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THE APLODONTOIDEA

BY

PAUL O. MCGREW

ASSISTANT CURATOR, PALEONTOLOGY



GEOLOGICAL SERIES
FIELD MUSEUM OF NATURAL HISTORY
VOLUME 9, NUMBER 1
DECEMBER 5, 1941

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THE APLODONTOIDEA

BY PAUL O. MCGREW

Among the specimens collected in 1940 by a Field Museum expedition are two apodontoid rodents from the Rosebud beds of South Dakota. These specimens are of unusual interest because they practically close the structural and time gap that has separated the John Day *Meniscomys* from the late Miocene and early Pliocene mylagaulids. Although the discovery of *Mylagaulodon* (Sinclair, 1903) had partially filled this gap, Matthew's conclusions, first, that the genus had no relationship to *Mylagaulus* and, second, that its type was a young individual of *Mylagaulus*, tended to mask the true significance of Sinclair's specimen. In general, the discovery of the new specimens herein described supports the widely accepted conclusions as to the relationship and ancestry of the Mylagaulidae; namely, that the family was descended from *Meniscomys* or a closely related form, and should be included in the Aplodontioidea.

I am deeply indebted to the authorities of the American Museum of Natural History, especially to the late Walter Granger, for permitting me to study important types, and to Mr. J. LeRoy Kay and Dr. John Clark of the Carnegie Museum for permission to study specimens in that institution. Drs. R. A. Stirton and C. L. Camp of the University of California have facilitated this study by loaning me specimens in their collections. I also wish to thank Mr. and Mrs. Harry Tylee of Wounded Knee, South Dakota, for the assistance and hospitality they provided our field party while collecting the new specimens described herein. Figure 1 was drawn by Mr. John J. Janecek, the remainder by Mr. John Conrad Hansen.

PREVIOUS WORK

Little confusion has existed regarding the origin and evolution of the Aplodontidae. Cope (1883 and 1884) recognized the resemblance between *Meniscomys* and *Aplodontia* and although he realized that the two were related, he referred *Meniscomys* to the Sciuridae. With the description of *Liodontia* (Furlong, 1910), the long gap between the John Day *Meniscomys* and the recent *Aplodontia* was partially closed by an intermediate form. It was Furlong's opinion that *Liodontia* was close to the ancestry of *Aplodontia* and a deriva-

tive of *Meniscomys*. These conclusions were substantiated by the work of Matthew (1904, 1910, 1924), Merriam (1916), Stock (1935), Gazin (1932), and Wilson (1937a).¹

As regards the Mylagaulidae there has been no such agreement. In his description of *Mylagaulus sesquipedalis* and *Mylagaulus monodon*, Cope (1878, 1881, 1883) compared the genus with the castorids and felt that it might bear some relationship to *Hystrix*. Riggs (1899) was the first to recognize a similarity between *Mylagaulus* and *Meniscomys* and he regarded the latter as nearly ancestral to *Mesogaulus* and *Mylagaulus*, basing his opinion on the lake pattern of the lower molars. In 1901 Matthew stated his disagreement with Riggs and considered *Mylagaulus* to be "related to the Sciuridae but not especially to any known member of the family." The following year the same author noted a resemblance between the skulls of *Ceratogaulus* and *Aplodontia*, but felt that the extreme difference in the teeth and the presence of horns in the former ruled out any possibility of relationship. In 1903 Sinclair described *Mylagaulodon* from the John Day beds and immediately recognized its position as intermediate between *Meniscomys hippodus* and *Mylagaulus*. Although this form now appears to have been properly interpreted by Sinclair, Matthew (1904) dismissed it with the following statement: "The genus *Mylagaulodon* Sinclair appears to be related to *Meniscomys* and *Haplodontia*, but we are unable to trace any relationship to *Mylagaulus*, whose teeth in our opinion are derived from a Castorid or Hystricomorph pattern with quadrate P^4 and no P^3 . *Meniscomys*, *Mylagaulodon* and *Haplodontia* have, like the Sciuridae, a triangular P^4 , and P^3 very persistent though small." After studying the skeleton of *Epigaulus hatcheri*, Gidley (1907) reached the following conclusions concerning the relationships of the Mylagaulidae: "It seems evident . . . that while this extinct group of highly specialized rodents apparently has some remote affinities to the Castoridae and a somewhat nearer relationship to the Sciuridae, as pointed out by Matthew, the family has a far greater number of characters in common with the Aplodontidae, and shows besides some striking resemblances of general proportions to some of the Asiatic forms of the Spalacidae. The resemblance to the latter family, however, seems to be due more to modifications of the skeleton for a similar special adaptation to burrowing habits than to any real relationship." In 1910 Matthew came a little closer

¹ Wilson pointed out certain characters indicating that *Liodontia* was not on the direct line of descent but he agreed that it was roughly intermediate between *Allomys* and *Aplodontia*.

to the views of Riggs (1899) and Sinclair (1903) by placing both the Mylagaulidae and the Aplodontidae in the superfamily Aplodontioidea. Miller and Gidley (1918) agreed that a relationship existed between *Meniscomys* and *Aplodontia* but placed them in different families. The Mylagaulidae, they believed, had a fundamentally different type of tooth structure "based on an underlying quadritubercular structure, the hypocone always entering into the essential mechanical scheme of the crown," whereas the teeth of the Allomyidae and the Aplodontidae were based on an "underlying tritubercular structure." *Mylagaulodon* they regarded as an "allomyid." The discovery of a good series of mylagaulids convinced Matthew (1924) that Riggs was correct—that the mylagaulids were an offshoot from the *Meniscomys* stock. Subsequently Gazin (1932), Stock (1935), and Wilson (1937a) have supported this view. Matthew (1924) also arrived at the conclusion that Sinclair's *Mylagaulodon* represented a young individual of *Mylagaulus*, bearing milk teeth, and that *Mylagaulodon* was therefore invalid. He was followed in this by Stock (1935), who made the last important contribution to our knowledge of the group with a description of the primitive *Eohaplomys*, a form from the Sespe Eocene which he regarded as intermediate between *Allomys* (also *Meniscomys*) and *Paramys*.¹

DESCRIPTION OF NEW MATERIAL

Promylagaulus gen. nov.

Genotype.—*Promylagaulus riggsi* sp. nov.

Distribution.—Early Miocene, South Dakota.

Diagnosis.—Facial region of skull similar to that of *Meniscomys*; dentition $I_{\frac{1}{1}}$, $P_{\frac{2}{1}}$, $M_{\frac{3}{3}}$; cheek teeth rooted; hypsodont but less so than those of *Mylagaulodon*; P^3 small and conical as in *Aplodontia*; P^4 approximately twice as large as M^1 , with mesostyle and four lakes in worn tooth. Molars with single lake when worn.

*Promylagaulus riggsi*² sp. nov.

Holotype.—F.M. No. P26256, facial region of skull with incisors and complete cheek-tooth series. Found by Henry Horback.

¹ Since this paper went to press Cook and Gregory (1941) have redefined *Mesogaulus* and concluded that it is intermediate between *Mylagaulodon* and *Mylagaulus*. *Mesogaulus*, then, includes those species which are referred to in this paper as "primitive species of *Mylagaulus*."

² In honor of Mr. Elmer S. Riggs, Curator of Paleontology in Field Museum of Natural History, who first recognized the relationship between the Mylagaulidae and *Meniscomys*.

Locality and horizon.—Four miles south of Porcupine, South Dakota; top of lower Rosebud beds.

Diagnosis.—Only known species of the genus. For measurements see page 28.

Description.—In the portion of the skull preserved, the part anterior to the parietals, there is a fundamental similarity to *Menis-*

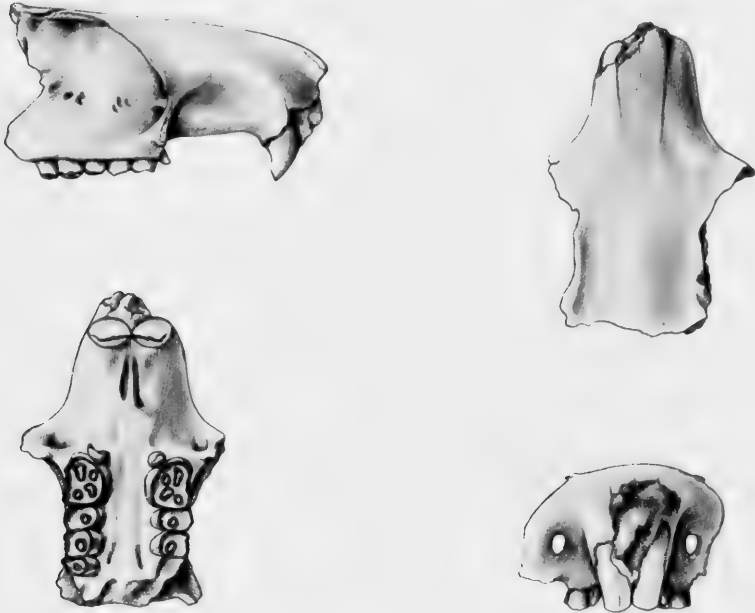


FIG. 1. *Promylagaulus riggsi* gen. et sp. nov. F.M. No. P26256. Partial skull; dorsal, ventral, lateral, and anterior views. $\times 2$.

comys combined with certain resemblances to *Aplodontia* and *Mylagaulus*. The few discernible differences from *Meniscomys* in skull structure are slight and proportional but approach in some degree the characters of *Mylagaulus*. The nasals are rather narrower than those of *Aplodontia* and extend more posteriorly, although not so far as in *Mylagaulus*. As in the living genus, the tips of the nasals, as well as the upper portion of the premaxillaries, pinch in anteriorly. The skull is not so much constricted between the orbits as that of *Aplodontia*. The dorsal rims of the orbits are so damaged that it is impossible to determine whether or not postorbital processes were present. The fact that the skull is relatively wide in this region may indicate that there were incipient processes.

The infraorbital foramen is the same relative size as that of *Mylagaulus*, and somewhat smaller than that of *Aplodontia*. The position of the foramen, as in *Aplodontia* and *Mylagaulus*, is above and external to P^3 (dP^3 in *Mylagaulus*). In *Promylagaulus*, however, it is relatively higher than in *Aplodontia* and lower than in *Mylagaulus*. The higher position in the Mylagaulidae apparently

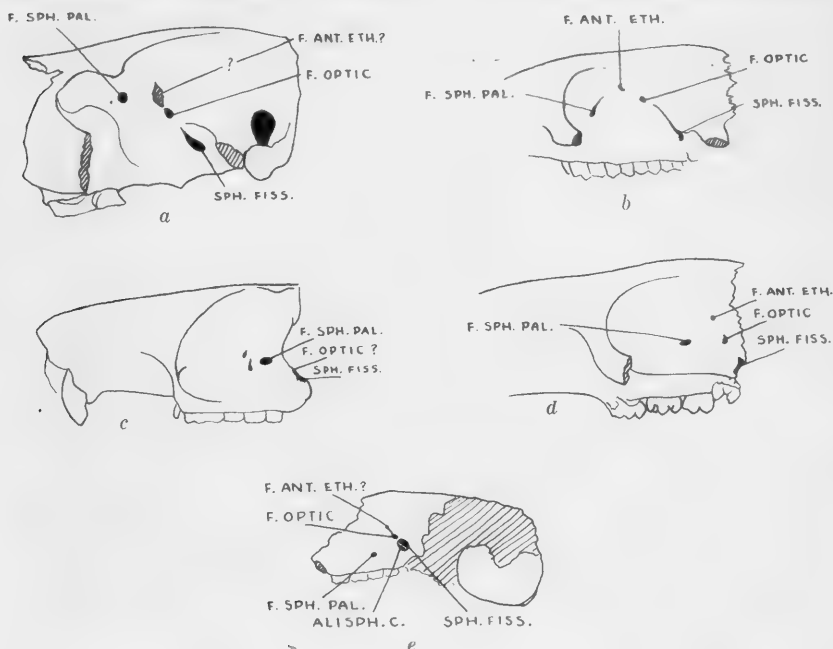


FIG. 2. Cranial foramina of a, *Mylagaulus*; b, *Aplodontia*; c, *Promylagaulus*; d, *Ischyromys*; and e, *Allomys*.

may be correlated with a progressive deepening of the maxillary brought about by the increase in size and length of P^4 .

The nasolacrimal foramen, lying immediately above the posterior opening of the infraorbital foramen, is large and does not differ significantly from that of other aplodontoids.

The sphenopalatine foramen is more posterior in position than in other aplodontoids examined but is otherwise typical.

Anterior to the sphenopalatine are two small foramina. In *Mylagaulus* one foramen occupies the same position but none is present in *Aplodontia*. Such foramina apparently are constant only in the *Mylagaulidae* and it would seem that they are nutrient, supplying the enlarged P^4 .

Unfortunately, the skull is broken away posterior to the optic foramen and sphenoidal fissure. A rounded portion of surface bone where the skull is broken seems to indicate the presence of these openings in much the same position as in *Mylagaulus*, but this is not certain.

The cranial foramina of *Ischyromys*,¹ *Allomys*, *Promylagaulus*, *Mylagaulus*, and *Aplodontia* show a distinct similarity of pattern—one which differs from that of other rodent groups. The similarity of these genera extends to *Ischyromys* (a skull of *Paramys* was not available), a fact that is in agreement with the primitive condition retained throughout the suborder.

The incisors of *Promylagaulus* are broader relatively than those of *Aplodontia* but not so broad as those of *Mylagaulus*. They are slightly convex anteriorly, as in the living genus.

P^3 is very small and conical, as in *Aplodontia* and as dP^3 of *Mylagaulus*. It differs from that of *Allomys* and *Meniscomys* in that it is more reduced and more perfectly conical in form.

P^4 is roughly quadrangular with an antero-external projection extending forward. It is nearly intermediate in form between that of *Meniscomys*, which is triangular, and that of *Mylagaulus*, which is oval. The enamel of the external border forms a low inverted W, the two projections being the mesostyle and an external projection from the parastyle. The tooth is relatively much larger than that of *Meniscomys* and is more hypsodont but much less so than that of *Mylagaulodon* and *Mylagaulus*. The cusps of P^4 may rather confidently be homologized with those of *Meniscomys* and *Aplodontia*. In an unworn condition the tooth probably would have resembled closely that of *Meniscomys* in cusp pattern. Four lakes extend deeply into the crown and they too can be homologized with depressions in P^4 of *Meniscomys* and *Aplodontia* and with lakes in P^4 of *Mylagaulodon* and *Mylagaulus*.

The molars of *Promylagaulus* are considerably reduced but not to the same extent as in *Mylagaulus*. Externally, only a trace of the mesostyle remains; the style was doubtless more prominent in less worn teeth. M^{1-2} are approximately square in outline and of nearly equal size. M^1 is somewhat more compressed antero-posteriorly than M^2 , a step toward *Mylagaulus*. M^3 is smaller than the other teeth of the series and nearly round. Each molar has but a single lake situated posterior to and slightly inside the center

¹ Because no figure showing the foramina was offered by Wood (1937) in his discussion of the cranial foramina of *Ischyromys* I have been unable to follow his interpretation. In this work the terminology of Hill (1935) is followed.

of the tooth. To which depression in the tooth of *Meniscomys* this lake is homologous cannot be determined until unworn upper molars of *Promylagaulus* are available.

Matthew (1904) has recorded a portion of a lower jaw from the Rosebud beds of South Dakota which he believed to represent

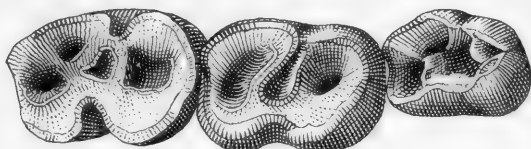


FIG. 3. *Promylagaulus* cf. *riggsi*. A.M. No. 10824. Left M_{T-3} ; crown view. $\times 10$.

a species of *Meniscomys* close to *hippodus*. Examination of this specimen convinces me that it is not referable to *Meniscomys*, but is a lower jaw of *Promylagaulus*, probably of *P. riggsi*. Although the molars are as small as those of *Meniscomys* they are set in a jaw that is much larger than any known specimen of the John Day genus. The teeth are more hypsodont than those of *Meniscomys*, and show an incipient *Mytagaulus* pattern. Although P^4 is missing from the specimen, its alveolus indicates that it was enlarged. The ascending ramus begins outside of M^2 , much farther forward than in *Meniscomys*, and more nearly in the position seen in *Mytagaulus*.

Mytagaulodon cf. *angulatus* Sinclair.

In the upper Rosebud beds of South Dakota, near Porcupine Butte, we were fortunate in finding a single P^4 which certainly



FIG. 4. *Mytagaulodon* cf. *angulatus*. F.M. No. P26266. P^4 ; lateral and crown views. $\times 4$.

represents *Mytagaulodon*. This tooth may be of a species distinct from the John Day specimen but no character unaccounted for by difference in wear can be found to distinguish it. The Rosebud speci-

men establishes *Mylagaulodon* as a valid genus and verifies Sinclair's conclusions as to its relationships. P^4 is strongly hypsodont but has two external and one internal root. At the stage of wear reached by this specimen two external styles are present. The posterior one, the mesostyle, is prominent and extends to the base of the crown. The anterior one is low and would disappear with a little more wear. In general form, the tooth is much like that of *Promylagaulus*, being roughly quadrangular with an antero-external projection. As in *Promylagaulus*, the lakes are four in number, but each is considerably longer than in that form. The antero-external lake



FIG. 5. *Allomys cavatus*. A.M. No. 6988. Type. Left P^4 — M^2 , right M^1 — M^2 ; crown views. $\times 10$.

branches anteriorly, one prong extending antero-externally, the other antero-internally. This lake is forked in all the later mylagaulids examined, and is suggested in *Promylagaulus* by a slight widening of the lake anteriorly. The two external lakes are elongated and almost meet near the center of the tooth. The postero-internal lake is oblique.

There can be no doubt that this tooth is a permanent premolar and not, as Matthew supposed, a member of the deciduous series. The roots bend together at the base and do not spread outward for the reception of the crown of a replacing tooth. Also, the degree of hypsodonty attained seems altogether too great for a milk tooth.

Allomys and Meniscomys

In 1884 Cope recognized four species of *Meniscomys*: *hippodus*, *liolophus*, *cavatus*, and *nitens*. The last was described by Marsh

in 1877 as the genotype of *Allomys*. Cope believed that the two genera were synonymous but attempted to justify his name, *Meniscomys*, by the brevity of the description given by Marsh, even though *Allomys nitens* was adequately figured. *Allomys*, of course, is valid with *nitens* as the genotype. The species *liolophus* was removed from *Allomys* by Miller and Gidley (1918) and made the type of *Haplomys* because of its more brachydont and generally more primitive dentition.

After examining Cope's specimens of *hippodus*, *cavatus*, and *nitens* I am convinced that further separation is necessary. Fortu-

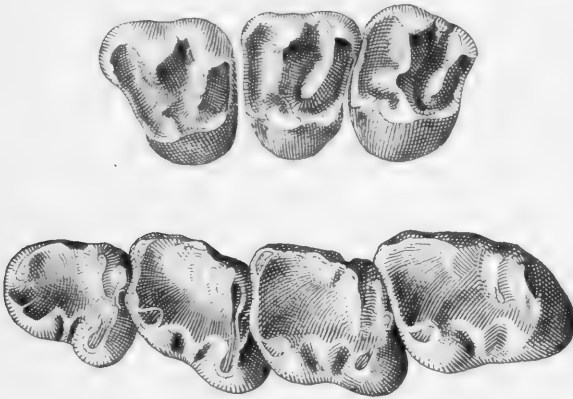


FIG. 6. *Prosciurus* cf. *relictus*. F.M. No. P25813, P⁴ - M²; and F.M. No. P25815, P₃ - M₃. × 10.

nately, it is *hippodus*, which was Cope's type of *Meniscomys*, that is generically distinct from the other two species, hence the original name may be retained. *Allomys cavatus* and *nitens* are very similar and may well represent the same species.

Allomys Marsh 1877

Genotype.—*Allomys nitens*.

Known species.—*Nitens* and *cavatus*.

Distribution.—John Day formation, Oregon. Distribution within the John Day unknown.

Diagnosis.—Cheek teeth lower crowned than those of *Meniscomys*; upper molars with high paramere, W-shaped ectoloph; metaloph and protoloph not well developed; protoloph complete, metaloph incomplete; protoloph not connected with anterior cingulum or

metaloph; hypocone distinct; basins of teeth not enclosed; lower molars basined; metaconid high and connected with protoconid by strong anterior cingulum; posterior cingulum extending inward from hypoconid, but not connecting with entoconid; hypoconulid present; entoconid with projection running to center of tooth (=hypoconulid I of *Prosciurus*); small mesoconid present; entoconid separated from metastylid and from posterior cingulum by shallow valleys; central basin complicated by numerous shallow pits, or lakes.

Meniscomys Cope 1878

Genotype.—*Meniscomys hippodus*.¹

Distribution.—John Day formation, Oregon.

Diagnosis.—Cheek teeth high crowned; upper molars with complete protoloph; protoconule large, connected with protoloph only by posterior edge, and extending to anterior cingulum; metaloph extending between metaconule and anterior base of metacone; metaconule connecting with protoloph and with posterior border of tooth; mesostyle constricted, crown with five well-defined lakes; no hypocone; lower cheek teeth not basined, completely lophodont, metastylid separated from metaconid by deep valley; entoconid and posterior cingulum completely united; molars with three lakes in antero-posterior row.

Discussion.—*Allomys*, as defined above, combines the characters of *Meniscomys* and *Prosciurus*. The complete protoloph, incomplete metaloph, presence of a hypocone, double metaconules and a mesoconid, separation of posterior cingulum from entoconid and the primitive-basined lower cheek teeth, are characters shared by *Prosciurus*, whereas the elevated paramere, with its crescentic paracone and metacone, and W-shaped ectoloph are characters of *Meniscomys*. The combination of characters in *Meniscomys* indicates affinities with *Liodontia* and *Aplodontia* and also with the mylagaulids. *Allomys* seems not to be related to any later types. The fact that the upper molariform teeth of *Eohaplomys* have a rather well-formed hypocone would indicate, but not prove, that the presence of that cusp is primitive. The variability of the hypocone in *Prosciurus*, a probable relative, suggests that the structure might readily

¹ Riggs (1899) recognized *hippodus* as generically distinct from the other species referred to *Meniscomys* and *Allomys* and placed the species in a new genus *Protogaulus*. He seems to have been correct in regarding the species as generically distinct but because *hippodus* is the genotypic species of *Meniscomys* this original term must stand.

be lost. If this is true the hypocone of the Aplodontidae was secondarily lost. The more unlikely alternative is that the absence of a hypocone was the primitive condition. This would require independent origin of *Allomys* and *Meniscomys* and more parallelism than is probable.

Meniscomys and *Allomys*, then, represent two related branches of the aplodontid stock, the two running parallel in the development of the paramere, but the former being much more progressive in the lengthening of the crown and development of an advanced tooth pattern.

The primitive condition and late appearance of *Haplomys* makes it probable that the genus is more closely related to *Allomys* than to *Meniscomys*.

EVOLUTION OF APLODONTID DENTITION

It is certain that the genera *Eohaplomys*, *Meniscomys*, *Liodontia*, and *Aplodontia* do not represent a direct line of descent. With the exception of a hypocone on the upper molars of *Eohaplomys* the general structure of this genus probably approaches the primitive condition for the *Meniscomys* line. The same may be said of *Prosciurus* which in many respects is more primitive than *Eohaplomys*. The dentitions of these genera do display a structurally progressive series, however, and from them may be learned the changes that took place between the early ancestors and *Aplodontia*.

P⁴ of *Eohaplomys* is brachydont and bears distinct, rounded cusps. Externally three cusps are present: the parastyle, paracone, and metacone. The proto- and metaconules are well developed as is the protocone. There are five incompletely enclosed basins: antero- and postero-external, antero- and postero-internal and transverse median. The last is bounded anteriorly by the paracone and protoconule and posteriorly by the metacone and metaconule. The remainder are bounded by adjacent cusps and low cingula. Two rather low and rounded external styles are present; the mesostyle between the para- and metacones and one between the parastylar cusp and the paracone.

In the position of cusps and basins, P⁴ of *Meniscomys* is very like that of *Eohaplomys*. The tooth is distinctly higher and the styles are more prominent. The ridges, which are incipient in *Eohaplomys*, are elevated so that the cusps are less distinct and the basins more completely enclosed. No hypocone is present in *Meniscomys*.

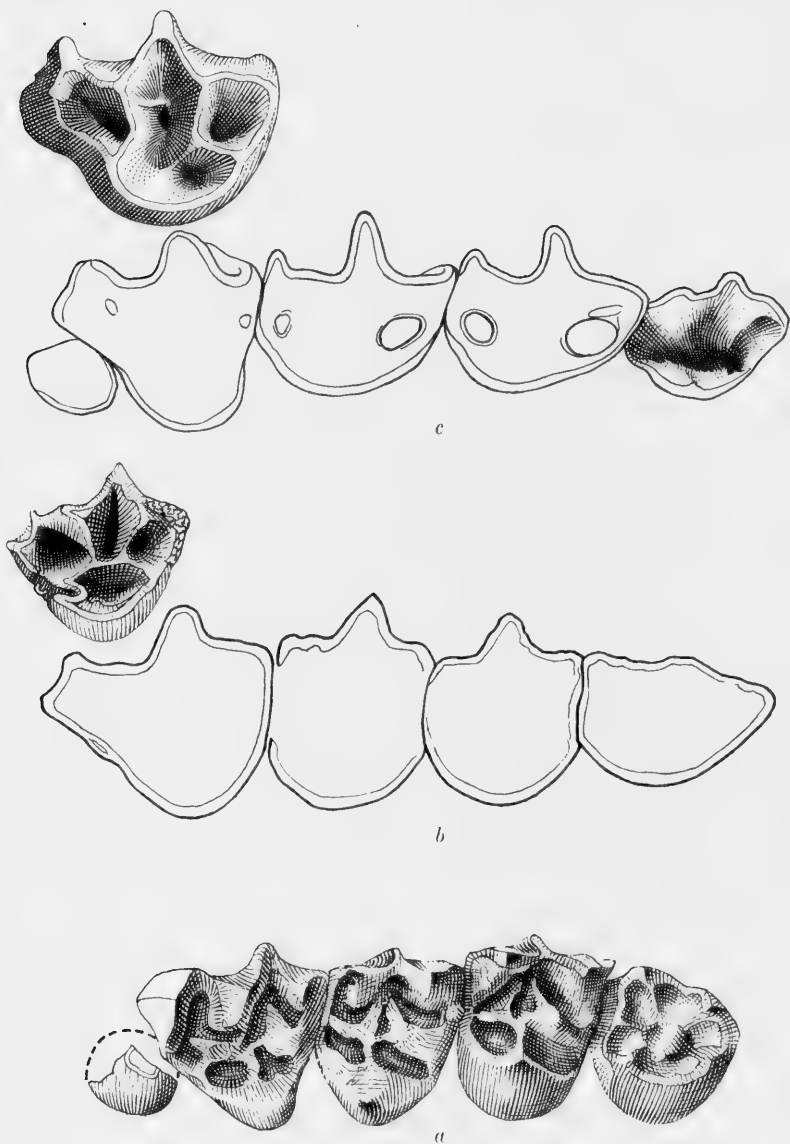
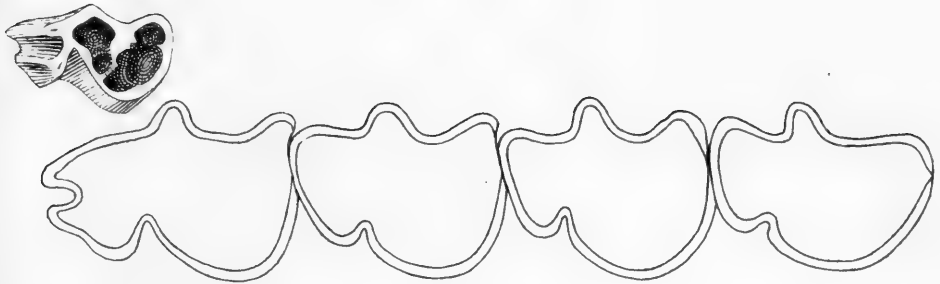
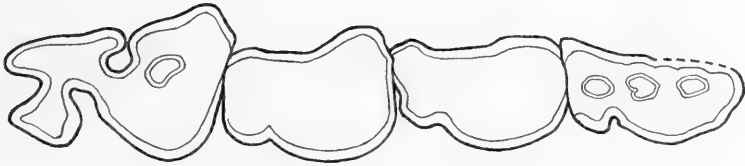


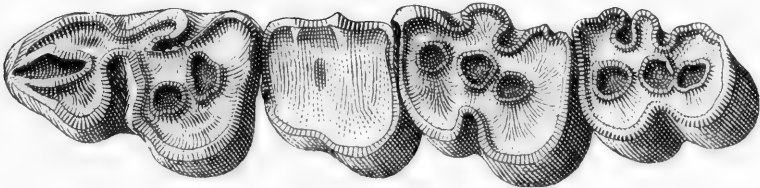
FIG. 7. Upper cheek teeth. a, *Meniscomys hippodus*, A.M. No. 6965; $\times 10$. b, *Liodontia alexandrae*, Univ. Calif. No. 31066; $\times 10$. c, *Aplodontia rufa* F.M. No. 41386; $\times 1$. Insets are unworn P^2 of *Liodontia* ($\times 10$) and *Aplodontia* ($\times 10$).



c



b



a

FIG. 8. Lower cheek teeth. a, *Meniscomys hippodus*, A.M. No. 6964; $\times 10$. b, *Liodontia alexandrae*, Univ. Calif. No. 11864; $\times 10$. c, *Aplodontia rufa*, F.M. No. 41386. Inset is unworn P_4 of *Aplodontia*.

Unfortunately no intermediate form between *Meniscomys* and *Liodontia* is known. However, the unworn P^4 of the latter genus displays a pattern that is amazingly like that of *Meniscomys*. The same progressive trends by which *Meniscomys* is advanced over *Eohaplomys* are carried further in *Liodontia*. P^4 is very high-crowned and rootless (at least in little-worn teeth). The cusps and basins are located as in *Meniscomys*. The cusps are hardly individual units, however, as the connecting ridges are elevated to the height of the cusps themselves. The styles are somewhat more prominent than those of *Meniscomys* and are more constricted. The antero-internal lake is opened anteriorly by the reduction of the cingular ridge that bounds it. The antero- and postero-external lakes are deepest and (as in *Aplodontia*) are the last to disappear with wear.

P^4 of *Aplodontia* does not differ greatly from that of *Liodontia*, but the small differences that do exist are significant. In the living genus the wall between the transverse-median and the postero-internal basins has been lost. The antero-internal basin too has completely disappeared through the loss of the bounding antero-internal cingular ridge. Thus P^4 of *Aplodontia* has only three completely enclosed lakes; the transverse-median plus the postero-internal, and the two external ones. By the loss of the antero-internal cingulum the protoconule is brought to the margin of the tooth. The fact that *Liodontia* approaches *Aplodontia* in the incipient loss of lakes indicates that the condition represented in the Tertiary genus was a step also attained in the development of the *Aplodontia* pattern, in spite of the probability that the genera are not on the same direct line.

In general the evolutionary course followed by the upper molars was much like that of P^4 . The basic structure of the molars differs from that of P^4 in the absence of a cuspsate parastyle. In the primitive members of the group there are five lakes, as in P^4 , bounded similarly by cingular ridges and ridges between cusps. There is a strong mesostyle and a much weaker parastylar column. As with P^4 the principal progressive change is in increased hypsodonty. There is also a progressive tendency toward transverse constriction of the individual teeth, more so in the posterior than in the anterior molars. The transverse-median lake exists throughout the series and is present with little modification in *Aplodontia*. The two anterior and two posterior lakes are brought progressively closer together by constriction of the teeth and in *Aplodontia* these lakes are either united or separated by a thin wall. The depth of the

lakes does not increase as the teeth become more hypsodont; thus they disappear very early in the life of the individuals.

The lower molars of *Aplodontia* differ from those of *Liodontia* in two principal characters. There is less reduction of the protoconid (hence also of the fold between protoconid and hypoconid). Of perhaps more significance is the presence of a prominent internal, median style which does not occur (or only on slightly worn teeth) in *Liodontia*.¹ In slightly, and only moderately worn teeth the metaconid and entoconid also project internally which, with the median style, makes three sharp angles on the internal border of the molars. It is probable that the absence of these styles in *Liodontia* represents the primitive condition and that in its development *Aplodontia* went through the stage represented by *Liodontia*, at least in this character. The further reduction of the protoconid in *Liodontia* seems to be a condition more specialized than that found in *Aplodontia* and for this reason the Tertiary genus can hardly be ancestral to the latter.

The greatest change in the lower cheek teeth from *Eohaplomys* to *Aplodontia* is, as in the uppers, in progressive hypsodonty. $P_{\frac{1}{4}}$ of *Meniscomys hippodus* is rather elongated antero-posteriorly. Anteriorly, a deep re-entrant is formed between spurs extending forward from the metaconid and protoconid. Posterior to the metaconid is a metastylid which projects postero-internally. On either side of the metastylid is a re-entrant valley: the anterior one, rather shallow, between the metaconid and metastylid and the posterior one, much deeper, between the metastylid and entoconid. The protoconid is separated from the hypoconid (and trigonid from talonid) by a deep valley extending two-thirds of the way across the tooth. In the talonid are two isolated lakes.

Except in its much more hypsodont condition, $P_{\frac{1}{4}}$ of *Liodontia* does not differ greatly from $P_{\frac{1}{4}}$ of *Meniscomys*. The anterior re-entrant is present but is not as deep as in *Meniscomys*. The antero-internal re-entrant is reduced so that there is only a slight concavity anterior to the metastylid. The postero-internal re-entrant is pinched off by a forward expansion of the entoconid, forming a lake which is open internally in unworn teeth. One lake is present in the talonid in a moderately worn specimen but two were probably present in a less worn tooth. The trigonid is somewhat broader than that of *Meniscomys*.

¹ Though usually referred to as the mesostylid this style is actually modified from the cusp I have interpreted as the metastylid. Whether it should be called mesostylid or metastylid is of no great importance.

The only important change in $P_{\bar{4}}$ between *Liodontia* and *Aplodontia* is the complete isolation in the latter of the main internal re-entrant. Apparently the wall between the two talonid lakes has broken down so that the entire talonid is occupied by a single large basin. In an unworn $P_{\bar{4}}$ of *Aplodontia* a slight enamel ridge partially dividing the basin into two lakes probably represents a remnant of this wall. These lakes, of course, disappear with slight wear.

The lower molars of *Meniscomys* are based on the primitive tribosphenic structure. The paraconid is lost. Of the four original cusps remaining (protoconid, metaconid, hypoconid, and entoconid), the metaconid is the highest. It is internal and slightly anterior to the protoconid. Behind the metaconid, and connected with it by a ridge, is a metastylid of the same size and height as the hypoconid and entoconid. A spur runs antero-internally from the rather large, V-shaped protoconid to the anterior base of the metaconid. A second ridge runs internally from the protoconid to the center of the tooth, then turns postero-internally to join the metastylid. Between and external to the metastylid and metaconid is a deep depression which connects with a somewhat shallower fossa between the protoconid and metaconid. The hypoconid is more U-shaped than the protoconid. Between these two cusps is a deep fold extending nearly to the center of the tooth. A ridge extends antero-internally from the hypoconid and joins the crest connecting the protoconid and metastylid. From the middle of this ridge a branch extends to a slight swelling on the posterior branch of the tooth. This swelling probably represents the hypoconulid. Between the last-mentioned ridge and the hypoconid is a lake. The entoconid, connected by a posterior ridge to the hypoconulid and hypoconid, is well separated from the metastylid by a deep internal re-entrant which divides the talonid from the trigonid. A spur runs antero-externally from the entoconid to connect with a ridge between the hypoconid and the posterior border of the trigonid.

Unfortunately, the detailed character of the lower molars is lost so early in life in *Liodontia* that the minor changes in crown structure cannot be traced. However, the more important changes are clear, and that the *Liodontia* molar is readily derived from that of *Meniscomys* cannot be doubted. The lower molars of *Liodontia* differ from those of *Meniscomys* in reduction of the protoconid (which causes the fold between the protoconid and hypoconid to become more shallow), reduction in depth of lakes (so that they disappear very early in life), and reduction or loss of internal re-entrant dividing the

talonid from trigonid. Of course, the teeth of *Liodontia* are much more hypsodont.

EVOLUTION OF MYLAGAULID DENTITION

The initial steps in the evolution of the Mylagaulidae were probably the same as in the Aplodontidae. As far as dental structure is concerned, *Meniscomys* could serve as an ancestor of both families. Judging from the structure of *Promylagaulus* and from its geologic

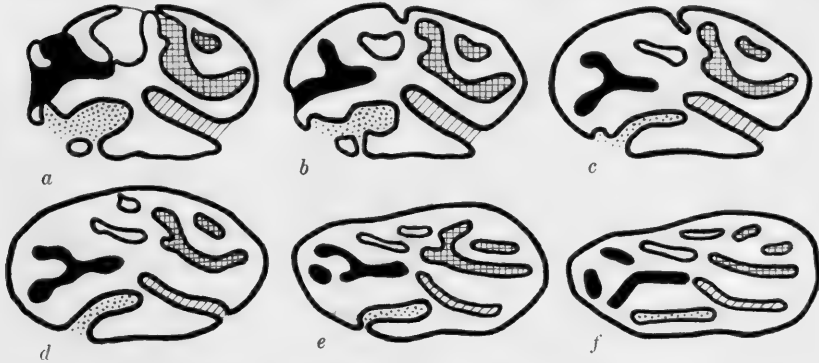
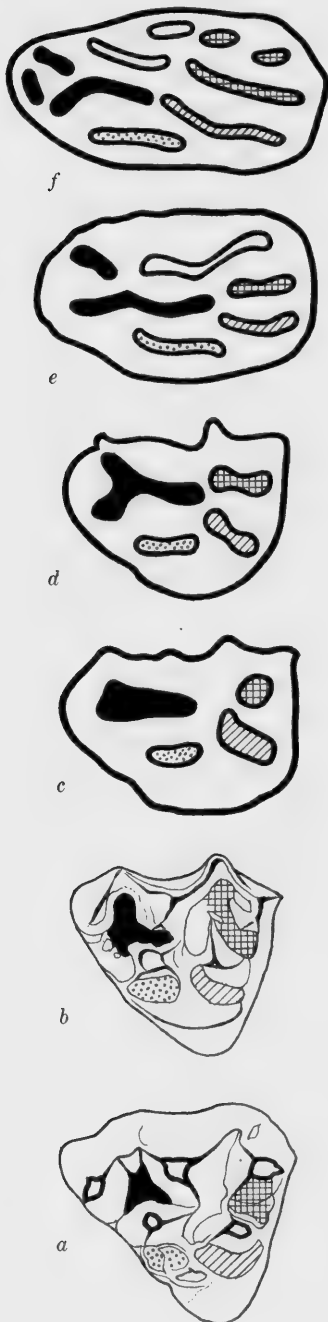


FIG. 9. *Mylagaulus* cf. *monodon*. Serial sections of P^4 showing successive stages of wear. Origin of lakes in worn tooth indicated by shading.

age, it would appear that this genus originated from some member of the aplodontid stock which, if not actually *Meniscomys*, was a form very close to it.

P^4 of *Promylagaulus* had advanced over that of *Meniscomys* primarily in attaining greater relative size, in becoming more hypsodont, and in having lost the transverse-median basin. Perhaps this latter basin is present in the unworn tooth of *Promylagaulus* but at least it did not deepen as the tooth increased in hypsodonty as the other basins did. The resulting pattern is one in which there are four lakes (in a worn tooth) almost certainly homologous with the antero- and postero-external and antero- and postero-internal basins of *Meniscomys*. The external styles of the only known specimen are rather low but this is undoubtedly due to heavy wear.

P^4 of *Mylagaulodon* is much larger and much more hypsodont than in *Promylagaulus*. In crown pattern it is much like that of the latter genus but the antero-external lake has an elongate antero-external projection which gives it the appearance of a horizontal Y. This extension is important as it is retained (with modification) in



later mylagaulids. The external styles are still well developed in this genus.

The crown pattern on P^4 of all the middle Miocene mylagaulids I have seen consists of six lakes, more elongate and better aligned antero-posteriorly than those of *Mylagaulodon*. The extension or projection of the antero-external lake is separated and has become an individual lake. The other new lake to appear is postero-external. I believe, judging from sections I made of *Mylagaulus* cf. *monodon*, that this lake is a portion of the original postero-external lake. This is not certain, however, as it may have originated as an invagination from the external wall of the tooth.

The Pliocene mylagaulids, as exemplified by specimens referred to *M. monodon* from Big Spring Canyon, may have as many as ten lakes in a well-worn P^4 . If a heavily worn tooth is compared with the more primitive types it is impossible to homologize the lakes. However, by making serial sections of an unworn tooth it has been possible to determine the homologies of nearly all the lakes with considerable certainty. This is best understood by referring to figures 9 and 10. The only point of doubt is the origin of the two small lakes (one in unworn teeth) left in white. Either they are "buds" of the antero-external lake, or they are closed invaginations from the external wall of the tooth.

FIG. 10. P^4 of a, *Haplomys*; b, *Meniscomyx*; c, *Promylagaulus*; d, *Mylagaulodon*; e, *Mesogaulus* cf. *pristinus* (middle Miocene); and f, *Mylagaulus* cf. *monodon* (early Pliocene).

It is more difficult to work out the details of development of the upper molars. The crown characters are lost with relatively little wear and sufficient unworn teeth are not available. As the premolar grew disproportionately large, the molars became reduced. The first molar became progressively compressed antero-posteriorly and by mid-Miocene was present only in young individuals. By Pliocene time this tooth had become almost entirely lost. In one specimen of *Mylagaulus* cf. *monodon* from the lower Pliocene Big Spring Canyon

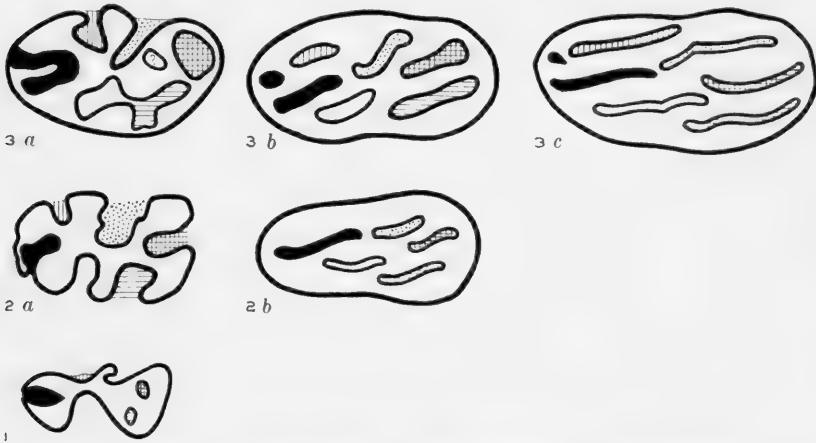


FIG. 11. P_4 of 1, *Meniscomys*; 2a, b, *Mesogaulus* cf. *pristinus*; and 3a, b, c, *Mylagaulus* cf. *monodon*, showing supposed structural development of pattern and successive stages of wear. Shading indicates homologous lakes.

(F.M. No. P15793) an M_1 exists, but this tooth is not present in much younger specimens from the same locality. In contrast with P_4 , the molars apparently became progressively more simplified.

Because lower premolars of *Promylagaulus* or *Mylagaulodon* are not known it is best to discuss first the molars, which are known from the unworn teeth in nearly every stage of evolutionary development.

The referred specimen of *Promylagaulus riggsi* (American Museum No. 10824) differs from *Meniscomys* in several molar characters, all of them progressive toward *Mylagaulus*. The molars are much more hypsodont. The external valley between the protoconid and hypoconid has become shallow. Internally the entoconid has migrated forward to lie close to the metastylid, cutting off the internal re-entrant and producing, with slight wear, an isolated lake. Two lakes are still present in the trigonid, but in the talonid, due to the absence of the ridge running forward from the hypoconulid,

the two lakes found in *Meniscomys* are united. However, this last character cannot be regarded as significant because the ridge between the talonid lakes is present in some specimens of *Mylagaulus* and absent in others belonging to the same species.

The differences between the lower molars of *Promylagaulus* and *Mylagaulus* are not great. In the latter genus they are more hypsodont and are smaller, relative to $P_{\frac{1}{4}}$. The lakes are somewhat better defined in young specimens of *Mylagaulus* but usually are of the same number and occupy the same relative positions as those of *Promylagaulus*.



FIG. 12. $M_{\frac{1}{4}}$ of
a, *Meniscomys*;
b, *Promylagaulus*;
and c, *Mylagaulus*.

Knowledge of the changes which take place in the lower molars permits a probably accurate deduction of the details in the evolution of $P_{\frac{1}{4}}$ between *Meniscomys* and *Mylagaulus*. In *Meniscomys*, $P_{\frac{1}{4}}$ is built on much the same plan as the molars. In the trigonid a deep re-entrant is formed between the spurs running forward from the metaconid and protoconid. Internally, between the metaconid and metastylid is a shallow valley which may be homologous with the internal lake in the molar trigonid. The external and internal re-entrants (between the talonid and trigonid) are present, as in the molars. Two lakes are again present in the talonid, as in the molars. Primitive species of *Mylagaulus*¹ have five lakes in $P_{\frac{1}{4}}$ that are sufficiently deep to persist in worn teeth: anterior, median-external and -internal, and postero-external and -internal. The anterior one is certainly homologous with the anterior re-entrant valley of *Meniscomys*, the median-external with the external re-entrant, the median-internal with the internal re-entrant and the two posterior ones with the two talonid lakes of *Meniscomys*. In the Pliocene form, *M. monodon*, six lakes are well developed. The extra lake is formed by the deepening of the valley between the metaconid and metastylid. In addition to these six rather large lakes is a small one which splits off from the anterior one but which is apparently constant and extends deep into the crown. The lake homologies in $P_{\frac{1}{4}}$ of the mylagaulids are shown in figure 11.

Sufficient material is not at hand to carry this study beyond the broader limits of mylagaulid development. As Wilson (1937) has

¹ These primitive species represent the genus *Mesogaulus* as defined by Cook and Gregory (1941).

pointed out it would be particularly desirable to undertake a study of the several genera and species of the late members of the family to determine their inter-relationships and the variation within and between the taxonomic units. If, as seems likely, there is considerable uniformity within the genera and species, the complicated pattern of $P\frac{1}{4}$ would facilitate such a study because differences of taxonomic importance might readily be ascertained. Because of the rapid and great change of pattern resulting from wear it will be essential to have sufficient material for making serial sections.

STRATIGRAPHIC RELATIONSHIPS OF APLODONTOIDS

It is surprising to find so many forms within the John Day representing such widely separated structural stages. This is true not only of the aplodontoid rodents but of many other mammalian groups as well. It is known that late Oligocene and early Miocene fossils occur in the John Day and it is entirely possible that *Haplomys* and *Meniscomys* are not contemporaneous but that the former is actually stratigraphically older as well as more primitive structurally. Even more surprising is the occurrence of *Mylagaulodon* as a possible contemporary of *Meniscomys*. The specimen of *Mylagaulodon* from the upper Rosebud is definitely later than lower Rosebud *Promylagaulus*, as its structure indicates it should be. It is most unfortunate that definite stratigraphic records are not available for the types from the John Day. In other regions the phylogenetic development of a group usually ties in rather well with its stratigraphic distribution. I should not be surprised if this would also be true of the John Day species if adequate data on the occurrence of the specimens were available.¹

ORIGIN OF THE APLODONTOIDEA

Stock (1935) described *Eohaplomys* from the Sespe Eocene as an ancestor of *Allomys* (including *Meniscomys*) and *Haplomys* and hence of all aplodontoids. It seems reasonable that *Eohaplomys* did occupy such a position. Going back in time from the late Eocene there is no rodent that seems to have characters that might be considered ancestral for the group. The similarity in basic structure, however, between *Prosciurus* and *Eohaplomys* suggests that the two genera have a common ancestor. The dentition of *Prosciurus*

¹ Dr. Lewis Gazin recently has informed me that the type of *Mylagaulodon angulatus* was found in some local deposits lying between the true John Day and the Mascall. Hence this specimen may well be of post-John Day age.

is structurally more primitive than that of *Eohaplomys*, particularly in the development of the paramere. I believe that the Aplodontioidea may well have originated as a branch of the *Prosciurus* stem, some time during the early or middle Eocene. To what ischyromyoid family *Prosciurus* belongs¹ is unknown, as no Eocene form has been found that might be ancestral to it. There seems to have been some evidence for Matthew's regarding *Prosciurus* as an ancestor of the aplodontoids. However, had *Eohaplomys* been known at that time he would undoubtedly have altered his views accordingly.

TAXONOMY

When the pertinent phylogenetic facts are known, the problem of classifying the incipient branches of a dichotomous pattern of evolution becomes an academic matter and must be settled arbitrarily. The aim, however, should be to denote relationships as clearly as possible in a manner no more complex than the facts.

Wood's (1937) reasons for recognizing the suborder Protrogomorpha seem valid. "It seems to be impossible to include these families² in any of the three generally accepted suborders. They are certainly not 'Histricomorphs'; they have practically nothing in common with the 'Myomorphs' and very little to do with the 'Sciurormorphs.' Neither can I see any justification for associating them with the Dipodidae. It is obvious, therefore, that they must represent an independent group, for which Zittel's term is available."

Actually there are no characters by which the Aplodontioidea may be separated from the Ischyromyoidea. Wood's statement that the cheek-tooth pattern of the Ischyromyoidea is based on transverse lophs, rather than on antero-posterior ones as in the Aplodontioidea, does not apply when the primitive members of the group are considered. Primitive aplodontoids grade imperceptibly into forms which are typically ischyromyoid in every respect. This is indicated by Stock's (1935) reference of *Eohaplomys* to the Ischyromyidae, although he recognized its relationships to the aplodontids.

The relationships of the aplodontoid families are known. The so-called ischyromyoids, however, are quite diversified and the inter-relationships of the families are not known. Some authors

¹ Since *Prosciurus* cannot be a descendant of any known sciuravid, its reference to that family (Wood, 1937) must remain tentative.

² Paramyidae, Sciuravidae, Ischyromyidae, Cylindrodontidae, (?)Protoptychidae, Aplodontidae, and Mylagaulidae.

have recognized but one major group for the inclusion of all these (Winge, 1924) while others would recognize the two (Wood, 1937). The Ischyromyoidea can hardly represent a natural group, and seems to be most useful as a basket in which to throw those primitive rodents which do not give rise to later types or those whose relation-

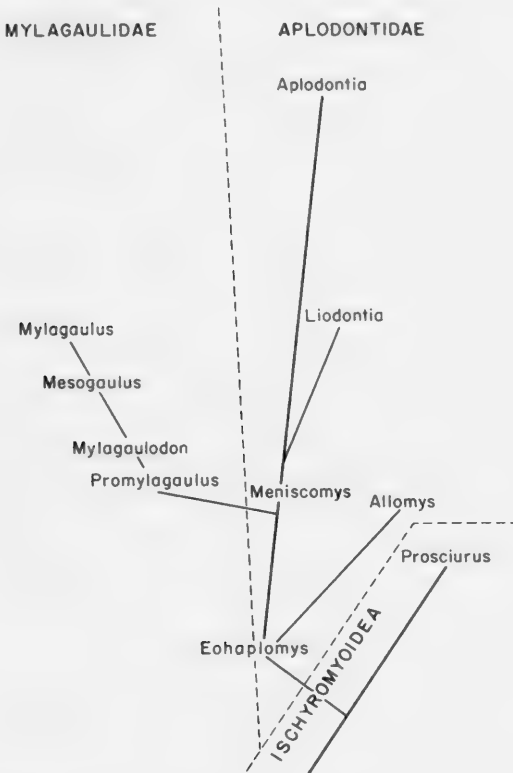


FIG. 13. Supposed relationships of the apodontoid genera.

ships are unknown. When the early history of other rodent groups is known their primitive ancestors will undoubtedly fall within the Ischyromyoidea as diagnosed. However, when any one of those primitive forms becomes sufficiently differentiated to be recognized as an ancestor of a particular later group, it may with justification be included in the group to which it is ancestral. Thus the relationship of *Eohaplomys* may be best implied if the genus is classified as a primitive apodontoid, although its characters are not such as to be distinct diagnostically from the Ischyromyoidea.

Within the Aplodontoidea two major and at least two minor lines of descent may be recognized. The more or less direct line from *Eohaplomys* to *Aplodontia* represents the basic stock and is of family rank. A major offshoot from the Aplodontidae is represented by the series from *Promylagaulus* to *Mylagaulus*, which because of its extreme divergence and specialization also should rank as a family, the Mylagaulidae. Smaller side branches which are closely related and parallel to the parent stock are represented by *Allomys* and *Liodontia* and probably *Haplomys*. They are not sufficiently divergent to rate as more than aberrant genera of the family Aplodontidae.

Thus the classification of the Aplodontoidea, according to my interpretation, should be as follows:

Suborder PROTROGOMORPHA	
Superfamily APLODONTOIDEA	
APLODONTIDAE	MYLAGAULIDAE
<i>Eohaplomys</i>	<i>Promylagaulus</i>
<i>Haplomys</i>	<i>Mylagaulodon</i>
<i>Allomys</i>	<i>Mesogaulus</i>
<i>Meniscomys</i>	<i>Mylagaulus</i>
<i>Liodontia</i>	
<i>Pseudaplodon</i>	
<i>Aplodontia</i>	

The relationships of these forms are best shown by the chart on page 25. It is necessary to stress the point that *Mylagaulodon* and *Meniscomys* are both from the John Day (see footnote on p. 23), and while structurally the two genera seem to bear ancestor-descendant relationships, there is a possibility that they are contemporaries.

DISTRIBUTION

The past and present distribution of the Aplodontidae is unique among mammalian families in that the range of *Aplodontia*, the only living member of the family and universally conceded to be the most primitive of living rodents, is limited to a small strip along the west coast of the United States. Not only is the range of the living genus thus limited, but as far as is known, every fossil form which might be ancestral to it also comes from the same general area. Such distribution cannot be explained by the principles of mammalian dispersal so ably advocated by Matthew (1915). Of *Aplodontia* Matthew said: "A marked exception to the rule is seen in the survival in the western Sonoran sub-region of *Aplodontia*,

the most primitive living sciurormorph in several respects. I have no explanation to offer of this anomaly, save that we have not yet balanced properly the essential qualities of progressiveness among Rodentia."

For broad application Matthew's thesis can hardly be disputed, but as Dunn (1926) has pointed out, it is not complete and must be expanded to account for certain exceptions, of which *Aplodontia* is notable.

Mammalian evolution and migration, according to Matthew, were stimulated primarily by climatic or environmental changes. These changes appeared first in the Holarctic realm, at the center of distribution, and spread toward the temperate and tropical regions. Thus a race "should be at first most progressive at its point of original dispersal, and . . . continue this progress at that point in response to whatever stimulus originally caused it and spread out in successive waves of migration, each wave a stage higher than the previous one. At any one time, therefore, the most advanced stages should be nearest the center of dispersal, the most conservative stage farthest from it." There are many exceptions, but generally the peripheral members of a group are most primitive.

There appears to have been little or no change in the distribution of *Aplodontia* and its ancestors since late Oligocene time; and in further contrast to the usual condition the peripheral forms, *Pseudaplodon* and *Liodontia*, are in some respects even more specialized than *Aplodontia*.

The aplodontids present a picture exactly the opposite of that required by the Matthewsian hypothesis. The range now occupied by *Aplodontia* is apparently near the center of origin and distribution of the family. This is suggested by the occurrence of *Eohaplomys*, *Haplomys*, and *Meniscomys* near or within the present range of *Aplodontia*, and at no other place. The occurrence of *Pseudaplodon* in the early Pliocene of Mongolia and *Liodontia* in the mid-Miocene of southeastern Oregon and mid-Pliocene of Nevada suggests an early unsuccessful attempt to extend the range. Of particular significance is the fact that in the limited parts known, these peripheral genera are somewhat more specialized than *Aplodontia*. This is indicated by the reduction of the antero-external folds (between protoconid and hypoconid) of the lower cheek teeth, which cannot be a primitive character. These dental modifications suggest migration into a different environment for which they were adaptive changes. In other words, it is most likely that these most specialized aplodontids moved into a new habitat instead of having a new

habitat move in on them. This distribution cannot be accounted for by any climatic or environmental change at the center of dispersal.

The environmental conditions along the west coast might have been quite stable during Tertiary time, at least sufficiently so that the aplodontids were able to maintain their range with relatively little structural modification. Those that migrated did so either because of population pressure or the inherent tendency of all animal life to expand. They were not successful in adapting themselves to new habitats, either because of harder environmental conditions or because of unsuccessful competition with better adapted forms. This apparently resulted in extinction of marginal forms and re-constriction of the family range to the original dispersal center.

The history of the Mylagaulidae, on the other hand, differs greatly. It appears that immediately after its inception the family spread to the Great Plains. In late Miocene and early Pliocene times its members are found in nearly every well-known fauna of the United States. This sudden expansion was probably due to the loss of some inhibiting factor, either structural or physiological, a change that permitted the group to occupy a much more extensive range than did the family from which it arose.

The above discussion is of necessity based largely on negative evidence, particularly the absence of ancestral aplodontids in regions outside the far west. I believe, however, that the faunae of the plains are sufficiently well known to warrant such a hypothesis.

MEASUREMENTS

(In millimeters)

	<i>Allomys cavatus</i> A.M. No. 6988	<i>Meniscomys hippodus</i> A.M. No. 6965	<i>Promylagaulus riggsi</i> F.M. No. P26255	<i>Mylagaulodon cf. angulatus</i> F.M. No. P26266
P ⁴ a-p.....	2.84	2.66	3.41	5.89
P ⁴ tr.....	2.80	2.43	2.60	4.40
M ¹ a-p.....	2.15	2.10	1.54	
M ¹ tr.....	2.80	2.35	2.25	
M ² a-p.....	2.10	2.10	1.84	
M ² tr.....	2.75	1.92	1.91	
M ³ a-p.....	2.10	2.10	1.30	
M ³ tr.....	2.47	1.76	1.52	
	A.M. No. 6988	A.M. No. 6964	A.M. No. 10824	
P ₄ a-p.....	3.45	3.45		
P ₄ tr.....	2.31	2.31		
M ₁ a-p.....	2.19	2.05	2.38	
M ₁ tr.....	1.61	1.93	1.87	
M ₂ a-p.....	2.11	2.78	2.00	
M ₂ tr.....	1.63	1.95	1.77	
M ₃ a-p.....	2.41	2.40	2.40	
M ₃ tr.....	1.68	1.76	1.25	

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