· 59.9, 32H:01

PHYLOGENY OF THE HETEROMYID RODENTS

By ALBERT ELMER WOOD

The Family Heteromyidæ includes a number of recent forms from North America, and several fossil forms, from the continental Tertiary beds of the western United States, ranging from the Oligocene to the Pliocene. The group has been rather neglected by palæontologists, due, probably, to the rarity of the fossil forms, and to their small size, the former probably being a function of the latter. A collection of rodents from the Deep River beds of Montana, which was recently turned over to me for study by Dr. C. C. Mook, contains an undescribed heteromyid which forms an important link between the earlier and the later members of the family.

The genera included in this family are: *Perognathus*, the pocket mouse; *Heteromys* and the very closely related form *Liomys*, the spiny pocket mice; *Dipodomys*, the kangaroo mouse; and *Microdipodops*, the pigmy kangaroo mouse, all living forms, found occasionally as fossils; *Diprionomys* from the Thousand Creek Pliocene of Nevada; *Peridiomys* from the Snake Creek Pliocene of Nebraska; **Mookomys**, new genus, from the Deep River Miocene of Montana, and from ?Colorado; and *Heliscomys* from the White River Oligocene of Colorado. These genera are discussed below in their stratigraphic sequence.

Order **RODENTIA**

Suborder **SCIUROMORPHA**

Family **Heteromyidæ**

$I\frac{1}{1}$, $C\frac{0}{0}$, $P\frac{1}{1}$, $M\frac{3}{3}$. Infraorbital foramen at the end of a long canal. Frontal without postorbital processes. Skull not of a fossorial character. Zygoma slender. Upper incisor sometimes grooved (in *Perognathus*, *Dipodomys*, *Mookomys* and *Microdipodops*, but not in *Heteromys* or *Liomys*). Teeth brachydont and bunodont in the Oligocene, becoming progressively more hypsodont and, especially, more lophodont. Range, western United States and Central America, and a small portion of southern British Columbia. Known time range, Oligocene to Recent.

HELISCOMYS Cope, 1873

White River Oligocene of Colorado. A small form, about the size of the recent pocket mouse, *Perognathus*, with a primitive dentition, fairly close to that of the Eocene stem rodent, *Paramys*. The tooth pattern of *Heliscomys* is easily derivable from a tritubercular type. There is no trace of lophs or crescents, but merely cusps. P_4 is tricuspidate, M_{1-3} quadritubercular, with a broad cingulum along the buccal margin. The upper dentition and the skull are unknown.

Heliscomys vetus Cope

Cope, 1873, and Cope, 1884, Pl. LXV, figs. 14, 16, 16a and 17.

TYPE.—Amer. Mus. No. 5461, a lower jaw, containing M_{1-2} left, from the White River Oligocene of Colorado.

PARATYPE.—Another lower jaw, Amer. Mus. No. 5462, containing P_4–M_1 left, from the same horizon.

This is the only known species of the genus. The teeth are bunodont and brachydont. P_4 is triangular, with the apex at the postero-external corner, and has but three cusps. If *Heliscomys* was descended from *Paramys* or a closely related form, as seems probable, the ancestral form had a protoconid, metaconid, hypoconid and entoconid on P_4. As there are, however, but three cusps on P_4 of *Heliscomys*, one of these must have been lost, and inspection of the specimen indicates that this was the metaconid. This explanation of the three cusps as the protoconid, hypoconid and entoconid, seems much more likely than that the tooth is primitive, and that the three cusps are protoconid, paraconid, and metaconid, as, in that case, there could be no known ancestors to *Heliscomys*, and it would be widely separated from the Oligocene rodents, which seems very improbable.

M_1 is essentially what would be expected in the lower teeth of an unspecialized Oligocene rodent, i.e., the pattern is dominated by four

subequal cusps arranged in a square. These are the protoconid, meta-
conid, hypoconid and entoconid. There is a small cusp, which may be
called the entoconulid, on the anterior side of the entoconid, in the
median valley. This valley is slightly deeper than are the antero-
posterior valleys, and opens unimpeded, at its lingual end. There is a
broad external cingulum running the entire length of the tooth. There
are slight elevations of this, which may be termed protostylid and hypo-
stylid, anticipating the condition found in the Miocene **Mookomys
altifluminis**, to be described below. Both of these stylids, but particu-
larly the hypostylid, are so small as to be almost indistinguishable.
There is an anterior cingulum, which may connect with the protoconid,
in which case it would perhaps be the remains of the paraconid.
M_2 is indistinguishable from M_1. The molars of the holotype are rhom-
bic; that of the paratype is quadrate. The teeth are two-rooted. The
incisors are long and slender.

These molars, then, could be readily derived from some form such
as an early Eocene paramyid, in which the lower molars were quad-
ritubercular, but which did not have the cingulum. The premolar is
different from that of any known paramyid, as these are all quadri-
tubercular, whereas *Heliscomys* is tritubercular, which is doubtless a
more specialized condition, due to reduction.

Heliscomys, however, could not have been descended from *Gymnop-
tychus* (*Adjidaumo*) as has been suggested, since, in this last form, the
hypoconids are developing into crescents, the posterior horn of which
connects with the entoconid, while the anterior runs forward on the
posterior side of the median valley. The premolar is quadritubercular.
There is no trace of an external cingulum on the molars. The teeth are
quite lophodont, indicating a stage of evolution further advanced than
that reached by *Heliscomys*, even though *Gymnoptychus* comes from the
Lower Oligocene Titanotherium beds and *Heliscomys* from the Middle
Oligocene. The characters of *Gymnoptychus* warrant its inclusion in the
Geomyidæ rather than in the Heteromyidæ. Nevertheless, it is doubtless
related to *Heliscomys*, the two probably being descended from a common
ancestor, perhaps in the Upper Eocene. Although in many respects
Heliscomys is more primitive than *Gymnoptychus*, yet there are enough
differences to indicate that *Heliscomys* could not have been ancestral to
Gymnoptychus.

MOOKOMYS, new genus

The genotype is **Mookomys altifluminis,** new species, described below. P_4 is quadritubercular. M_{1-3} are bilophodont, each loph formed of three cusps in a transverse row, the outer cusp of each loph being derived from the external cingulum, which is so well developed in *Heliscomys.* The antero-posterior valleys between the cusps of each loph, draining into the median valley, are much shallower than are those of *Heliscomys,* and become progressively shallower in the later species, approaching the conditions found in *Perognathus.* The teeth become progressively hypsodont. The upper incisor is grooved on its anterior face. The external cingular cusps are more elevated in the later species. *Mookomys* differs from *Perognathus* in the more primitive characters of
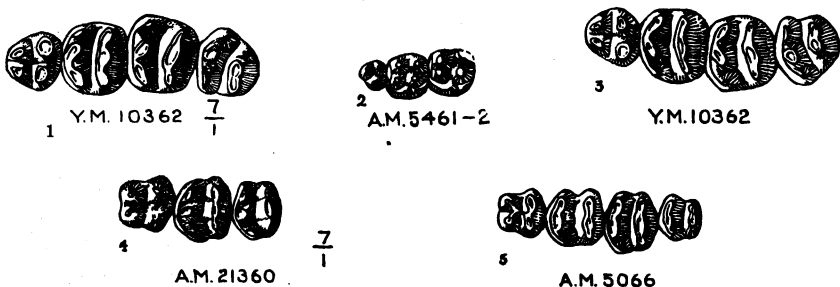

Fig. 1.   *Mookomys parvus.* P_4-M_3 right. Y. M. No. 10362.

Fig. 2.   *Heliscomys vetus.* P_4-M_2 left. Composite of A. M. No. 5461 and No. 5462.

Fig. 3.   *Mookomys parvus.* P_4-M_3 right, reversed, so as to correspond with the other figures. Y. M. No. 10362.

Fig. 4.   *Mookomys altifluminis.* P_4-M_2 left. A. M. No. 21360.

Fig. 5.   *Perognathus fallax.* P_4-M_3 left. A. M. No. 5066.

The lingual surfaces in Figs. 2-5 are toward the top of the page.   All figures seven times natural size.

P_4, which is quadritubercular in the fossil genus and bilophodont in the living one. In *Perognathus,* the premolar is fully molariform. Also, the cusps of the molars of *Mookomys* are distinct for much of the animal's life, which is not the case with *Perognathus.* Finally, the tibia and fibula of *Mookomys* are not ankylosed as are those of *Perognathus.*

Diplolophus parvus Troxell, which was referred to *Heliscomys* by Hay (1930), is much nearer to the type species of *Mookomys* than to that of *Heliscomys,* as the molars are definitely lophodont and the premolar is quadritubercular instead of tritubercular, and the species has for this reason been referred to *Mookomys.*

Mookomys altifluminis is made the genotype, rather than *M. parvus*, as the horizon of the former is definitely known, whereas that of the latter is highly speculative.   Moreover, the specimen of *M. altifluminis* is more complete, there being associated part of the skull and portions of the skeleton, as well as parts of both rami of the lower jaw, instead of being only a ramus of the lower jaw, as in the case of *M. parvus*.

The genus is named for Dr. C. C. Mook, who has very kindly allowed me to describe the rodents which he collected in Montana in 1925.

Mookomys parvus (Troxell)

TROXELL, 1923, Figs. 3–5.
SYNONYMY:
    Diplolophus parvus TROXELL, 1923.
    Heliscomys parvus HAY, 1930.
    TYPE.—Yale Mus. No. 10362, one ramus of the lower jaw, containing the incisor and P_4–M_3 right, perhaps from Colorado.

There is little real relationship between this species and *Diplolophus insolens* Troxell, the genotype, whose teeth are much more hypsodont, as well as more fully lophodont, and which has lost P_4.   In addition, the cusp pattern of the teeth is quite different in the two forms. The relationship of *Mookomys parvus* to *Heliscomys vetus*, as indicated by Hay, seems to be quite genuine.   This species, however, is more specialized than *H. vetus*, as two cusps, the protostylid and hypostylid, have been developed on the elevated external cingulum, from which they are differentiated, though slightly, leaving no doubt as to their mode of origin.   Moreover, the individual cusps are much less independent of each other than in *H. vetus*, and they are beginning to unite into lophs, due to the obliteration of the antero-posterior valleys.   The teeth are more hypsodont than in *H. vetus*.   These differences are those listed above as generic characters of *Mookomys*, and warrant its inclusion in that genus, rather than in *Heliscomys*.

P_4 is essentially quadritubercular, composed of four cusps.   If this form is descended from *Heliscomys*, as seems likely, the two posterior cusps would be the entoconid and the hypoconid.   Doctor Gregory suggested that the two anterior cusps are the protoconid and a pseudometaconid, developed, by splitting, from the protoconid.   The shape of P_4 in *M. parvus* and *M. altifluminis* is an indication of the correctness of this opinion, as the two anterior cusps are much closer together in *M. parvus* than they are in *M. altifluminis*, and the general appearance

of the former fits with its being derived from the tricuspidate *Heliscomys*. This is a considerable advance over the conditions in *Heliscomys*, but it is not as great a one as it would be if any other interpretation of cusps were used. The median valley is but little deeper than the antero-posterior ones. There is a small posterior cingulum. In M_1, the two stylids are present, though the protostylid is much lower than are the primitive cusps, having been only slightly worn before the death of the animal, which was fully adult. This cusp can easily be seen to be merely an expansion and further elevation of the external cingulum. The hypostylid shows a strong incipient tendency to fuse with the hypoconid. The external cingulum continues, anteriorly to the protostylid, and curves around to the anterior border of the protoconid. There is a well developed posterior cingulum. The structure of M_2 is almost identical with that of M_1. The protoconid is separated slightly from the elevated anterior portion of the cingulum by a shallow valley, and but little more wear would be required to cause the two to unite. The hypostylid is here very closely joined to the hypoconid. In M_3, the protoconid is similar to that in M_2. The protostylid, however, is not very well developed, being an elevated point on the cingulum, which is but little enlarged in diameter. The hypostylid is a very small cuspule on the postero-buccal surface of the hypoconid. It is much lower than are the other cusps, and would not be worn until the tooth was reduced almost to the roots. *Mookomys parvus*, then, is similar to *Heliscomys vetus*, but is definitely more specialized.   •

The horizon from which *Mookomys parvus* came is, unfortunately, not known. The original label and the Yale catalog give no information as to the date, locality, horizon, collector, or anything else. For this reason, any reference of this fossil to a given formation or locality must involve considerable doubt. *Diplolophus insolens*, Yale Mus. No. 10368, is from the White River of Colorado. As the catalog numbers of the two specimens are so nearly the same (10362 and 10368), it is probable that they were parts of the same season's collection. On the basis of this, Troxell describes *Mookomys* (*Diplolophus*) *parvus* as from the "Oreodon Beds of the Middle Oligocene, probably from Colorado." Since the catalog numbers were not given in the field, but after the specimens were in the Museum, the fact that the numbers were so close to each other does not prove that they were collected in the same locality, but, at most, only that they were sent in to the Museum together. As there are Miocene as well as Oligocene beds scattered throughout northeastern Colorado, *M. parvus* might as well have been from the former as

from the latter beds. Since, however, *M. parvus* is structurally so far advanced over *H. vetus* from the White River, and close to, but more primitive than, *M. altifluminis* of the Deep River, it is perhaps legitimate to guess that it may have been from the Pawnee Creek or Martin Canyon Lower Miocene beds, rather than from the Cedar Creek Oligocene beds. It would seem unlikely that two forms, so close together as are the two species of *Mookomys*, should be separated by the length of time from the Middle Oligocene to the Middle Miocene, and that two forms as distinct as *M. parvus* and *H. vetus* should be found in the same beds. If, however, *M. parvus* were from the Lower Miocene, there would be time intervals of about the right size, both below and above it, to account for its differences from *H. vetus* and *M. altifluminis*. Nevertheless, even if *M. parvus* were from the White River, it would still be morphologically an intermediate stage between an early heteromyid, almost identical with *Heliscomys vetus*, and the later members of the family.

Mookomys altifluminis, new species

TYPE.—Amer. Mus. No. 21360. Both rami of the lower jaw, with the posterior portions broken off, containing I_2, P_4, M_{1-2} left, I_2 right and the alveoli of P_4 and M_1 right, a fragment of the skull with I^2 left, and various portions of the skeleton, of a young individual.

Collected by Dr. C. C. Mook, August 16, 1925.

HORIZON AND LOCALITY.—Deep River beds, seven miles south of Logan, Montana.

DIAGNOSIS.—The specific characters, as far as determinable, are M_{1-2} made up of two lophs, which, in a young individual, are each visibly formed by the union of three cusps in a buccolingual row. Moderate wear would cause the disappearance of all trace of these cusps as individual entities. The stylids are of almost the same height as are the primary cusps. There is practically no trace of an external cingulum across the median valleys. The teeth differ from those of *M. parvus* in being much more lophodont, more hypsodont, and in having shallower antero-posterior valleys. The tibia and fibula are separate throughout, instead of being united distally as in *Perognathus*.

This species is evidently congeneric with *Mookomys parvus*. In spite of the incompleteness of the material, there are sufficient structural advances in this form over *Heliscomys vetus*, in both premolar and molars, to warrant its being made a new genus. Moreover, the fact that one is Deep River and the other White River gives corroborative support to their separation, as apparently no genera of mammals are known to extend, unchanged, through this period of time.

The teeth show a marked advance over *M. parvus* toward *Perognathus*. The cusps are much less distinct in *M. altifluminis*, a young individual with P_4 just beginning to be worn, than in *M. parvus*, an adult, whose teeth had been in use for some

time. This form, then, is a structural intermediate between *Heliscomys* and *Perognathus*, with *M. parvus* intercalated between *Heliscomys* and *M. altifluminis*.

The fragment of the skull contains part of the premaxillary and maxillary of the left side, and extends as far posteriorly as the end of the diastema. The upper incisor is very similar to that of *Perognathus fallax*, having about the same radius of curvature, being of about the same width, and likewise having a groove on the anterior surface. The extreme tip of the upper incisor is broken off. The diastema is of similar length in the two animals. The lower incisor is complete to its tip. Its radius of curvature is similar to that of *Perognathus*, but the portion of the tooth above the alveolus is much shorter in the fossil form.

P_4 shows a slight advance over that of *M. parvus* in specialization toward the *Perognathus* type. This tooth is formed by four subequal cusps, which have just begun to show wear on their tips. The pseudo-metaconid and protoconid are closer together than are the entoconid and hypoconid, and are slightly smaller. They are, however, farther apart than are the corresponding cusps of *M. parvus*. The median valley opens widely at its lingual end. Buccally, it is partially dammed by a small external cingulum. The anterior and posterior tributary valleys are slightly closed at their ends farthest from the median valley. There are two subcircular roots, one anterior and one posterior.

M_1 is divided into a well marked metalophid and hypolophid, with a deep median valley between them. The metalophid is somewhat higher than the hypolophid. Under each loph is a transversely elongate root, extending the entire width of the tooth. The metaconid forms the narrowest part of the triangular metalophid. It is marked off from the protoconid, at the stage of wear in the present individual, by a slight groove. Lateral to this is a well developed protostylid, which is, however, a shade lower than the other cusps of the metalophid, so that, in the stage of wear that the tooth has reached, this cusp shows only very slight traces of wear. The enamel forms a continuous crest along the anterior margin of the metalophid. The three cusps of the hypolophid are more nearly equal in size than are those of the metalophid. The hypoconid is the largest, the entoconid the next, and the lateral cusp, the hypostylid, the smallest. The hypolophid is bounded posteriorly by a continuous enamel crest, which is not, however, as straight as is the crest of the metalophid, being indented between the cusps. The median valley is deep and opens widely, both buccally and lingually, with only a very slight trace of an external cingulum. The side valleys are good examples of "hanging valleys," entering well up on the sides of the median valley.

M_2 is quite similar to M_1, but there is more difference in height between the metalophid and hypolophid than in M_1. The antero-posterior diameter of the tooth is considerably less. The metalophid is more nearly of a uniform width, instead of being expanded in the region of the protoconid, as it is in M_1. There is no external cingulum at the buccal end of the median valley.

The extension of the nasals anterior to the edge of the alveolus of the incisor is quite similar in its proportions and size to that in *Perognathus*. Associated fragments of the skeleton are an astragalus and calcaneum, part of the pelvis, the head and shaft of both humeri, the distal end of the femur, portions of the tibia and fibula, several metapodials, a dorsal vertebra, two caudal vertebræ, and some fragments.

The tibia and fibula were separate for their entire length, instead of being co-ossified in the distal half, as are those of *Perognathus*. Other than this, the skeleton, so

far as it is known, is essentially similar to that of *Perognathus*. These parts of the skeleton would indicate that *Mookomys* was a quadrupedal, swift-running animal, similar to *Perognathus*, which had not yet begun to specialize on the line leading to the kangaroo rats, and which probably could not run on its hind legs for even the few steps that *Perognathus* sometimes does.

It is possible that *M. altifluminis* is directly descended from *M. parvus*, as the tooth patterns of the two forms are so closely alike, the differences consisting largely of a few changes along the lines already laid down by the evolution of *M. parvus* from *H. vetus*. The chief reason for doubting whether this could be a direct phylogenetic sequence is that *M. parvus* is slightly larger than *M. altifluminis*. There is a general assumption that in any phylogenetic line, the ancestral forms are always either the same size as the descendants, or else of smaller size. In general, this is likely to be correct. But I do not believe that there is any innate force causing such an effect, but merely that the forms that have been studied the most, and which are the most fully known, are those that are the largest. As the modern mammals have all been derived from small ancestors in the Eocene, these well-known forms all show a derivation from smaller ancestors. Certainly there is no genetic reason why the descendant might not be smaller than the ancestor. Moreover, the difference is so small as to be almost negligible, and might be merely an individual variation. There is a small hypostylid on M_3 of *M. parvus*, which is not present in *Perognathus fallax*. This may indicate that *M. parvus* is slightly off the direct line to *Perognathus*. In any case, however, it does not make much difference whether *M. parvus* is really the ancestor of *M. altifluminis* or is merely so closely related to its ancestor as to be practically indistinguishable from it. In *M. parvus*, M_2 is slightly larger than M_1. In both *M. altifluminis* and *Perognathus*, the reverse is the case.

PERIDIOMYS Matthew

Peridiomys rusticus Matthew

MATTHEW, 1924, Fig. 9.

The type, Amer. Mus. No. 18894, from the Lower Snake Creek Pliocene of Sioux County, western Nebraska, is the lower jaw containing P_4-M_2 left, of a member of this family, related to *Mookomys* and *Perognathus*, but not intermediate between the two. The teeth are more hypsodont than in *Perognathus*, and the median valley is shallower, particularly on the lateral side of the tooth. In this respect, *Peridiomys* is more like *Heteromys*, to which it may be ancestral. The teeth are considerably worn, so that the cusp pattern cannot be accurately deter-

mined. In P_4, however, four main cusps can be seen. The pseudo-metaconid and entoconid are considerably larger than are the protoconid and hypoconid. There is a small cusp which may be called a pseudo-metaconulid, on the inner side of the pseudo-metaconid. The cusps have united into two transverse lophs, though the median valley has been almost worn away. Before being worn, the antero-posterior valleys were probably quite deep, though perhaps more shallow than those of *Mookomys*. In M_1 and M_2, nothing can be told of the pattern other than that there are two transverse lophs. These are so very similar in size and shape to those of *Mookomys* and *Perognathus* as to indicate that they were probably formed in the same way, by the union of three cusps in a buccolingual row. The lateral portion of the metalophid was large. This form cannot have been ancestral to *Perognathus*, as it is too large, the structure of P_4 is different, and the teeth are more hypsodont.

Hall suggests that *Peridiomys* may be synonymous with *Diprionomys* Kellogg, the differences being due to greater wear in the specimens of the latter genus. I have not been able to study the specimens of *Diprionomys*, but I have compared Hall's figures and descriptions with *Peridiomys*. The differences in pattern between the molars of the two forms could easily be due to wear. The premolars, however, have slightly different patterns—that of *Peridiomys* having the metaconulid mentioned above, and being bilophodont for a larger portion of the animal's life than that of *Diprionomys*. The premolar of *Peridiomys* is shorter antero-posteriorly in proportion to its width than are the premolars of the various species of *Diprionomys*. A more important distinction is that of the shape of the teeth—those of *Diprionomys* being essentially circular, and those of *Peridiomys* being much wider than they are long (for details of the comparison, see the table of measurements). For these reasons, although further material may prove the two genera to be identical, for the time being I believe it best to keep them separate. *Peridiomys*, it seems to me, may well be ancestral to the closely related *Heteromys* and *Liomys*. The lower premolar of *Peridiomys* is simpler than that of *Heteromys*, but is essentially the same as that of *Liomys*. *Peridiomys* is slightly larger than *Liomys*. It is practically the same size as some species of *Heteromys*, as *H. nelsoni*.

DIPRIONOMYS Kellogg

KELLOGG, 1910, Figs. 17, 17b and 18; HALL, 1930, Figs. 2–12.

This genus, from the Thousand Creek Pliocene of Nevada, is also known chiefly from lower jaws, though fragments of skulls have recently been described by Hall for two of the four species. The teeth of most of the specimens are in an advanced stage of wear, so that no trace of the cusps remains. In P_4, there are a functional metalophid and a hypolophid. In worn teeth, these unite in the middle of the tooth. The shape of the "metalophid" varies in different species as well as with wear. M_1, in an unworn specimen, is made on the same pattern as that of *Mookomys*—having two lophs, each composed of three cusps. In a worn tooth, the lophs unite, beginning with the lingual side, and, in an old animal, the tooth is reduced to a circle of enamel surrounding a dentine area in the center. The upper teeth resemble those of *Perognathus* and *Liomys*. They differ from those of *Perognathus*, however, in being more hypsodont, resulting in a much shallower median valley, so that the protoloph and metaloph are united much earlier in the animal's life than in the case of *Perognathus*. In this respect *Diprionomys* is much like *Liomys*. *D. parvus* is the most primitive member of the genus, and may be ancestral to the others. A more specialized member of the genus, as *D. quartus*, may have been ancestral to the kangaroo rats, *Dipodomys* and *Microdipodops*, as Hall suggested, though it does not have the grooved incisor characteristic of the modern genera. P_4 of these animals is more specialized than in *Diprionomys*, but the characters of the two forms are such as to allow *Diprionomys* to be their ancestor. I do not believe, however, that Hall is correct in deriving *Perognathus* and *Liomys* from *Diprionomys*. The proportions of P_4 in *Perognathus fallax* and *Diprionomys tertius* are quite different, the former being essentially of equal dimensions, and the latter elongate antero-posteriorly. The diastema of *Diprionomys* is much longer than that of *Perognathus* and the dentary is much deeper. It seems to me that *Peridiomys* is more closely related to *Liomys* than is *D. quartus*. If *Diprionomys* is ancestral to the kangaroo rats, which are the only members of the family known to be jumping forms, it is probable that *Diprionomys* was tending in this direction. But just what stage had been reached cannot be told until fossils are found showing the hind feet. It is, perhaps, justifiable to assume that they were more or less in the stage reached by *Perognathus*, which very occasionally rises onto its hind legs.

PEROGNATHUS Maximilian

Perognathus fallax Merriam

MERRIAM, 1889, Fig. 12.

This species was selected to represent the genus, chiefly because a young specimen was available, showing the pattern of the unworn dentition. In this genus, the molars are hypsodont and lophodont, and the separate cusps are reduced to small rugosities on the upper surface of the unworn teeth. A very little wear causes all trace of these cusps to disappear, leaving nothing but the two transverse lophs. There are no traces of cingula. P_4 is quadritubercular, with a connection between the middle of the two lophs. M_1 and $_2$ are sextitubercular. M_3 is quinquetubercular, with no trace of a hypostylid. This would seem to indicate either a slight retrogressive evolution from the *Mookomys parvus* stage, where there is a minute hypostylid, or else that *Perognathus* is descended from a form related to *M. parvus*, but which did not have the hypostylid. What this tooth indicates about the unknown M_3 of *Mookomys altifluminis* is difficult to say. It seems reasonable to assume, however, that either the hypostylid was absent, or, if present, extremely small. There is no trace of an external cingulum closing the median valley on any of the lower teeth, although in an old skull the two lophs begin to connect on the median side.

P^4 has a small, apparently unicuspular protoloph, followed by a tricuspid metaloph. The cusps of this seem to be the metacone, hypocone, and either a hypostyle or hypoconule. Whether the protoloph is formed by the protocone, the paracone, or by a fusion of the two, is impossible to determine from this form alone. *Dipodomys* (see below) seems to indicate that the anterior crest is formed by the protocone and paracone. M^1 and ^{2} are essentially similar to the lower molars, being formed of two transverse lophs, made up of paracone, protocone, and protostyle, and metacone, hypocone and hypostyle, respectively. In M^2, there is an internal cingulum which tends to close the median valley. M^3 is formed of the four primitive cusps, together with a protostyle, continued posteriorly as a very strong internal cingulum of essentially the same height as the two lophs. There is, however, no distinct hypostyle.

The incisors are stouter than in *Mookomys*, and the upper incisors are grooved. The tooth pattern of this genus is very easily to be derived from that of *Mookomys*. The tibia and fibula are ankylosed at their distal ends. All that is required to form *Perognathus* from *Mookomys*

is a further specialization of the teeth along the lines followed in the evolution leading up to *M. altifluminis*, and a specialization of the limb bones, as indicated by the union of the tibia and fibula.

Perognathus furlongi Gazin

GAZIN, 1930, Pl. III, Figs. 5, 5a and 6.

The type, Cal. Inst. Tech. No. 35, is the anterior portion of a skull containing the cheek teeth of both sides, from the Cuyama Miocene beds of California, which have been correlated with the Upper Miocene Barstow beds. This makes this specimen but slightly younger than *Mookomys altifluminis*. The portions preserved are distinctly perognathoid in character. While this may be the upper dentition of *Mookomys*, it is so close to *Perognathus* that I believe Gazin was correct in referring it to that genus. From Gazin's figures, it would seem that the anterior loph of P^4 is composed of but a single cusp, and the posterior of three, just as in the living species of the genus. M^1 is sufficiently little worn to show three cusps on the protoloph. The median valley is closed internally by an elevated cingulum. This shows that this species is more advanced than *M. altifluminis*, since, in that form, the cingulum does not close the valley until the teeth have been considerably worn. It is also more advanced than *P. fallax*. M^2 is similar to M^1, but smaller. The figure does not show any cusps. M^3 is broken off.

This species, it seems to me, though the earliest known member of *Perognathus*, is probably not ancestral to all the later members of the genus. It is not very far removed from *Mookomys altifluminis*. There are, however, more differences between *M. altifluminis* and *P. furlongi* than between the latter and *P. fallax*, so I have drawn the dividing line here.

HETEROMYS Desmarest

GOLDMAN, 1911, Pl. I, Figs. 1-2.

The teeth of an adult of this genus, in which the original crown pattern has been lost, are not very different from those of the other members of the family. The lower molars seem to have had the same basic pattern as those of *Mookomys*, and do not seem to have been greatly modified beyond that. However, in some species, there is a cusp developed from a posterior cingulum on M_3, in the center of the posterior side of the tooth. This is, however, inconstant, being sometimes present on one side of the animal and not on the other. There has also been a union of the metalophid and hypolophid, on the buccal border of the tooth, so

that the crown pattern is a U. This connection is a portion of the external cingulum which has not been elevated as high as the protostylid and hypostylid portions were. This would indicate, perhaps, that *Heteromys* cannot be derived from *Mookomys altifluminis*, as there is practically no trace of the cingulum closing the valley in that form. *M. parvus*, however, would be a satisfactory ancestor, as it possesses the complete cingulum. *Peridiomys*, however, could be an intermediate stage between *M. altifluminis* and *Heteromys*.

P$_4$ is much more advanced in its pattern than is that of *Mookomys*. The cusps have fused into two transverse lophs, connected at their external margins, as in the molars. This lends strength to the supposition that an external cingulum has developed, with the formation of the two stylids, as in the molars. Furthermore, an anterior loph has appeared in front of the "metalophid." This may have developed from an anterior cingulum, as it is connected with the "metalophid" at the external margin of the tooth, where the "metalophid" has been derived from the elevated external cingulum. It is also connected with the middle part of the "metalophid." This crest is in about the right place to be homologized with the paraconid, though it is probably not that cusp, which seems to have disappeared in the Heteromyidæ by the Miocene.

The pattern of the upper molars is identical with that of the lowers, except that, as so very frequently occurs among mammals in general and rodents in particular, the pattern is reversed. The only visible difference in a worn tooth is that the lophs are connected at their median instead of at their lateral ends. In P^4, however, the pattern is quite different from that of P$_4$. The posterior loph curves around on the median side, in a hook-shaped process, toward the single anterior cusp. It is impossible to say, on the basis of this genus alone, whether the hook on the metaloph properly belongs to the protoloph, or whether it is a metastyle moving toward the protoloph. Comparison with *Dipodomys*, however, tends to support the latter explanation.

The upper incisor is not grooved. The tibia and fibula are fused for their distal halves. This form is quadrupedal at all times.

As *Heteromys* and *Liomys* do not have a grooved upper incisor, it is possible that the upper incisor of *Peridiomys* was not grooved. If this were so, it would indicate that *Peridiomys* was probably derived from a form related to *Mookomys altifluminis*, but without the groove, although this groove may have been secondarily lost in the recent genera.

Liomys Merriam

GOLDMAN, 1911, Pl. I, Fig. 3.

This genus is a very close relative of *Heteromys*, but is a more primitive type. The lower molars have the same pattern as do those of *Heteromys*. In the premolar, however, the pattern is much simpler than that of *Heteromys*. The hypolophid is essentially similar in the premolars of the two genera. The protoconid and pseudo-metaconid of *Liomys*, however, are quite distinct from each other, and remain separate for some time. Moreover, there is no trace of the additional anterior loph. There seems to be a tendency for the antero-posterior connection of the lophs of the molars to show itself later in life than in *Heteromys*. The upper teeth, also, have essentially the same pattern as in this last genus, again the only important difference being in the premolar. Here the median hook of the metaloph is less well developed and looks much more like a metastyle than it does in *Heteromys*. It seems obvious that *Liomys* and *Heteromys* have had a common ancestor at a not very distant period. Probably this ancestor was more nearly related to *Liomys* than to *Heteromys*, and may have been close to *Peridiomys*.

Dipodomys Gray

GRINNELL, 1922, Fig. C.

The genus is the kangaroo rat of western North America. P_4 has an anterior loph as in *Heteromys*. This form is, however, in a different line, since the anterior loph is connected at both ends with the "metalophid." There are two median cusps and one lateral cusp on the "metalophid." This anterior crest seems to be pushed out from the "metalophid," though this appearance may be a secondary development. The hypolophid is formed of three cusps. The separation of the cusps from each other is about as distinct as in *Perognathus*. There is no trace of an external cingulum. In the molars, there are six cusps, arranged in two rows, with practically no separation between the cusps of each row. There is, however, a strong external cingulum closing the median valley. The upper premolar shows the protoloph to be formed by two cusps. It thus seems to be in a stage structurally ancestral to those of *Heteromys* and *Perognathus*, where no such division is discernible. In the metaloph are three cusps, the hypostyle being continued anteriorly as a cingulum which partially closes the median valley. The upper molars, like the lower, are composed of three cusps in each loph. The median valley is closed by an internal cingulum, which connects the protostyle and hypo-

style. The upper incisor has a groove on its anterior face. The lower half of the tibia and fibula are ankylosed. This animal is saltatorial, being entirely bipedal.

MICRODIPODOPS Merriam

This genus is closely related to *Dipodomys*, and has a similar habitat. The chief difference between them is one of size. In the teeth, M$\frac{3}{3}$ of *Microdipodops* are very small in proportion to the other teeth, being minute nodules. The teeth, when worn, become enamel ovals, surrounding an area of dentine in the center. The upper incisor is grooved. The tibia and fibula are united throughout, so that this process reaches its culmination in this genus.

These two genera of kangaroo rats are probably derived from a common ancestor in the Pleistocene or late Pliocene. They were very possibly ultimately derived from *Diprionomys quartus*, by a specialization of P_4.

Would it not now be possible, on the basis of our knowledge of the tooth pattern of the upper teeth of the recent forms, to reconstruct that of the fossil genera? Since in most of the more specialized rodents, including the Heteromyidæ, the patterns of the upper and lower teeth are essentially mirror images of each other, it follows that, when we know the lower teeth, we can determine, with reasonable accuracy, the pattern of the uppers. And, also, when two forms have similar lower teeth, their upper teeth ought also to be similar. In *Mookomys*, the pattern of the lower molars is essentially that of the lower molars of *Perognathus*. This should mean, in accordance with the principle cited above, that the pattern of the upper molars was also essentially the same. Of course, this should be considered only a hypothesis until the upper teeth are found. This resemblance in pattern of the upper and lower teeth is of considerable value to the palæontologist, as it makes the lower jaws of rodents as serviceable for identification as an upper dentition. This is especially important, as, for some reason, the lowers are much more common as fossils than are the uppers.

The resemblance between the upper and lower premolars of *Mookomys* was probably not quite as great as that between the molars. The upper premolar was, however, probably more primitive than a *Perognathus* premolar, and more quadritubercular, thus resembling the lower premolar.

We should have, then, in Miocene heteromyids, a series of parallel ridges, which, in mastication, would oppose each other, and wear on the

surface of the corresponding ridge on the other jaw. This would be a necessity, as the motion of the jaws of a rodent has a backward and forward component when chewing, and no motion of this sort would be possible if the crests interlocked. An occlusion of this sort, with the lower jaw moving antero-posteriorly, would give only a limited grinding surface, and would seem to supply a sufficient reason for the positive selection of forms in which the teeth were elevated into lophs, and the median valleys were reduced in depth and width. A tooth of this sort, after a very moderate amount of wear, has a much larger grinding surface than does one of the type of *Mookomys*. It is interesting to note, as supporting this theory as to the origin of the tooth pattern of the more specialized forms, that all the recent genera of the family have undergone modifications of this sort, and that there are no living rodents in which the teeth are of the *Mookomys* type. In the lagomorphs, whose jaws move transversely during mastication, the teeth have antero-posterior differences in height. These facts suggest that there is a positive selection of forms with the perognathoid type of dentition, as opposed to those with teeth of the *Mookomys* variety.

This picture of the upper teeth of *Mookomys* was based partly on the upper teeth of *Perognathus* and partly on a mirror image of the lower teeth of *Mookomys*. It could, however, have been derived equally well by determining, from a study of the recent genera, what their common ancestor should have been like. This lends support to the essential accuracy of the description.

The accompanying phylogenetic chart indicates the probable inter-relationships of the different members of the family. *Mookomys* is probably descended from *Heliscomys*, and *Perognathus* and *Peridiomys* from *M. altifluminis*. *Heteromys* and *Liomys* are perhaps derived from *Peridiomys*. *Dipodomys* and *Microdipodops* may have been descended from a stage similar to *Mookomys parvus*, through *Diprionomys*.

One of the aspects of this phylogenetic series which will be of interest to the palæontologist is the manner in which it shows, clearly and definitely, that, in this family of rodents, at least, the teeth have been derived from a tritubercular pattern which existed in the Eocene or Oligocene. While it has long been suspected that such was the case for all the rodents, as well as for other mammals, proof has been wanting for most of the members of the order. This series also shows, in some of the later forms (as *Heteromys*), the early stages in the multiplication of crests which is so common among the rodents, and which is carried to such extremes among the Hystricomorpha.

PHYLOGENETIC CHART OF THE HETEROMYIDÆ

		Heteromys	Liomys	Perognathus	Microdipodops	Dipodomys
RECENT						Dipodomys
PLEISTO-CENE	Rancho la Brea			Perognathus		Dipodomys
	Thousand Creek					Dipodomys / Diprionomys quartus / Diprionomys parvus
PLIO-CENE	Lower Snake Creek	Peridiomys rusticus				
	Cuyama (cf. Barstow)			Perognathus furlongi		
MIOCENE	Deep River			Mookomys altifluminis		
	?			Mookomys parvus		
OLIGO-CENE	White River	HETEROMYIDÆ		Heliscomys vetus		Gymnoptychus / GEOMYIDÆ
UPPER EOCENE	Uinta					?

CONCLUSIONS

1.   *Heliscomys* from the White River Oligocene is probably the common ancestor of the Heteromyidæ.   A form similar to *Mookomys parvus* of the ??Lower Miocene was probably essentially ancestral to all the later forms.   *M. altifluminis* of the Deep River Miocene is ancestral to *Perognathus* and *Peridiomys* and perhaps to *Heteromys* and *Liomys*.

2.   *Gymnoptychus* (*Adjidaumo*) is not ancestral to the Heteromyidæ.   Probably it and *Heliscomys* are descended from a common ancestor in the Upper Eocene or lowest Oligocene.

3.   The dental evolution of the family was presumably caused by the comparatively inefficient pattern of the teeth in the earlier forms. Since the crests of one jaw could grind only against the crests of the other, the tendency was toward the increase in the size of the crests and the reduction in size of the valleys and interlophic spaces, which are functionless.

BIBLIOGRAPHY

Cope, E. D.   1873.   Synopsis of new vertebrates from Colorado.   Misc. Publ. U. S. Geol: Surv. Terr., p. 3.

1874.   Report on the Vertebrate Paleontology of Colorado.   Ann. Rept. U. S. Geol. Surv. Terr., 1873 (1874), p. 475.

1884.   Tertiary Vertebrata of North America.   Rept. U. S. Geol. Surv. Terr., III, I, pp. 845–847.

Gazin, C. L.   1930.   A Tertiary vertebrate fauna from the Upper Cuyama drainage basin, California.   Contr. Carn. Instn. Wash. Publ. 404, pp. 66–67.

Goldman, E. A.   1911.   Revision of the spiny pocket-mice.   North American Fauna No. 34.   U. S. Dept. Agri., Biol. Surv.

Grinnell, J.   1922.   A geographical study of the Kangaroo Rats of California. Univ. Cal. Zool. Publ., XXIV, 1, pp. 1–124.

Hall, E. R.   1930.   Rodents and Lagomorphs from the later Tertiary of Fish Lake Valley, Nevada.   Univ. Cal. Publ., Bull. Dept. Geol. Sci., XIX, 12, pp. 295–312.

Hay, O. P.   1930.   Second Bibliography and Catalog of the Fossil Vertebrates of North America.   Carn. Instn. Wash. Publ. 390.

Kellogg, L.   1910.   Rodent fauna of the late Tertiary beds at Virgin Valley and Thousand Creek, Nevada.   Univ. Cal. Publ., Bull. Dept. Geol. Sci., V, 29, pp. 411–437.

Matthew, W. D.   1924.   Third contribution to the Snake Creek Fauna.   Bull. Amer. Mus. Nat. Hist., L, 2.

Matthew, W. D., Granger, W., and Simpson, G. G.   1929.   Additions to the fauna of the Gashato Formation of Mongolia.   Amer. Mus. Nov., No. 376.

Merriam, C. H.   1889.   Revision of the North American Pocket Mice, North American Fauna No. 1.   U. S. Dept. Agri., Biol. Surv.

Troxell, E. L.   1923.   *Diplolophus*, a new genus of Rodents.   Amer. Jour. Sci., V, pp. 158–159.

MEASUREMENTS OF RECENT AND FOSSIL HETEROMYID RODENTS

All Measurements in Millimeters

	Heliscomys setus, A.M.N.H. 5461. M₁-₃ left, Measured by Wood.	*Heliscomys setus*, A.M.N.H. No. 5462. P₄-M₁ left. Measured by Wood.	*Mookomys parvus*, Y.M. No. 10362. P₄-M₁ right. Measured by Wood.	*M. altifluminis*, A.M.N.H. No. 21360. P₄-M₃ left. Measured by Wood.	*Peridiomys rusticus*, A.M.N.H. No. 18894. P₄-M₃ left. Measured by Wood.	*Perognathus fallax*, A.M.N.H. No. 5066. P₄-M³ left. Measured by Wood.	*P. furlongi*, Cal. Inst. Tech. No. 35. P₄-M³ left. After Gazin.	*Diprionomys parvus*, U. Cal. No. 12566. P₄-M₁ right. From Kellogg's figures.	*D. magnus*, U. Cal. No. 12567. P₄-M₂ left. From Kellogg's figures.	*D. tertius*, U. Cal. No. 29632. P₄-M₃ right. After Hall.	*D. quartus*, U. Cal. No. 29639. P₄-M³ right. No. 29631. P₄-M₁ right. After Hall.	*Dipodomys merriami*, A.M.N.H. No. 6878. P₄-M₃ left. Measured by Wood.	*Microdipodops megacephalus*, A.M.N.H. No. 54815. P₄-M₃ left. Measured by Wood.	*Heteromys desmarestianus*, U.S.N.M. No. 100007. P₄-M₃ left. From Goldman's figures.	*Liomys inornatus*, U.S.N.M. No. 93914. P₄-M₃ left. From Goldman's figures.
Length of Lower Cheek Teeth	....	....	4.85	....	....	3.55	....	....	....	....	5.1	....	2.65	4.86	4.95
Length of Lower Diastema	2.85	2.23	....	3.5	....	2.65	....	4.11	....	4.22	5.00	2.65	2.72	4.20	4.36
Depth of Dentary at P_4	....	2.23	4.1	2.8	4.89	2.4	....	2.62	4.05	3.37	4.2	3.50	2.30	2.20	2.24
Depth of Dentary at M_3	....	....	....	....	3.23	1.30	....	....	....	3.02	....	....	1.83	....	....
Length of Metalophid, P_4	....	0.55	0.92	0.80	1.40	0.65	....	1.08	1.03	0.51	1.15	1.0	0.75	1.22	1.24
Length of Hypolophid, P_4	....	0.55	1.02	0.95	1.98	0.90	....	1.29	1.52	0.71	1.25	1.22	0.85	1.25	1.59
Antero-posterior length, P_4	....	0.48	0.99	1.05	1.53	0.90	....	1.32	1.53	1.2	1.5	1.45	1.00	1.35	2.00
Length of Metalophid, M_1	0.83	0.79	1.32	1.15	2.20	1.05	....	1.25	1.40	0.82	1.2	1.07	1.05	1.22	1.46
Length of Hypolophid, M_1	0.84	0.79	1.22	1.15	2.32	1.00	....	1.43	1.53	0.97	1.1	1.08	1.05	1.29	1.58
Antero-posterior length, M_1	0.84	0.84	1.28	1.10	1.57	1.05	....	1.06	1.06	1.2	1.2	1.00	0.56	1.03	1.20
Length of Metalophid, M_2	0.82	....	1.44	1.10	2.13	1.10	....	....	1.48	0.90	1.2	....	1.05	1.45	1.48
Length of Hypolophid, M^2	0.83	....	1.32	1.10	2.12	1.05	....	....	1.62	0.82	1.1	....	1.05	1.54	1.43
Antero-posterior length, M_2	0.82	....	1.30	1.00	1.82	0.95	....	....	1.02	1.0	1.3	....	0.54	0.95	1.12
Length of Metalophid, M_3	....	....	1.23	....	....	0.80	....	....	....	....	1.2	....	0.70	1.35	1.33
Length of Hypolophid, M_3	....	....	1.03	....	....	0.70	....	....	....	....	1.0	....	0.70	1.24	1.30
Antero-posterior length, M_3	....	....	1.20	....	....	0.80	....	....	....	....	1.2	....	0.45	1.29	1.12
Crown length of Upper Creek Teeth Series	....	....	....	....	....	3.32	3.4	....	....	3.77	....	....	2.70	4.59	4.54
Length of Upper Diastema	....	....	....	5.68	....	5.51	....	....	....	....	7.20	4.90	5.25	10.67	9.80
Width of P^4	....	....	....	....	....	1.23	1.2	....	....	1.25	1.40	1.34	1.02	1.44	1.81
Antero-posterior crown length, P^4	....	....	....	....	....	1.00	0.92	....	....	1.39	1.36	1.20	0.71	1.33	1.64
Width, M^1	....	....	....	....	....	1.24	1.3	....	....	1.31	1.36	1.25	1.11	1.46	1.68
Antero-posterior length, M^1	....	....	....	....	....	0.97	0.9	....	....	1.03	0.98	0.90	0.57	1.19	1.21
Width, M^2	....	....	....	....	....	1.05	1.2	....	....	0.95	1.31	1.16	0.86	1.54	1.50
Antero-posterior length, M^2	....	....	....	....	....	0.77	0.8	....	....	0.88	0.89	0.85	0.55	1.18	0.98
Width, M^3	....	....	....	....	....	0.70	0.9	....	....	0.76	....	....	0.63	1.16	1.20
Antero-posterior length, M^3	....	....	....	....	....	0.82	0.7	....	....	0.56	....	....	0.51	1.01	0.96