbital foramen, and limited to a narrow, horizontal zygomatic plate. No part of the masseter extends onto the rostrum. In the second and more advanced type, the zygomatic plate is broad and inclined upward so that some part of the masseter lateralis comes to lie above the infraorbital canal, and on the muzzle. The masseter superficialis forms a distinct head, and is therefore not spread out along the anterior border of the zygomatic arch. It is attached to some part of the rostrum, frequently by a distinct process. These two types when typically developed are so distinct that various authors have tended to place their representatives in separate suborders. Thus Miller and Gidley (1918) include the primitive sciuriforms with the jumping mice and jerboas under their Dipodoidae. A. E. Wood (1937a) has resurrected Zittel's old name *Protrogomorpha*, used in a somewhat different sense, for this group. The advanced *Sciuromorpha*, excluding the *Anomaluroidea*, about which no agreement exists, have usually been kept together in modern treatments of the order, with or without expression of doubt as to the validity of such an arrangement.

#### SUPERFAMILY APLODONTOIDEA

The term *Aplodontoidea* as here used is synonymous with the *Protrogomorpha* of Wood, and is nearly the equivalent of the primitive *Sciuromorpha* of Romer (1945). It should also be recalled that authors who recognize the group as of subordinal rank may retain the name for a superfamily, including only the mountain beavers and mylagaulids within it.

The aplodontoids are, as was indicated earlier, the most primitive of rodent groups. They range in time from late Paleocene to Recent, and exceed by a considerable margin the known span of any other group. Typically Eocene, during which time they are almost the only known rodents, they are also important but declining members of the Oligocene fauna. Thereafter, they are relatively inconspicuous, and only one genus, *Aplodontia*, the mountain beaver, still exists with restricted range in Pacific North America. Classically, the aplodontoids are held to be in part the ancestors of existing rodents, and in part to represent various specialized but archaic offshoots of the primitive rodent stock. In this regard, their position may be compared roughly to that of the Eocene *Creodonta* among carnivores. Miller and Gidley, however, have rejected this view, and other modern workers have been cautious in accepting it.

The zygomaseteric structure and dental formula of the *Aplodontoidea* have already been described. In addition, the tibia and fibula remain separate. The arrangement of the cranial foramina probably will prove distinctive in typical cases when better known. Many other features are present which are not characteristic throughout, and may appear in higher types, but which on the whole tend to stamp the superfamily as primitive.

#### FAMILY ISCHYROMYIDAE

The family *Ischyromyidae* as here defined, following Simpson, includes paramyines, prosciurines, cylindrodontines, sciuravines, and ischyromyines. It is

very nearly equivalent to the Ischyromyoidea of Wood. If any stem family of rodents is known, it is this group. Direct evidence based on actual specimens is largely lacking, at least in the same sense in which we speak of horse or camel phylogenies. The evidence such as it is will be presented on later pages.

Ischyromyids first appear in the late Paleocene and constitute the common rodents of the Eocene. Statistically, the number of Oligocene genera progressively declines. It cannot be stated when the Ischyromyidae became extinct, although for all practical purposes they died out in North America with the close of the Oligocene. *Sespemys*, an ischyromyid of the upper Sespe, may be early Miocene rather than late Oligocene in age. *Kansasimys* from the Kansan Edson beds (Hemphillian) may possibly represent an exceedingly late survivor of the family. Lastly, an undescribed rodent from the lower Chanac (Clarendonian) of the Great Valley of California may likewise be ischyromyid. These forms, based on only five specimens, seem to be the only possible candidates for designation as post-Oligocene members of the family.

The family as here used is too inclusive for ready definition. Broadly speaking, it comprises the relatively unspecialized members of the Aplodontioidea with, usually, short-crowned dentitions which are basined or imperfectly crested. Matthew (1910, pp. 44-45) has given an extended definition which fits most of them so far as they are known.

#### SUBFAMILY PARAMYINAE

At present the paramyines are defined almost entirely on the basis of their dental features. The dental formula is complete (for rodents), the cheek teeth are brachydont, and the pattern thereof is more sciurid in character than that in any other ischyromyid group. Typically, the tympanic bullae are incompletely ossified or loosely attached, and the skull generally lacks any specialization, except perhaps slight ones to fit into the different habitats of the paramyines. The skeleton is also apparently without any special peculiarities, and certainly not specialized to any degree, although arboreal, terrestrial, and semifossorial types were probably developed.

*Paramys* and its relatives had upper cheek teeth in which the hypocone, though variable, is of slight structural importance. Usually it is small to absent, with little distinct separation from the protocone, and the pattern can be termed tritubercular. The metaconule is a large and important cusp. The corresponding protoconule is usually distinct but reduced. The imperfect crests formed by the paracone-protoconule and metacone-metaconule converge inward toward the protocone. Development of the parastyle and mesostyle is variable. The lower cheek teeth are more or less basined. Typically, the entoconid is marginal, but distinct. It unites with the curving posterolophid,<sup>2</sup> and, although rising distinctly above it, is seldom separated from that crest by more than a slight notch. Hypolophids are absent or only incipient.

The members of the Paramyinae range in time from late Paleocene to the

<sup>2</sup> For the tooth-cusp nomenclature used throughout this paper see fig. 3; see also Wood and Wilson, 1936.

Orellan inclusive. For the first part of the range, to the close of the Wasatchian, they are either essentially or actually the only known rodents. Hence, their position in the geologic record suggests an ancestral relation to the later rodents. Their many primitive features, and lack of any significantly specialized ones so far as is known, suggest the same thing.<sup>3</sup> The primitive nature of the paramyine group has been actively advocated or tacitly assumed by all American workers. Matthew (1910, pp. 64-66) has described many primitive characters, most of which are listed below. Some not mentioned by him are also given. As Matthew pointed out, many of these are characters of primitive Eutheria generally:

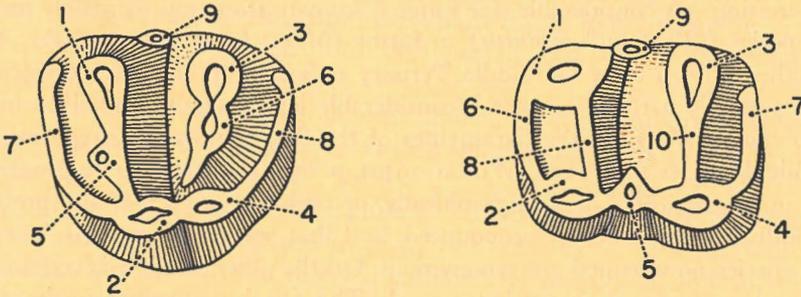


FIG. 3. Principal nomenclature employed in cheek-tooth descriptions

*Upper molar*

- |                |                       |
|----------------|-----------------------|
| 1, paracone    | 7, anterior cingulum  |
| 2, protocone   | or anteroloph         |
| 3, metacone    | 8, posterior cingulum |
| 4, hypocone    | or posteroloph        |
| 5, protoconule | 9, mesostyle          |
| 6, metaconule  |                       |

*Lower molar*

- |                                      |                        |
|--------------------------------------|------------------------|
| 1, metaconid                         | 7, posterior cingulum  |
| 2, protoconid                        | or posterolophid       |
| 3, entoconid                         | 8, metalophulid II     |
| 4, hypoconid                         | 9, mesostylid or meta- |
| 5, mesoconid and                     | stylid                 |
| ectolophid                           | 10, hypolophid         |
| 6, anterior cingulum or anterolophid |                        |
| or metalophulid I                    |                        |

(1) Dental formula  $1/1, 0/0, 2/1, 3/3$ , the maximum found in any known rodent. (2) Cheek teeth brachydont. (3) Cheek teeth with pattern structurally capable of evolution into other types so far as is known. (4) Zygomaseteric structure of primitive type, that is, resembling most nearly that found in other mammals, and particularly in primitive mammals. (5) Tympanic bullae incompletely ossified or loosely attached. (6) Paroccipital processes short, directed away from bullae. (7) Pronounced interorbital constriction. (8) No postorbital processes. (9) Jugal in contact with a relatively large lachrymal. (10) Considerable squamosal extension behind postglenoid process, with small mastoid exposure. (11) Incisive foramina relatively small. (12) Foramen ovale distinct from foramen lacerum medium. (13) Sphenopterygoid and alisphenoid canals present and separate. (14) Posterior region of skull shallow. (15) Vertical, uninflected angle. (16) Scaphoid and lunar separate, at least in some. (17) Tail very long and heavy. (18) Humerus with entepicondylar foramen. (19) Tibia

<sup>3</sup> A. E. Wood, 1946 (abstract) states, "The family [=Paramyinae of this paper] cannot have the fundamental ancestral position usually given it, since most members are too highly specialized." This brief statement, however, is as yet undocumented.

and fibula separate. (20) Femur with third trochanter. Presumably, many additional features might be mentioned, but no complete description of an Eocene ischyromyid exists. For example, it seems quite probable that the optic foramen was well separated from the sphenoidal fissure.

Although from first to last the paramyines, as currently recognized, are a remarkably stable group, minor distinctions are numerous, and the list of named species is very long. In general, as Matthew points out (1910, p. 50), a trend exists from Wasatchian species "with broad flat crowns and low marginal cusps, to those of the Uinta with higher cusps, reduced basins, and a tendency to cross-cresting." A considerable size range is known, from approximately mouse-like species ("*Paramys*" *minutus*) to forms (*Manitsha tanka*) far larger than any other known early or middle Tertiary rodent. The long list of species is perhaps largely a reflection of the considerable length of time involved in the group range. Work on the paramyines of the Sespe, however, suggested that individual species may have (Wilson, 1940a, p. 65) "a limited range geographically and ecologically, or stratigraphically, or perhaps both." It is also probable that individual variation is pronounced, and that several of the two dozen or more species now named are synonymous. On the other hand, it is certain that the number of named genera is too small. This fact is recognized in the stratigraphic lists by assigning numerous species, as was done in the past, to *Paramys*, but in quotation marks.

Problems of individual variation, and several other more important ones, may be solved or partly solved in the near future, for Dr. A. E. Wood is now engaged in reviewing the Paramyinae. In the absence of announced results from this study, the information for the present synopsis has been taken chiefly from Matthew (1910; Matthew and Granger, 1918), reinforced for the later paramyines from the more or less incidental work of Burke (1934a, 1935b), Simpson (1941), and Wilson (1937b, 1940a).

The known paramyine species fall into several different groups, which in part represent natural lines of descent, but in part may be artificial. The three groups with the greatest geologic range are: (1) *Pseudotomus-Ischyrotomus-Manitsha*, representing the tribe Manitshini. This is a natural group of relatively robust rodents with flanged symphysis, and broad incisors and cheek teeth. Presumably this group is terrestrial to semifossorial. It ranges from early Bridgerian to Orellan inclusive. Wasatchian representatives appear to be unknown at present. (2) "*Paramys*" *copei-Paramys-Leptotomus*. This group is probably natural, especially as regards the Bridgerian and later forms. The species are on the whole medium-sized, without a pronounced symphyseal flange, with moderately compressed incisors, and with narrower cheek teeth than in the Manitshini. Cheek-tooth enamel typically is quite rugose. They are the arboreal paramyines of Matthew. In time, the group is early Wasatchian to early Duchesnean. (3) "*Paramys*" *buccatus* group. Species included are: "*P.*" *buccatus*, "*P.*" *murinus*, "*P.*" *atwateri*, "*P.*" *minutus*, "*P.*" *tricus*. Possibly also "*Mysops kalicola*" should be placed here, and "*Sciuravus depressus*" may be an offshoot of the same line. As here constituted, this assemblage may be in large

part artificial. It includes very small paramyines with subquadrate molars in which the hypocone plays a relatively important part. The upper molars in some at least have decidedly concave occlusal surfaces with reduced conules. The lower dentition in "*Mysops kalicola*" and "*P.*" *tricus* shows in the talonids slight trends toward the sciuravine and cylindrodontine cresting of the entoconids. The geologic range is from early Wasatchian to early Duchesnean inclusive.

Other less well known lines are those represented by *Reithroparamys*, apparently an offshoot from the *Paramys* group; *Rapamys*; and possibly *Cedromus*.

Progressive differentiation within the paramyines is indicated by the presence of two, possibly three groups in the Wasatchian; four in the Bridgerian; and four, possibly five in the Uintan.

One or two lines other than those mentioned are apparently represented, but the known species can be fairly well distributed among those named—at least judging from published work.

It has been pointed out that the antiquity and primitive nature of paramyines suggests that they are ancestral to many or even all later rodents. This view, advocated by Matthew, has received considerable support, if only in the way of attempts to derive the dental pattern of various rodents from the *Paramys* type. It must be admitted, however, that very little direct evidence has been forthcoming to substantiate this hypothesis. The main argument apparently still has to be based on (1) the antiquity and primitiveness of the group, and (2) the fact that no better theory with any geological evidence at all has been advanced. This theory will be the subject of extended discussion on later pages, so it is reviewed here only briefly.

Aside from (1) derivation of the aplodontid-mylagaulid rodents from the paramyines, a derivation perhaps not accepted by all, and not involving the higher rodents in any case, the evidence is certainly scant. As based on some evidence, however weak and improbable it may seem, the following theories may be listed with regard to North American forms: (2) The Bridger sciuravines and *Mysops* may have been derived from middle and late Wasatchian members of the "*Paramys*" *buccatus* group; here also, however, only aplodontoids are involved. (3) The Prosciurinae with paramyine-type upper teeth and imperfect hypolophids in the lower cheek teeth may have branched from the Paramyinae by way of the *Rapamys*<sup>4</sup> line, although not directly. (4) The Sciuridae were possibly derived from the Paramyinae, as is suggested by real resemblances in the teeth, and a zygomasseteric structure in primitive squirrels not too remote from the aplodontoid. (5) The Eutypomyidae may be castoroid, and the upper molars of *Eutypomys* resemble, grossly but not in detail, the molars of *Paramys*. (6) The upper molars of *Florentiamys*, probably heteromyid, also show distinct resemblances to paramyine teeth. In addition, the Eurasiatic Gliroidea (dormice) have teeth which might possibly be derivable from the dentition of some members of the "*Paramys*" *buccatus* group. It may be noted

<sup>4</sup> *Rapamys*, though retaining a paramyine upper dentition and a nearly typical lower dentition, shows changes in the entoconid-posterolophid paralleling the sciuravines.

that, extremely speculative as the above list may sound, it involves chiefly and directly groups usually referred to the Sciuromorpha.

Negatively, in respect to Matthew's theory, the Paramyinae seem a remarkably stable group on the whole, with few and minor departures from the typical. Further, the paramyine groups or lines of descent previously listed (pp. 90-91) do not lead noticeably toward any other group, with the exception of members of the "*P.*" *buccatus* group, and possibly *Rapamys*. Moreover, the lines represented in the Bridger lead far enough upward in time to make it almost impossible that any higher type evolved from them with the exception of the Sciuridae. Thus, in general, if any higher group evolved directly from the Paramyinae, it must have been from unknown or little-known members of the subfamily. On the other hand, the presence of *Rapamys* in the late Eocene suggests that the paramyines were capable of some fairly significant dental changes at a rather late date in their history. Indirectly, the Paramyinae, if they gave rise to the Sciuravinae, would also be ancestral to any descendants of the latter.

Apparently three paramyine genera have been reported from Europe. These are "*Paramys*" and *Decticadapis* of the early Eocene, and *Plesiarctomys* of the late Eocene. The former two are the only early Eocene rodents reported from Europe. No paramyines are known from Asia, and, indeed, no Eocene rodents are certainly known from that continent.

The earliest paramyines are completely characteristic of the order so far as known. Certainly, the Rodentia would not merge into a generalized eutherian stock short of the late Cretaceous or early Paleocene, so that the order is one of the more ancient.

#### SUBFAMILY PROSCIURINAE

The Prosciurinae include for the present only the Oligocene genus *Prosciurus* and, tentatively, *Sespermys* (Whitneyan or Arikareean). The name *Prosciurus*, however, probably covers more than a single generic type. Specimens referred to *Prosciurus* have been found not only in North America, where the genus is widely represented in the White River, but also in Mongolia and southwestern Asiatic Russia (Kazakstan).

The group is characterized by a *Paramys*-like upper dentition, and a highly variable but usually distinct hypolophid in the lower cheek teeth which approaches the sciuravine type. The skull is very poorly known. The single basicranial fragment, of uncertain reference to the genus, shows several sciurid-like features, but the zygomatic structure is certainly aplodontoid.

Earlier writers placed *Prosciurus* in the Sciuridae. As the genus became better known, this assignment was recognized as incorrect on the basis of the zygomatic structure. Miller and Gidley (1918) allocated the genus to the Paramyidae (Paramyinae of this paper). A. E. Wood (1937a) assigned it to the Sciuravidae (including Sciuravinae and Bridger *Mysops* of this paper). Simpson (1945) placed it in the Sciuravinae, otherwise constituted as in the present paper. The wide difference in pattern of the upper molars seems to the

writer to indicate that *Prosciurus* cannot be assigned to any group built chiefly around the genus *Sciuravus*. Superficially, the dentition resembles the cylindrodontine type in both uppers and lowers, but the details suggest lack of the close relationship necessary if assignment is to be made to the relatively compact Cylindrodontinae. Both Matthew (1910, p. 67) and McGrew (1941c, pp. 23-24) have thought that *Prosciurus* is structurally ancestral to the aplodontids. The discovery of *Eohaplomys* in the late Eocene, however, as recognized by McGrew, seems reason enough for not viewing the Oligocene genus as a genetic ancestor. It may be an Oligocene survivor of an Eocene stock which gave rise to the aplodontids. This stock appears to be closely related to the Paramyinae, but the different construction of the talonid in typical cases prevents assignment of *Prosciurus* to the latter group. Thus it seems best to treat *Prosciurus* and its relatives as a separate group, but most closely related to the particular paramyines which gave rise to the Aplodontidae (Wilson, 1949a, pp. 14-17). *Rapamys* indicates that derivation from the Paramyinae is not impossible, and ?*Prosciurus jeffersoni*, *Cedromus wardi* are forms which narrow the structural gap between typical paramyine and typical prosciurine.

In addition to the aplodontid relationship suggested by some species of *Prosciurus*, other species indicate that a special relationship to the Sciuridae may not be altogether beyond credence (Wilson, 1949b, pp. 31-32). Much depends on determination of the affinities of several still imperfectly known types, and also on the acquisition of definitely associated skull material.

Whatever are the true relations of *Prosciurus*, its direct Eocene ancestor is unknown, at best only faintly suggested (i.e., *Rapamys*). The small paramyines of the "*Paramys*" *buccatus* group are apparently barred on the basis of hypocone development and some other features, but the poor material and lack of definite assurance that the group is natural permit this group to remain a possibility.

More extended exposition of various views on the relationship of the Prosciurinae may be found in McGrew, 1941c; Wood, 1937a; and Wilson, 1940a, 1949a, 1949b. The affinities of *Sespemys* with the type genus are discussed in Wilson, 1949c.

#### SUBFAMILY CYLINDRODONTINAE

The Cylindrodontinae as now constituted apparently include as North American forms the Bridgerian *Mysops*, the Uintan and Duchesnean *Pareumys*, and the Chadronian *Ardynomys*, *Pseudocylindrodon*, and *Cylindrodon*. *Ardynomys* is also known from the early Oligocene of Mongolia; and *Tsaganomys* and *Cyclomytus*, from the later Oligocene of the same region, have been rather generally accepted as highly specialized cylindrodontines. *Pareumys* has been placed in the Ischyromyidae (Ischyromyinae of this paper) by Wood (1937a, p. 173), but the affinities of this genus (and *Mysops*) are distinctly cylindrodontine (see especially Burke, 1938, p. 255; Wilson, 1940c, pp. 105-108). *Sespemys* has also been included in the Cylindrodontinae, but there is at least as much evidence for placing this genus in the Prosciurinae (Wilson, 1949c, pp. 54-55). Pre-Bridgerian species are not known, but some late Wasatchian specimens

suggest that the group arose from the Paramyinae during Wind River time. The group, then, ranges from early Bridgerian through Chadronian on this continent, with some chance of an earlier and a later span.

The dental formula of the Cylindrodontinae is  $1/1, 0/0, 2-1/1, 3/3$ . The upper cheek teeth retain the paramyine pattern in greater or less degree. Usually the hypocone is weakly developed, and even when not, is not distinctly separate from the protocone. The protoloph is complete, but the metaloph is either weakly connected with the protocone or incomplete. The protoconule is nearly, or in advanced forms completely, fused into the protoloph. The corresponding metaconule is large, and is a much more distinct cusp. In the lower cheek teeth, the hypolophid is well developed, the posterior trigonid wall steep, and the ectolophid without a distinct mesoconid. In both upper and lower cheek teeth, the basins are relatively deep and pocketed, especially the central ones. Typically, the intervening crests are in consequence high, and rather thin as well. Progressively, the difference in elevation of the trigonid and talonid tends to be reduced. The dentition is brachydont to hypsodont (to evergrowing, if the late Oligocene Mongolian forms are included). The only complete and fully described skull is that of *Pseudocylindrodon medius* of the early Oligocene (Burke, 1938). This species apparently retains, in greater degree than any other Oligocene type, the primitive construction of its ancestors, and has advanced beyond such rodents as *Paramys* and *Sciuravus* principally in "expansion of the brain case, modifications in the occipital region and an advanced type of auditory bulla" (*ibid.*, p. 268). The other Oligocene genera show various stages leading toward fossorial adaptation, or so they have been interpreted. The postcranial skeleton is unknown. There seems to have been a general increase in size with time.

"*Mysops*" *kalicola*, of the late Wasatchian, is more nearly paramyine than anything else; yet this species, here tentatively referred to the "*Paramys*" *buccatus* group, shows certain features suggestive of the cylindrodontines. At best, however, "*M.*" *kalicola* and similar types indicate only the possibility of a middle and late Wasatchian origin of the cylindrodontines. Some other members of this paramyine group may have a similar position in respect to the Sciuravinae. If these forms are actually ancestral to both, they presumably should not be placed together in the same paramyine group.

The Cylindrodontinae are well established by early Bridgerian time with the appearance of *Mysops*. This genus already shows the beginnings of the characteristic dental specializations of the later types. It is altogether likely that within *Mysops* can be recognized initiation of the several lines of later cylindrodontines, but the individual and temporal variations present make it unfeasible to distinguish these in practice.

*Pareumys* is known from two stages of the Uintan and one of the Duchesnean. In general, there is not only an advance of *Pareumys* over *Mysops*, but also of the late Uintan and early Duchesnean over the early Uintan. The teeth become progressively higher-crowned, the cresting more pronounced, and the talonid-trigonid heights equalized. In the upper molars, the more primitive species

have transverse and detached metalophs, an advance over the oblique and more complete loph of typical *Mysops*. The later species apparently undergo further backward shift in the alignment of the metaloph, with the metaconule becoming rather decidedly united to the posteroloph. Present evidence suggests that *Pareumys* left no known descendants; at least, the Chadronian cylindrodontines are more readily derived from *Mysops* than through an intermediate *Pareumys* stage. The ancestors of the Oligocene genera, however, were in existence during the Uintan, and these may be recorded, but simply confused with *Pareumys*, the diagnostic upper cheek teeth being of rare occurrence.

The early Oligocene cylindrodontines appear as three separate lines of descent—in part separated by individual specializations, and in part by different rates of evolutionary progress from *Mysops*. With respect to dentition, *Cylindrodon* seems to represent the culmination of the general advance toward a hypsodont and evenly crested type, already seen in *Pareumys*. The relationships may be expressed approximately by means of the accompanying diagram (fig. 4).

*Pseudocylindrodon* is broadly the most conservative of the early Oligocene

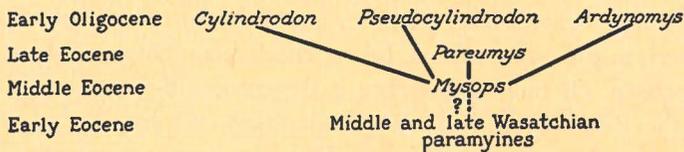


FIG. 4. Phylogeny of the Cylindrodontinae

genera. As Wood (1937a, p. 204) suggests, it seems to be a surviving relict of the Eocene type which gave rise to *Cylindrodon*, but with some otherwise distinctive features. *Cylindrodon* has higher-crowned teeth, and has progressed in skull features slightly beyond it, in the same direction as *Ardynomys*. In *Ardynomys*, the skull is definitely specialized in the "robust construction throughout, the flattened brain-case, the sharply constricted and narrow interorbital region, and the antorbital breadth, coupled with an angular and heavy type of rostrum" (Burke, 1936, p. 136). These features have been interpreted as pointing to a fossorial existence, but Simpson urges caution in this regard (1941, pp. 14-15). The cheek teeth of *Ardynomys* are less specialized than those of *Cylindrodon*, and also on the whole than those of *Pseudocylindrodon*. At least, *Pseudocylindrodon neglectus* resembles *Cylindrodon* more closely than does *Ardynomys*. The dentition of *P. medius*, however, is closer to that of *Mysops* than is that of any other Oligocene member of the group. *Cylindrodon* and *Pseudocylindrodon* appear to be more closely related to each other than either is to *Ardynomys*.

Progressive differentiation within the Cylindrodontinae is indicated by the development of several distinct Oligocene lines in place of the single known Bridger genus.

Other than *Tsaganomys* and *Cyclomyilus*, the cylindrodontines seem to have

left no descendants. Thus, of the three subfamilies of rodents known from the Bridger, one, the Cylindrodontinae, is almost certainly a dead-end group.

Extended discussion of the genera may be found in Burke, 1935<sup>a</sup>, 1935<sup>b</sup>, 1936, 1938; Wilson, 1938, 1940<sup>c</sup>; and A. E. Wood, 1937<sup>a</sup>. The detailed relationships of these are too complex, and on the whole not of sufficient importance to the present paper, to be treated more fully here.

Mention should be made of the Sespe genus *Presbymys* from the Pearson Ranch stage (Wilson, 1949<sup>a</sup>, pp. 7-12), here assigned tentatively to the Cylindrodontinae. The assignment is chiefly on the basis of similarity of the worn upper dentition of the paratype of *Presbymys lophatus* to worn dentitions of the cylindrodontines. The type lower dentition is bilophate, somewhat geomyoid in appearance, and distinctly less similar to that of cylindrodontines. Resemblances have also been noted to the Protoptychidae. Whatever the affinities of this genus, the dental pattern is highly specialized, and no other Eocene or Oligocene rodent has a directly comparable tooth structure.

#### SUBFAMILY SCIURAVINAE

The preceding ischryomyids all have, but in varying detail, the basic paramyine pattern in the upper molars. Lower cheek teeth, however, show a greater range in pattern. Of most importance is the entoconid-posterolophid development. In the Prosciurinae and Cylindrodontinae, the hypolophid is present, whereas in the Paramyinae it is not. This has been considered of decided systematic importance. On the other hand, these and other rodents show intermediate stages between typical ones, and apparently transformation from the *Paramys* type to those with a strong hypolophid has been accomplished a number of times. What is now known suggests that more stress should be placed on the pattern of the superior cheek teeth than on that of the lower. In the Sciuravinae, a very distinct type of upper molar is found which the writer believes to be of prime importance in determining the broader relations of the Eocene rodents. So far as is known, the only intermediates which bridge the gap between the upper molar of *Paramys* and that of *Sciuravus* in any degree occur in a group, "*Paramys*" *buccatus*, which may represent the paramyine stem that gave rise to the Sciuravinae.

The Sciuravinae have molars in which the hypocone not only is well developed, but also is distinctly separated from the protocone by a pronounced intervening valley. In correlation with this type of hypocone development, a reduction of the conules has occurred. This is especially evident in comparing the metaconule of the paramyine type with that of *Sciuravus*. As a matter of fact, it remains to be demonstrated that the structures in *Sciuravus* usually identified as the conules really represent these primary tubercles. The metaloph is of quite different design, and no longer tends to trend obliquely forward and inward to join the protocone, the common but not universal condition in the paramyine type. Because the loph structure is variable, it will be described independently at the end of this section. The lower molars show a hypolophid development of

varying degree. The entoconid is separate from the posterolophid and compressed anteroposteriorly so that it projects into the basin of the tooth. It does not necessarily join the hypoconid-ectolophid to make a complete hypolophid, but generally it does so. When it does, it is more obviously the result of extension of the entoconid across the basin than in, say, the *Cylindrodontinae*, in which the impression is gained of a more marginal entoconid, with the connecting crest independently developed. Cheek teeth are brachydont, or essentially so. The dental formula is  $1/1, 0/0, 2/1, 3/3$ , but  $P_4$  is notably reduced in some species.

The skull of *Sciuravus* in general resembles that of *Paramys* "except for a longer muzzle, more slender proportions, and absence of sagittal crest. . . . The tympanic bulla is incompletely ossified and loosely attached to the skull; it has no tubular meatus, the ossification comprising little besides the tympanic ring. What is known of the skeleton agrees with *Paramys* except for the lesser width of the distal end of the humerus" (Matthew, 1910, p. 60). The orbit is larger, and the eyes looked more outward than in *Paramys*. The small infra-orbital foramen is visible when viewed from the side of the skull, whereas this is not true of *Paramys* (Miller and Gidley, 1918, pp. 439, 442). The sciuravines are generally small animals, ratlike in size, and hence average considerably less in bulk than the paramyines.

In time, the Sciuravinae are known to have ranged from early Bridgerian to early Uintan inclusive. If "*Sciuravus depressus*" is a sciuravine, the downward limit is middle Wasatchian. Records of the group later than early Uintan are vague, but Burke (1934a, p. 391) speaks of teeth of the *Sciuravus* type persisting into the basal Duchesne River beds.

The ancestors of the Sciuravinae are not certainly known at present. The single possibility lies in members of the "*Paramys*" *buccatus* assemblage, the group favored by Matthew.

*Sciuravus* has been suggested, with little or no evidence brought forward in support, as a possible ancestor of a number of later types. Among these may be mentioned ischyromyines, cylindrodontines, eomyids, castoroids, geomyoids, and muroids. So far as any direct and convincing evidence goes, the Sciuravinae could well have died out without any Oligocene or later descendants. Several authorities (Matthew and Burke, for example) have considered the Ischyromyinae possible descendants, and for more than speculative reasons. Moreover, if the geomyoid, muroid, and dipodoid groups have any special ancestors among the known Eocene aplodontoid rodents, they apparently lie in the Sciuravinae. Especially to be noted is the possible affinity of the Sciuravinae with the Muroidea. Still more speculatively, it may be suggested that the Gliroidea originated from peripheral species of the "*Paramys*" *buccatus* and sciuravine groups. These possibilities, and the evidence, will be discussed fully on later pages.

Material hardly exists in sufficient quantity to justify the establishment of lines of descent. Most of it is from the Bridger, and here, because of considerable individual variation, uncertainty of level in many instances, and several other

factors (see Wilson, 1938, pp. 131-132), the evolutionary pattern, if any, is obscured. The later Bridgerian types are on the whole more progressive, and depart more widely from the paramyine type than do the early ones, as is recognized for example by increase in size, and increase in strength of hypolophid. *Sciuravus? rarus* has  $P_4$  distinctly reduced, and this species is apparently on a line distinct from the common *S. nitidus* of the Bridger. *Sciuravus eucristadens* of the early Bridgerian of the Green River formation shows certain features pointing to an *Ischyromys*-like type of dentition. In addition to the common Bridger genus, *Sciuravus*, other sciuravines are *Tillomys* and *Taxymys*. These latter are so imperfectly known that their relation to *Sciuravus* is not entirely clear, but *Taxymys* certainly represents a divergent line. *Pauromys* also is clearly on a separate line, but assignment to the Sciuravinae is not certain. *Sciuravus altidens* is the only described Uinta species. It seems to be a direct descendant of the Bridger *S. nitidus*. *Sciuravus powayensis* of corresponding age from the Poway of California can hardly be so regarded. Instead, suggestive similarities to *S. eucristadens* are found, but not to *Ischyromys*. Thus, it is at least clear that a number of different lines are known, most of them contemporaneous, and varied descendants could be expected.

Several somewhat different types of upper molar pattern are found in the Sciuravinae. The usual type is seen in *Sciuravus nitidus* and *S. altidens*. In these, the protoloph and metaloph are incomplete. That is, the conules (?) appear to be present but fused with the inner cusps; the demiloph thus formed are somewhat oblique and alternate with the paracone and metacone. In *S. powayensis* this characteristic of the loph is strengthened, and the pattern approaches the fundamental plan of the muroids. On the other hand, in *Taxymys* the protoloph and metaloph are complete, and the teeth hence more crested transversely than in *S. nitidus*, so that a closer approach is made to a bilophate pattern. Lastly, some specimens suggest possible loss of the conules without cresting, thus leaving as major units of the pattern four more or less isolated cusps. These last two patterns approach, but at a great distance, the geomyoid plan.

#### SUBFAMILY ISCHYROMYINAE

The Ischyromyinae include only two genera, *Ischyromys* and *Titanotheriomys*. The dental formula is  $1/1, 0/0, 2/1, 3/3$ , and the cheek teeth are brachydont. In the superior cheek teeth, a hypocone is well developed although the valley between the principal inner cusps does not cut very low, and the cusps are rather distinctly joined by their edges. Thus, the hypocone development is not quite like that of *Sciuravus*, and suggests an extreme development of the paramyine type. The conules are absent or essentially so as discrete structures, the basic pattern consisting of two strongly developed transverse lophs. There is no mesocone. In the lower cheek teeth, a strong hypolophid is present, but the ectolophid is short and without a mesoconid. The skull is aplodontoid in zygomasseteric structure, but a subsciuroid structure develops in *Titanotheriomys*. The tympanic bullae are ossified and attached. The skeleton shows many re-

semblances to that of *Aplodontia*, but is more primitive (paramyine). Wood refers to the members of the group as slow-moving, subfossorial types.

The Ischyromyinae range from Chadronian to Whitneyan inclusive. *Ischyromys* is known throughout the Oligocene, and *Titanotheriomys* is a Chadronian genus, with some possibility of an Orellan record. The latter genus is distinguished from *Ischyromys* by somewhat different skull proportions, by some distinctions in the tooth pattern, and by failure of the temporal crests to unite into a sagittal crest. Moreover, the zygomasseteric structure of *Titanotheriomys* departs from the aplodontoid type, and takes on the previously noted subsciuroid appearance.

Although *Ischyromys* is probably represented by more complete material than any other early Tertiary rodent genus, the exact affinities of the Ischyromyinae are still in doubt, other than that they are closely related to other members of the family. Troxell (1923c, pp. 393-396) thought that *Ischyromys* had descended from *Mysops* (as now defined). In an earlier paper (1922) he reached the conclusion that the White River genus was a forerunner of *Cynomys*, the prairie dog. Later workers have sought a relative in one or another of the Bridger rodents, but have assumed that *Ischyromys* left no known descendants. It is reasonably certain that the Bridger sciuravine-cylindrodontine groups include the ancestor of the genus, although its identity has not been definitely established. It may be that no known form stands in a direct ancestral relation.

Matthew (1910, p. 61) considered the dentition of *Ischyromys* to be a direct outgrowth of that of *Sciuravus* with conversion of the cusps into crests. More recently, Burke (1937, pp. 6-8) has pointed out noteworthy resemblances between certain species of the two genera. On the other hand, Wood (1937a, p. 186), by inference at least, has suggested *Mysops* as the ancestor.

That the Bridger ancestor of *Ischyromys* is to be sought in *Sciuravus*, or at least in the Sciuravinae, is indicated by: (1) the small importance of the conules as discrete structures in both groups; (2) the presence of a well developed hypocone; (3) a still closer approach to upper teeth of the *Ischyromys* type by the Bridger *Taxymys*, if this genus is actually sciuravine; and (4) details of the lower dentition pointed out by Burke. The alternate view is favored by: (1) lack of a mesoconid in *Ischyromys*; (2) the manner of union of protocone and hypocone; and perhaps (3) the general features of the skeleton, which suggest very indirectly a relationship to some other group than the Sciuravinae.

Although the writer studied the pertinent Bridgerian forms in some detail, he found no convincing demonstration of the relation of *Ischyromys* to either group. Therefore, the current uncertainty is sufficient reason, among others, for retaining the subfamily as distinct from either the Sciuravinae or the Cylindrodontinae. The Ischyromyinae may, however, be more closely allied to the former group.

#### FAMILY PROTOPTYCHIDAE

The Uinta genus *Protoptychus* is the sole representative of this family known at present. The type of *P. hatcheri*, represented by a single specimen, consists

of the major part of a skull. *Protoptychus? smithi* has been tentatively assigned to the genus, and is likewise known only from its type, a maxillary fragment. *Protoptychus hatcheri* is recorded as coming from Wagonhound strata. *Protoptychus? smithi* is of uncertain stratigraphic position, but may be from comparable beds of the Washakie Basin. Matthew (1910), however, refers *P. hatcheri* to the upper Uinta, and although this assignment is presumably not correct, the characters exhibited by the skull suggest the later rather than earlier date.

The dentition of the type skull is worn and the details of pattern are obscured. The upper cheek teeth of *P.? smithi* are clear enough in pattern, but doubt exists as to its proper reference to the genus. In any case, the superior tooth pattern is ischyromyid, and in particular has greatest resemblance to that of the *Cylindrodontinae* except for prominent hypocone development, and of the *Ischyromyinae*. It consists of one deep median external inflection of enamel flanked by two shorter, shallower ones; the median basin being retained for a time after the anterior and posterior ones have disappeared. The cheek teeth are relatively hypsodont. The dental formula of the type is  $1/$ ,  $0/$ ,  $2/$ ,  $3/$ ; that of *P.? smithi*, apparently  $1/$ ,  $0/$ ,  $1/$ ,  $3/$ . The lower cheek teeth are unknown. If *Presbymys* of the Pearson Ranch Sespe should prove to be related (Wilson, 1949a, pp. 10-11), then the lower dentition may be quite different from what might be expected, and bilophate, somewhat geomyoid-like in pattern.

It is in the skull, however, not the dentition, that characters are seen which suggest the necessity of maintaining a separate group for *Protoptychus*. Instead of being of the expected Eocene ischyromyid type, the skull bears a rather striking resemblance in many features to that of the dipodoids, and to a lesser extent the heteromyids. These resemblances are reflected in the tendency until rather recent years to classify *Protoptychus* with the Dipodidae (Matthew; Miller and Gidley) or Geomyoidea (Zittel, 1925). Particularly noteworthy in this connection is the considerable inflation of the bullae, especially the mastoid part. Other significant departures from the paramyine type are seen in the fully ossified bullae; the large incisive foramina; the absence of a sagittal crest; the absence of pronounced interorbital constriction; and the large, high, and narrow infraorbital foramen. On the other hand, the jugal is still in contact with the lachrymal, a primitive feature.

Scott, in his comprehensive and original description of *Protoptychus* (1895), thought of the genus as an ancestral dipodoid, and one not too far removed from the ancestral heteromyid type as well. Wood (1935a, p. 239) has suggested that it is simply a sterile but highly specialized aplodontoid. This view, based primarily on the dentition, is adopted here, but other ideas of affinity should be remembered, for the skull features may well prove to be of real significance. *Protoptychus* is the only known early Uintan rodent which is without either direct or indirect Bridger relatives, in that it does not seem to belong to the paramyine-cylindrodontine-sciuravine groups. Obviously, there are no certainly known descendants.

## FAMILY APLODONTIDAE

The Apododontidae are represented in the present North American fauna by the genus *Aplodontia*, the mountain beaver or sewellel. Although *Aplodontia* has survived as a highly specialized type, it still is of considerable interest as the only living representative of the primitive rodent stock. Its present range is restricted to the coastal region from southern British Columbia southward to the San Francisco Bay region of northern California. In the past, the range of the Apododontidae has been more extensive, but in general still confined to the area west of the Rocky Mountains. No authoritative North American Tertiary record is known outside of California, Nevada, and Oregon. However, a seemingly authentic occurrence of an apodontid in the Pliocene of Mongolia (*Pseudaplodon asiatica*) should be mentioned, and *Allomys* has been identified in the European Phosphorites of Quercy by Piveteau (1934).

The known geologic range of the Apododontidae is from late Uintan to Recent. No pre-Uintan rodent extends the record further, but it is probable that in Bridger times the apodontids were hardly to be distinguished from the paramyines. Absence of a Bridgerian ancestor may well be accounted for by the absence of nonmarine deposits of that age in the Pacific coast region.

The Apododontidae retain the primitive zygomaseteric structure. The dental formula,  $1/1, 0/0, 2/1, 3/3$ , is also primitive. The fourth premolars tend to enlarge somewhat in most members. The upper molar pattern is of paramyine type, but anteroposterior connecting crests develop, converting the occlusal surface into a series of basins. These basins are apical features, and are gradually lost from the adult pattern as the cheek teeth are converted from brachydont to hypsodont with persistent growth. Hypocones are of variable development, but later forms are without them. Prominent mesostyles are characteristic features. In the lower molars, a similar series of basins forms. A metastylid (or mesostylid) comparable to the mesostyle of the uppers may be developed. Even the earliest apodontids exhibit in lower molar pattern a departure from the typical paramyine type in that a weak hypolophid may be present, and the entoconid is separate from the posterolophid. Nevertheless, the writer feels that the Apododontidae originated within the Paramyinae, and never passed through a stage in which the dentition could be associated with either the cylindrodontines or the sciuravines (Wilson, 1949a, pp. 15-17). The skull progressively widens posteriorly, and takes on a fossorial appearance, although the Arikareean genera are rather squirrel-like. This sciuroid aspect is heightened by the presence of postorbital processes in these genera. The angle of the ramus, except in the earlier species, becomes greatly inflected, the posterior end everted. This feature is strikingly different from the vertical, uninflected angle of the Ischyromyidae. After John Day time at least, fossorial features become pronounced.

The earliest and only known Eocene apodont is *Eohaplomys* of the Tapo Ranch Sespe. In this form, the cheek teeth are brachydont and ischyromyid in pattern, but the details already suggest the later types. The angle of the ramus

is still unspecialized. *Eohaplomys* may be regarded as an approximate structural ancestor to both the later aplodontids and the mylagaulids.

A considerable interval in time separates *Eohaplomys* from the next younger aplodontids, those of the John Day formation. Within this interval, apparently the only rodents which may be related to the aplodontids are the Prosciurinae (see earlier section on the Prosciurinae). Again, as in the case of the pre-Uintan ancestors of *Eohaplomys*, this absence from the Oligocene may be merely a reflection of scarcity of rodent remains for that epoch in the area of evolution.

Three Arikareean (John Day) aplodont genera have been described: *Haplomys*, *Allomys*, and *Meniscomys*. These appear to be valid and distinguishable genera. They have been placed in a distinct family, Allomyidae, by Miller and Gidley (1918), and this arrangement has been followed by A. E. Wood (1937a, p. 261). However, even if the John Day genera should prove to be highly divergent from the later aplodontids, which seems very doubtful, this taxonomic treatment would be extreme. Consequently, earlier authors and McGrew (1941c) are followed here, and the John Day genera united with *Liodontia* and *Aplodontia* in a single family.

*Haplomys* is brachydont and its tooth pattern relatively primitive. In these features a close approach is made to *Eohaplomys*. The genus seems to be a relict of unknown Oligocene forms, although not necessarily close to the main line of descent. Postorbital processes are apparently present. Because of its late appearance, this genus cannot be ancestral to younger types.

*Allomys* is more hypsodont than *Haplomys*, with a more complicated occlusal pattern, but like *Haplomys* it does not seem to be related to later types. Primarily, but not entirely, this statement is based on the presence of the more advanced *Meniscomys* in the same beds. As in *Haplomys*, postorbital processes are present.

*Meniscomys* is the most hypsodont of the John Day genera. In addition, the cheek-tooth pattern is more advanced in the direction of the later aplodontids. McGrew (1941c) has reiterated the opinion of most authors that this genus is approximately ancestral to *Liodontia* and *Aplodontia*, and at least structurally ancestral to the mylagaulids. He has presented detailed dental evidence for this view. There is, however, considerable difference in the shape of the skull and bullae, and a decided increase in hypsodonty which must have taken place between Arikareean and early Barstovian time. Therefore, if the relation of *Meniscomys* to *Liodontia* is ancestral, this instance at least indicates rapid evolution of a rodent line. It is not without parallel, despite frequent comments by authors on the slowness of rodent evolution.

Cope has reported *Meniscomys* as bearing postorbital processes on the skull. It should be remembered, however, that he included the genera *Allomys* and *Haplomys* in his genus, and these do exhibit those structures. *Meniscomys hippodus*, as figured by Cope (1884, pl. 63, fig. 10a), shows what may be small postorbital structures. *Aplodontia* (and *Liodontia*?) is without them, and if all the John Day genera are alike in this feature, then these may be somewhat off the line of descent leading to the later Tertiary forms.

Acquaintance with the details of aplodontid dental evolution may be gained by consulting McGrew, 1941c; Stock, 1935; and Wilson, 1949a. These are the most recent contributions, and McGrew's paper contains a comprehensive bibliography.

#### FAMILY MYLAGAULIDAE

The Mylagaulidae are now known to be merely a rather highly divergent branch of the general aplodontid stock. They make their first known appearance in the Arikareean, where some of them (i.e. *Promylagaulus*) are very like *Meniscomys*. This resemblance is soon partially masked by their own peculiar specializations. The last mylagaulids disappear with the close of the Hemphillian Pliocene. Although accorded separate family status, the Mylagaulidae might well be regarded as a subfamily of the Aplodontidae, and this arrangement would have the merit of indicating the close relationship of these two groups, which is not so apparent in the classification here employed. The family has not been recorded outside North America. They differ from the aplodontids, however, in that they migrated almost upon their inception to the Great Plains area, where their remains are common throughout the geologic span of the group.

The dentition is basically that of the Aplodontidae. The fourth premolars, however, rapidly enlarge beyond their condition in that family. Concomitantly, the molars are reduced. Moreover, the premolars in the more advanced types expand toward the base of the tooth, a process which results in forcing  $M_{1/1}$  out of the jaws during life. Indeed, in extreme cases  $M_{2/2}$  and  $M_{3/3}$  may apparently drop out in the same way.  $P^3$  is present in the primitive types, but is later lost. The dental formula may be expressed as  $1/1, 0/0, 2-1/1, 3-0/3-0$ . An additional difference from the Aplodontidae is seen in the retention of the modified elements of the premolar pattern throughout life, progressively more so in the later genera, as a series of enamel lakes, whereas in the mountain beaver these lakes are progressively lost. Thus, the number of lakes retained into an advanced stage of tooth wear increases, and in the later species these exceed in number the original basins of the teeth. The premolars are progressively higher-crowned. The skull of advanced mylagaulids exhibits many features also shown in *Aplodontia*, but in exaggerated fashion. These similarities are the result not only of a common inheritance from a primitive ancestor, but also of a common fossorial habitat. The skeleton is strikingly fossorial, with powerful digging forequarters. In this regard, the later mylagaulids are more modified for subterranean life than is *Aplodontia*, and it is probably true that the former have always held this position since initiation of a fossorial habit in both. Heavy postorbital processes are present. Some at least of the post-Arikareean species have heavy twinned horn cores on the nasals, a unique feature. The angle of the ramus is turned inward and the posterior border everted, more or less as in the later aplodontids, but less markedly.

Arikareean mylagaulid genera are *Promylagaulus*, *Mylagaulodon*, and *Mesogaulus*, in order of increasing advancement. The first named differs so little

in dentition and what is known of the skull from the nearly if not exactly contemporaneous *Meniscomys* that it needs careful observation to prevent confusion with the latter. Whether *Meniscomys* could be actually ancestral to this and more advanced mylagaulids can only be established with the exact correlation of the John Day faunas with respect to those of the Arikarean of the Great Plains. *Promylagaulus* is from the top of the lower Rosebud beds of South Dakota, and *Meniscomys* is confined to the John Day, Matthew's record of the latter from the Rosebud apparently pertaining to the former genus (McGrew, 1941c, p. 9).

*Mylagaulodon* is the only John Day mylagaulid. Actually, the material representing it was found in local deposits lying between the typical John Day and the Mascall, and hence may be post-John Day (see footnote in McGrew, 1941c, p. 23). This genus is also recorded from the upper Rosebud. Hence, available stratigraphic evidence suggests that *Mylagaulodon* and *Promylagaulus* although essentially contemporaneous may be slightly separated in time. This suggestion is supported by the fact that the former is more advanced in tooth pattern, although primitive enough to have been referred at one time to the Aplodontidae by Matthew. A mesostyle is still present and riblike, an aplodontid feature.

*Mesogaulus* first appears in the late Arikarean and persists into the Barstovian. It is distinctly more advanced than either of the other Arikarean genera. The skull has assumed the proportions of the later mylagaulids, the premolars are higher-crowned, and the mesostyles, although present, are no longer riblike.

The three Arikarean genera bridge the gap between *Meniscomys* and *Mylagaulus*, and indicate that quite probably the Mylagaulidae originated from the aplodontids as late as Whitneyan time, perhaps even slightly later. A detailed discussion of the dental evolution as currently interpreted on the basis of available material is given by McGrew (1941c).

#### ADVANCED SCIUROMORPHA

It has already been pointed out that two types of zygomaseteric structure are found within the Sciuromorpha. The more advanced type, in which the zygomatic plate is broadened and inclined, is found in the Sciuroida, Castoroidea, and Geomyoidea. In conjunction with this feature, the infraorbital foramen generally no longer pierces the zygomatic root, but has migrated forward on the rostrum. The dental formula is  $1/1, 0/0, 2-1/1, 3/3$ . If *Diplolophus* should prove to be a geomyoid, then the cheek-tooth formula may be  $0/0, 3/3$  in rare cases, but the fourth premolars usually are strong, functional teeth. Tibia and fibula may be free (squirrels), fused at their distal ends (some beavers), or considerably fused (pocket mice and gophers). The advanced Sciuromorpha of this paper corresponds to the "Sciuromorpha" of A. E. Wood (1937a, p. 261). It is difficult to escape the conclusion that the members of this group are polyphyletic in origin.

In general, the first appearance of the advanced sciuromorph rodents is in

the Oligocene. None is known from beds older than late Eocene. More specifically for this continent, the oldest record is late Uintan. The pre-Oligocene forms are: *Protadidaumo* (Eomyidae), late Duchesnean; and *Griphomys* (?Geomyoidea, but more certainly not aplodontoid), late Uintan and early Duchesnean. *Presbymys* (early Duchesnean), if not cylindrodontine, might conceivably have some remote affinity with the Geomyoidea. The late Eocene European forms are: *Eomys* (Eomyidae), and several genera doubtfully assignable to the Anomaluroidea. The anomaluroids, however, can hardly be regarded as advanced sciuriforms as this term is here employed.

No Eocene rodents are known which can be termed typically sciuriform, castoroid, or geomyoid, and hence the living advanced sciuriforms are without demonstrable Eocene roots. The first undoubted sciuriform record seems to be early Arikareean (John Day) and Aquitanian in age. Castoroids and geomyoids appear distinctly earlier, with more or less reliable Chadronian records.

#### SUPERFAMILY SCIUROIDEA

The superfamily Sciuroidea includes only a single family, the Scuridae or squirrels. Some authors have separated the flying squirrels as a distinct family of rodents, but there seems no very cogent reason for their individual recognition at this taxonomic level.

The Sciuroidea retain in greater degree than any other existing rodent group the primitive dentition of the paramyines. It is even doubtful if any dental characters are present which would separate all known squirrels, fossil and living, from all paramyines. North American squirrels of the later Cenozoic, however, are distinguishable in general on the basis of less distinct conules and more crested lophs, pronounced posterior lobe of  $M^3$ , greater development of the anterior cingula in the upper teeth; and anterior position and reduction of the entoconids, rhombic rather than quadrate or subquadrate outlines in the lower teeth. The cheek teeth are brachydont and rooted; progressively, in ground-dwelling types, mesodont or unilaterally hypsodont. Almost always, the dental formula is  $1/1, 0/0, 2/1, 3/3$ ; rarely, it is  $1/1, 0/0, 1/1, 3/3$ .

The skull differs from the paramyine type in a number of important respects. The brain case is more inflated (although this character is less marked in the earlier types), and apparently sufficiently so to prevent, with rare exceptions, the formation of a sagittal crest. The skull is somewhat arched in nearly all types. Tympanic bullae are not excessively large, but are inflated, fully ossified, and attached to the skull. It should be mentioned, however, that *Reithroparamys* is exceptional among paramyines in having ossified bullae. Postorbital processes are usually well developed. The bony palate is broad. Typically, the zygomatic plate is broadened and inclined sufficiently to reach the dorsal surface of the skull. This feature, however, is variable in living squirrels; in such forms as *Belomys* (living flying squirrel of southern Asia), the zygomatic plate is so narrow that a close approach is made to the condition found in *Aplodontia*; and most of the Miocene types have less extensive plates.

The small and ventrally placed infraorbital foramen has usually migrated a

varying distance forward from its primitive position, although not so far forward as in the Castoroidea and Geomyoidea. In a few (i.e., some individuals of *Tamias*, A. E. Wood, 1935a, pp. 245-246), it has nearly the same close relationship to the zygoma as in *Paramys*. A distinct knob for attachment of the masseter lateralis superficialis is present. The masseteric fossa normally terminates beneath  $P_4$ . This forward position is correlated with development of the zygomatic plate and forward migration of the masseter. In the earlier Miocene squirrels the fossa is intermediate in position between this condition and the normal paramyine one, in which the fossa ends beneath  $M_2$  (Bryant, 1945, p. 367). The late Miocene or early Pliocene *Protospermophilus quatalensis* also shows an approach to paramyine structure in the profile of the superior border of the ramus between  $P_4$  and the incisor, in that it is less concave than in the modern sciurids (Gazin, 1930, p. 64). Tibia and fibula are incompletely fused. Squirrels may be arboreal, terrestrial, or fossorial, but the skull never becomes distinctly fossorial in appearance. The known geologic range of the Sciuroidea is that of the family Sciuridae, Arikarean (John Day) to Recent. The Sciuridae are apparently the last sciuriform group to make their appearance.

The origins of the Sciuroidea seem to lie in the Paramyinae, although this is inferred rather than proved. Scott has indicated certain sciurid-like features in "*Paramys*" *sciuroides* (1890, pp. 475-477), and Wilson has observed some sciurid trends in the ramus and dentition of *Cedromus wardi* (1949b, pp. 31-32). Conversely, Gazin has noted some paramyine features in the brain case of early Barstovian squirrels (1932, p. 57). Several authors have viewed *Prosciurus* as an ancestral type (see especially Matthew, 1910). Any such relationship for *Prosciurus* has been denied by Wood, but he figures and describes a skull fragment, tentatively assigned to *Prosciurus*, which exhibits several sciurid features, including strong postorbital processes (1937a, pp. 163-165). Certain Old World squirrels show dental patterns reminiscent of the prosciurines and apodonts.

A number of similarities tend to unite the Paramyinae, Prosciurinae, Apodontidae (and Mylagaulidae), and Sciuroidea. These may be rather vague parallelisms for the most part, but it seems to the writer that all the above-named groups are more closely related to one another than they are to any other Oligocene or later North American rodents with the possible exception of the castoroids. If so, the relationship is complex, and not likely to be easily comprehended. Further, the writer believes the evidence at present favors a late development of the Sciuroidea, or at least of types clearly recognizable as such, and more or less directly from the Paramyinae.

#### FAMILY SCIURIDAE

The North American Sciuridae are represented by tree squirrels, ground squirrels (more exactly, terrestrial squirrels and chipmunks), and flying squirrels. The flying squirrels are very poorly represented in the fossil record, presumably because of their habits, and have not been recognized in North American

deposits earlier than the Pleistocene. The remaining two groups are more abundantly recorded, with skull material known for several of the species. The oldest known terrestrial squirrels, however, are apparently early Barstovian in age. This suggests, but does not prove, that the terrestrial types originated during the Miocene. On the other hand, Bryant (1945, p. 384), in his comprehensive and very valuable recent review of the North American Sciuridae, presents a phylogenetic chart with a separate terrestrial line extending back into the Oligocene. The oldest undoubted sciurids of certain stratigraphic position are from the John Day and Tecuya (Arikareean of southern California) formations. These are placed in the genus *Sciurus* by Bryant. It is doubtful whether any forms so old could actually represent a modern genus, but in any case they apparently are tree squirrels. If squirrels in Oligocene time were fully distinct from the Paramyinae, and this is a definite possibility, their apparent absence from the record might be explained on the basis of the scarcity of tree-dwelling types generally. The first undoubted European sciurids seem to be Aquitanian, and nearly equivalent in time to the John Day species.

What appears to be a true sciurid is recorded from the Kew Quarry Sespe. If the quarry fauna should prove to be Whitneyan (H. E. Wood *et al.*, 1941, p. 23) rather than Arikareean, the authentic range of the Sciuridae would be slightly increased. Bryant records the age of this indeterminate Sespe species as upper Eocene (1945, pp. 339, 340-341). This is an error, for the fauna is undoubtedly either Whitneyan or Arikareean.

#### SUPERFAMILY CASTOROIDEA

The Castoroidea include the family Castoridae (beavers) and, doubtfully, the extinct Eutypomyidae. The former is represented today by a single genus, *Castor*, but the group is well represented in the fossil record by a number of genera belonging to several distinct phyla. Past differentiation is marked enough so that some authors have subdivided the Castoridae into separate families (Chalicomyidae, Castoridae, and Castoroididae), but this procedure is extreme, and has not been followed recently by American workers. The Eutypomyidae are known at present only by *Eutypomys*.

As here constituted, the Castoroidea range from early Oligocene (Chadronian) to Recent. Even if the Eutypomyidae are removed, a doubtful record is known from the Chadron, and there are authentic records from the Orellan.

The cheek-tooth pattern of advanced castorids in the upper dentition consists of one internal inflection of enamel and three external inflections. This pattern is reversed in the inferior teeth. Cheek teeth are mesodont to hypsodont to evergrowing. In the earlier, less hypsodont forms, the enamel inflections may be converted into lakes upon wear. The hypocone is well developed. The dental formula is  $1/1, 0/0, 2-1/1, 3/3$ , but except in the Oligocene species, the third premolar is lost (possible exception in *?Agnotocastor montanus*). In all known instances, the pattern of the cheek teeth is already well advanced, and is isolated from that in other sciuriforms. No known Eocene type seems directly ancestral. The closest resemblances are to certain hystricomorphs, but these are in

end members of each group, and apparently of no genetic significance. A possible clue as to origin may be obtained from the fact that *Eutypomys* upper molars are superficially like those of *Paramys*.

In the Castoroidea, the zygomaseteric structure is similar to that in advanced squirrels. The zygomatic plate is broad and inclined, reaching to the dorsum. The narrow and small infraorbital foramen has migrated forward on the rostrum, and is usually separated by a ridge from the area of masseter lateralis origin. Postorbital processes are absent. The zygomatic arches are deep anteriorly. The tympanic bullae are ossified and firmly attached; the auditory meatus is long, and directed upward and outward. Mastoids are uninflated. The skull and skeleton are usually rather noticeably modified for fossorial or aquatic life. The size is large for rodents, some late types being gigantic.

Most authorities have regarded the Castoroidea as relatively closely related to the Sciuroidea, some (e.g. Romer, 1945) even placing the Castoridae in the latter. Tullberg (1899) has indicated that the beavers show certain features which suggest a myomorph affinity. What can be made out of the dental pattern likewise points to both sciuriform and myomorph affinities. The writer, at present, is inclined to view the Castoroidea as showing closer relationship with the Sciuroidea than with the Geomyoidea or any other non-aplodontoid rodent group.

#### FAMILY EUTYPOMYIDAE

The Eutypomyidae are represented solely by the genus *Eutypomys* of the Chadronian and Orellan stages of the White River and Cypress Hills. The position of this family is uncertain, but it can be tentatively assigned to the Castoroidea. *Eutypomys* is an advanced sciuriform, although a primitive one, and shows similarities to both the Sciuridae and the Castoridae, with perhaps more to link it with the latter.

The dentition is mesodont; the tooth formula,  $1/1, 0/0, 2/1, 3/3$ . An outstanding feature of the tooth pattern is the presence of a large number of small enamel lakes distributed over the entire occlusal surface, and tending to obscure the fundamental pattern. This latter appears, in the maxillary teeth, to be based on a quadrituberculate plan with connecting crests. A. E. Wood states that there is no clear indication of the conules (1937a, p. 224), but this may be taken to mean merely that they are lost in the pattern complexities. The pattern suggests derivation from a sciuravine rather than a paramyine type. Wood, however, has also written that "One of the closest analogies in tooth pattern that I have seen to that of *Eutypomys* occurs in *Paramys sensu strictu* (i.e., in the Bridger species). Here there is a similar development of complex wrinkles in the enamel, although they do not become so prominent a part of the pattern. In the upper molars, this similarity reaches such a point that it is almost suggestive of genetic relationships. The lower molars, however, clearly show that this resemblance is merely parallelism" (*ibid.*, p. 226). A hypolophid is present in the lower cheek teeth, and sometimes a post-hypolophid valley, sometimes not. The pattern of the lower teeth shows certain resemblances to that in *Agnotocastor* (Wilson,

1949*b*, pp. 33-34), or so it seems to the present writer. To Wood, the only similarity between eutypomyid and castorid patterns is that between the former and advanced members of the latter (i.e. *Amblycastor*).

Judging from Wood's illustrations (1937*a*, pl. 29), the skull of *Eutypomys* is somewhat more like the squirrels, particularly the primitive squirrels, than the castoroids in the details of the zygomatic plate, except that the inferior border is more emarginate. A relatively broad palate is also suggestive of the sciurids. The infraorbital foramen, however, is relatively high in position. Postorbital processes are lacking. The brain case is not enlarged, so that the primitive rodent features of a sagittal crest and narrow interorbital region are present. These last give the skull a castoroid appearance. A small optic foramen is likewise a beaver feature.

The pes is rather unusual. Metatarsals I and II are relatively long, slender, and divergent from the others. Metatarsals III, IV, and V are robust and compact, rather strongly interlocked. Wood compares the interlocking arrangement of these outer metatarsals with a similar construction in the Geomyidae. This feature, however, is perhaps no more developed than in some beavers, for example *Dipoides stirtoni*. Comparison of the pes of *Eutypomys* with that of many rodents and other mammals by Wood failed to give any clue as to the locomotor habits of the animal.

The presence of *Eutypomys* in the fossil record, with its mingling of sciurid and castorid features in both skull and skeleton, is perhaps an additional reason to those usually given for regarding the beavers and squirrels as related, although it must be held in mind that many of those features are primitive, retained in varying degree by the later sciuriforms. *Eutypomys* may also give a clue as to what the ancestral tooth pattern was like in the beavers, but it still does not suggest any immediate Eocene ancestor for either group. Neither does the tooth pattern give any decisive answer as to its possible derivation from either paramyine or sciuravine type. Other evidence suggests very inconclusively that both the Eutypomyidae and the Castoridae are more closely related to the paramyines than to the sciuravines of the Bridger, although *Sciuravus* is usually cited as the most probable Eocene ancestor.

#### FAMILY CASTORIDAE

The North American Castoridae appear to be divisible into two general groups (Stirton, 1935). These are (1) a group leading into the Recent *Castor*, characterized by semiflattened incisors; and (2) one developing into the Pleistocene giant beaver, *Castoroides*, with rounded incisors and somewhat different cheek-tooth pattern. The first has been termed the Castorinae; the second, the Castoroidinae (Simpson, 1945). Both appear to be present as far back as the Oligocene.

The only member of the family to be described from Oligocene beds in North America is *Agnotocastor*. This genus appears to represent the group having rounded incisors (see Wood, 1937*a*, p. 223; Wilson, 1949*b*, p. 33). Apparently some material, not yet distinguished from *Agnotocastor*, indicates the presence

of a beaver with flat incisors as early as the Orellan. From the Arikareean are to be recorded *Palaeocastor* and *Euhapsis*, both of which belong to the flat-incisor group.

*Agnotocastor* ranges from Chadronian? to Arikareean?. The only skull material which has been described is from the Whitneyan, and we cannot be certain that in such features as zygomaseteric structure the earlier Oligocene species were as modernized as *Agnotocastor*, although they may well have been. The known specimens indicate a form with skull intermediate between those of *Eutypomys* and *Palaeocastor*. It is hence less fossorial than the latter, but that it was becoming fossorial is indicated by the short nasals, small, upward-directed eyes, and other characters. The dentition is mesodont; the dental formula, 1/1, 0/0, 2/1, 3/3. Cheek-tooth pattern in the known specimens is too heavily worn to indicate much. In general, the pattern shown is that of *Palaeocastor*. That of the lower dentition of *Agnotocastor coloradensis* is perhaps more complex than in the usual Arikareean *Palaeocastor*, and faintly reminiscent of *Eutypomys* in this respect.

*Palaeocastor* replaces *Agnotocastor* in the Arikareean, where the former genus is common not only in the Great Plains fauna, but also in the John Day. Fossorial characters are emphasized, the teeth hypsodont, but not excessively so. In connection with this genus, the structures called *Daemonelix* should be mentioned. These are vertical, spirally coiled tubes, usually expanding into inflated, horizontal chambers at the base. They vary in size over a considerable range. The larger ones are fully seven feet in length, with tube diameters up to a foot and a half. *Daemonelix* has been called a plant, and also the burrow of *Palaeocastor*. The latter is the generally accepted view at present. At least it may be safely stated that *Palaeocastor* lived in the more typical structures, and probably built them. The less typical ones may have had other origins.

*Euhapsis* is known only by a single specimen. It represents an extreme fossorial type, with very wide skull and forward-sloping occiput.

As indicated before, the Eocene ancestors of the Castoridae have not been recognized. The castorids are common only after the disappearance of *Eutypomys*, but even if the latter is representative of a pre-castorid group, the ultimate ancestry is still uncertain. In Europe, the oldest beavers (*Steneofiber*) are only upper Stampian (= late Orellan or early Whitneyan?) in age, and so are of no help in this connection.

#### SUPERFAMILY GEOMYOIDEA

The Geomyoidea are represented by two exclusively New World families: the Heteromyidae (pocket mice and kangaroo rats), and the Geomyidae (pocket gophers). These are closely related, and, indeed, an argument can be made for uniting them in a single group. In addition, the present classification includes a third family, the extinct Eomyidae, which are both New and Old World in distribution, and of uncertain reference to the Geomyoidea.

Undoubted heteromyids appear in the fossil record as early as Chadronian; geomyids, not until the Arikareean. In addition, *Griphomys*, a possible geo-

myoid, is of late Uintan and early Duchesnean age; and *Diplolophus*, possibly geomyid, is found in the Orellan. North American Eomyidae are first known from the late Duchesnean, and persist into the Whitneyan. Old World records of this family suggest a late Eocene (*Eomys*) to early Miocene (?) range for the family.

The cheek teeth of the geomyoids, exclusive of the Eomyidae, are of transversely bilophate type, becoming in advanced forms simple ovals of enamel surrounding dentine, and finally anterior or posterior enamel plates or both, united by dentine. Conules are absent, but strong internal (upper teeth) and external (lower teeth) cingula are present in the primitive forms. Apparently the presence of a distinct hypocone, together with modification of the cingula into cusps, resulted in a sextubercular system in spite of conule loss. The six cusps are arranged in two transverse rows of three each, usually indistinctly separate or fused with each other. Cheek teeth are brachydont to evergrowing; inferior teeth are mirror images of the superior ones. The Eomyidae have brachydont to mesodont cheek teeth of cricetodont-like pattern. In all three families the dental formula, except in one doubtful genus (*Diplolophus*), is  $1/1, 0/0, 1/1, 3/3$ .

The skull is murine in general form, especially in the less specialized terrestrial types, but the zygomatic structure is that of the advanced sciuriforms, with the zygomatic plate fully developed. The infraorbital foramen has migrated forward approximately halfway to the incisors, and is normally without trace of protecting knob or crest. Mastoid exposure is large, and the bone inflated, sometimes considerably so in those members whose skulls are not modified for underground life. Postorbital processes are never present. Tympanic bullae are ossified and firmly attached to the periotics, except in the Eomyidae. The optic foramen is closely associated with the sphenoidal fissure. Tibia and fibula are fused throughout a considerable part of their length, and the latter is reduced. All forms so far as known are either terrestrial or fossorial.

*Heliscomys* is an Oligocene and early Miocene heteromyid which A. E. Wood regards as probably ancestral to all later members of the family, and structurally ancestral to all Geomyidae. However, the dental pattern in this form (see section on Heteromyidae) is completely unlike any known Eocene type, so that the ancestry of the Geomyoidea (exclusive of the Eomyidae, at least) is unknown at present. Upper molars have well developed hypocones and no conules, and this fact suggests as the only possibility the Sciuravinae. Likewise, the eomyid tooth pattern is cricetodont, and indicates the same thing only more strongly. On the other hand, *Florentiamys* (Arikarean), supposedly an aberrant heteromyid, has a dentition suggestive of the paramyines (A. E. Wood, 1936d, pp. 44-47). *Griphomys* is late Eocene in age, and has been questionably referred to the Geomyoidea by the writer. In details of dental structure this genus is unlike *Heliscomys*, and bears little resemblance to any Bridger rodent group. The upper molars are becoming bilophate, and are quadrituberculate in structure, with anterior and posterior cingula. The lower molars are approximate mirror images, but show single posterior crests rather than the bifurcate or double crests required for a true reversed pattern. A highly modified sciuravine

pattern is perhaps suggested. Among known geomyoids, however, the closest resemblance, distant though it may be, is to *Florentiamys*.

The possible relation of certain other Eocene genera (*Presbymys*, *Protoptychus*) to the Geomyoidea has been indicated in previous sections. None of the Eocene genera contributes anything directly to the solution of the problem of geomyoid ancestry. If any one of them has special affinity with this group, it merely serves to increase the complexity of the problem. Despite this uncertainty, however, it seems to the writer that if any Bridger group has the remotest genetic affinity, it is the Sciuravinae. At least, this is not impossible.

For approximately the past half-century, the Geomyoidea have been placed in the Sciuromorpha because of their zygomassteric structure. Many of the earlier zoologists, however, regarded them as myomorphs. Although it would be contrary to the thought of recent years to return to this classification, if such a procedure were to prove valid on genetic grounds it would offer a somewhat more satisfying explanation for many characters present in the geomyoids (*s.l.*) than does the assumption of parallelism in subordinally distinct groups. It would, however, force the abandonment of zygomassteric structure as a conclusive criterion for genetic relationship, and in the absence of real evolutionary evidence, may be highly objectionable to most workers on this ground alone. Further discussion of the question is best postponed to later pages.

#### FAMILY EOMYIDAE

The Eomyidae may be broadly defined as rodents with cricetodont-like tooth pattern but not tooth formula, and an advanced sciuromorph type of zygomassteric structure. They still, however, retain many primitive rodent characters. The earliest North American genus is *Protadjidaumo* of the late Duchesnean. Oligocene forms are represented by *Adjidaumo* (Chadronian-Whitneyan) and *Paradjidaumo* (Chadronian-Orellan). These American forms have been included in a separate family, Adjidaumidae, but they seem to be clearly in the same group as *Eomys*, *Omegodus*, and *Rhodanomys* of the European Tertiary (see A. E. Wood, 1937a, pp. 234-235).

The tooth pattern in the relatively primitive American forms, *Protadjidaumo* and *Adjidaumo*, is similar to that described as cricetodont, but, of course, not identical. It also resembles that of *Simimys*, an Eocene myomorph, and, to a lesser extent, that of *Sciuravus*. The upper molar plan consists of four main cusps with connecting crests. The anterior and posterior crests are cingular in origin. A deeply indented mure is present. The mesocone is somewhat compressed to form a short mesoloph. Paracone and metacone unite with the inner elements by means of a protolophule I and metalophule I respectively. A small mesostyle may be present. Conules appear to be absent. The lower cheek teeth are essentially mirror images of the uppers. Hence, the hypolophid tends to connect entoconid with posterolophid rather than directly with the hypoconid. The dental formula is 1/1, 0/0, 1/1, 3/3, and the cheek teeth are brachydont. *Protadjidaumo* is somewhat more primitive than *Adjidaumo*, and may be directly ancestral.

*Paradjidaumo* is more advanced than the preceding genera in height of crown (mesodont), and with wear the pattern assumes an omega-like form. The dental formula remains the same. Although closely related to the other two, this genus apparently represents a distinct line of eomyid rodents (Burke, 1934a, p. 394).

The skull is murine in general appearance, and indicates a terrestrial habitat. The only reasonably complete description is that by the writer (1949b), and applies particularly to *Paradjidaumo*, but no outstanding difference was evident on comparison with the available skull fragments of *Adjidaumo*. The skull of *Protadjidaumo* is unknown. The eomyid skull shows a number of primitive aplodontoid features, such as interorbital constriction; shallow brain case; loosely attached, hollow, although ossified bullae; and contact of lachrymal with jugal. Aside from its aplodontoid aspects, it is quite like unspecialized skulls of the Heteromyidae (e.g. *Liomys*) and various cricetids, but particularly the former, for it has a fully developed zygomaseteric structure of advanced sciuromorph type. The infraorbital foramen is rather far forward on the muzzle, but not so advanced in position as in typical heteromyids. The mastoids are of considerable exposure, and somewhat inflated, roughly comparable to those of *Liomys*. The optic foramen is apparently separated from the sphenoidal fissure by a narrow bony bar. Fibula and tibia appear to be fused in geomyoid-myomorph fashion.

The position of the Eomyidae is uncertain. This problem is discussed at length by the writer elsewhere (Wilson, 1949b). It is evident that the eomyids show more resemblance to the geomyoids than to any other rodent group above the aplodontoid level. A. E. Wood is of the opinion that these forms do not belong to the Geomyoidea, where several workers have placed them. Wood bases his conclusions on (1) the structure of the infraorbital foramen, and (2) the tooth pattern. The former may not be particularly critical. Although it is true that the structure of the cheek teeth is not like that of any Oligocene or later geomyoid, it should be noted that the muroids have produced two quite different types of tooth pattern. The cricetid type bears a marked resemblance to that of the eomyids; the murid type shows some similarity to that of typical heteromyids, more so certainly than to that of any other sciuromorph group. If the muroids could produce two such types, and many authors do not grant separate family status to the Muridae, there seems no reason why a similar situation could not prevail in the Geomyoidea. If the Eomyidae are geomyoids, then the cheek-tooth pattern of the more primitive of them may be taken as suggestive of the basic plan in the superfamily. This in turn would point to the sciuravines rather than any other known Eocene group.

If the Eomyidae are not geomyoids, then either they are myomorphs, and the zygomaseteric structure must be discounted, or they represent an independent superfamily. This last suggestion will appeal strongly to some, but is purely negative, whereas it seems to the writer that a considerable body of evidence suggests that the Geomyoidea (as used here), Muroidea, and Dipodoidea all may have evolved from the sciuravine stock, in contrast with the aplodont-

sciuroid-(?)castoroid groups, which suggest derivation more directly from the paramyines.

#### FAMILY HETEROMYIDAE

The Heteromyidae (pocket mice in a general sense) are a family of New World rodents, chiefly of western North America, but ranging southward into northern South America, and, in the past, eastward into Florida. Living forms include *Perognathus* (pocket mouse), *Microdipodops* (pygmy kangaroo rat or kangaroo mouse), *Dipodomys* (kangaroo rat), and *Liomys* and *Heteromys* (spiny pocket mice). Extinct types are rather common, and have been made known by several workers, but particularly by A. E. Wood (1935a). The Recent genera fall into either two or three subfamilies. According to the latter arrangement, *Perognathus* and ?*Microdipodops* are placed in the Perognathinae, *Dipodomys* in the Dipodomyinae, and *Liomys* and *Heteromys* in the Heteromyinae. The Perognathinae, however, have been included with the Dipodomyinae as a single subfamily (Ellerman, 1940, pp. 470-471). In any case, the kangaroo rats developed after Arikareean time, and do not enter into the scope of the present paper. The remaining two groups are apparently known from as far back as the Whitneyan. In addition to these, the subfamily Florentiamyinae has been established for the aberrant Arikareean genus *Florentiamys*.

The dentition of the Heteromyidae is similar to that of the Geomyidae, but is less advanced for the same stage of geologic time. Primitively, as stated before, the molars consist of six cusps arranged in two transverse rows of three each. Four of these are primary, and two develop from the cingulum. At a later stage in development, as hypsodonty is acquired, the cusps unite to form a bilophate pattern. Rarely, as in *Dipodomys*, the cheek teeth are of persistent growth, and the pattern is reduced to enamel ovals, or, in very advanced species, enamel plates united by dentine.

Heteromyids are terrestrial or subfossorial types, and the skull is not modified for underground existence. A bipedal, ricochetal skeletal modification may develop. Hence, the skull is lightly constructed, and the nasals project beyond the incisors. The bullae may be greatly expanded. The interorbital region is relatively broad; the zygomatic arches are extremely slender.

The oldest undoubted pocket mouse is *Heliscomys*, not readily assignable to any of the recognized subfamilies. This genus is now known to range from the Chadronian into the Arikareean (McGrew, 1941b). Almost all the material is from the Orellan, and no Whitneyan types have been found. A. E. Wood in 1935 viewed this genus as ancestral to all later types. The discovery of *Florentiamys*, and of additional material of *Heliscomys*, introduced doubt as to the strict validity of this concept (Wood, 1936d; 1939, pp. 560-561), which however is still considered by Wood to be a distinct possibility. In any case, the molars of *Heliscomys* are primitive in comparison with those of the later Perognathinae, Dipodomyinae, and Heteromyinae, and their pattern appears to be close to the immediately ancestral one for these groups. That this pattern is truly primi-

tive is doubtful, for it would completely isolate the Heteromyidae and Geomyidae from all other early Tertiary rodents, the only approach at all being made by the late Tertiary Muridae. Whether *Heliscomys* is actually ancestral to the later heteromyids depends largely on the true significance of the premolar structure.  $P_4$  typically has only three cusps (*H. vetus*). Other species (*H. hatcheri*, *H. senex*) show, in addition, a poorly developed fourth cusp. The pre-*Heliscomys* ancestor of the group must have had a fourth cusp, as do almost all post-Oligocene types. In the living *Perognathus spinatus nelsoni* a three-cusped condition is reached through known degeneration. Therefore, it seems much more likely to the writer that *Heliscomys* is undergoing cusp loss than gain, as Wood originally thought. Confirming this conclusion to a certain extent is the fact that *Heliscomys woodi*, the last known species of the genus, has only three cusps (McGrew, 1941*b*, p. 55).  $P_4$  is comparatively small, and if cusp reduction is actually operative, it may be a clue indicating the eventual loss of the tooth. This does not seem to be true of  $P^4$ , however. Even so, a suggestive parallelism to the Muroidea is present which should be held in mind in connection with the peculiar genus *Diplolophus*.

Whitneyan heteromyids are represented by the heteromyine *Proheteromys* (A. E. Wood, 1937*a*, pp. 215-216), and possibly the perognathine *Mookomys* (*Mookomys*(?) *bodei* Wilson, 1949*c*, pp. 58-60). The forms mentioned show only imperfectly the characteristics of the Heteromyinae and Perognathinae, but presumably indicate (1) that these groups developed as early as Whitneyan, and (2) that the common ancestor was not much more remote in time (Orellan?).

Arikareean heteromyid genera are *Heliscomys*, *Mookomys*, *Proheteromys*, and *Florentiamys*. *Mookomys* is close to *Heliscomys* in the general distinctness of individual cusps, and in shortness of crown, but differs in having a quadrituberculate  $P_4$  and generally more progressive features such as greater tendency toward loph formation. It probably leads upward into the Recent genus *Perognathus*, and possibly also into the aberrant perognathine *Perognathoides*, and the dipodomysines.

*Proheteromys* has about the same degree of molar development as *Mookomys*, but suggests the later Heteromyinae in a tendency of the premolar cusps to enclose a central basin, and in development of the Y pattern in the molars (see A. E. Wood, 1935*a*, p. 165).

*Florentiamys* is so aberrant that it has been made the type of a distinct subfamily, Florentiamyinae (A. E. Wood, 1936*d*). The skull is typically heteromyid, but the dental structure is not like that of other types. Of *Florentiamys* Wood states in defining the subfamily, "well-developed anterior and posterior cingula on all teeth except the last two upper molars, which have only anterior ones." Wood also noted the similarity of tooth pattern to that in *Paramys*. If this similarity is indicative of real affinity, it is the only instance in which the superior cheek-tooth pattern of a heteromyid resembles the paramyine type. *Griphomys* also shows a resemblance to *Florentiamys*, but lacks the internal ridge of the upper teeth, or the external one of the lower. If these two genera are related,

then the internal ridge of the upper teeth does not correspond to the protocone-hypocone area in *Paramys*, and similarity to the pattern of *Paramys* is without significance. In any case, it seems difficult to view *Florentiamys* as anything other than a heteromyid, and it and *Griphomys* together suggest that the ancestors of the Miocene and later geomyoids may have passed through a series of changes somewhat comparable to a *Taxymys* (or *Sciuravus*)–*Griphomys*–*Floren-*

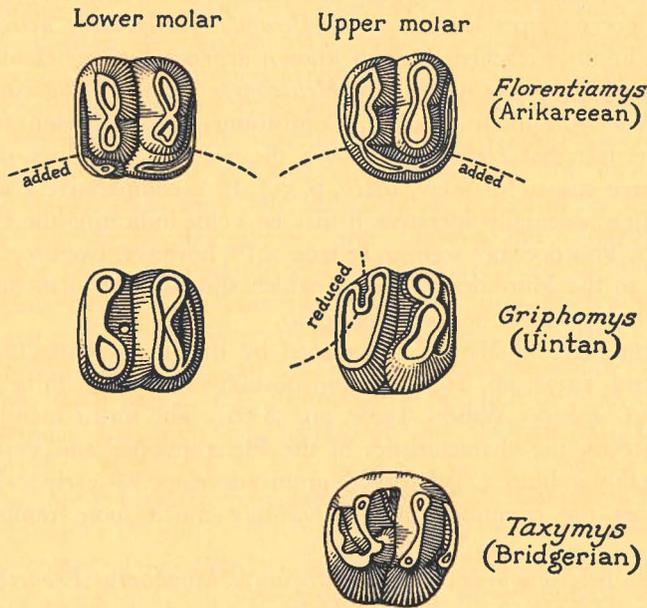


FIG. 5. Tooth patterns of *Taxymys*, *Griphomys*, and *Florentiamys* compared. (*Taxymys* after A. E. Wood in Wilson, 1938; *Griphomys* after Wilson, 1940b; *Florentiamys* after A. E. Wood, 1936d.)

*tiamys* structural series (fig. 5). The relatively isolated and conical cusps in *Heliscomys* may be in part an end result, not necessarily passed through by all later forms. Of course, this series should not be taken literally, or the thought as anything more than a suggestion, but in view of the current lack of information on the early stages of geomyoid tooth development, it is worth noting.

#### FAMILY GEOMYIDAE

The Geomyidae have marked fossorial adaptations in both the skull and the skeleton. The skull is thick-walled, the zygomatic arches are relatively heavy, and the interorbital breadth is less than in the Heteromyidae. The mastoids have considerable surface exposure, and are somewhat bullate, but little inflated. A grooved and ridged palate, and nasals which terminate behind rather than in front of the superior incisors, are other features distinguishing these forms from the Heteromyidae. The dentition is hypsodont, usually extremely so. In the living forms, the molars, except for some M<sup>3</sup>'s, consist of single columns of

persistent growth, with the enamel differentiated into bands. The pre-Pleistocene forms have less hypsodont cheek teeth, and more marked bilophate patterns.

No pre-Arikareean geomyids are definitely known. *Diplolophus* of the lower Brule (Orellan) may belong to this family, but has lost the premolars in both jaws. This genus was first described by Troxell (1923*b*) on the basis of a lower dentition. A. E. Wood, in commenting on the affinities of this dentition, said, "The most obvious similarity of the cheek teeth is to the geomyoids. In this fossil, however, there are only three teeth, and the details of the pattern are different from anything within the geomyoids. . . . If this rodent is not a geomyoid, I can think of no other group with which it could possibly be associated. . . . As suggested by Dr. G. E. Lewis . . . , there are certain interesting similarities to the Muridae in the pattern of *Diplolophus*, which may or may not be of significance" (1937*a*, pp. 258-259). The first described upper dentition of this genus was not in association with the lower teeth, nor were more than the first two cheek teeth present. This dentition was mistakenly made the type of a new genus, *Gidleumys*, by Wood (1936*b*, pp. 3-4). At that time, *Gidleumys* was placed in the Geomyidae, and Wood commented, "This form unquestionably represents an Oligocene geomyid." Later, it was discovered that the two genera were synonymous, and this fact, together with description of several additional specimens, was reported by Barbour and Stout (1939). These authors, however, offered nothing further on the relationships of the genus, except perhaps to stress the differences from the geomyoids. If *Diplolophus* is geomyoid, it offers an interesting parallel with the Muridae in tooth reduction. Moreover, the development of accessory cuspules along the external margins of the lower teeth, and to a lesser extent internally in the uppers, offers a further parallel with the murids.

The Arikareean rodent fauna is characterized by the considerable number of types referred to the Entoptychinae. These forms are found, so far as is definitely known, only in this geologic stage, where they occur both in the John Day and in the Arikareean of the Great Plains. Four genera have now been described: *Pleurolicus*, *Gregorymys*, *Grangerimus*, and *Entoptychus*. In addition, the Arikareean has yielded the rare Great Plains genus *Dikkomys*, which appears to represent a true gopher of the subfamily Geomyinae.

The entoptychines are imperfectly differentiated geomyoids. A resemblance to the gophers is particularly evident in the skull of *Entoptychus*, with its long rostrum and relatively short postorbital region. The inferior border of the rostrum likewise is geomyid in its arching and divergence from the palatal plane. The cheek teeth show a closer resemblance to those of the heteromyids, except in the highly specialized *Entoptychus*, but this is not unexpected in view of the geologic age. Likewise, what is known of the skeleton indicates lack of the pronounced fossorial adaptation present in modern gophers. These forms differ from members of the Geomyinae in that the angular part of the mandible is mostly below the alveolar level; in the greater similarity of P<sub>4/4</sub> to the molars in pattern; and in the union of the two lophs of the cheek teeth at the ends rather than medially.

A noteworthy feature of the Entoptychinae is the occurrence of several stages of specialization in beds which are essentially contemporaneous. Their absence from Oligocene deposits may be, and probably is, fortuitous. Several features, however, suggest precocious and rapid development from their ancestral stock.

In many respects the Entoptychinae are a group intermediate between the Geomyinae and the Heteromyidae, but they seem best to be classed with the former on the basis of skull structure, since the pattern of the cheek-teeth is indecisive in this case. The habitus of this subfamily, in part at least, seems to have been fossorial, though they were not as far advanced along these lines as are the Geomyinae. The apparent sudden disappearance of the entoptychines after John Day and Rosebud time may be due to competition with the better-fitted Geomyinae, or may merely indicate that we have not as yet found the later Entoptychinae, microfauna being relatively rare in most Miocene deposits. The appearance of the earliest known geomyine in the same beds as the later entoptychines may or may not be of significance in this connection (A. E. Wood, 1936*b*, p. 28).

*Pleurolicus*, *Gregorymys*, and *Grangerimus* agree in having short, broad skulls. The cheek teeth are rooted in all three genera, but with varying stages of hypsodonty represented. *Pleurolicus* has been recorded from both the John Day and the Great Plains. *Grangerimus*, more hypsodont in dentition, is known only from the former; *Gregorymys*, only from the Great Plains. The latter differs from the others in having relatively larger premolars, and in showing a well developed, cusped anterior cingulum on P<sub>4</sub>.

*Entoptychus* is long-skulled and more fossorial than the others. The cheek teeth are rootless. After wear the enamel becomes interrupted, confined to a central lake and the anterior and posterior borders. In the lower molars, the enamel is also absent from the anterior surface. The genus is from the John Day only.

*Dikkomys* from the Harrison of Nebraska has hypsodont but rooted cheek teeth. Apparently it is a true, but primitive, geomyine, as indicated by the structure of the lower premolar.

The only modern work on the Arikarean geomyids is that of A. E. Wood, 1936*b*. Recent references on *Diplolophus* are: Wood, 1936*b*, 1937*a*; Barbour and Stout, 1939.

#### ?SCIUROMORPHA INCERTAE SEDIS: SUPERFAMILY ?ANOMALUROIDEA

The upper Eocene deposits of Europe contain, in addition to paramyines, comyids, and gliroids (?), remains of members of two other rodent groups. These are *Pseudosciurus*, *Suevosciurus*, and *Sciuroides*, representing the extinct Pseudosciuridae; and *Trechomys*, a member of the Theridomyidae. Although no comparable forms have been recognized in North America, mention should be made of them because of their relative antiquity. Unfortunately, the relationships of both the Pseudosciuridae and the Theridomyidae, either to each other or to other rodents, are uncertain at present. Their assignment to the Anomaluroidea is open to serious question, and assignment of either the Anomaluroidea

or these two families, if they are not anomaluroids, to the Sciuromorpha is a subjective matter. In this, the writer has followed Simpson (1945), in the absence of any actual acquaintance with either group.

The Pseudosciuridae have skulls with large infraorbital foramina which may have transmitted a branch of the masseter muscle. The dental formula is  $1/1, 0/0, 1/1, 3/3$ , and the premolars are relatively large. Hypocones are well developed on the cheek teeth, but, typically at least, the conules are retained as distinct structures. Judging from the few illustrations available, the dental pattern seems more closely allied to the paramyine than to the sciuravine type, although hypocone development is suggestive of the latter. The tibia and fibula are not fused. Whatever else the pseudosciurids may be, they do not seem to be typical myomorphs.

The theridomyids show certain resemblances to the hystricomorphs, and several authors have held that members of this group are the early Tertiary ancestors of the porcupine-like rodents. In tooth pattern, dental formula, prominence of the inferior border of the masseteric fossa, and lack of fused tibia and fibula, an approach to the latter forms is seen, and *Trechomys* is apparently no exception. Whether any real affinity is expressed by these similarities can be determined only after extensive study of the available fossil material by a careful modern student. Schlosser (1884, p. 129) regarded *Trechomys* as ancestral to *Erethizon*, but such a view, even considered broadly, is difficult to maintain, and involves, as does any assumption of theridomyid-hystricomorph affinity, the problem of the relationship of the South American hystricomorphs to those of the Old World.

Of the pseudosciurids and theridomyids, Matthew (1910, pp. 66-68) says:

The most primitive European rodents, the Theridomyidae and Pseudosciuridae, although imperfectly known, approach very nearly to the Ischyromyidae, but appear to be transitional in several respects between this family and the Hystricomorpha. The antorbital region agrees with Ischyromyidae except for the somewhat larger size of the infra-orbital foramen, which also faces forward instead of partly downward, so that it could, and according to Zittel . . . did transmit a branch of the masseter, as in Myomorphs and Hystricomorphs. They agree with Hystricomorpha in dental formula, and several of the Theridomyidae show a marked approach in tooth pattern toward certain Hystricomorph families, and also a very noticeable prominence of the antero-inferior border of the masseteric fossa, the jaw being otherwise constructed as in Ischyromyidae. This feature may fairly be interpreted as prophetic of the Hystricomorph construction of the angle.

It is, however, open to very serious question whether the differences of these two groups from the Ischyromyidae are any greater than may be found among different members of some of the modern families of the Rodentia, and their retention as distinct families should be regarded rather as a matter of convenience in classification than as indicating any very wide structural differences.

These families, first appearing in the European late Eocene, but also present in the Oligocene, by their late appearance and uncertain position perhaps suggest more strongly the correctness of Matthew's theory of differentiation from a

common Eocene ancestor than they do the alternative concept of pre-Eocene divergence implied by Miller and Gidley. At least, the existence of these groups in the late Eocene is not inconsistent with the former interpretation of rodent history.

#### SUBORDER MYOMORPHA

Throughout most of Tertiary time, myomorphs held a subordinate place in the North American rodent fauna. Even today, the number of major groups is less than for the sciuromorphs, in contrast with the representation in the Old World, where conditions are decidedly reversed. The existing North American myomorphs are the Cricetidae, including voles, lemmings, and a number of New World rats and mice such as deer mice, wood rats, and cotton rats; and the Zapodidae or jumping mice. The Muridae, the Old World rats and mice, are doubtfully represented in the fossil record of this continent.

The first known myomorphs are of late Eocene age. In North America, they are represented by *Simimys* from the late Uintan and early Duchesnean Sespe. This genus is of uncertain affinities, but it is either a muroid (cricetid?) or a zapodid. In the Old World, the gliroids or dormice appear possibly as early as late Eocene in Europe; and *Cricetodon schaubii* has been reported in Asiatic deposits assigned to that age by Young (1931), although this species is regarded by Zdansky as probably Sannoisian (1930, p. 83). No direct ancestors of earlier age are known. Certain sciuravines, however, show suggestive similarities in dental pattern to primitive members of the muroid-dipodoid groups. Thus, in *Sciuravus powayensis* the inner crests of the upper molars are oblique and separate from the outer primary cusps. The conules, particularly the metaconule, tend to disappear as distinct structures in the sciuravines, the hypocone is always well developed and distinctly separate from the protocone, and several forms have quite reduced premolars. No other Bridgerian or early Uintan groups show any pertinent resemblance in tooth structure. Hence, it seems possible, and perhaps even probable, that the Sciuravinae occupy an ancestral position in relation to the more typical myomorphs. Possible ancestors of the relatively isolated gliroids can hardly be even suggested. It is just possible, however, that members of the "*Paramys*" *buccatus* group gave rise not only to the sciuravines, but also to the gliroids, as previously noted.

In the Myomorpha, in contrast with the Sciuromorpha, the masseter medialis muscle invades the infraorbital canal to issue forth on the side of the rostrum, and, in consequence, the canal is enlarged and modified in varying degree. The zygomatic plate may remain horizontal, narrow, and beneath the infraorbital canal, as in the Dipodoidea; or the plate may be relatively broad and inclined, as in the Muroidea, although not to the same extent as in the advanced sciuromorphs. Postorbital processes are never present. Tooth reduction is advanced over the sciuromorph condition. The dental formula for the suborder as a whole is  $1/1, 0/0, 1-0/1-0, 3-2/3-2$ , but typically, and in the vast majority of forms, the premolars are lost, and the formula becomes  $1/1, 0/0, 0/0, 3/3$ . The fibula

is extensively fused with the tibia in all but some groups of exceedingly dubious affinities (i.e. Ctenodactyloidea, Anomaluroidea).

#### SUPERFAMILY GLIROIDEA

The Gliroidea or dormice are an Old World group of rodents. Although they are unknown from North America, they are mentioned briefly in this review because of their reported occurrence in the late Eocene of Europe, and because their tooth pattern seems so unlike that of the more typical myomorphs.

In the gliroids, the infraorbital foramen is of moderate size. It is distinctly higher than wide, and lacks almost entirely any differentiation into nerve-bearing and muscle-bearing parts. The zygomatic plate is usually broadened and inclined, but in one subdivision, the Graphiurinae, it is narrow and horizontal. Miller and Gidley have placed the latter group under the dipodoid rodents because of this feature, but other authors regard *Graphiurus* simply as a primitive member of the dormouse group. As in myomorphs generally, the optic foramen is closely associated with the sphenoidal fissure, and separated from it only by a slender bony bar. The dental formula is  $1/1, 0/0, 1-0/1-0, 3/3$ , but typically the premolars are retained. The cheek teeth are brachydont. The molar pattern is usually termed sciuroid, but it is far from typical. Miller and Gidley refer to it as trituberculate, but there is a strong suggestion of quadrituberculate structure in the long inner border of the upper molars. Basically, as in *Eliomys*, the upper molar pattern consists of four relatively low transverse ridges, each pair terminating externally in a single cusp (paracone and metacone respectively). In the lowers, the pattern is comparable, but with three external cusps (protoconid, mesoconid, and hypoconid) instead of two. The anterior (cingulum) and second ridges unite with the anteroexternal cusp (protoconid). Internally, these ridges, in both upper and lower teeth, join with an anteroposterior one which may be partly divided in the upper molars, again, as in the length, suggesting a quadrituberculate structure. Additional ridges may develop in other genera. An outstanding feature of the pattern is the very external position of the mesoconid, and the long mesolophid extending inward from it. The occlusal surfaces of the molars in the more primitive genera are decidedly concave. The tibia and fibula are strongly fused.

The Gliroidea appear to be a relatively ancient group, having existed throughout most of Tertiary time with strikingly small modification. They seem to have become differentiated from other myomorphs well back in the Eocene, although the known record is no older than late Eocene. The gliroids are typically myomorphs on the basis of skull characters, but the dentition is not like that of the muroids and dipodoids. Even so, it may eventually prove to bear more resemblance to the sciuravine type, which the writer believes to be approximately ancestral to these in dentition, than to the paramyine-sciuroid type, which it is supposed to resemble. If not, and if Matthew's theory of Eocene rodent differentiation from known fossil groups is correct, then only certain members of the "*Paramys*" *buccatus* group seem to stand in any way close to

the dormice. These<sup>5</sup> have upper molars with relatively well developed hypocoines, and with concave occlusal surfaces. The cross-lophs of the upper molars are low, with indistinct intermediate tubercles. The lower molars exhibit long and distinct anterior cingula. The forms in question in part suggest a trend toward the sciuravines, and it is just barely possible that within this group lie the ancestors of the gliroids. The group is not so highly evolved as to preclude a gliroid relationship, and yet it is within a rodent section with sciuravine dental trends—the sciuravine tooth pattern in turn suggesting muroid-dipodoid affini-

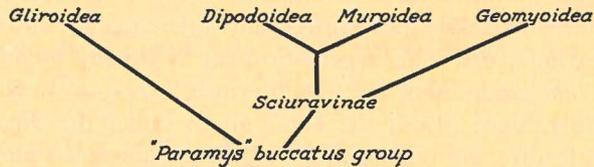


FIG. 6. Possible relationship of Scieuravinae to Myomorpha

ties. As based on dentition, the accompanying diagram (fig. 6) illustrates the relationships indicated above.

It should be emphasized, however, that this theory of relationships results primarily, but not entirely, from two assumptions: (1) Eocene differentiation from a common paramyine ancestor; and (2) a complete geologic record of the larger groups (subfamilies and higher ranks, but not genera). An obvious difficulty in this scheme is the apparently closer affinity of the muroids to the geomyoids than to the gliroids, a degree of relationship not indicated otherwise than in the dentition, although the gliroids have some other sciuroid features.

#### SUPERFAMILY MUROIDEA

The superfamily Muroidea contains the Cricetidae, the Muridae, and some less important Old World families. The muroids probably first appear in the late Eocene. If *Simimys* is not a muroid, and if *Cricetodon schaubii* is not Eocene in age, then their first authentic record is in the early Oligocene. Their earliest appearance in North America is contingent upon the systematic position of *Simimys*. Should *Simimys* prove to be a dipodoid rodent, the oldest muroid record is Orellan or mid-Oligocene, although the eventual recognition of early Oligocene cricetids on this continent is perhaps to be expected. The Muridae, disregarding dubious New World reports, appear at a distinctly later time than the Cricetidae, and the stratigraphic evidence in general bears out the opinion that the murids have developed from the cricetids in relatively late geologic time.

Recent muroids are in general characterized by a specialized infraorbital foramen in which the upper part is enlarged for muscle transmission; the inferior part is more slitlike, and permits the passage of nerves and blood vessels without pressure from the masseter medialis. The anterior part of the mas-

<sup>5</sup> "*Paramys*" *tricus* (early Duchesnean); "*P.*" cf. *minutus* (late Uintan); "*P.*" *minutus* (Bridgerian); and undescribed species from the late Wasatchian.

seter medialis is lodged in a depression on the side of the muzzle. The zygomatic plate is wide and inclined, but some variation exists, and *Deomys* has the plate nearly as in the Dipodoidea. Moreover, fossil forms such as *Cricetops* and Oligocene species of *Cricetodon* indicate clearly that the infraorbital canal and zygomatic plate of the existing muroids developed during late Eocene and Oligocene times from a dipodoid-like type. The anterior head of the masseter lateralis superficialis is distinct (except in *Deomys*?). The dental formula is  $1/1, 0/0, 0/0, 3-2/3-2$ , but except in a very few, all three molariform teeth are retained.

#### FAMILY CRICETIDAE

The Cricetidae include a more primitive subfamily, the cricetines (deer mice, hamsters, and the like), forms in which the cheek teeth are rooted and tuberculate, more rarely prismatic; and an advanced group, the microtines (voles and lemmings), with prismatic, usually rootless, teeth. The latter group does not appear before the Pliocene, at least as definitely recognizable types, and the following remarks refer to the cricetines.

The cricetine cheek-tooth pattern appears to be based on four primary cusps with connecting crests, basically more or less as in some species of *Sciuravus*. The upper cheek teeth are without recognizable conules, unless perhaps in the most ancient types. Usually the earlier genera have teeth with distinct mesocones and mesoconids. Anterocones and anteroconids are almost always well developed. The lower cheek teeth have strong hypolophids. The dental formula is  $1/1, 0/0, 0/0, 3/3$ . The skull is usually not much modified for special habitats.

*Simimys* (late Uintan and early Duchesnean) may well be the oldest known cricetid. In *S.*(?) *murinus*, probably the most primitive known species of the genus, the cricetid superior cheek-tooth pattern is represented in its essentials. The outer cusps (paracone and metacone) are almost completely isolated. The inner cusps (protocone and hypocone) are obliquely compressed, and lengthened (by fusion with the conules?) to form diagonal crests. This pattern is strongly reminiscent of that in some sciuravines (e.g. *S. powayensis*), although no species of the latter group are known which could be considered even approximately ancestral. In other species of *Simimys* (*S. vetus* and *S. simplex*), the connecting crests are more strongly developed. The lower molars of *S. vetus* and *S. simplex* also resemble somewhat the comparable teeth in the sciuravines, but again none are known which could be considered genetically ancestral. Relatively long, true mesolophids are present, and the ectolophids are usually oblique in orientation. Anterocones and anteroconids are absent or essentially so. The dental formula is  $1/1, 0/0, 0?/0, 3/3$ .  $P^4$  may possibly be present, but apparently is not. The zygomatic plate is relatively narrow and nearly horizontal, and lies completely beneath the infraorbital foramen. The character of the infraorbital canal cannot be satisfactorily demonstrated. Some evidence indicates that it was unspecialized, but transmitted a part of the masseter muscle. A knob of bone is present medial to the zygomatic plate to which apparently a distinct anterior head of the masseter superficialis was attached. The problem of the systematic position of

*Simimys* has been discussed at length in another place (Wilson, 1949a, pp. 21-23). Only a summary will be given here.

*Simimys* in its dentition bears a striking resemblance to the Oligocene sicistine (Zapodidae) *Plesiosminthus* of Europe. A sicistine relationship has been recognized as possible by the writer (1935a, pp. 31-32; 1949a, pp. 21-23), advocated as probable by A. E. Wood (1937a, p. 249), and affirmed by S. Schaub (written communication to A. E. Wood). On the whole, the similarity to *Plesiosminthus* in dental pattern is greater than to any cricetine. Nevertheless, in this connection, it should be recalled that the cheek-tooth pattern of *Plesiosminthus* is notably like that of the earlier Old World cricetines, so that resemblance to the cricetine pattern is also shown. The present writer believes that the Sespe genus is probably a primitive muroid because (1) the dental formula is apparently  $1/1, 0/0, 0/0, 3/3$ , and (2) a distinct anterior head of the masseter lateralis superficialis muscle is apparently present. The similarity of the dental pattern to that of *Plesiosminthus* may possibly indicate that *Simimys* is close to the common ancestor of both muroids and dipodoids.

If *Simimys* is muroid, it probably is to be assigned to the Cricetidae, although it might belong to a primitive and extinct group. It seems to have left no known descendants.

No early Oligocene muroids have been recognized in North America. Undoubted cricetines, however, appear in the Orellan stage of the White River, where they are known by several genera. The most common type is *Eumys*. Others are the closely related *Leidymys*, and the more distantly related *Cricetodon*, a common Old World genus. *Eumys* differs from *Cricetodon* and other European types in that the mesolophid is quite short, or even absent, and the metalophulid II crest is long and separate from the trigonid, replacing this crest in the tooth pattern. The crests of the upper cheek teeth are more inclined than in the cricetodonts. *Eumys* shows an infraorbital foramen of typical cricetid type, although the zygomatic plate is less extensive. In this feature, it is advanced beyond some Oligocene species of *Cricetodon*, for in the latter the inferior border of the foramen is little narrowed, and the plate has barely begun its transformation from the dipodoid type. Miocene species of *Cricetodon* are much more modernized in zygomaseteric structure than the earlier species of the genus. It may be noted here that the Asiatic *Cricetops* is still more primitive, and almost completely dipodoid in zygomaseteric structure. *Eumys*, primitive species of *Cricetodon*, and *Cricetops* are broadly contemporaneous; this fact indicates independent evolutionary rates of masseteric development, and considerable modification even after relatively minor taxonomic groups had been established. In cricetids, at least, we have considerable direct evidence that tooth pattern may be more significant than zygomaseteric structure in determining broad relationships (Schaub, 1925, p. 88).

*Leidymys* differs from *Eumys* particularly in the development of widely separated temporal crests rather than a sagittal crest as in the latter genus. It is clearly in the same group (tribe Eumyini of Simpson, 1945) as *Eumys*.

Both *Eumys* and *Leidymys* continue into the upper Oligocene (Whitneyan),

but the latter genus has not been recorded as yet. In addition, the genus *Scottimus* has been described by Wood (1937a, pp. 255-256). This genus is characterized by development of anteroposterior crests at the expense of the more primitive transverse lophs. *Scottimus* is evidently an outgrowth from certain species of *Eumys* (*E. exiguus*), but apparently left no descendants.

Early Miocene cricetids are represented by *Leidymys* (type stratigraphic level), *Schaubeumys*, and *Paciculus*. *Eumys* apparently had become extinct. *Schaubeumys* seems to represent a development from species of *Eumys* type, but somewhat more divergent than *Leidymys*. The mesolophid is entirely absent except in  $M_1$ , where it is strongly developed. A pseudo mesolophid formed by metalophulid II is present in the posterior two molars, as in *Eumys*. The anteroconid of  $M_1$  is small. A mesoloph is present in  $M^2$ . The principal cusps tend to alternate in position. Other features are set forth in Wood's original description of the genus (1935b, pp. 1-2). According to him, the characters of *Schaubeumys* suggest "specializations of the *Eumys* type of tooth toward what is found in *Peromyscus*." Wood concludes, however, that some features indicate that the genus does not lead directly to *Peromyscus*, the living deer mouse.

*Paciculus* is more widely separated from *Eumys* than either of the other two Arikareean types. This genus has been assigned to the dipodoid rodents by Matthew (1910) and Hay (1930), but A. E. Wood (1936a) maintains that cricetid affinities are strongly indicated, and that the genus cannot be a dipodoid. Sicistine features are seen in the elongate mesoloph and the anteroposterior compression of the paracone and metacone, but the absence of  $P^4$  and the large anterocone of  $M^1$  are definitely cricetid characters. It is of interest to note that according to Wood (*ibid.*, p. 5), "there is a considerable resemblance between *Paciculus* and some of the more primitive Sicistids, especially *Plesiosminthus myarion* from the Aquitanian." It is this sicistine species which also shows the greatest resemblance in tooth pattern to *Simimys*, but its similarity is more notable than that of *Paciculus*.

#### FAMILY MURIDAE

The Muridae, the typical rats and mice of the Old World, are by far the most prolific of rodent groups. Strangely enough, the fossil record is very poor until relatively recent geologic times, and does not extend back beyond the Pontian for a certainty. The earliest fossils are quite modern in cheek-tooth pattern; hence they not only are very distinct from the cricetid type, but also suggest a considerable previous history. Apparently bearing out this long pre-Pontian development is the occurrence in the John Day of *Palustrimus*, a genus described by A. E. Wood (1935c, pp. 370-371), and assigned by him to the Muridae. It has also been suggested that *Diplolophus* (Orellan stage of White River) is possibly a murid. Even if one or both of these genera are murid, however, the fossil record suggests very strongly that the pre-Pontian forms were of restricted distribution (and largely tropical?), and that most of the development has occurred in post-Miocene times with almost explosive energy. Indeed, it

may even be that the earlier records are in error, and that the Muridae did not arise until late in Miocene times. This suggestion has been made by Simpson (1945, pp. 205-208), and the present writer feels that it is very probably correct.

The Muridae are closely related to the Cricetidae, and many authors maintain with good reason that they should be placed in the same family. The skull is entirely comparable to that in the typical Cricetidae; the dental formula is  $1/1, 0/0, 0/0, 3-2/3-2$ , but with few exceptions, three molariform teeth are present. In dental pattern, however, the two groups are quite distinct. The Muridae have rooted, generally brachydont, tuberculate teeth. In most, three "anteroposterior rows" of tubercles are evident, but those of the inner row in the uppers, and particularly those of the outer row in the lowers, are of lesser development. Adjacent tubercles may unite to form transverse lophs. The connecting crests in the cricetids are scarcely in evidence, and the greatest superficial similarity in pattern is to the Heteromyidae. It seems altogether probable, however, that the Muridae have developed from the Cricetidae, although direct fossil evidence is lacking.

Miller and Gidley, Schaub, and others have maintained that the inner (third) row of tubercles in the upper teeth is later, and not a fundamental element of the murid pattern. It is apparently added in the same way as in the Geomyoidea, by development from a cingulum. The same is true of the outer row in the lower teeth. On the other hand, Hinton, Ellerman, and others have argued that the primitive pattern had three anteroposterior rows with subsequent reduction in some groups. In this connection, it may be mentioned that some have held the Muridae to be primitive, and close to the ancestral group out of which other muroids developed. Suffice it to say that the latter theories are opposed by evidence which appears to be conclusive.

Of the two North American forms with possible murid affinities, the more dubious one is *Diplolophus*. This genus is probably a geomyoid, notwithstanding its obvious peculiarities. *Palustrimus* Wood from the John Day deserves more serious consideration, for the describer has referred it unequivocally to the Muridae. The type and only known specimen is a single tooth, probably  $M^1$ . This tooth has three transverse lophs, each loph bearing three cusps of which the median one is the largest, the inner one the smallest. The rear two lophs are concave forward. The characters seen in this tooth are not matched apparently by any Old World murid, nor is there any approach to a cricetid pattern. These facts, the fragmentary nature of the material, and the geologic and geographical distribution of other murids make it seem unwise to accept this murid record without reservation. If not murid, however, it is hardly possible to suggest what *Palustrimus* might be. Perhaps it is a geomyoid.

#### SUPERFAMILY DIPODOIDEA

The Dipodoidea include two families, the Zapodidae (jumping mice, striped mice) and the Dipodidae (jerboas). The former family is known from North America for a certainty only from the Pliocene and Quaternary faunas. The Old World Dipodidae are unrecorded from this continent unless *Protoptychus*

should prove after all to be a true dipodid. Some other pre-Pliocene American forms have been referred to the superfamily, but these, with the exception of *Simimys*, can no longer be considered even possible representatives of either group. If European genera are included, the dipodoids range in time from middle or late Oligocene (upper Stampian) to Recent. If *Simimys* is one, however, then the range can be extended back into late Eocene.

In the Dipodoidea, the infraorbital canal is enlarged for transmission of part of the masseter muscle. Typically, it is not only larger than in the Muroidea, but of different shape, more or less triangular with the narrower part dorsal. The zygomatic plate is narrow, horizontal, and beneath the foramen. There is no distinct anterior head for the masseter lateralis superficialis. Instead, the origin of this division of the masseter is spread out over a considerable area along the zygomatic plate. The jugal is a large and important element, either in contact with the lachrymal or nearly so. The dental formula is  $1/1, 0/0, 1-0/0, 3/3$ . In primitive forms the cheek-tooth pattern is of cricetid type; the more advanced genera have molar patterns which are derivable from this type.

Schaub (1934, p. 24) has suggested that future work may demonstrate a closer relationship between the muroids and dipodoids than is usually held to exist. As he has indicated, the basic plan of the molars is the same in the two groups, and the difference in zygomaseteric structure largely disappears if all known forms are considered. Certainly, of the three chief groups generally assigned to the Myomorpha, gliroids, muroids, and dipodoids, the latter two stand in much closer relationship to each other than either does to the first named. Present evidence, however, seems to indicate that the muroids and dipodoids, although arising from a common (mid-Eocene?) ancestor, have been distinct groups since the late Eocene. Moreover, this common ancestor apparently arose from the sciuravines, if any stem is known at present.

#### FAMILY ZAPODIDAE

In the Zapodidae, the skull retains its murine appearance. The metatarsals are neither fused nor reduced, although the hind limbs may be lengthened in the more advanced types. Some authorities prefer to unite the Zapodidae with the Dipodidae as a single family. Because of the late appearance of the jerboas in the fossil record, and for other reasons as well, this latter arrangement may be more desirable. Regardless of this, a subfamily grouping is usually employed in which authors recognize the Sicistinae (striped mice), the least specialized of the dipodoids; and the Zapodinae (jumping mice proper). The sicistines have brachydont, tuberculate dentitions, and hind legs of normal proportions. In the zapodines, the cheek teeth are subhypsodont and flat-topped, the hind legs lengthened. Only the former group appears to have any known pre-Pontian record.

The European *Plesiosminthus* is the only sicistine so far reported from beds older than Pontian. It ranges from late Stampian through the Aquitanian. If *Simimys* is dipodoid, then it also is a sicistine and related to *Plesiosminthus*. Reasons for referring it to the Muroidea have already been discussed. *Plesio-*

*sminthus* is unrecorded from the New World; it may be noted that according to Schaub it is a relatively isolated genus, not close in its affinities to either *Sicista* or *Zapus* (Schaub, 1930, pp. 635-636; 1934, pp. 18-19, 22). He also states that *Sicista* and *Zapus* have tooth patterns modified from a "pre-cricetodontid" structure. These statements are based, in part at least, on relative development of the anterior trigonid cusp in  $M_1$ , which Schaub terms the paraconid. In *Plesiosminthus* it is small to essentially absent, whereas in *Sicista* and particularly *Zapus* it becomes considerably enlarged. This cusp corresponds to the anteroconid of the Wood and Wilson nomenclature (1936). If it is actually a paraconid, Schaub is certainly justified in his view. Possession of a true paraconid, however, would be an unusual feature, and would point to a long history, independent of that of other rodents. The explanation of the cusp as a secondary development seems much more likely to the writer. This is perhaps borne out by *Simimys*, for here the anteroconid is nearly absent, although this genus is much older. Nevertheless, Schaub's opinion as to the relationship of *Plesiosminthus* may well be correct, because it is founded on other features as well as on anteroconid development.

The Sicistinae as a group may have been ancestral to the Zapodinae on the one hand, and to the Dipodidae on the other. Paleontological proof of this is lacking, but the stratigraphic sequence in the known forms is in agreement, and the structural features of the living forms suggest it.

#### FAMILY DIPODIDAE

In contrast with the jumping mice, the jerboas show a highly developed foot structure, in which the inner and outer metatarsals are reduced or absent, and the median ones (II, III, IV) are fused. Mastoid and tympanic bullae are expanded, and the skull in consequence is widened in comparison with that of the zapodids. The cheek teeth are more hypsodont, but, as in the zapodids, the pattern is basically of cricetid type. A resemblance to that of *Plesiosminthus* is seen in the failure of the anteroconid of  $M_1$  to develop. In this feature, the dipodids resemble *Plesiosminthus* more closely than do *Sicista* and *Zapus*.

The oldest dipodids are late Miocene in age. None is known from North America. Miller and Gidley (1918, p. 443) have referred *Protoptychus hatcheri* to the Dipodidae, and Hay (1930, p. 911) has assigned *Pacculus insolitus* and *Leidymys lockingtonianus* to the same family, but none of these appears correctly assignable to either the Dipodidae or the Zapodidae. Their affinities have been discussed in earlier sections of this review.

#### SUBORDER HYSTRICOMORPHA

The hystricomorph rodents, as the name implies, include among their number the "porcupines," and also a great variety of other and chiefly South American types, such as guinea pigs, chinchillas, and hutias. In all these forms, the infraorbital foramen is much enlarged for muscle transmission, and the zygomatic plate resembles that of the dipodoids in being narrow and beneath the foramen. The masseter lateralis superficialis does not extend forward on the

rostrum. Typically, the angular process appears to arise from the side of the ramus. This outward distortion permits the passage of "a specialized and enlarged distal anterior limb of the masseter lateralis superficialis" (Miller and Gidley, 1918, pp. 443-444). It should be noted, however, that in the Caviioidea (guinea pigs) a different condition usually prevails, in which the masseter medialis modifies the jaw shape instead to develop a horizontal ridge just below the alveolar level. In other rodent suborders, the angular process takes origin from the inferior margin of the ramus, and is not modified in either of the above ways (except in the Bathyergoidea, the systematic position of which is uncertain). The hystricomorph skull is without postorbital processes. The dental formula is  $1/1, 0/0, 1/1, 3/3$ . The premolars are large and important molari-form teeth. The cheek teeth are usually flat-topped and hypsodont, frequently of persistent growth. The pattern is highly variable. One noteworthy type simulates rather closely that of some castoroids. The tibia and fibula are never fully fused.

The Hystricomorpha are chiefly South American. This is true not only in respect to the number of major divisions, but especially in so far as the suborder involves a demonstrably natural group. They first appear there in the Oligocene, already, or shortly after, differentiated into four groups (Simpson, 1945, pp. 210-211). Hystricomorphs have also been reported from the Oligocene of Europe and Africa (?), but some, at least, of these records are dubious. Thus, "*Hystrix? lamandini*" of the Quercy Phosphorites does not show the characteristic microscopic structure of the incisors, and according to Korvenkontio (1934) is to be excluded from the "Stammreihe" of the hystricomorphs. This author finds nothing in his histological studies which would preclude a theridomyid origin for the hystricomorphs (see section on Anomaluroidea). On the other hand, Simpson notes that at the time of the first appearance of hystricomorphs in these two widely separated areas, the representatives of each region are quite distinct from one another.

No hystricomorphs are known from North America until late in the Cenozoic. The earliest ones clearly have migrated from South America. Occasionally, individual ischyromyids show certain features reminiscent of the hystricomorphs, but these cannot be of direct phylogenetic importance, for North America was isolated from the continent to the south by the beginning of Eocene times at least. The connection was not re-established until the Pliocene.

The apparent close relationship of the New and Old World hystricomorphs raises serious geographic problems, as has been pointed out on numerous occasions. If the South American rodents were introduced through North America, they have originated from Paleocene types which so far as known were exclusively paramyine. In this case, the Old World forms are an amazing example of morphological convergence. If they were introduced into South America from the Old World, the most logical of several doubtful explanations is that of migration by natural rafts. Development in the Old World from the theridomyids, and subsequent migration to South America, is perhaps the usually accepted theory.

## ORDER LAGOMORPHA

Although lagomorphs are now recognized as occurring as early as late Paleocene, remains are strangely rare until the beginning of Oligocene times. Indeed, they have been recorded only recently from the late Paleocene and late Eocene, and still have not been recognized in the interval between these two ages. This pre-Oligocene material is very fragmentary, and little besides the tooth patterns may be studied. With the White River Oligocene, nearly complete skulls and skeletons become available, but these pertain almost entirely to a single generic type, *Palaeolagus*. Other genera are known chiefly by their dental characteristics. Thereafter, lagomorph remains are abundant but frequently very fragmentary. Nevertheless, considerable progress has been made in research on fossil lagomorphs. We now know that they constitute an independent order, with little or perhaps nothing to unite them with the rodents; that their evolution, although extremely slow and lacking in the diversity shown by rodents, is somewhat more complex than was thought; and that the upper cheek-tooth pattern is quite unlike that of most other mammals, even if we do not know how to interpret it. Future work will undoubtedly bring knowledge of the order to a relatively high degree of completeness—much higher than we can reasonably expect from study of the complex ramifications of the Rodentia.

Three lagomorph families are now known: the Eurymylidae, aberrant, and at present recorded only from the late Paleocene of Mongolia; the Ochotonidae (pikas), the more primitive of the two living families; and the Leporidae (hares, rabbits), the more advanced living family, and the only group with fossil representatives on this continent as old as Arikareean.

The Lagomorpha must be a very ancient order, distinct from other mammalian orders as far back as early Paleocene, or more probably Cretaceous, times. "The origin of the lagomorphs, or of the Cohort Glires if this be accepted, is entirely unknown. Despite some earlier theories of deviation from marsupials, or even direct from reptiles, there is now no doubt that they are Eutheria and so derivable from the postulated proto-insectivoran ancestry of the whole infraclass, but this is no more than to repeat that they are Eutheria. Theories of relationship to particular later Eutheria, for instance, the Eocene artiodactyl †caenotheres, are quite untenable at present" (Simpson, 1945, p. 196).

## FAMILY EURYMYLIDAE

The first recorded lagomorphs are from the late Paleocene (Gashato formation) of Mongolia, and represent a family, Eurymylidae, known only by a single genus, *Eurymylus*. This family has not been found outside the type area.

Specimens representing the Eurymylidae were first described by Matthew and Granger (1925a), and placed in two distinct and widely separate divisions of mammals. Lower jaw material was referred to a new genus, *Baënomys*, of the Glires, family indeterminate. Characters of the lower dentition seemed to sug-

gest most strongly the lagomorphs. The corresponding upper dentition was referred to another new genus, *Eurymylus*, of uncertain systematic position, but tentatively assigned to the Menotyphla. Subsequently, Matthew, Granger, and Simpson (1929) demonstrated that the two genera were synonyms, and all material was allocated to *Eurymylus*, which was made the type of a new family, Eurymylidae. Superficial resemblances to the lagomorphs in both upper and lower dentitions were noted, and the family was referred questionably to the Glires. In 1940, A. E. Wood, in his monograph on the White River lagomorphs, tentatively assigned *Eurymylus* to the Lagomorpha, and this was followed in 1942 by definite assignment of the Eurymylidae to the lagomorphs, and a full discussion of important systematic characters shown by *Eurymylus*.

Wood demonstrated that *Eurymylus* shows many characters similar to those of the more modern lagomorphs, and that it also has features necessarily ancestral to those of the two existing families. Among these may be mentioned: (1) incipient fenestration of maxilla, present as pitting; (2) orientation of lower cheek teeth so that the talonid of one tooth is on the level of the following trigonid; and (3) general mechanics of tooth occlusion. Dissimilarities demonstrate only a more primitive evolutionary stage than that of the later types, or, as in the loss of P<sup>2</sup> and the different area of maxillary pitting, that *Eurymylus* is on a side line not directly ancestral to any known lagomorph.

Wood concluded that "the Eurymylidae represent an ancestral stock from which the Leporidae and Ochotonidae have been derived" (1942, p. 7). If *Eurymylus* is a lagomorph, then the orders Rodentia and Lagomorpha have equally ancient known records, and both are unlike other orders, and each other, as far back as the late Paleocene. The fact that *Eurymylus* was first referred to the Menotyphla also suggests derivation from a proto-insectivoran ancestor.

#### FAMILY OCHOTONIDAE

Broadly, the Ochotonidae may be defined as lagomorphs with low, depressed skull, without supraorbital processes; zygomatic arch a slender rod; dental formula 2/1, 0/0, 3/2, 3-2/3-2; limbs of approximately equal length; no external tail; and ears short, orbicular.

The Ochotonidae are in general a more primitive group of lagomorphs than the Leporidae, although not demonstrably more ancient. Because of this fact, it appears that several of the older leporids (e.g. *Desmatolagus*) have been determined by some authors as ochotonids, although in reality these forms have simply shown primitive and not necessarily ochotonid characters. The fragmentary nature of the material in several of the ochotonid-like genera has made a determination of significant systematic characters difficult, but it seems on the basis of work by Burke (1934*b*, 1936, 1941) that late Eocene lagomorphs are all leporids, and that no known ochotonid is older than late Oligocene. On this continent the most ancient record is somewhat later—early Hemingfordian (*Oreolagus*, see McGrew, 1941*a*; Wilson, 1949*c*, p. 56). Thus, no undoubted North American ochotonid falls within the time range covered in this paper.

## FAMILY LEPORIDAE

The Leporidae are distinguished from the Ochotonidae by greater arching of the skull; the presence of supraorbital processes; platelike rather than rod-like zygoma; dental formula  $2/1, 0/0, 3/2, 3/3$ , rarely with third upper molar absent; hind legs elongate; and ears long. They are the larger and more progressive lagomorphs. In North America, *Mytonolagus* is known from the Uintan and early Duchesnean; *Palaeolagus* from the Chadronian to Whitneyan inclusive; *Megalagus* from the Chadronian and Orellan, possibly Whitneyan; *Desmatolagus* from the Chadronian and Orellan, possibly Whitneyan or Arikareean; and *Archaeolagus* from the Arikareean, and possibly early Hemingfordian. The forms named represent several lines of descent, and their arrangement within valid subfamily units is uncertain at present. A number of other genera are also known, but these are all post-Arikareean.

The oldest North American leporid, *Mytonolagus*, has been fully described by Burke (1934b, 1941). The cheek teeth are rooted and without cement.  $P_3$  bears three re-entrant folds, one external and two internal (these two not actually shown in the well worn known material, but present in the closely related Asiatic genera), but the latter two are not persistent with wear. The external fold extends not more than halfway across the occlusal surface. *Mytonolagus* and its Asiatic allies (*Shamolagus*, *Gobiolagus*) belong to a primitive group apparently ancestral to all later leporids (Burke, 1941, p. 21). Hence, the Oligocene forms may be regarded as representing three separate developments from this stock.

*Palaeolagus* is the common Oligocene rabbit. Indeed, it is probably the most abundantly represented genus in the White River, the only near rival being *Merycoidodon*. It is also the only early Tertiary rabbit known by very complete material. The skull is already essentially that of a modern lagomorph. It is distinguished, however, on the basis of a number of characters which have been pointed out by several authors (Matthew, 1902, 1903; Troxell, 1921; Wood, 1940). The supraorbital processes are smaller than in *Lepus* or *Sylvilagus*, the palate is less reduced, the maxillary fenestration less developed, the skull less arched, a distinctly larger coronoid process is present on the mandible, and the lower incisor terminates more posteriorly (under  $M_1$  or anterior part of  $M_2$ ). The skeleton is less adapted for leaping than in *Lepus*, or even *Sylvilagus*.

The dentition is modernized, but still shows several distinctive features. It is less high-crowned than in the modern genera, but differs from *Mytonolagus* in having abundant cement, and in lacking clearly defined roots on the upper teeth. The lower cheek teeth are quite hypsodont, but apparently are rooted after considerable growth. The dental pattern changes with wear, but a typical one developed with moderate wear may be characterized as follows:  $P^2$  usually has two anterior folds; only one may be present in advanced wear. The more molariform upper teeth in back of this show short, uncrenulated internal folds, and, except after considerable wear, a more external "crescent" of enamel which may open to the external wall of the tooth.  $M^3$  is simplified, and is essentially

an enamel tube surrounding dentine.  $P_3$  shows a characteristic "hourglass" shape of the occlusal surface, formed as the result of more or less opposed enamel inflections. With tooth wear, the internal fold is reduced to an islet, and a slight groove on the internal face of the tooth; finally all trace of the internal fold may be lost. The internal re-entrant, however, is a much more persistent feature than in the other genera under consideration.  $P_4$ - $M_2$  are double-columned teeth not differing in major features, at least after moderate wear, from other lagomorph teeth.  $M_3$  throughout most of its life is a single column of dentine surrounded by enamel, and with a single external inflection. *Palaeolagus* has been fully described by A. E. Wood (1940).

*Megalagus* is a much less common White River genus which seems to be more directly derivable from *Mytonolagus* than is *Palaeolagus*. The known species are much larger than those of *Palaeolagus*, the cheek teeth shorter-crowned and weakly cemented. Small buccal roots are always present on the upper molariform teeth.  $P^2$  is somewhat different from the comparable tooth in *Palaeolagus* in the lesser development of the more external of the two inflections, and hence with wear it approaches more rapidly the pattern of this tooth in *Archaeolagus*.  $P^3$  is not so molariform as in *Palaeolagus*. Wear rapidly reduces the internal re-entrant of the upper molariform teeth to a shallow groove. The two genera are to be distinguished particularly by the structure of  $P_3$ . In *Megalagus*, this tooth shows an early reduction of the internal fold so that the average pattern shows only a single, external inflection. *Megalagus* is not too well known other than by the dentition, but Olson (1942) has shown that the skull also has differences of generic value. The skeleton is likewise poorly known, but it is more cursorial than that of *Palaeolagus*. In this regard, it is about comparable to *Sylvilagus*, the modern cottontail. The known remains are fully described by Wood (1940) and Olson (1942).

The typically Mongolian genus, *Desmatolagus*, has only recently been recognized in North America. It is more widely separated from *Palaeolagus* than is *Megalagus*, and appears to represent a type which has retained many primitive, *Mytonolagus*-like features, but which has progressed in the reduction in size of the terminal teeth ( $P^2$ ,  $M^3$ ;  $P_3$ ,  $M_3$ ). It is close enough to *Megalagus* to have been confused with this genus in North America until Burke (1936) showed its distinctness. *Desmatolagus* is particularly close to *Megalagus* in pattern of  $P_3$ , and in the shallow internal re-entrants of the upper molariform teeth. It may be distinguished, however, not only by the small size of the terminal teeth, but also by lesser height of crown, greater transverse diameter of the upper molariform teeth, and the decided persistence of the external openings of the "crescents." *Desmatolagus* appears to be a descendant of the Mongolian genus *Shamolagus* (Burke, 1941, pp. 21-22). This genus has been reviewed by both Burke (1936, 1941) and Wood (1940).

The typical but perhaps not the sole Arikareean leporid is *Archaeolagus*. In this genus,  $P^2$  has only a single inflection, but a second one is faintly indicated in some specimens; "crescents" are present in the upper teeth only in early stages of wear; and the internal re-entrant is more persistent than in the upper

teeth of *Megalagus*, even though relatively short and simple as compared with late Tertiary types.  $P_3$  shows the usual posteroexternal fold, and, in addition, a quite shallow but distinct flexure is present in advance of it. The internal inflection is absent except in a few specimens showing slight wear. The teeth are cemented.

On the whole, *Archaeolagus* is considerably more progressive than either *Palaeolagus* or *Megalagus*. It seems to represent an outgrowth of one or the other, but which one is not clear. By inference at least, Burke has favored a closer relation to *Megalagus* (1941, p. 22), and Wood, more positively, to *Palaeolagus* (1940, pp. 335, 339). The writer is of the present opinion that *Archaeolagus* is a descendant, or at least a near relative, of *Palaeolagus*. There is little reason to doubt that it gave rise to the common later Tertiary genus *Hypolagus*. The interrelationships of all these genera are indicated tentatively in the accompanying diagram (fig. 7).

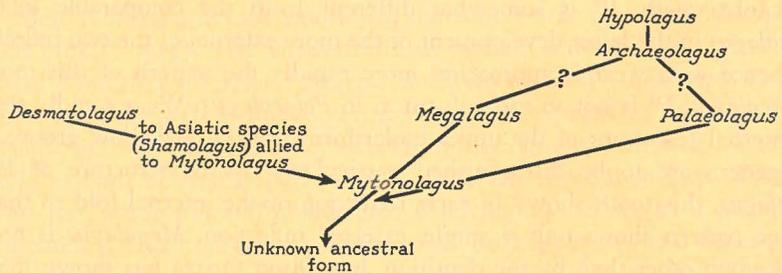


FIG. 7. Phylogeny of some early Tertiary leporids

#### *Evolutionary Tendencies in North American Leporidae*

Certain general evolutionary tendencies are seen in most of the Tertiary leporids of North America. These have been described before by other authors, but may be summarized here:

*Skull*: (1) increased bending downward of facial part of skull in respect to the basicranial axis; (2) reduction of palate to a narrow bony bridge; (3) enlargement and forward shift of posterior narial opening; (4) reduction of coronoid process of mandible; (5) forward shift of incisor base.

*Dentition*: (1) increased hypsodonty and deposition of cement; (2) continued molarification of upper premolars; (3) progressive loss of "crescents"; increase in length of internal re-entrant of molariform maxillary teeth with increasing plication of enamel borders; (4) increasing complexity of  $P^2$ ; (5) development of anteroexternal fold on  $P_3$ .

*Skeleton*: changes in skeleton associated with increased running and leaping ability.

#### *Subfamily Classification of North American Leporidae*

Subdivision of the Leporidae was first undertaken by Dice in 1929. At that time three subfamilies were recognized, namely, the Palaeolaginae, Archaeolaginae, and Leporinae. These groups were established principally on the basis

of the structure of  $P_3$ . This division has been maintained by Hibbard (1941a). Many workers, however, have reduced the original divisions to two, the Palaeolaginae (including Archaeolaginae) and Leporinae (see Kormos, 1934; Schreuder, 1936; Wood, 1940; Simpson, 1945). On the other hand, Burke (1941) has seen fit to increase the number of subfamilies to five—Mytonolaginae, Palaeolaginae, Megalaginae, Desmatolaginae, Leporinae—and obviously more for those late Cenozoic forms not discussed in his paper. On this basis, each of the five genera discussed here would fall into a separate subfamily. Burke based this tentative classification on grounds only incidentally concerned with the structure of  $P_3$ . For other authors, the ground for division seems always to have been primarily  $P_3$ , although not entirely so by any means.

It seems that in a classification of general utility, the refinement expressed in Burke's is hardly necessary at present (Simpson, 1945, p. 197). In regard to the others, recent work of Hibbard suggests rather strongly that some change in taxonomy is necessary. Thus, the Palaeolaginae could well be used for most of the primitive forms of Oligocene and earlier age (i.e. *Mytonolagus*, *Palaeolagus*, *Desmatolagus*); the Archaeolaginae for a small, compact group (? *Megalagus*, *Archaeolagus*, *Hypolagus*, *Notolagus*) without living descendants; and the Leporinae for the living types and a few extinct genera (*Nekrolagus*, *Pratilepus*). Although somewhat beyond the intended scope of this paper, it is perhaps desirable to present some of the argument on which the above statements are founded.

*The posterointernal re-entrant fold of  $P_3$ .* The known late Eocene and Oligocene leporids all have an internal re-entrant fold on  $P_3$  which is more or less opposite a similar fold from the buccal side, and the two together bring about the hourglass pattern of the Palaeolaginae of Dice. These folds apparently separate trigonid from talonid. The internal fold may be present throughout most of the life of the animal, as in *Palaeolagus*, or it may be quickly lost even in comparative youth, as in *Megalagus*. It is difficult to avoid the conclusion that *Lepus*, *Hypolagus*, *Archaeolagus*, and in fact all Miocene and later leporids had ancestors with an internal re-entrant fold. Not only does the occurrence of the fold in primitive types suggest this, but also the fold or a comparable enamel lake is sometimes found in little-worn  $P_3$ 's of later forms, and must have some significance. Kormos (1934) in his work on *Pliolagus* describes such structures, and regards their presence as showing the invalidity of the Archaeolaginae. A fold or a lake has been seen by the writer in some specimens of *Archaeolagus* from the John Day, and in individuals of *Hypolagus*? *apachensis*. The internal fold is consistently present as a lake in *Nekrolagus*, which Hibbard considers to be a forerunner of *Lepus*, and in some individuals of *Lepus* (Hibbard, 1944). The structure is also consistently present in *Alilepus* and *Pratilepus*, and as a variant (?) in some young individuals of *Hypolagus browni*.

The posterointernal re-entrant would seem to be a dominant element in most third lower premolars, (a) if actual re-entrant folds are considered, as in *Palaeolagus*, *Pentalagus*, *Pronolagus*, *Alilepus*; (b) if isolated lakes internal to posteroexternal re-entrants are regarded as homologous to the folds, as in

*Romerolagus*, *Pratilepus*, *Nekrolagus*; and (c) if it be assumed that the deep posteroexternal re-entrant angle in *Lepus* is the result of the isolated lakes of (b) cutting through to the outside, as in *Lepus*, *Sylvilagus*, and others (see Hibbard, 1944, pp. 64-65). Post-Oligocene North American genera in which the structure is not persistent are *Archaeolagus*, *Hypolagus*, and *Notolagus*, the Archaeolaginae in a restricted sense. Whether the element is present as an open fold or an enamel islet does not seem to be of subfamily importance.

*Palaeolaginae*. The Palaeolaginae of Dice and Hibbard include the primitive members of the Leporidae, and later forms, some still extant, in which the primitive character of a posteroexternal re-entrant fold structure has been retained. Hence, it is neither a vertical phylogenetic unit nor a horizontal taxonomic unit for geologically ancient leporids. Neither is it a repository for all primitive types, living or extinct, if defined in this way. Forms which invariably show a persistent internal inflection may be advanced in most other dental characters. Such types as the living Old World *Pentalagus* and *Pronolagus* are much advanced over *Palaeolagus* in dentition, and in some other ways as well. Wood's suggestion (1940, p. 276) that the subfamily is better defined by the smooth enamel wall of the anterior (trigonid) lobe of  $P_3$  would result in a much better allocation of genera, but a group so constituted would still be somewhat imperfect.

*Archaeolaginae*. Regardless of whether or not the Archaeolaginae should be granted recognition as a distinct subfamily, the North American members represent a distinct line which was the chief or sole representative of the Leporidae on this continent during Miocene and most of Pliocene time. Certainly to be assigned to the line are *Archaeolagus* (Arikareean) and *Hypolagus* (Barstovian-early Pleistocene). The latter genus perhaps shows more typical archaeolagine characters than the former, if this is technically possible. To this line the writer has also assigned *Notolagus*, mid?-Pliocene of Mexico (Wilson, 1937c). Hibbard, however, has maintained that *Notolagus* and the related *Dicea* (late Pliocene of Kansas) are members of the Palaeolaginae (1941a). Finally, the Oligocene *Palaeolagus* and *Megalagus* are approximately ancestral to *Archaeolagus*, if one of them is not actually so.

*Archaeolagus* shows a number of points of resemblance to *Palaeolagus*, but in most features it is distinctly more advanced. Aside from progressive development in several characters, the former also shows two points of difference which should be noted. In *Archaeolagus*,  $P^2$  typically has only one instead of two inflections, and  $P_3$  has a shallow anteroexternal fold. In respect to the first character, it is possible that all specimens are relatively advanced in wear, and the shallower of the two principal folds has disappeared. The additional inflection in  $P_3$  is apparently a recently acquired feature, becoming more prominent in *Hypolagus*. If this is true, however, the anteroexternal fold has probably been more or less independently acquired in several distinct lines, for it is present in all post-Oligocene types. It is possible that *Megalagus*, characterized by an early disappearance of the internal inflection of  $P_3$ , is closer to *Archaeolagus* than is

*Palaeolagus*. *Palaeolagus*, however, agrees more closely in (1) size, (2) hypsodonty of cheek teeth, and (3) length and persistence of median valley of upper cheek teeth.

The dentition in *Palaeolagus*, *Archaeolagus*, and *Hypolagus* shows evolutionary tendencies which in part are shared by all leporids, but in part serve to define imperfectly the "Archaeolaginae." These are: (1) progressive loss of the posterointernal inflection of  $P_3$  in earlier and earlier stages of wear; (2) failure to produce more than two re-entrant folds on the occlusal surface of  $P^2$  (except in *Dicea*). The first is of considerably more importance than has been hitherto recognized, even with all the taxonomic weight given this tooth.

The Pliocene *Notolagus* is here placed in the "Archaeolaginae." Hibbard in reviewing the genus has disagreed altogether with this assignment, and has placed it in the Palaeolaginae on the basis of a well developed internal re-entrant fold and the resulting hourglass figure. The writer stills feels, however, that assignment to the Archaeolaginae, at least as an indication of affinities with *Hypolagus*, is justified. This assignment is based on the following considerations: (1) If all the material from the type locality represents *Notolagus*, then the only dental character separating the genus from *Hypolagus* lies in the anterior half of  $P_3$ . Otherwise, even in the two folds of  $P^2$ , the material is within the limits of *Hypolagus*. (2) The internal re-entrant angle does not seem to be homologous with the defining angle of the "Palaeolaginae." Instead, it is anterior to the posteroexternal angle, and is probably comparable to the antero-internal angle of *Pentalagus* and *Caprolagus*. In the former genus both anterior and posterior internal re-entrants are present, the posterior one apparently comparable to the single fold in *Palaeolagus*. In *Caprolagus*, the posterior fold is absent but the deep posteroexternal fold presumably represents both postero-internal and -external re-entrants. Hence, although the antero-internal fold is a rarity, it does occur in two other genera of late Cenozoic rabbits. It should also be noted that a shallow but distinct antero-internal re-entrant has been seen in some specimens of *Hypolagus? apachensis*. (3) *Notolagus* apparently is mid-Pliocene at its type locality. This is somewhat earlier than the first appearance of *Nekrolagus* and *Pratilepus*, presumably migrants from the Old World. The Hemphillian fauna as a whole shows some Old World elements, but no leporine-palaeolagine rabbits are otherwise known, nor are they known for the interval between Arikareean and Hemphillian. Thus, derivation from a pre-existing North American archaeolagine stock is suggested.

On the other hand, it must be admitted that the complicated  $P_3$  of *Notolagus* is in strange contrast with the simple  $P_3$  of *Hypolagus* and *Archaeolagus*. Moreover, although  $P^2$  shows only two folds, the related or synonymous *Dicea* apparently has three, a number unknown (or rare?) in *Hypolagus*.

*Leporinae*. Most specialists have divided the Leporidae into the "Palaeolaginae" and "Leporinae." Under this arrangement, the former subfamily includes the primitive and geologically old members of the group, the "Archaeolaginae," and some late Cenozoic types as stated before. The latter would

include most of the existing leporids, which are in general advanced in all structures, are not known before the Pliocene, and have a deep posteroexternal fold extending nearly across  $P_3$ .

It seems to the writer that if we accept the suggestions of Hibbard in regard to the pattern origin of  $P_3$  in *Lepus*, and hold in mind the position in time of *Nekrolagus* and *Pratilepus*, it becomes necessary to (1) revise the content of these subfamilies, or (2) abandon all attempt to maintain any subfamilies, or (3) expand considerably the number of subfamilies, in line with what Burke has already done for the early Tertiary rabbits. The second alternative may seem to be a backward step, and the third too complex for the nonspecialist.

If we accept the first suggestion, the Palaeolaginae should contain only the primitive Eocene-Oligocene members of the Leporidae, and thus represent the usual horizontal base of all classifications if these are pursued back far enough in time. Eventually, it might be more desirable to substitute the "Mytonolaginae" for the basal group, and restrict the time range still more, but not enough is known about the relations of *Palaeolagus* and *Megalagus* to do this at present. The Leporinae should contain not only the usual members, but also the late Cenozoic "Palaeolaginae" of most authors. Under such a scheme of classification, the Archaeolaginae could well be recognized as a third subfamily. The arguments in favor of revision of the Palaeolaginae and Leporinae may not be as convincing as they should be, but it is felt that the suggested rearrangement results in a classification more in accord with present evidence than those heretofore used.

Hibbard's work on *Nekrolagus* and *Pratilepus* (1941a, 1944) indicates, as pointed out previously, that the deep re-entrant in  $P_3$  of *Lepus* has resulted from (1) isolation of the posterointernal re-entrant as an enamel islet, and (2) union of this with the posteroexternal fold, rather than from deepening of the external re-entrant angle in a tooth devoid of an internal fold structure. This obviously brings forms considered to be late Cenozoic palaeolagines into much closer union with the leporines than was imagined possible a relatively few years ago. As a matter of fact, present evidence suggests that the posteroexternal fold never extends completely across the occlusal surface of the tooth in any leporid, except when aided by union with an opposed fold.

The suggested rearrangement of genera is also in harmony with the complex nature of the dentition in such forms as *Pentalagus*, although in these the skeleton and skull possess certain features which are regarded as primitive. These forms, previously assigned to the Palaeolaginae, are distinctly more advanced than the Oligocene palaeolagines, and an appeal to the time interval since the Oligocene to explain the changes might be made almost equally well in the case of those forms invariably placed in the Leporinae, and result in the logical union of Palaeolaginae and Leporinae as a single group. If these later forms are palaeolagines, they do not appear anywhere in the stratigraphic record until late Pliocene (Blancan) time (typical *Alilepus* excepted, which could be palaeolagine), at best do not appear significantly earlier than true leporines, and are essentially contemporaneous with the latter.

If *Nekrolagus* is a structural ancestor to *Lepus*, it probably is not directly ancestral, for *Lepus* appears only slightly later in time, and presumably other modern leporines were also differentiated by then (e.g. *Sylvilagus*, etc.). Moreover, *Caprolagus*, a leporine, has been recorded from Pliocene beds, and although the age assignment or generic determination, or both, may be regarded as doubtful, the available evidence would place the transition to *Lepus*-like types as probably pre-Blancan. The presence of *Nekrolagus* in Blancan deposits, however, does imply a late origin (Pliocene) for *Lepus* and its close allies. This origin would seem to be too late for separate subfamily recognition for the latter forms on the basis of a long posteroexternal re-entrant with disappearance of the internal re-entrant as a distinct and separate structure.

Perhaps such rabbits as *Pentalagus*, *Pronolagus*, and *Romerolagus* should be regarded not as palaeolagines peripheral in distribution as a result of an older development and radiation of palaeolagines followed by contraction of range and isolation during leporine dispersal, but as leporines peripheral in respect to *Lepus*-like types as a result of Pliocene dispersal of the latter. Some of their peculiar characters may be due to environment and may have been acquired in Quaternary times. Characters not due to habitat are perhaps those which would be found in Pliocene leporines in general, except that the living types have advanced somewhat since that time in general dental development. In the case of *Pentalagus*, this change has resulted in the development of the most complex leporid dentition known, even if it be not regarded as the most advanced.

### SIGNIFICANCE OF THE STRATIGRAPHIC SEQUENCE

A summary of the stratigraphic record of North American rodents is given in the accompanying chart (fig. 8). Few comments are necessary. The chart emphasizes the facts that (1) the early faunas, Tiffanian to early Uintan inclusive, are entirely aplodontoid, (2) the Arikareean faunas are composed essentially of higher rodent types, and (3) the intervening late Uintan to Whitneyean faunas, inclusive, show intermingling of the two elements. Not so apparent because of the large size of the chart units is the decided break between the Eocene lines of descent and the later ones. To a very large degree it is true that the Oligocene and Arikareean genera can be traced back only with difficulty, if at all, into the late Eocene; and the Eocene lines at best are only approximately ancestral to Oligocene phyla. In general, however, this situation is no different from that prevailing in several other orders, the Carnivora and Artiodactyla for example.

A progressive increase with time in the number of families and subfamilies is also to be noted until a more or less stable constitution is reached in the Arikareean stage. Although graphing is necessarily somewhat arbitrary, it is of interest to plot the number of groups against time as in figure 9. The geological stages are spaced approximately according to their assumed duration. Dotted parts of the curves smoothe out irregularities caused by inadequacies of collecting, plotting, and the like, but they are not strictly speaking development curves

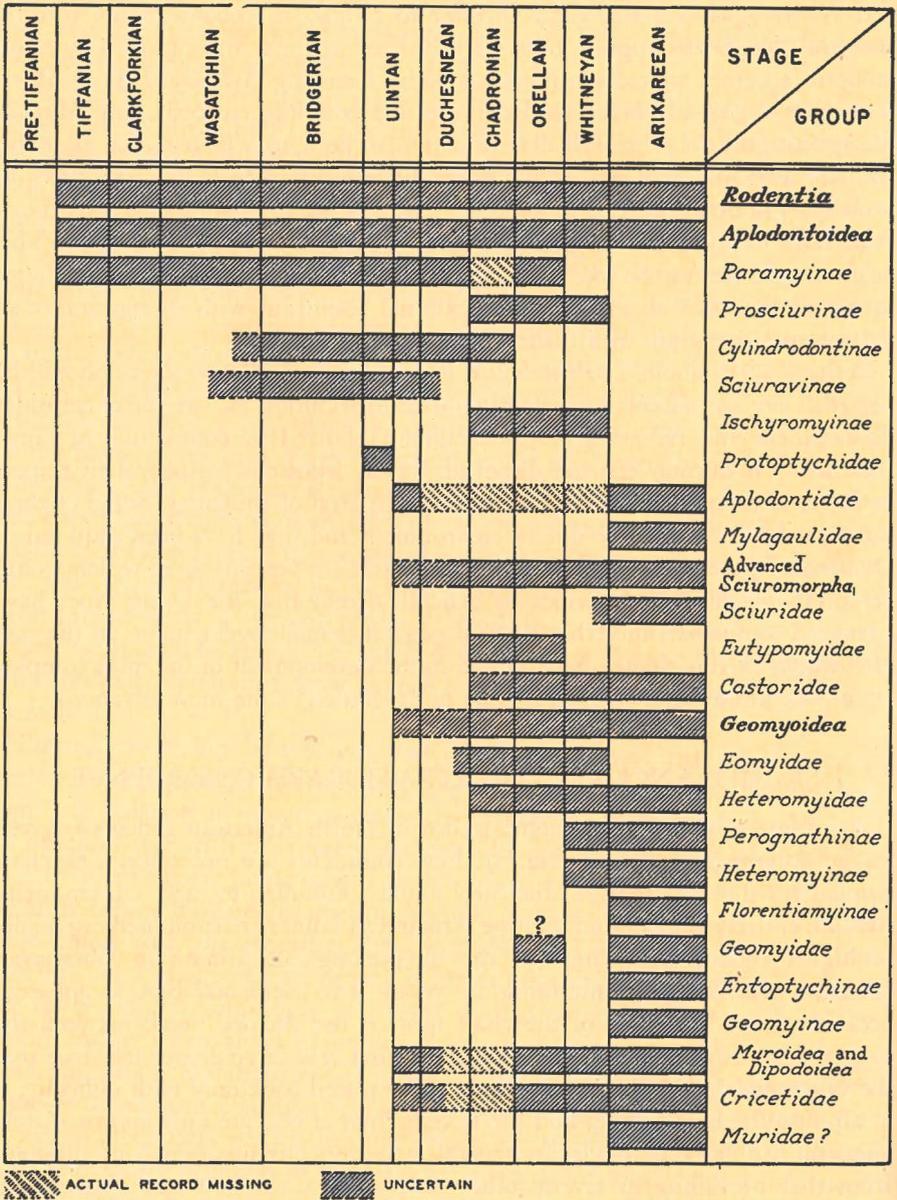


FIG. 8. Distribution of rodent groups in North American early Tertiary stages

because the effect of intercontinental migration, whatever its magnitude, is included.

Progressive expansion of the North American rodent fauna is clearly expressed. The curves also bring out one other fact. The aplodontoids rise steadily throughout the earlier Eocene. Shortly after the first appearance of higher groups a marked decline sets in, with a dwindling to two groups (*Aplodontidae* and

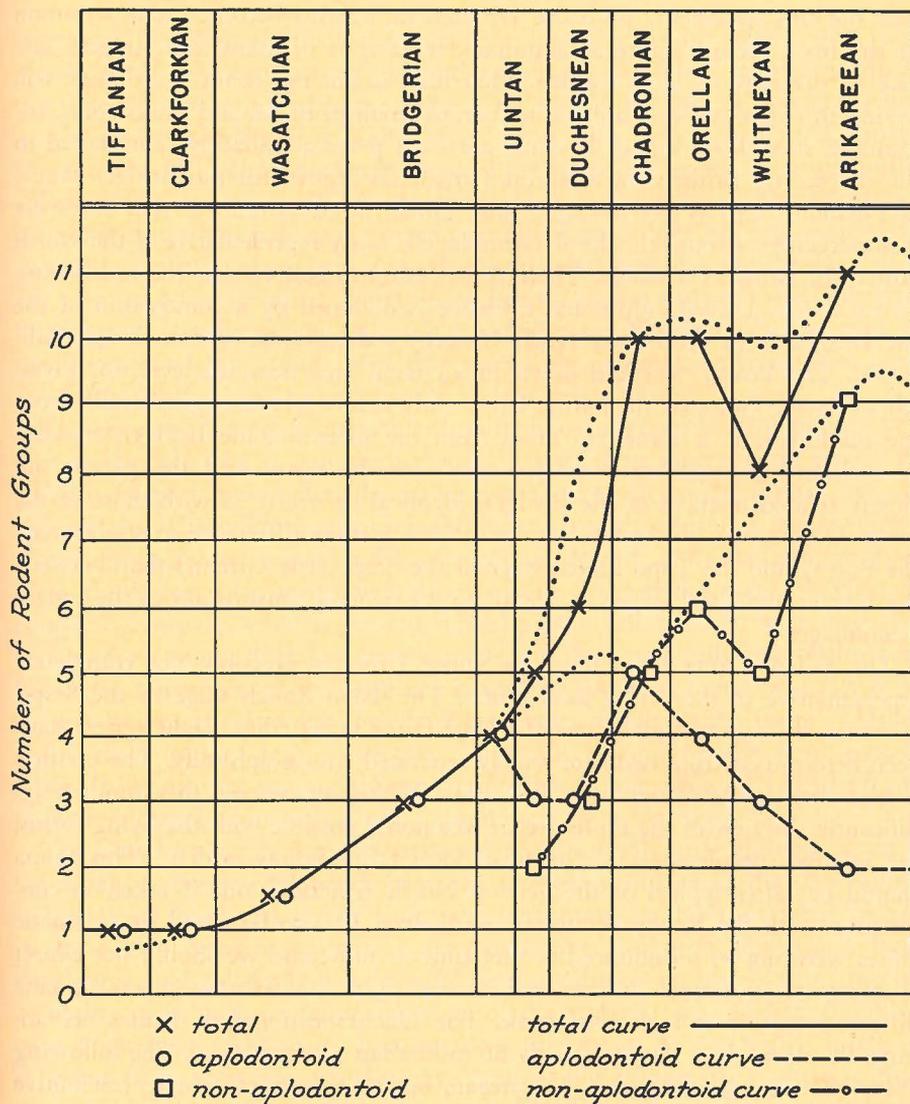


FIG. 9. Curves of rodent evolution

Mylagaulidae) by Arikarean time. Incidentally, this decline apparently more than offsets the continued expansion of the higher rodents, resulting in a slight drop in total representation during the Orellan and Whitneyan stages.

In an earlier section the opinion was expressed that the known North American early Tertiary rodent record is fairly representative of the real fauna at the level of family and subfamily. This theory can be proved only by further exploration, and is perhaps contradicted by the lessons recently learned as a result of the late discovery of lagomorphs in the Eocene, and of paramyines in the Paleocene and Orellan. Nevertheless, it is believed that several lines of evidence

bear out this statement. With the Wasatchian, rodents become rather common in the fossil record—quite as abundant, in fact, as in many later stages. The lack of diversity of these forms at that time is not the result of selective collecting in respect to size, because numerous small primates and insectivores, for example, have been found. Rodents are even more abundantly represented in the succeeding Bridgerian. Simpson (1936) has argued for the Bridger fauna, and demonstrated as well as can be done under the circumstances, that in respect to supergeneric groups this local assemblage is fairly representative of the North American fauna as a whole. There is no reason to believe that the rodents are an exception. Indeed, additional evidence is obtained by a comparison of the late Bridger with the Poway (early Uintan) rodent fauna of San Diego, California. The Poway was laid down in a coastal area near sea level, for invertebrates were collected in marine lenses only a few feet stratigraphically from the mammals. It is some 700 miles from the intermontane Bridger deposits. Nonetheless, the subfamilies represented are the same, and the genera are closely related to those of the Bridger, identical or nearly so with those of the lower Uinta. As a matter of fact, considerably more difference exists between the Poway and the Tapo Ranch stage of the Sespe (late Uintan) than between the former and the Bridger in regard to the general constitution of the rodent assemblage.

The rodent fauna from the type upper Uinta is probably not completely representative of the actual local fauna. The Tapo Ranch stage of the Sespe, however, is large enough to record a local fauna in actuality. Eight genera have been determined from beds not widely separated stratigraphically. The existing local rodent fauna of the same area probably does not exceed this number significantly. In view of the more precise taxonomy possible with the living forms, the relative completeness of the fossil local fauna seems evident. This fauna should be fairly typical of the general North American one if taken in conjunction with the Rocky Mountain equivalent. It is to be noted that climatic zones were not so pronounced at that time as now, and we should not expect so many major faunal differences between areas as exist now, when climatic differentiation is at a decided peak. The Duchesnean rodent faunas are admittedly incomplete, but apparently no more than moderately so. The following White River, John Day, and Arikarean, however, certainly are representative of the general fauna, although even here the late discovery of paramyines, and the rarity of some types, suggest something less than complete information.

That the lack of diversity on a supergeneric level in the earlier Eocene faunas is real is further suggested by comparison with the very scant upper Sespe (Whitneyan? and Arikarean) rodent fauna. Only seven specimens are known, but these represent five families. Four of the eight living families of North American rodents are present, and one of the latter at least could not possibly be present. A similar situation has been noted by Matthew (1924, pp. 74-75) for the Snake Creek fauna. It is difficult to believe that the observed primitive nature of the Eocene fauna is imaginary and the result of collecting caprice.

The curves previously cited (fig. 9) also point to the same conclusion, as is

suggested by comparison of that of the aplodontoids with that of the non-aplodontoids. The peak of aplodontoid expansion is reached approximately at the time of appearance of higher types, and shortly declines. This coincidence can hardly be accidental. If higher types were really present on this continent at an earlier date, their presence should have been felt by the more primitive aplodontoids, preventing their expansion. Perhaps if the more advanced types were present in highland areas, more primitive types might have persisted with success in lowland areas (or the reverse, for that matter), but this situation does not seem to have prevailed. The known Eocene faunas were for the most part inhabitants of intermontane basins, but not all were. Moreover, during most of the Eocene and Oligocene, relief was apparently not sufficiently great to have any marked differentiating effect on the rodent fauna.

The conclusion appears inevitable that the known record is a fair approximation to the real North American record in respect to supergeneric groups of rodents. If so, it must reflect the actual evolution of the rodent groups, even if imperfectly. The only completely valid method of determining the evolution of any group is one based on the stratigraphic record. If the latter were complete, the history of a group would be obvious. Even if this record is very incomplete, however, what is present should permit reliable inferences as to the course of evolution. Mistakes may be made, but it seems highly improbable that "no extinct member of the [rodent] order has yet been found which can be regarded as ancestral to any considerable number of subsequent forms" (Miller and Gidley, 1918, p. 432), if we take "ancestral" in an approximate or general sense. It is certainly against all expectation that a long geologic record of any order is incomplete in such a way as to be wholly misleading.

The record in North America, however, is that of only one continent. Even if we admit a complete sequence here, the possibility still exists that the higher rodent types developed in the Eurasiatic land mass. In this case, what we see in the North American picture is not continuous evolution, but largely local development of aplodontoid rodents followed by migration into North America of higher types with consequent decline of the native stocks. The stratigraphic record obtained under such circumstances might not be noticeably, if at all, different from what we actually have, and would explain the failure to find direct Bridger ancestors of the higher types of late Eocene and Oligocene rodents. Moreover, intercontinental migration affecting this continent did occur in the late Eocene, reaching a climax in the Chadronian. *Simimys* (Muroidea?), *Griphomys* (advanced Sciuromorpha?), and *Protadjidaumo* (Eomyidae) appear to be the only American Eocene forms which could be foreign in origin, and are not aplodontoid. Of these, *Protadjidaumo* and to a lesser extent *Simimys* suggest most strongly an outside origin, for related forms are found in essentially contemporaneous deposits in the Old World. Nevertheless, *Simimys* is somewhat older than any other recognized myomorph. How significantly the factor of migration distorts the picture of rodent evolution obtained from study of North American rodents alone is not too clear. It is perhaps of less importance than usually thought.

The Eocene record of other continents does not contribute much to an interpretation of the North American fauna. Early Eocene rodents are known from Europe, and they are apparently all paramyines just as the American ones are. Middle Eocene rodent faunas seem to be completely lacking outside North America. Late Eocene rodents are also known from Europe. These are partly similar to American forms and partly different, but are apparently comparable in stage of evolution. *Cricetodon* has been reported from the latest Eocene or earliest Oligocene of Asia, but otherwise the important Asiatic Eocene faunas remain to be discovered. If the Old World Eocene rodents do not clearly substantiate the American record, neither do they alter the picture.

That the North American stratigraphic sequence is a fair indicator of the actual course of evolution, whether influenced by migration or not, is suggested by the state of development of several forms. For example, *Simimys* of the late Eocene and early Duchesnean, if it is a muroid, is very primitive in zygomaseteric structure, and gives no indication of a long previous specialization. Further, authentic Oligocene muroids show various stages of zygomaseteric evolution, which suggest no great lapse of time since initial differentiation (see section on Cricetidae). Although this argument is partly negated by the continuance into Recent times of similar transitional types, progressive changes in Oligocene and Miocene species of *Cricetodon* can be observed in the stratigraphic record. Hence, the first appearance in North America of several advanced rodent types may indicate, even if only very approximately, the time of their development (see also p. 147).

Matthew's argument that rodents have developed within the present limits of the fossil record from the Wasatchian paramyines seems to be supported by the known stratigraphic facts. At least, there is no reason for abandoning the theory, and some positive and much inferential evidence is in its favor. Generally, the rodent record is in agreement with that of several other orders, the Carnivora and Artiodactyla, for example, as to the first appearance in time of higher groups (see fig. 10). We should hardly expect to find a true cat or camel in the Wasatchian or its equivalents in the Old World, and there is no actual evidence to indicate anything but a comparable situation in respect to the rodents.

If the known North American rodent record is taken as an approximation of the true record of development, then a summary statement of early Tertiary rodent history, in its application particularly to this continent, may be made as follows:

*Late Paleocene:* Paramyinae only. Ancestral dentition and zygomaseteric structure.  
*Eocene*

Wasatchian: Paramyinae; beginning of rodent dental differentiation in middle and late Wasatchian times.

Bridgerian: Paramyinae, Cylindrodontinae, Sciuravinae. Complete differentiation of these ischyromyid groups with consequent development of diverse, but brachydont, dental patterns. Probable initial development of non-aplodontoids.

STAGE	CARNIVORA		RODENTIA		ARTIODACTYLA	
OLIGOCENE	Representatives of modern families widespread and common	Decline of creodonts	First appearance of many modern families	Decline of aplodontoids	First appearance of several typical Tertiary artiodactyl groups	
UINTAN and DUCHESNEAN	First higher types (first canids, felids, viverrids?)		First higher types; first modern families		First appearance of modern families; first North American selenodont artiodactyls	
BRIDGERIAN	No modern families	Increasing differentiation of creodonts	No modern families	Increasing differentiation of aplodontoids	No modern families; first development of selenodont dentition	Only primitive bunodont artiodactyls in North America
WASATCHIAN	First hyaenodonts		Beginning of rodent differentiation		First Artiodactyla	
TIFFANIAN and CLARKFORKIAN	First oxyaenids		First Rodentia	None		
TORREJONIAN	First miacids (and fissipedes, s.l.); and mesonychids		None	None		
OLDER PALEOCENE	First Carnivora		None	None		

FIG. 10. Comparison of major evolutionary changes in three orders of mammals

Early Uintan: Paramyinae, Cylindrodontinae, Sciuravinae, Protoptychidae.

Fauna still aplodontoid so far as known, but higher types undoubtedly developing. Beginning of hypsodonty in some types.

Late Uintan: Paramyinae, Cylindrodontinae, Sciuravinae(?), Aplodontidae, Geomyoidea(?), Muroidea(?). Sciuravinae in decline or extinct (record questionable after early Uintan). First appearance of recognizable aplodontids, myomorphs, and possibly advanced sciuromorphs, although these groups presumably arose somewhat earlier. Non-aplodontoid differentiation well under way.

Duchesnean: Paramyinae, Cylindrodontinae, Sciuravinae(?), Aplodontidae, Eomyidae, Muroidea(?). First appearance of forms usually accepted as unquestioned advanced sciuromorphs. Maximum expansion of Aplodontioidea about at this time.

*Oligocene*

Chadronian: Paramyinae, Prosciurinae, Cylirodontinae, Ischyromyinae, Aplodontidae, Eutyromyidae, Castoridae(?), Eomyidae, Heteromyidae, Muroidea(?). First appearance of recognizable Prosciurinae and Ischyromyinae. First appearance of unquestioned heteromyids, castoroids.

Orellan: Paramyinae, Prosciurinae, Ischyromyinae, Aplodontidae, Eutyromyidae, Castoridae, Eomyidae, Heteromyidae, Cricetidae. Decline of aplodontoids. Last known appearance of paramyines and eutyromyids. Appearance of unquestioned cricetids. Possible beginning of sciurid differentiation? Possible aberrant geomyids (*Diplolophus*)?

Whitneyan: Prosciurinae, Ischyromyinae, Aplodontidae, Sciuridae(?), Castoridae, Eomyidae, Perognathinae, Heteromyinae, Cricetidae. Continued decline of aplodontoids. Last appearance of Prosciurinae?, Ischyromyinae, Eomyidae. Beginning of heteromyid differentiation. Rise of mylagaulids?

*Miocene*

Arikareean: Aplodontidae, Mylagaulidae, Sciuridae, Castoridae, Perognathinae, Heteromyinae, Florentiamyinae, Entoptychinae, Geomyinae, Cricetidae, Muridae(?). Extinction of Ischyromyidae? First appearance of Mylagaulidae. Appearance of undoubted Sciuridae as tree squirrels. Appearance and differentiation of unquestioned geomyids. Faunal constitution essentially unchanged until close of Hemphillian.

## RODENT EVOLUTION

Opinions have been expressed by many workers on rodents which if correct would make this order somewhat exceptional. In the first place, it has been repeatedly stated or implied that rodents evolve very slowly. Many of the older paleontologists thought of rodents as essentially useless for stratigraphic work, a view which suggests a slow rate of change; and even excellent modern authority (Burke, 1935*b*, p. 12; Wood, 1940, p. 275) lends support to this view. If evolution was always as slow as is implied, it is difficult to see how the rodents reached their present diversity at all, and the stratigraphic record would have to be recognized as very misleading. Secondly, parallelism is usually thought to be the outstanding evolutionary phenomenon of the order. That this is the truth is admitted, but the impression is gained at times that assumptions as to its manifestations have been carried to improbable lengths by some. Lastly, zygomaseteric structure is regarded as the key to rodent classification even by authorities who are unwilling to accept the extreme views of its value propounded by Miller and Gidley. This almost universal acceptance of the criterion of zygomaseteric structure is perhaps all the more striking in the light of the certainly great role parallelism has played in development of other structures in rodents.

## RATE OF EVOLUTION

If the stratigraphic record of the rodents is interpreted literally, the establishment of the major taxonomic divisions must have proceeded rapidly. In some instances, the speed of necessary changes would seem to exceed what is at all probable. Further, the expected intermediate types are rarely found, and if

found are more often than not associated stratigraphically with more advanced forms, and consequently are not actually ancestral. The failure to find real "missing links" is not, however, restricted to rodents. It is likewise true of most orders in respect to the evolution of family and higher units. To explain this common phenomenon, it has been argued that evolution at this level takes place rapidly, and in numerically small sections of the population, and hence the chance of finding the intermediates is small (Simpson, 1944, pp. 117-118). Evolution of specific lines within families or subfamilies takes place more slowly, with much greater numbers involved, and hence under more favorable conditions for a fossil record. The rate of change of these lines is what is usually employed in estimations of speed. Even here, however, the rate varies, and in certain instances has been rapid. The short life span of rodents would seem to argue for more rapid evolution than in the larger mammals, although only rarely if at all do we find much evidence of this (*ibid.*, p. 20). Jepsen has even suggested that "long intergeneration spans might correlate more successfully, at least theoretically, with rapid than with slow evolution, depending upon how and when mutations occur" (1946, p. 540).

Because intermediate stages in the development of a new group from an ancestral stock are rarely found, the first appearance of the new group in the record practically never corresponds to the time of origin. It is probably not necessary, however, to assume a long previous history for rodent groups of superfamily or family size. More specifically, an interval of a stage or less (e.g. Bridgerian, Arikareean) may frequently be sufficient. For example, the first appearance of the typical myomorphs (muroid-dipodoid groups) is late Uintan in North America, latest Eocene or earliest Oligocene in eastern Asia, and early Stampian in Europe. This record in itself strongly suggests origin of the myomorphs not too long before their first appearance on this continent. Moreover, if descent of the myomorphs is from early aplodontoids, their origin occurred after the early Wasatchian at earliest. If, further, their origin lies in the sciuravine division, they would seem to have developed most probably in the late Bridgerian or early Uintan, dubious as this may sound. It should be remembered that even so, such an interval may well represent a time range of nearly four million years with a possible five million generations of rodents, at a rough estimate.

Regardless of the rate of evolution for the larger taxonomic groups, the rate of change of individual lines apparently need not be always slow. An example concerned with size may be taken from the development of the giant-beaver phylum (*Castoroidinae*). During the earlier part of its history, the constituent forms (*Monosaulax*, *Eucastor*, *Dipoides*) increase in average size very slowly and apparently almost steadily, but do not show any tendency toward gigantism. Indeed, the Hemphillian *Dipoides* is apparently distinctly smaller than the contemporary true beavers, although these are poorly known. *Procastoroides* of the Blancan is larger than modern *Castor*, and the rate of size change has obviously increased. The Pleistocene *Castoroides* has a tooth row twice as long as that in *Castor*, and the animal itself was many times the size of any living

beaver (of eight to nine times greater bulk?). An approximate growth curve, anteroposterior length of  $P_4-M_3$  against time, is plotted in figure 11. In this an appropriate interval has been maintained for the apparent faunal discontinuity separating Hemphillian and Blancan. If this interval were to be omitted, an even greater acceleration in growth would be shown. Although the generic series is based on dental characters, there is little reason to question its authenticity. The curve would seem to indicate both rapid increase in size and change in rate.

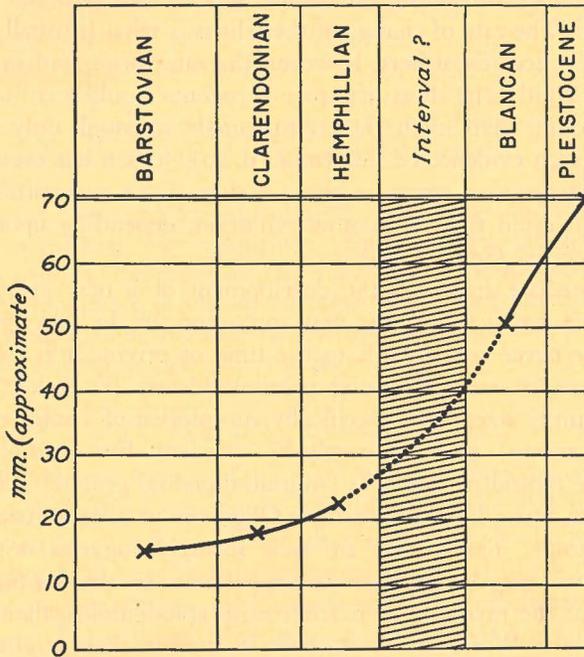


FIG. 11. Rate of change of length,  $P_4-M_3$ , in Castoroidinae

Hypsodonty may also be rather rapidly acquired. The John Day *Meniscomys* has hypsodont but rooted cheek teeth. *Liodontia* of the early Barstovian is characterized by rootless teeth several times as high at any time during wear as in *Meniscomys*. If it be admitted that *Liodontia* is derived from *Meniscomys* or a form in the stage of dental evolution of the latter, a proportionately greater increase in effective hypsodonty has been acquired than is seen in the contemporary horses. With increased hypsodonty, changes of tooth pattern took place, although they resulted chiefly in obliteration of most of the recognizable crown elements.

An equally great change is seen in skull proportions in the above genera. Apparently, the John Day type has a rather squirrel-like skull in which the peculiarities of the aplodonts are only beginning to appear. In *Liodontia*, the modern shape has been acquired, at least in its essentials. A similar change is seen if comparisons are made between the earliest mylagaulids of the Rosebud

(*Promylagaulus*) and those of the Hemingfordian (*Mesogaulus*) and early Barstovian (*Mesogaulus* and *Mylagaulus*). Only slight differences between *Promylagaulus* and *Meniscomys* are apparent in the rather fragmentary skull material available, but the late Hemingfordian and early Barstovian mylagaulids are as characteristically mylagaulid as *Liodontia* is aplodontid.

Aside from these changes in size, hypsodonty, and skull proportions in general lines of descent, rapid development of diverse if closely related genera is also indicated by the history of certain groups. Among these may be mentioned the Microtinae, the Murinae, and the South American Cricetinae. The stratigraphic record and some other features of their history suggest that the major development of each occurred in post-Miocene times. Lastly, it is difficult to explain the appearance and characteristics of the Arikarean Entoptychinae except by assuming a rather rapid development of this subfamily in the later Oligocene.

#### PARALLELISM

The more striking instances of parallelism in dental patterns are found in the more recent, end members of lines with hypsodont teeth (e.g. *Castoroides* and *Amblyrhiza*; *Myospalax* and various microtines). Less striking are those between brachydont types (e.g. *Perognathus* and *Mus*; *Eliomys* and various sciurids). It is generally although not always true that the degree of parallelism developed is an expression of degree of relationship, and particularly is this so of the earlier brachydont forms. Even here, caution is necessary, but there is hardly reason for regarding tooth pattern in the older types as being distinctly less significant than for other mammalian orders. Schaub, in discussing the relationships of *Cricetops*, has maintained the value of tooth pattern as opposed to zygomaseteric structure (1925, p. 88) in the cricetids. Likewise, the writer believes it will be found true in general of the brachydont early Tertiary forms that the dental structure reveals real relationships, and that the closer the correspondence in dental pattern between two groups, the closer the degree of kinship. Conversely, it is unlikely that groups which are related will exhibit completely unlike tooth patterns during late Eocene and early Oligocene times.

#### ZYGOMASETERIC STRUCTURE

Comments on the zygomaseteric structure have been made in earlier sections. Here only a summary will be given.

The fundamental premise of the Miller and Gidley classification is that the zygomaseteric structure of rodents has not changed significantly within the limits of the known record (late Paleocene to Recent). Hence, five main types of structure are made the criteria for five major divisions. Most other modern authors have likewise stressed the importance of the zygomaseteric structure, but have not made it a sole and rigid basis for determination of the systematic position of each species, if the total of other characters indicated that the assignment was very unlikely. In either case, however, the assumption is made that the zygomaseteric structure furnishes a natural means of classification, with no parallel development of this structure in unrelated groups.

That Miller and Gidley were extreme in their views seems to be admitted by all recent commentators. A certain number of living types are known which bridge the gaps between dipodoid and muroid (*Deomys*), sciuroid (*Belomys*, some *Tamias*) and aplodontoid types. The fossil record also exhibits annectent structures in these same groups (*Cricetops*, *Simimys*, and to a certain extent *Protospermophilus*), and various Oligocene and Miocene species of *Cricetodon* (*C. incertum*, *C. minus*, *C. gregarium*, and *C. affine*) demonstrate that zygomaseteric modification of a significant sort may take place. Although no specific line of rodents can be traced in which transformation from one type to another is completely demonstrated, the varying stages of development shown by fossil and living forms together with the known stratigraphic record make it all but actually demonstrated (1) that the aplodontoid zygomaseteric structure is primitive and gave rise to the other types, and (2) that this transformation is Eocene in age, possibly Oligocene in part. Further, not all individual lines within a family show the same degree of progress in zygomaseteric development at a particular time. The Oligocene Cricetidae, for example, exhibit a wide range in the shape of the infraorbital foramen and the breadth and inclination of the zygomatic plate in different lines at comparable levels (*Cricetops*, *Cricetodon*, *Eumys*). To a lesser extent the same variation appears to be found in the Miocene North American Sciuridae. The families of the advanced Sciuromorpha likewise apparently show the same phenomenon on a larger scale, inasmuch as the Sciuridae not only is the last to appear, but has the most primitive forms within its members. In this case, however, the superfamilies grouped together may really have little in common. As a matter of fact, if this group is a natural one, the Castoroidea and Geomyoidea must have become separated from the Sciuroidea when the zygomaseteric structure was in an aplodontoid stage, or nearly so.

Although the hypothesis has not been seriously proposed by any modern student, it may be that the use of zygomaseteric structure as a means of classification does not always lead to a natural arrangement. In particular this may be true of the union of the Geomyoidea with the Sciuroidea and Castoroidea. Discussion, however, is reserved for a following section.

A very tentative outline of the evolution of zygomaseteric structure based on the present stratigraphic record is given below. It should be noted that only rarely is the first appearance of a group accompanied by direct information as to skull structure. Thus, in North American forms:

Group	First appearance	Zygomaseteric structure preserved
Sciuridae.....	Whitneyan?	Arikareean (John Day)
Eutypomyidae.....	Chadronian	Orellan
Castoridae.....	Chadronian?	Orellan?, probably Whitneyan
Eomyidae.....	Late Duchesnean	Chadronian
Heteromyidae.....	Chadronian	Orellan?
Geomyoidea?.....	Late Uintan	Late Uintan, but very poorly
Muroidea?.....	Late Uintan	Late Uintan

- Wasatchian: Zygomatic plate narrow, horizontal. Infraorbital foramen not invaded by masseter medialis.
- Bridgerian: Same as above so far as known, but probable invasion of infraorbital canal taking place in some groups.
- Early Uintan: Beginning of formation of a distinct anterior head for masseter lateralis superficialis in muroids, but zygomatic plate still almost horizontal. Beginning of broadening and tilting of plate in some advanced sciuriforms.
- Late Uintan: Masseter lateralis superficialis in muroids with anterior head distinct, zygomatic plate slightly tilted but still beneath infraorbital foramen and essentially horizontal. Some tilting of plate in geomyoids?
- Duchesnean: Continued development of zygomatic plate in some advanced sciuriforms (Eomyidae, Heteromyidae?, Castoridae?).
- Chadronian: Muroid zygomatic plate still largely beneath infraorbital foramen, lower border of infraorbital canal little narrowed. Advanced sciuriform type completely developed in Eomyidae, perhaps not at all in Sciuridae.
- Orellan: Muroid zygomatic structure nearly modernized in some phyla. Castorids modernized. Sciuridae perhaps still largely of aplodontoid type.
- Whitneyan: Sciuridae with zygomatic plate becoming inclined and broadened?
- Arikarean: Zygomatic structure essentially modernized in all groups.

#### RODENT EVOLUTION IN RELATION TO CLASSIFICATION

If Matthew was correct in proposing a derivation of higher rodent types from the Eocene aplodontoids, and if the Bridgerian rodent groups are representative as to the true state of rodent evolution at that time, certain facts regarding rodent classification must necessarily follow. It should be held in mind, however, that neither of these premises can be established as fact, or even as partially true. On the other hand, neither can they be disproved, and a considerable body of information suggests their possible correctness, and the validity of the inferences drawn from them.

The early Wasatchian rodents are all paramyines. During the middle and late Wasatchian, certain poorly known forms make their appearance which may foreshadow the differentiation of cylindrodontines and sciuravines, and suggest their derivation from the paramyines. With the Bridgerian, the rodent dentition has evolved into several distinct types which may well represent the first fundamental divergence in the rodent stock. At this time two quite distinct kinds of upper molar pattern are present. The first type is the paramyine, with distinct conules, imperfect protoloph and metaloph convergent toward the protocone, and weak hypocone, poorly separated from the primary internal cusp. The second is the sciuravine, with less distinct conules, especially metaconule, well developed and fully separate hypocone, and perhaps on the whole stronger protoloph and metaloph; these latter tend to be parallel and slightly inclined crests somewhat as in the earlier horses. Broadly, two types of lower molar pattern are also known, although the distinctions are of considerably less importance than those between the two upper molar patterns (see earlier section on Sciuravinae). The more primitive paramyine type retains a basined talonid. In the type represented by the cylindrodontines and sciuravines this basined

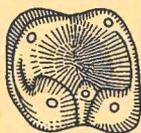
heel is interrupted by a crest (hypolophid) from the entoconid to the ectolophid-hypoconid. These types are diagrammatically illustrated in figure 12. Four combinations of pattern are possible, of which three are represented by the Bridger Paramyinae, *Cylindrodontinae*, and *Sciuravinae*.<sup>6</sup> The fourth, with a sciuravine-type upper and paramyine lower, is suggested only in some of the more poorly known late Wasatchian and younger specimens. At present, the *Cylindrodontinae* appear to be a sterile line terminating in the Oligocene. Hence, if any groups are known which are broadly ancestral to the later rodents, they must be the *Paramyinae* and *Sciuravinae*.



Paramyine type  
upper molar



Sciuravine type  
upper molar



Paramyine type  
lower molar



*Cylindrodontine* and  
*sciuravine* type  
lower molar

FIG. 12. Molar patterns of the Bridgerian. (*Sciuravine* type upper from A. E. Wood, 1937*a*; others from original material.)

Appearance of the higher non-aplodontoid types is sufficiently rapid beyond the Bridgerian stage to preclude in large measure the possibility of an evolution of any post-Bridger paramyines through a sciuravine stage to advanced types. Consequently, we should expect to find two groups of more advanced rodents: first, those that still retain the fundamental pattern of the paramyines in their upper molars; and second, those which have well developed and separate hypocones, reduced or absent conules, and greater loph development, either as transverse or as more or less parallel diagonal crests. Those of the first type would be more closely related among themselves than to other rodents, and, moreover, could be regarded as direct derivatives of the paramyines. Those of the second type would suggest derivation from the sciuravines, although less positively because

<sup>6</sup> It should be mentioned, however, that because of the lesser value of the lower molar construction, the pattern combinations do not in themselves serve to define these groups. The *Cylindrodontinae* are not merely forms with paramyine-type upper molars and hypolophids, nor are all known forms with this pattern combination *cylindrodontines*.

of the greater chance for later parallelism in tooth structure to confuse the picture.

The upper molar pattern has been utilized by Miller and Gidley in their classification of 1918 as a secondary basis for division. The results, at least in certain instances, were far from satisfactory. To employ it now as a primary basis is obviously much more hazardous. Nevertheless, if the basic assumptions are found to be correct, it would be difficult to avoid its use, because the first recognizable cleavage in the rodents is indicated in the dentition, and only at a later date by other characters. It must be acknowledged, however, that even Oligocene types do not always seem to indicate very clearly their affinities with either pattern, and the application of the criterion of molar structure becomes increasingly difficult with later types, especially forms with hypsodont dentition. Its present application, particularly with respect to North American forms, is discussed below.

The following groups show the paramyine type of upper molar pattern: Prosciurinae, Cylindrodontinae, Aplodontidae, Mylagaulidae, and Sciuridae. Other characters than the dentition bear out the contention that these groups are closely related to one another. All but the Sciuridae are aplodontoids, and the Sciuridae are the most primitive of advanced Sciuromorpha in dentition and zygomaseteric structure. Such forms as *Belomys* are little advanced beyond the aplodontoids in the latter respect. The postorbital processes of the Sciuridae are also present in the Mylagaulidae and some aplodontids, and not in other rodents. Finally, the late appearance of the squirrels in the stratigraphic record suggests, even if it does not prove, that the sciurids are a late development from the aplodontoid stock, and rather distinct from other advanced sciuromorphs.

The above list also suggests the appropriateness of including the aplodontoids in the Sciuromorpha even if it should prove necessary eventually to exclude the Castoroidea and Geomyoidea from this suborder. Tentatively, the Castoroidea may be included in the division with paramyine dental affinities. Most workers have recognized a close relation between the squirrels and beavers, some including the two in a single superfamily. Tullberg, however (1899, pp. 460-461), has also indicated characters which would tend to separate both castoroids and geomyoids from the sciuromorphs, and unite them with the myomorphs. The dentition of the oldest castoroids still remains rather isolated from all contemporary patterns. *Eutyptomys*, however, does show certain superficial similarities to *Paramys*, and with no definite evidence to the contrary, the castoroids may be placed in the Sciuromorpha. The Protoptychidae might possibly be a paramyine offshoot of the Aplodontoidea, but perhaps better general evidence suggests derivation from the sciuravine division. There is no real evidence that it is related to either (see section on Protoptychidae). Other North American rodents, including the Geomyoidea, do not seem directly derivable from the paramyines. Hence, of the rodent groups above the aplodontoid level of specialization only the Sciuridae (and tentatively the Castoroidea) can be cited as probably descended from any paramyine in a direct sense. Consequently, most advanced rodents seem to be derived from other aplodontoids.

Of the remaining rodent groups, the muroids and dipodoids show the greatest resemblance to the sciuravines in basic molar pattern. Evidence for a relatively close union of these two modern groups has been reviewed in an earlier section. There seems little reason to doubt the validity of the suborder Myomorpha, at least as regards a nucleus formed by the Muroidea and Dipodoidea. It may be assumed that if any of the aplodontoids is ancestral to the myomorphs, it is the Sciuravinae. If so, then the suborder has its roots as far back as the middle Eocene at least, and from this time on exhibits certain characteristic dental differences which grow increasingly pronounced.

The Old World Gliroidea, or dormice, on the basis of many characters, apparently should be referred to the Myomorpha. The tooth pattern and formula, and other features as well, suggest a relatively primitive group within the suborder. Little evidence of sciuravine affinities is seen in the teeth, however, although it appears barely possible that a peripheral relationship exists (see earlier sections on Gliroidea and Sciuravinae). The Ischyromyinae demonstrate the frequent practical difficulty of attempting to apply dental differences in classification even with excellent material, and with types not too far removed in time from those of the Bridger. Present evidence may slightly favor a closer relationship to the sciuravines than to any other group.

Relationships of all the above groups as expressed in fundamental tooth pattern either generally agree with the consensus based on other characters or are of uncertain significance. The Geomyoidea, however, are an apparent exception. The tooth pattern, although not nearly so close to that of the Sciuravinae as are those of the Dipodoidea and Muroidea, still bears considerably more resemblance to that of certain sciuravines than it does to the paramyine type. Thus, the hypocone is well developed and completely separate from the protocone, conules have disappeared, and the remaining structures tend to be present as transverse rows of cusps generally united to form lophes. One outstanding difference to be noted is the development of lateral cingula in the Geomyoidea. Nevertheless, if either the paramyine or the sciuravine type is ancestral to the geomyoid, the resemblance of the sciuravine is much more marked. If the Eomyidae are related to the more typical geomyoids, this resemblance is greatly increased. Certainly, the dentition of the Geomyoidea suggests association with the Myomorpha rather than with the Sciuromorpha. How close this relation is, remains to be established, but it should be recalled that at one time the geomyoids were classified as myomorphs.

In opposition is the important zygomaseteric structure, and to a lesser extent the retention of the premolars as functional teeth. These features have been deemed conclusive evidence for approximately the past fifty years. It may be suggested, however, that in addition to characters previously thought to indicate myomorph affinities, the dental history of the rodents lends support to the older assignment. Many striking similarities are seen in comparing the muroids and geomyoids, whereas any real resemblance between geomyoids and sciurids seems limited essentially to the zygomaseteric structure, and retention in both of some primitive characters. The main points of osteological resemblance between the

geomyoids and muroids may be listed as follows: (1) General murine skull. Both produce in specialized types highly modified skulls as a result of inflation of the bullae. (2) "Muroid" dentition. This is the result of parallel development, but both are derivable from the sciuravine pattern, whether or not they have actually descended from forms with such a pattern. If the Eomyidae are included in the Geomyoidea, a considerable dental resemblance is seen in comparison with the Cricetidae. Otherwise, comparisons can be made between the Heteromyidae and the more typical Muridae. (3) Optic foramen closely associated with sphenoidal fissure. These are separated usually by a slender bony bar. Although this close association is in part a function of size of the optic foramen, and although it may be regarded as a primitive feature in other orders of mammals, it still seems to be a significant character in rodents. (4) Sphenopterygoid canal absent, vestigial, or reduced to a foramen. (5) Inflation of mastoids and reduction of the postglenoid branch of the squamosal. (6) Reduction of the jugal. This is usually extreme. Contact with the lachrymal is lost in all living muroids and geomyoids. (7) Short alisphenoid canal. (8) Fusion of tibia and fibula. This occurs in other groups, but fusion is not so extensive. It may be suggested that a return to classifying the Geomyoidea as Myomorpha is permissible, or at least that the Geomyoidea be separated from the Sciuromorpha and placed nearer the Muroidea (and Dipodoidea), whatever the arrangement.

In addition to the Sciuromorpha and Myomorpha, the South American Hystricomorpha certainly warrant subordinal recognition. Notwithstanding the considerable geographic and geologic difficulties involved, the Old World hystricomorphs seem to be really related to the American forms. Any alternative presumably would involve introduction of paramyine rodents into South America by way of North America in Paleocene times. In this case, it is difficult to understand why the South American rodent radiation was not more productive than appears to have been the case. For, great as it was, it seems to have been the result of development from forms already more specialized than the early aplodontoids. Moreover, absence of rodents from the Eocene record of South America implies their introduction during Oligocene times. In either case, the South American record is basis enough for subordinal recognition.

The geologic record of the rodents suggests that the classic division into three suborders is well founded. Whether or not several other groups of equal rank should be established cannot be demonstrated on the basis of the present geologic record.

#### SUMMARY OF PRINCIPAL PHYLOGENETIC CONCLUSIONS

1. The known record suggests primary differentiation of the rodents from the paramyine group within Eocene times (fig. 13).
2. Molar patterns probably form a fundamental criterion for rodent division, but a criterion difficult to apply.
3. Some basic patterns, at least, are established before recognizable zygomaseteric evolution begins, and may outweigh the latter in importance.
4. There is no reason to doubt the evolution of zygomaseteric structure

from the aplodontoid type, principally within the Eocene and Oligocene. No specific line of rodents is known at present, however, in which evolution from a primitive to a higher type can be traced.

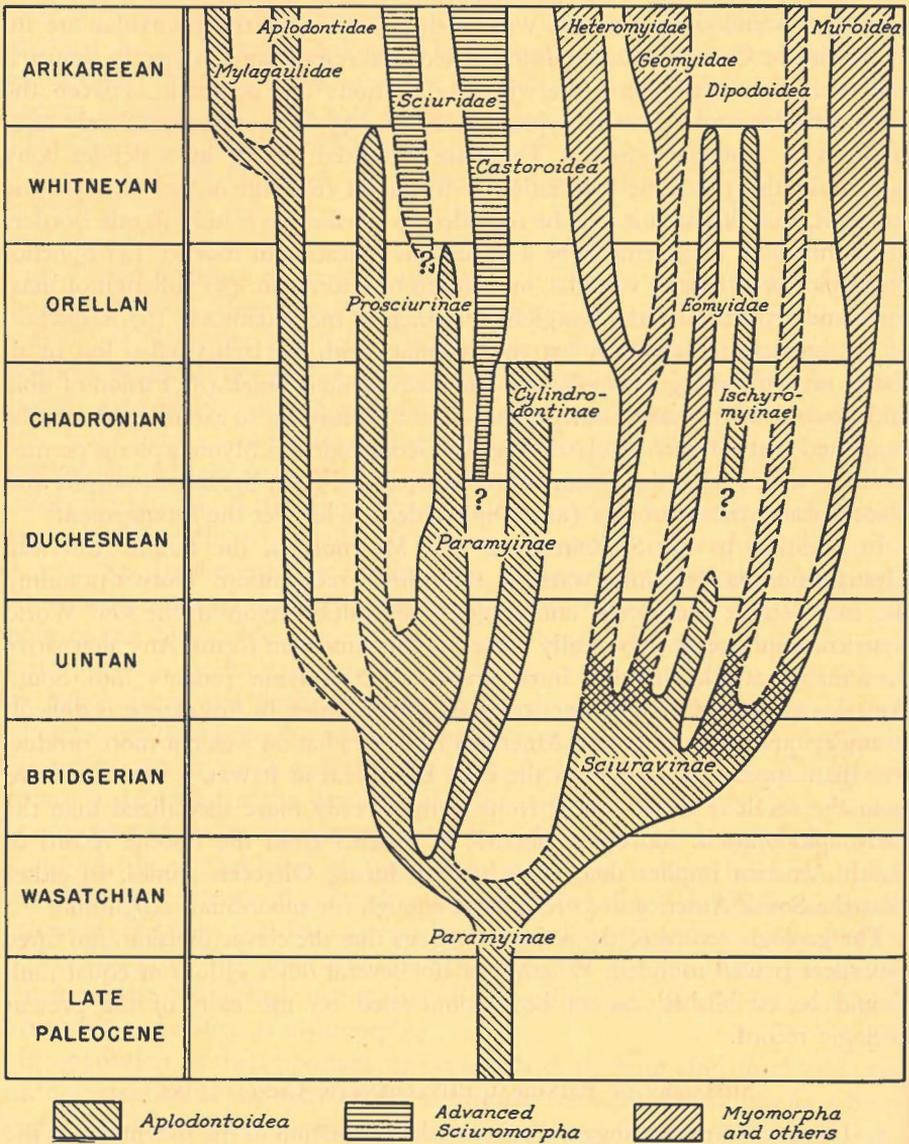


FIG. 13. Tentative phylogenetic chart of North American rodents

5. Zygomasseteric evolution proceeds at different rates even in phyla within a single family.

6. The Sciuromorpha, Myomorpha, and Hystricomorpha apparently represent valid, natural suborders, but some superfamilies remain to be accurately

placed. The Geomyoidea, for example, show every evidence of being widely separated from the "advanced Sciuromorpha" as represented by the Sciuroidea. On the other hand, the Muroidea and Dipodoidea apparently are closely related to each other, and more distantly to the Geomyoidea.

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