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EVOLUTION OF GEOMYINE RODENTS WITH ROOTED CHEEK TEETH

by

William Andrew Akersten

A dissertation submitted in partial fulfillment  
of the requirements for the degree of  
Doctor of Philosophy  
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## INTRODUCTION

This study began as a biometric examination of speciation, in space and time, among late Pliocene and early Pleistocene Geomyini (including Nerterogeomys). It soon became apparent that more than one major lineage of geomyines was included in my concept of the Geomyinae. The composition and relationships of these lineages would have to be defined before any study of speciation could begin. My attempt to sort out the different possible lineages led to working with more archaic geomyines and, finally, to restriction of this study to only those forms which have rooted cheek teeth.

During preliminary work on the more advanced geomyines, I noted a number of problems which would make any biometric study of fossil geomyines impractical if not impossible. Modern geomyine populations become almost completely reproductively isolated from one another quite readily. These strongly fossorial forms find moderately large rivers, rocky areas, or soils with certain characteristics almost impassable barriers. Consequently, they show a tremendous amount of interpopulational variability. This variability has led to the naming of many subspecies and considerable uncertainty as to the relationships of many living forms. In living Thomomys, I found that the biometric parameters of two subspecies assigned to the same species may differ more than in two populations assigned to

two different species. If the usual biometric standards, measuring degree of relationship, are difficult to apply in the two-dimensional modern situation, the three-dimensional fossil situation would be so difficult as to render interpretation of the results impossible. It did prove quite easy to biometrically separate different species of geomyines in a single fossil fauna. In most cases this was easily verified by qualitative characters as two different genera were usually present. However, it did prove quite difficult to interpret biometric differences between fossil populations belonging to the same genus but from different faunas. Differences could be temporal or geographic, of specific, subspecific, or populational rank. These difficulties are compounded in taxa with hypsodont or evergrowing cheek teeth because the occlusal outline and dimensions of the teeth change with age. There is also a considerable amount of sexual dimorphism in Holocene geomyines (Bailey, 1915; Merriam, 1895; Russell, 1968b).

A biometric approach to the study of fossil geomyines will not be possible until the relationships and biometry of living geomyines are understood. Even then, any such study would probably be very difficult.

In summary, this study evolved from its original objective to a study of the phylogenetic relationships of those geomyines with rooted cheek teeth and relies on qualitative rather than quantitative data. Measurements are not considered to be taxonomically significant except

in extreme cases. Therefore, they are included in the Appendix rather than within the description of each taxon.

Previous work.— The only previous work which included an attempt to synthesize the relationships of geomyines with rooted cheek teeth was by Russell (1968a). Unfortunately, his paper had gone to press before the major contribution of Shotwell (1967b) became available. Shotwell described much of the material which forms the basis for this review, but he did not attempt a complete synthesis. Russell also relied only on a few key characters to assess phylogenetic relationships, an approach likely to yield poor results even when the best of characters are chosen. One of his key characters, the supposed occurrence of H-shaped occlusal patterns on the molars with a primary medial loph or lophid connection, is based on a misinterpretation of the evidence. As will be shown later, a C-shaped pattern is basic for geomyine molars and the presence of an H-shaped pattern in a geomyoid rodent with rooted cheek teeth is a good criterion for exclusion from the Geomyinae. Another of Russell's key characters, which he considered to be a relict of a primitive bicolumnar condition, was an elongate  $M^3$  with mid-labial and mid-lingual constrictions. In the preliminary stages of this study, I examined several unworn  $M^3$ 's belonging to taxa having this "bilobate"  $M^3$ . The elongate posterior lobe is the result of elaboration of the posterior cingulum or posterior portion of the hypostylar ridge; the constrict-

tions occur between the metaloph and the elaborated cingulum. An elongate, bilobed  $M^3$  is an advanced characteristic, not primitive, and could easily develop in parallel among different lineages. Russell also noted that the posterior enamel plate of the geomyine  $P^4$  becomes progressively reduced with advancing evolutionary grade, a type of characteristic not very useful for evaluating phylogenetic relationships. He then used the presence of a partial enamel plate as a character to unite Nerterogeomys (here considered to be of valid generic rank) with Zygogeomys, members of distinct lineages.

The use of incisor grooves as a key characteristic has been discussed elsewhere (Akersten, 1973). Suffice it to say that the groove patterns of living geomyines have been misinterpreted and that number of grooves is very probably another character primarily indicative of evolutionary grade. Gross development of the masseteric crest and fossa are also tied to evolutionary grade more than to phylogenetic relationships. The skull characteristics discussed by Russell (1968a) seem to be of phylogenetic importance but they are not available for the fossil material I studied.

I disagree with so many previously published statements that it would be impractical to contrast all my findings with those of previous workers. Therefore, I have often left out detailed descriptions of just how my interpretations differ from those of others.

Approach.- A study based on all the preserved remains of these geomyines would be, of course, the most desirable approach. However, a survey of the existing specimens in collections showed that in most samples only dental elements and the mandible were common enough to be of real value. The occasional skull and limb fragments cannot add to the phylogenetic picture at this stage and are only mentioned rather than described systematically. I describe all qualitative features observed on the dentition and mandible in the systematic sections of this paper, whether or not they are considered to be of taxonomic importance. This procedure led to several "discoveries" of important characteristics which I had overlooked until reaching the stage where I could synthesize the data.

Phylogenetic interpretations are based on all available data, at least to the extent that none of the data conflict with the conclusions. I subjectively weighted some characters more strongly than others since they seemed to be more indicative of phylogenetic relationships than evolutionary stages. However, I know of no way to definitely prove or disprove either possibility. Samples of primitive geomyines are rarely large enough to include many significant characters. Quantitative systems of measuring phyletic distances and relationships, such as Prim networks and Wagner trees, require the same data base for each included group. In order to use one of these methods, I would have to reduce either the number of groups

or the number of characters to the point that the exercise would become meaningless.

In order to estimate phylogenetic relationships, I have leaned most heavily on the cusp patterns of the unworn teeth and certain features of the masseteric fossa and crest complex on the mandible. The cusp patterns of the deciduous teeth are very conservative. That of the  $DP_{\overline{4}}^4$  is so conservative that it is almost useless as a phylogenetic character. However, the  $DP_{\overline{4}}^4$  does help to distinguish geomyines from other geomyoid rodents. The  $DP_{\overline{4}}^4$  is a little less conservative than the  $DP_{\overline{4}}^4$  and helps to distinguish individual tribes within the Geomyinae. The  $DP_{\overline{4}}^4$ 's of Brachygeomys drewseyensis n. gen. and sp. and Pliogeomys buisi, the latter species being far more advanced than the former, differ only in size but they differ enough from other geomyines to indicate that these species probably are members of the same lineage. Deciduous teeth are subject to different "evolutionary forces" than are the permanent teeth because they function during a different part of the animal's life and, very probably, are specialized for a different manner of mastication. The occlusal patterns of unworn permanent teeth evolve even faster but do not show as great a percentage of change as do crown height or root reduction, though these estimates are also very subjective. As the crown height of the geomyine cheek teeth increased, the occlusal pattern was present for an increasingly shorter percentage of the life

of the animal and became less important to that animal in adaption to its feeding habits. Two main patterns of the masseteric fossa and crest region on the mandible seem to persist independently throughout much of known geomyine history.

Measurements were made with a Gaertner measuring microscope to 0.001 mm. They were then rounded to 0.01, 0.1, or 1.0 mm according to the absolute magnitude of the measurements. The stereo pairs of photographs were made with the tilt-table described by Wienert (1960).

Abbreviations.— The prefixes L and R before a skeletal or dental element indicate left and right, respectively. The following is a list of abbreviations pertaining to collections or localities.

|         |                                                                                                               |
|---------|---------------------------------------------------------------------------------------------------------------|
| AMNH    | American Museum of Natural History                                                                            |
| CIT     | California Institute of Technology (now part of the Los Angeles County Museum of Natural History collections) |
| KU Loc. | University of Kansas Vertebrate Paleontology Locality                                                         |
| LACM    | Los Angeles County Museum of Natural History                                                                  |
| SDSM    | South Dakota State Museum                                                                                     |
| UCMP    | University of California Museum of Paleontology                                                               |
| UCMPloc | University of California Museum of Paleontology Fossil Locality                                               |

|        |                                                                 |
|--------|-----------------------------------------------------------------|
| UM-Ida | University of Michigan Vertebrate Paleontology Locality, Idaho  |
| UMMP V | University of Michigan Museum of Paleontology Fossil Vertebrate |
| UO     | University of Oregon                                            |
| UOloc. | University of Oregon Fossil Vertebrate Locality                 |

## AGE AND CORRELATION OF FAUNAS

The following are interpretations of the relative and absolute ages of the faunas which contain remains of geomysines with rooted cheek teeth. I attempted to assign each fauna to either the early, middle, or late portion of a North American Land-Mammal Provincial Age. The assigned age and correlation of several of the Oregon faunas is very tentative. Text-figure 1 shows the ages and correlations of the faunas and text-figure 2 shows their geographic distribution.

Meade Basin, Kansas and Oklahoma.- Two of the many vertebrate faunas in the Meade Basin, the Buis Ranch and Saw Rock Canyon local faunas, include the remains of geomysines with rooted cheek teeth. The Buis Ranch local fauna was first considered to be early Blancan because of the presence of Buisnictis, Gopherus riggsi, and Perognathus cf. P. mclaughlini (Hibbard, 1954). In this same paper, Hibbard assigned the deposits containing the fauna to the base of the Rexroad Formation and considered them to be equivalent to, or slightly older than, the XI Member of the Rexroad Formation which contains the Saw Rock Canyon local fauna. Tihen (1955) assigned the Buis Ranch local fauna to the Hemphillian and the deposits containing the fauna to the upper part of the Ogallala Formation, citing personal communication with Hibbard for the change. Hibbard (1963) then described a mandible of Tanupolama vera, a Hemphillian

species, from the Buis Ranch local fauna. He described the reasons for reassignment of the deposits to the upper Ogallala Formation and considered the fauna to be late Hemphillian. Stevens (1966) followed Hibbard as to the age and correlation of the fauna and cited the additional occurrences of Prosthenops sp. and Nannippus minor. The former genus does not occur in the Blancan but the latter species may range into late Blancan (Akersten, 1972). Additional confirmation of a Hemphillian age for the Buis Ranch local fauna is provided by the presence of cf. Teleoceras sp., UMMP V41870 - an upper incisor of a rhinoceros, and Pliohippus sp., UMMP V31382 - a partial lower molariform tooth. The Buis Ranch local fauna best fits an advanced Hemphillian fauna and is assigned to the late Hemphillian. Three localities within one-half mile of each other yielded elements of this fauna.

The first descriptions of fossil vertebrates from the Saw Rock Canyon local fauna, KU Loc. 6, was by Hibbard (1944a,b). He considered the fauna to be Hemphillian, occurring in the Ogallala Formation. Later, Hibbard (1949, 1953) assigned the deposits containing the Saw Rock Canyon local fauna to a new, basal member of the Rexroad Formation, the XI Member, and considered the fauna to be near the boundary between the Hemphillian and the Blancan. However, in his systematic descriptions it was assigned to lower upper Pliocene or early Blancan. This

Text-fig. 1- Correlation of vertebrate local faunas which contain geomyines with rooted cheek teeth. Those faunas with lower case letters in name do not contain geomyines with rooted cheek teeth and are included for purposes of comparison.

| Mammal Age / Area |              | Meade Basin,<br>Kansas & Oklahoma    | Idaho    | Juntura Basin,<br>Oregon                      | Northern Oregon                | Nevada                              |
|-------------------|--------------|--------------------------------------|----------|-----------------------------------------------|--------------------------------|-------------------------------------|
| Middle            | Blancan      |                                      | HAGERMAN |                                               |                                |                                     |
| Early             |              | Rexroad<br>Wendell Fox<br>Fox Canyon |          |                                               |                                |                                     |
| Late              | Hemphillian  | SAW ROCK CANYON<br>BUIS RANCH        |          |                                               | McKAY RESERVOIR<br>KREBS RANCH |                                     |
| Middle            |              |                                      |          |                                               |                                |                                     |
| Early             |              |                                      |          | BARTLETT MOUNTAIN<br>OTIS BASIN<br>Drinkwater |                                | SMITHS VALLEY and<br>THOUSAND CREEK |
| Late              | Clarendonian |                                      |          | BLACK BUTTE I & II                            |                                |                                     |

Text-figure 1.

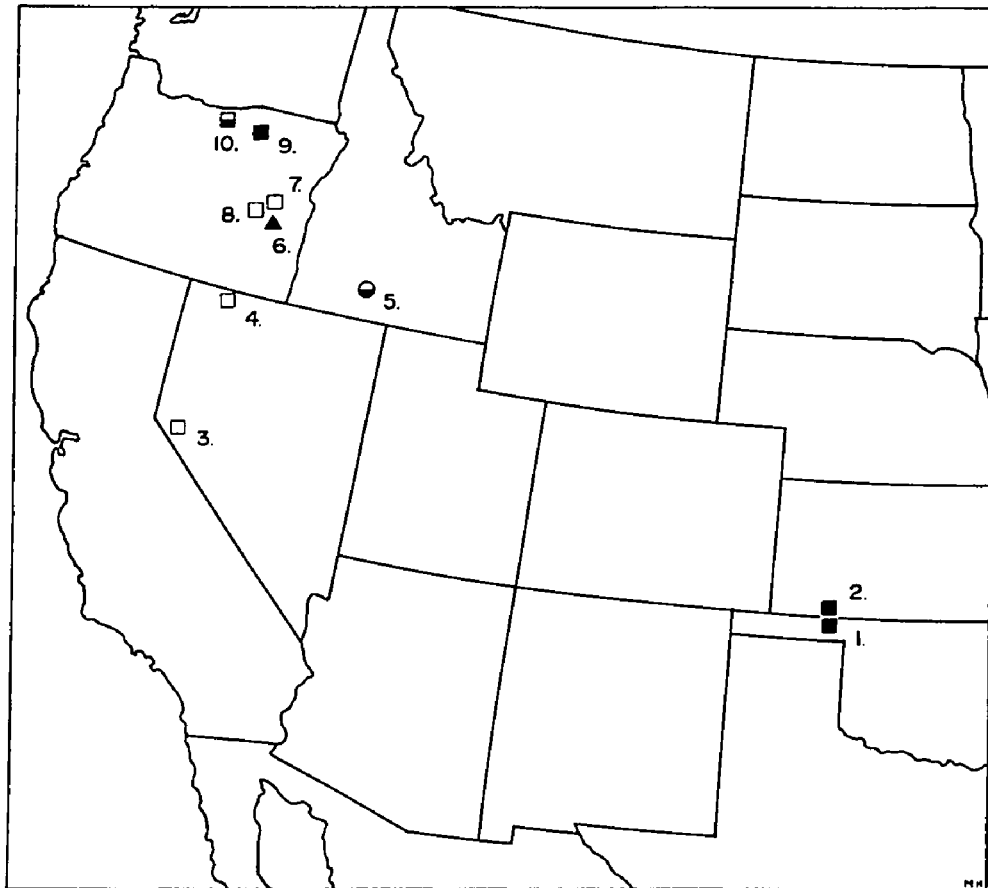
was done on the basis that many of the forms in the fauna were more similar to related Rexroad (early Blancan) forms than to related Edson Quarry (lower or middle Hemphillian) forms. Hibbard (1967) referred to the fauna as lower upper Pliocene but placed it on the boundary between the Hemphillian and Blancan on a correlation chart (his fig. 1). Subsequent to this publication, the humerus of a mylagaulid, UMMP V56996, was recovered from the fauna. This specimen, although not specifically referred to, apparently led Zakrzewski (1967, 1970) and Bjork (1970) to refer the Saw Rock Canyon local fauna to the late Hemphillian. This fauna is transitional between the Hemphillian and the Blancan but the geomyine in it is much closer to the one in the Hemphillian Buis Ranch local fauna than to those in the Blancan Fox Canyon and Rexroad local faunas. Since standard paleontological practice is to pigeonhole a fauna rather than calling it transitional, it seems best to rely on the geomyine and the mylagaulid and assign the Saw Rock Canyon local fauna to the latest Hemphillian, slightly later than the Buis Ranch local fauna. The Saw Rock Canyon local fauna comes from several localities in a small area.

Hagerman, Idaho.— A great number of localities which span about 500' of section in the Glens Ferry Formation near Hagerman, Idaho have yielded the Hagerman local fauna. The history of the various studies on this fauna and different ages assigned to it has recently been summarized by Zakrzewski (1969) and Bjork (1970). Their conclusion,

Text-fig. 2- Geographic distribution of vertebrate local faunas which contain geomyines with rooted cheek teeth. 1, Buis Ranch. 2, Saw Rock Canyon. 3, Smiths Valley. 4, Thousand Creek. 5, Hagerman. 6, Black Butte. 7, Otis Basin. 8, Bartlett Mountain. 9, McKay Reservoir. 10, Krebs Ranch.

**EXPLANATION**

- MIDDLE BLANCAN
- LATE HEMPHILLIAN
- ▣ MIDDLE HEMPHILLIAN
- EARLY HEMPHILLIAN
- ▲ LATE CLARENDONIAN



Text-figure 2.

after thorough studies of the fauna, is that the Hagerman local fauna is middle Blancan, younger than the Rexroad fauna from Kansas but older than Pleistocene. K-Ar dates of  $3.2 \times 10^6$  to  $3.48 \times 10^6$  years (Everndon et al., 1964, KA 831, 832, 1173), from volcanic rocks within the Hagerman section or correlatable with it, confirm the age assignment. The Hagerman local fauna is the youngest that contains remains of a geomyine with rooted cheek teeth.

Juntura Basin, Oregon.- J. A. Shotwell has collected Pliocene faunas from a number of localities in Oregon. These are so isolated from other Pliocene faunas, either by distance or physiographic barriers, that detailed correlations and age assignments are very difficult. In most cases, Shotwell and his students have not attempted to correlate these faunas at a scale any finer than the North American Land-Mammal Provincial Age.

A series of localities, combined into three faunas, from the Juntura Basin of Oregon have yielded remains of geomyines with rooted cheek teeth. The oldest of these is the Clarendonian Black Butte local fauna, UOlocs. 2337 and 2500, which was collected from the Juntura Formation. The first mention of Clarendonian fossil material from this area is in Shotwell (1958a) but the specimens are from a different locality, UOloc. 2343. The first major description of the Black Butte fauna was by Shotwell and Russell (1963) who considered all the localities in the Juntura Formation to represent a single fauna. The fauna was

assigned to the late Clarendonian because of the lack of Hypohippus and the advanced nature of Eucastor malheuren-  
sis. Numerous other megafaunal elements placed the fauna  
somewhere in the Clarendonian. Shotwell and Russell also  
noted that UOloc. 2337 was the lowest stratigraphically of  
all the Black Butte localities, fifty feet or more below  
the main localities which yielded the megafauna. UOloc.  
2500 is first mentioned by Shotwell (1967a,b) and Hutchison  
(1968) as being stratigraphically equivalent to UOloc. 2337  
but neither locality was assigned to any particular part of  
the Clarendonian. A more extensive description of the 1963  
discovery of a new locality equivalent to UOloc. 2337  
appears to relate to UOloc. 2500 (Shotwell, 1970). Again,  
the age assignment is simply Clarendonian. UOlocs. 2337  
and 2500 are clearly Clarendonian, a K-Ar date on the  
Stinking Water Flora from a lower level in the Juntura  
Formation is  $12.1 \times 10^6$  years (Everndon and James, 1964, KA  
1240), but their placement within the Clarendonian is very  
much open to question. No identifiable megafauna is known  
from either locality (Shotwell, 1970), and most of the  
microfauna which can be identified to species is not known  
from other faunas which can be placed in a specific part of  
the Clarendonian. The advanced Eucastor and the presence  
of a tooth fragment assignable to Microtoscoptes are  
suggestive of a rather late Clarendonian age. The Black  
Butte microfauna localities are very tentatively assigned  
to the late Clarendonian.

The first mention of Hemphillian faunas from the Drewsey Formation in the Juntura Basin was by Wilson (1937) and Hall (1944) as discussed by Shotwell (1963). Bowen et al. (1963) and Shotwell (1963) delineated three Hemphillian faunas from the Drewsey Formation and were able to demonstrate their superposition. The Drinkwater local fauna is the lowest stratigraphically; the Otis Basin local fauna, UOloc. 2347, occurs about 150' higher in the section; and the Bartlett Mountain local fauna, UOloc. 2517, is highest, about 350' above the Otis Basin local fauna. The Drinkwater has only yielded megavertebrate remains (Shotwell, 1970), but the other two faunas have yielded microvertebrate remains including geomyines. Neither Shotwell (1963, 1967a, 1967b, 1970) nor Hutchison (1968) make any attempt to correlate these faunas more closely than simply Hemphillian. A K-Ar date of  $8.6 \times 10^6$  years, early Hemphillian, has been determined for the base of the Drewsey Formation (Everndon et al., 1964, KA 1225). As discussed by Hibbard (1970), Microtoscoptes disjunctus is associated with Dipoides stirtoni in the Rome, Stroud Claim, and Kelly Road local faunas. Shotwell (1970) reported both species from the Bartlett Mountain local fauna. Faunal correlation of the Bartlett Mountain local fauna with the Rome, Stroud Claim, and Kelly Road local faunas appears quite tenable. The latter two faunas have been K-Ar dated as early Hemphillian at  $10.0 \times 10^6$  and  $9.2 \times 10^6$  years, respectively (Everndon et al., 1964, KA 830 and 929). Hibbard (personal

communication, 1972) considers the Stroud Claim date as too old. The sum of the evidence is that all three faunas from the Drewsey Formation are assignable to the early Hemphillian.

Northern Oregon faunas.— Two Hemphillian local faunas from northern Oregon, the McKay Reservoir, UOloc. 2222, and Krebs Ranch, UOlocs. 2322 and 2323, have yielded remains of geomyines with rooted cheek teeth. In spite of numerous references to fossil vertebrates in one or more of these faunas (Shotwell 1955a, 1955b, 1956, 1958a, 1958b, 1967a, 1967b; Brodkorb 1958; Hutchison 1968; and Repenning 1968), their exact correlation is still obscure. The only reference I could find relative to stratigraphy was by Shotwell (1958b) in which he stated that both faunas came from a relatively thin rock unit. He considered them to be nearly contemporaneous but the McKay Reservoir local fauna may be slightly older. He also notes that there is no way to determine their relative stratigraphic position. Shotwell (1967b) reiterates this evaluation of the relative ages of the two faunas. Hutchison (1968) lists the age of the McKay Reservoir local fauna as Hemphillian and the age of Krebs Ranch I, UOloc. 2322, as late Hemphillian without explanation. The only taxa which appear to provide an indication of the relative ages of these faunas are the geomyines. The Krebs Ranch geomyine is more primitive than the one from McKay Reservoir. This may simply reflect the presence of different lineages of geomyines in the area but,

within such a short distance, it seems more likely that the Krebs Ranch local fauna is slightly older than the McKay Reservoir local fauna. Correlation of these faunas with other Hemphillian faunas is inconclusive. The primitive microtine Prosomys mimus shotwell, which occurs in the McKay Reservoir local fauna, is also known from the Christmas Valley local fauna (Repenning, 1968), another fauna of uncertain age. Repenning (1968) placed Prosomys in synonymy with Promimomys but Kretzoi (1969) considers them to be distinct genera. The presence of relatively advanced geomyines and a true microtine show that the McKay Reservoir and Krebs Ranch faunas are advanced over early Hemphillian faunas. Prosomys is more primitive than Ogmodontomys from the Sawrock Canyon local fauna (Hibbard, personal communication, 1972). The best age estimate of both faunas on the basis of available faunal evidence is middle to late Hemphillian, older than the Saw Rock Canyon local fauna.

Nevada.-- Wilson (1936) described the Smith Valley local fauna from central western Nevada, including a geomyine with rooted cheek teeth. He correlated this fauna with the Hemphillian Thousand Creek local fauna, also from Nevada. MacDonald (1959) reviewed the Smith Valley fauna and revised its age to early Hemphillian. A K-Ar date of  $9.3 \times 10^6$  years (Everndon et al., 1964, KA 485) confirms an early Hemphillian age. The Smith Valley and Thousand Creek local faunas should be very close to the same age as the

Bartlett Mountain and Otis Basin local faunas of Oregon.

## SYSTEMATIC PALEONTOLOGY

### Terminology of cheek teeth cusps and mandible

The terminology and homologies of the cusps used in this paper are largely taken from Rensberger (1971) with the exception of the  $DP_{\overline{4}}$  cusps and a few other minor changes. The basic descriptions refer primarily to more primitive forms. Some changes have occurred in advanced forms and are discussed in the systematic and evolutionary trend sections. Mandibular terminology is taken partially from Hill (1937) and Repenning (1968) with numerous new terms introduced here. The figures of teeth used to illustrate the terminology are idealized from specimens showing primitive conditions. The illustrations for mandibular terminology are of a recent Geomys pinetus and Pliogeomys parvus. Measurements are given in the appendix, not in the text of each systematic description.

Lower incisor.— No special terminology is necessary in lower incisor descriptions.

Lower deciduous premolar.— The  $DP_{\overline{4}}$  is an elongate tooth, usually broader posteriorly than anteriorly (Text-fig. 3A). It possesses either one broad or two narrow posterior roots and a narrow anterior one. Several possible schemes of homology can be drawn between the cusps of the geomyine  $DP_{\overline{4}}$  and the entoptychine  $DP_{\overline{4}}$  described by Rensberger (1971) or those of the Gregorymys  $DP_{\overline{4}}$  described by Wood (1936). However, none of the possible schemes is

totally satisfactory. At this time it seems safer to describe and name the cusps of the geomyine  $DP_4$  without attempting to force them into homology with those of other geomyids. The names applied to these cusps are based on comparison with the basic cusp pattern of other lower geomyine teeth and the assumptions that a strong posterior cingulum has been developed and that the protolophid has shifted anteriorly with the addition of a cusp (the neoconid, new name) in the space between it and the hypolophid.

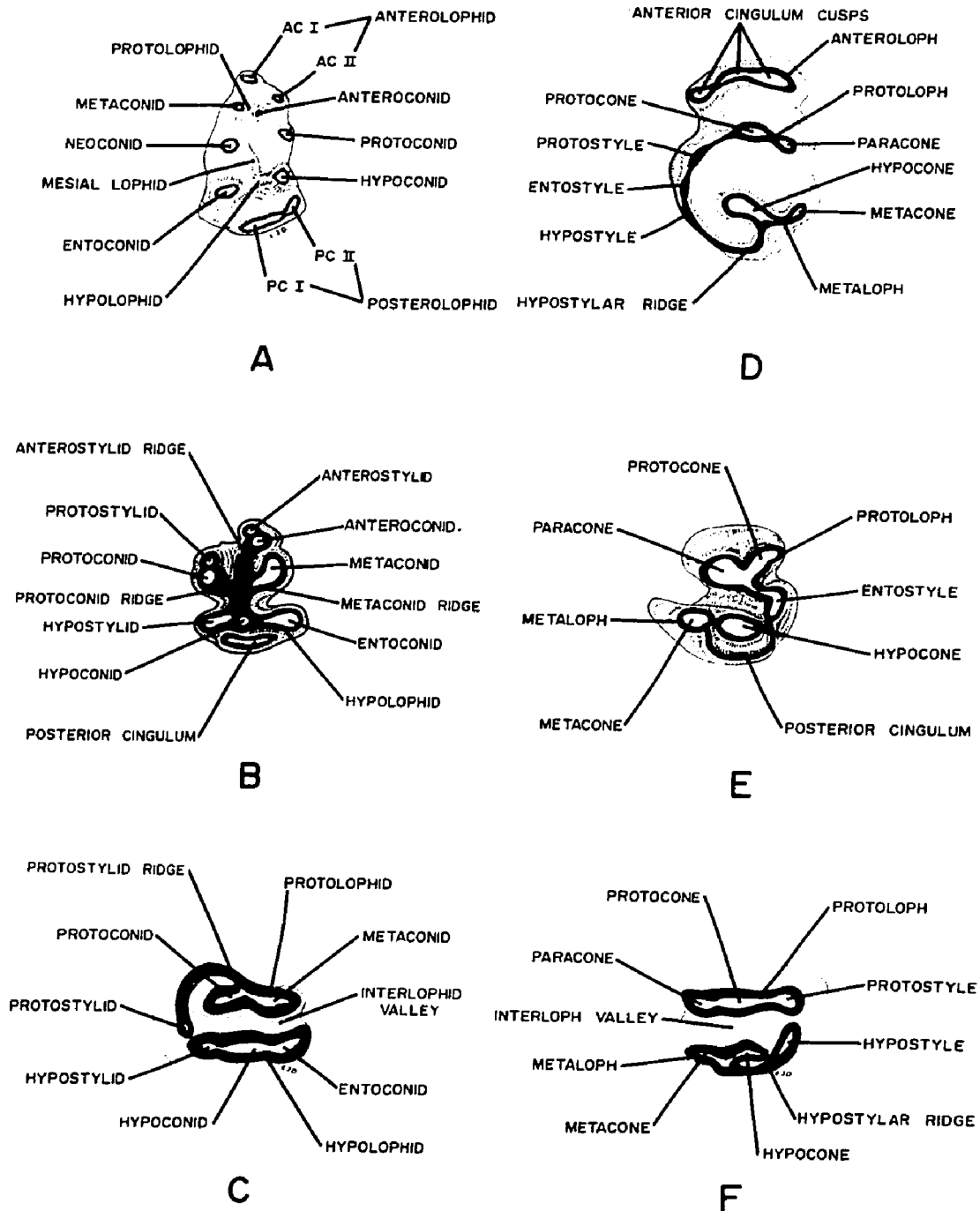
The occlusal pattern of the  $DP_4$ , as a whole, varies from highly cuspsate to highly lophodont. The bicuspsate posterior cingulum, or posterolophid, is moderately to very strongly developed. The lingual cusp, PC I, is larger and laterally elongate and the labial cusp, PC II is nearly equidimensional or slightly anterolabially elongate. The hypolophid is separated from the posterolophid by a deep valley except for a low connection between the hypoconid and PC II. A lower, secondary ridge may connect the entoconid to PC I. The hypoconid and entoconid are nearly round in outline and are connected by a transverse ridge to form the hypolophid. Anterior to the entoconid is the neoconid, mentioned above, which appears to have filled the gap between the protolophid and hypolophid. The neoconid is also nearly round in outline. Anterior to it is the rounded metaconid which is connected by a ridge to the more posteriorly placed, oval protoconid

to form the protolophid. An anteroposteriorly directed mesial lophid connects the approximate midpoint of the protolophid to that of the hypolophid. The mesial lophid also connects to the medial side of the neoconid. A minute cusp, considered to represent the anteroconid, is sometimes present where the mesial lophid connects to the protolophid. The anterolophid usually bears two cusps; the lingual is termed AC I and the labial, AC II. They are normally connected by a low ridge and AC II is often similarly connected to the anteroconid. The metaconid and AC I are occasionally connected by a very low ridge.

With the exception of the minute anteroconid, all cusps are on the margin of the tooth. There is no evidence for the presence of a protostylid or a hypostylid but if they were ever present in an ancestral form, they may have merged with the protoconid and hypoconid, respectively, in the known Geomyinae.

Lower fourth premolar.— The  $P_4$  is a bicolumnar tooth with a medial connection, the isthmus, between the columns (Text-fig 3B). The anterior column is almost round in outline; the posterior one is anteroposteriorly flattened. The anterior column bears the cusps of the protolophid (metaconid, protoconid, and protostylid), an anteroconid, and an anterostylid. The unworn occlusal pattern on the anterior column consists of three cusped ridges radiating from the posteromedial part of the column. The lingual, or metaconid ridge, terminates at the metaconid; the labial,

Text-fig. 3- Cusp nomenclature. A,  $RDP_{\bar{4}}$ . B,  $LP_{\bar{4}}$ . C, left lower molar. D,  $LDP_{\bar{4}}$ . E,  $RP_{\bar{4}}$ . F, right upper molar.



Text-figure 3.

or protoconid ridge, includes the protoconid and proto-stylid; and the medial, or anterostylid ridge, includes the anteroconid and anterostylid. The protoconid ridge usually runs slightly lingual from the point of confluence of the ridges and is closer to the metaconid ridge than to the anterostylid ridge. A low ridge often connects the protoconid and protostylid, enclosing a shallow pit. In advanced geomyines, a large number of accessory cuspules encrust the surface of the tooth and obscure the primary pattern.

The occlusal pattern on the posterior column consists of a tricuspid hypolophid and a variably developed posterior cingulum. From lingual to labial, the cusps of the hypolophid are entoconid, hypoconid, and hypostylid. The entoconid and hypostylid are transversely elongate and the hypoconid is subcircular in outline. The hypoconid, when present, occurs at the posterior end of the isthmus. The posterior cingulum, when present, varies in strength of development and degree of cuspidity. Generally speaking, it is better developed in the more advanced forms. Accessory cuspules also tend to occur on the posterior column in advanced forms but usually less than on the anterior column.

Dentine tracts develop on the lingual and labial sides of both columns with increasing hypsodonty of the tooth and, after the occlusal pattern is worn away, interrupt the enamel pattern to form four enamel plates; anterior, poste-

rior, labial, and lingual. The labial and lingual plates outline the reentrants which form the sides of the isthmus and may be V, U, or squared-U in shape and in advanced forms, they are filled with cement.

Lower molars.- The lower molars have an ovoid occlusal outline, usually with the lingual margin relatively pointed and the labial margin relatively broader and sometimes flattened. Their occlusal pattern is basically bilophodont. A small hypostylid, a larger, laterally elongate entoconid, and a medial hypoconid make up the hypolophid (Text-fig. 3C). In advanced forms, the hypostylid may become lost or merged with the hypoconid. The protolophid is separated from the hypolophid by the interlophid valley and consists of the posterolabially elongate protoconid and posterolingually elongate metaconid which join at their anteromedial margins, a small protostylid which is usually well separated from the protoconid, and a protostylid ridge which runs anteriorly from the protostylid then turns lingually to connect with the juncture of the protoconid and metaconid. The protostylid ridge appears to have developed from a condition similar to that found in entoptychines where there is an arcuate anterolabial cingular cusp (Rensberger, 1971). In geomyines the anterolingual end of this cusp is elongated to connect with the protoconid and metaconid while the posterolabial end, also elongated, connects with the protostylid. Within the Geomyinae there is normally no trace of cusp development on

this ridge except for the protostylid.

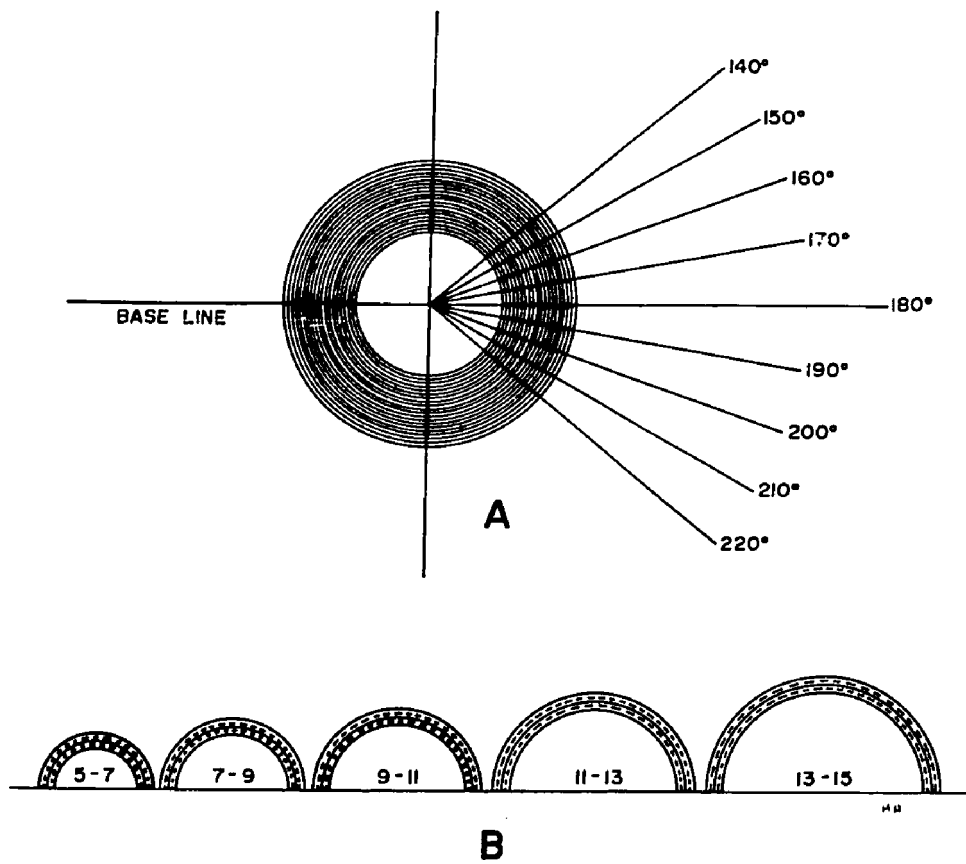
With wear, the protolophid and hypolophid may connect in two ways: by means of a ridge between the protostylid and hypostylid or a ridge near the midpoints of the lophids. A connection is not considered to be complete until all of the ridge has undergone wear. Usually, both connections occur in the  $M_1$  and  $M_2$  but one may develop at an earlier stage of wear than the other.

Dentine tracts are absent or very poorly developed in primitive forms. They first develop on the lingual and labial sides of the molars, separating an anterior enamel plate from a posterior one. The anterior enamel plate is progressively reduced in most advanced forms until it is only present in very early stages of wear.

Upper incisor.-- Geomyine upper incisors are usually grooved on their anterior surfaces. The most common grooves occur either near the middle of the incisor, medial grooves, or near the lingual margin, lingual grooves.

Measurements of length in rodent incisors, whether taken in a straight line or along the curvature, are misleading because their length is a function of two different factors: the gross size of the incisor and the amount of arc through which the incisor grows from root to tip. A geomyine upper incisor grows in a very uniform arc with a uniform radius of curvature. This radius of curvature provides a good estimate of gross size and was measured by constructing a chart of arcs having radii of curvature

Text-fig. 4- Graphs for measuring incisor parameters. See text for use. A, subtended angle. B, radius of curvature. Solid semicircles indicate even millimeters, dashed semicircles indicate half-millimeters. Numbers within each group indicate the range of radii of that group.



Text-figure 4.

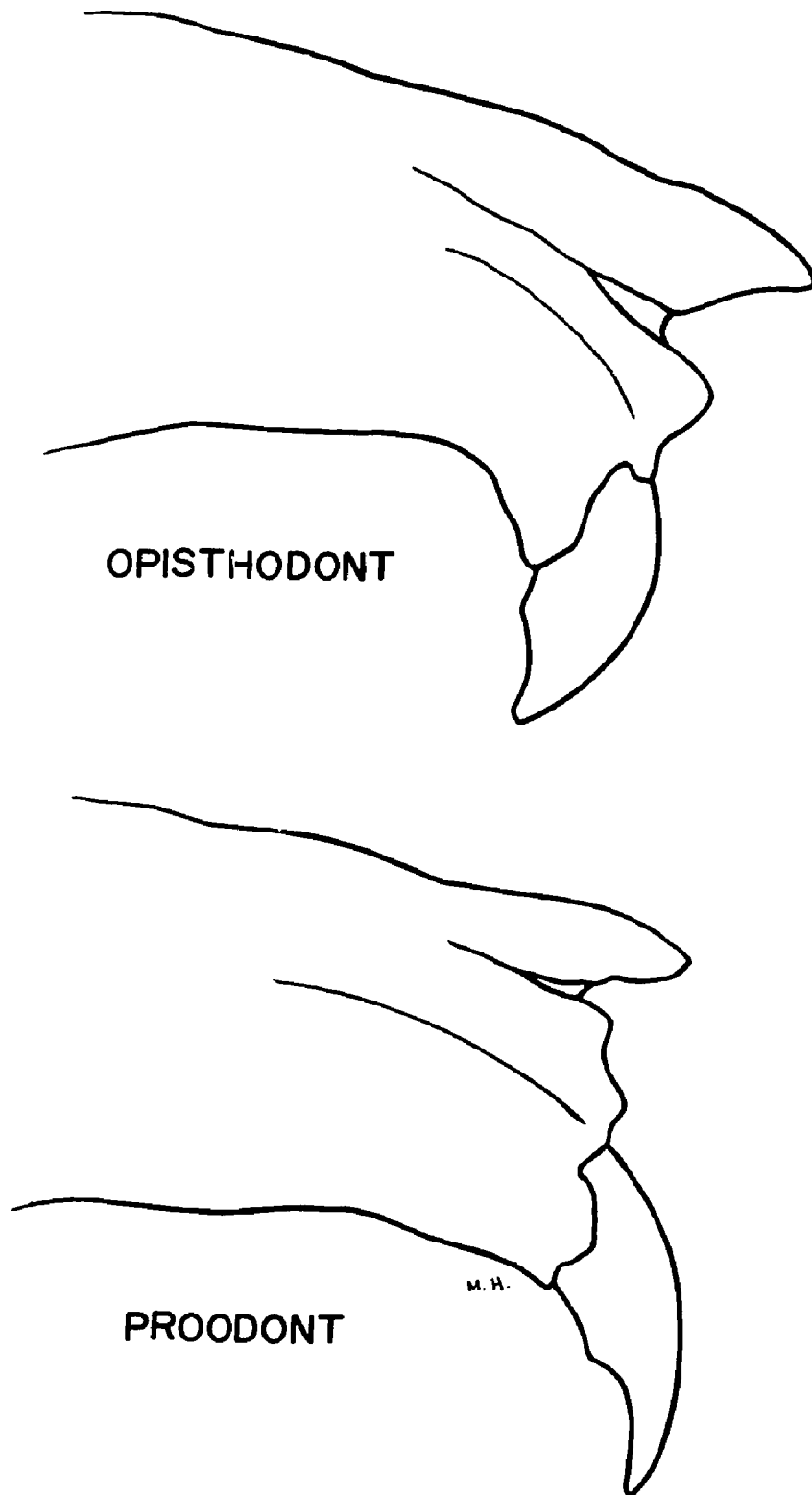
differing by 0.5 mm increments (Text-fig. 4B). The outer margin of each incisor was compared to the chart by matching it to the arc which best fit it. An estimate of the arc through which an incisor grows was made by constructing another chart of similar arcs divided by radii  $10^{\circ}$  of arc apart (Text-fig. 4A). The incisor was aligned with the arc matching its external curvature and with one end on the baseline. The angle subtended by the arc of the incisor was then determined to the nearest  $10^{\circ}$  by the radian closest to the other end.

This measure of the subtended angle appears to provide a good estimate of relative proodonty or opisthodonty (Text-fig. 5). Proodont incisors are recurved posteriorly and opisthodont incisors are projected anteriorly (HersHKovitz, 1962).

Upper deciduous premolar.- The basic pattern of the DP<sup>4</sup> consists of three transverse lophs separated by anterior and posterior interloph valleys (Text-fig. 3D). The most anterior loph, the anteroloph, bears two or three anterior cingulum cusps. A low lingual ridge usually connects the anteroloph to the protoloph which bears a large medial protocone and a smaller labial paracone. On unworn specimens, conspicuous enamel loops, directed anterolabial and anterolingual, show the respective positions of the metacone and the larger hypocone. The hypostylar ridge connects to the posterior margin of the juncture of these cusps, runs posteriad for a short

Text-fig. 5- Opisthodont and proodont rodent incisors.

After Hershkovitz (1962, fig. 19).



Text-figure 5.

distance, then curves anterolingual to connect with the protoloph. The cusps on this ridge are difficult to make out on the available material but three very small ones appear to be present. These are tentatively named, from anterior to posterior: protostyle, entostyle, and hypostyle. Dentine tracts may occur on the lateral margins of the protoloph.

Upper fourth premolar.- The  $P_4$  is bicolumnar with the anterior column bearing the protoloph (Text-fig. 3E). In primitive forms, an anterior groove separates the protocone and paracone. In more advanced forms, these cusps usually cannot be distinguished. A ridge runs posterolingual from about the midpoint of the protoloph to a lingual cusp (entostyle) on the isthmus between the columns. The homologies of this cusp are not clear; it may be the result of fusion of several styler cusps, but it is herein termed the entostyle. The isthmus gradually shifts labial to a more or less medial position with wear. The metaloph, on the posterior column, bears two large cusps: a labial metacone and a medial hypocone. A posterior cingulum usually attaches to the metacone and the lingual end of the hypocone. In advanced forms, small irregular cuspules often encrust part or all of the occlusal surface. Dentine tracts occur on the labial and lingual sides of both columns in advanced forms, dividing the enamel into anterior, posterior, labial, and lingual plates. The posterior plate is usually reduced or absent

in advanced forms. On worn specimens, the reentrants between the columns may be V, U, or squared-U in shape, and in advanced forms, they are filled with cement.

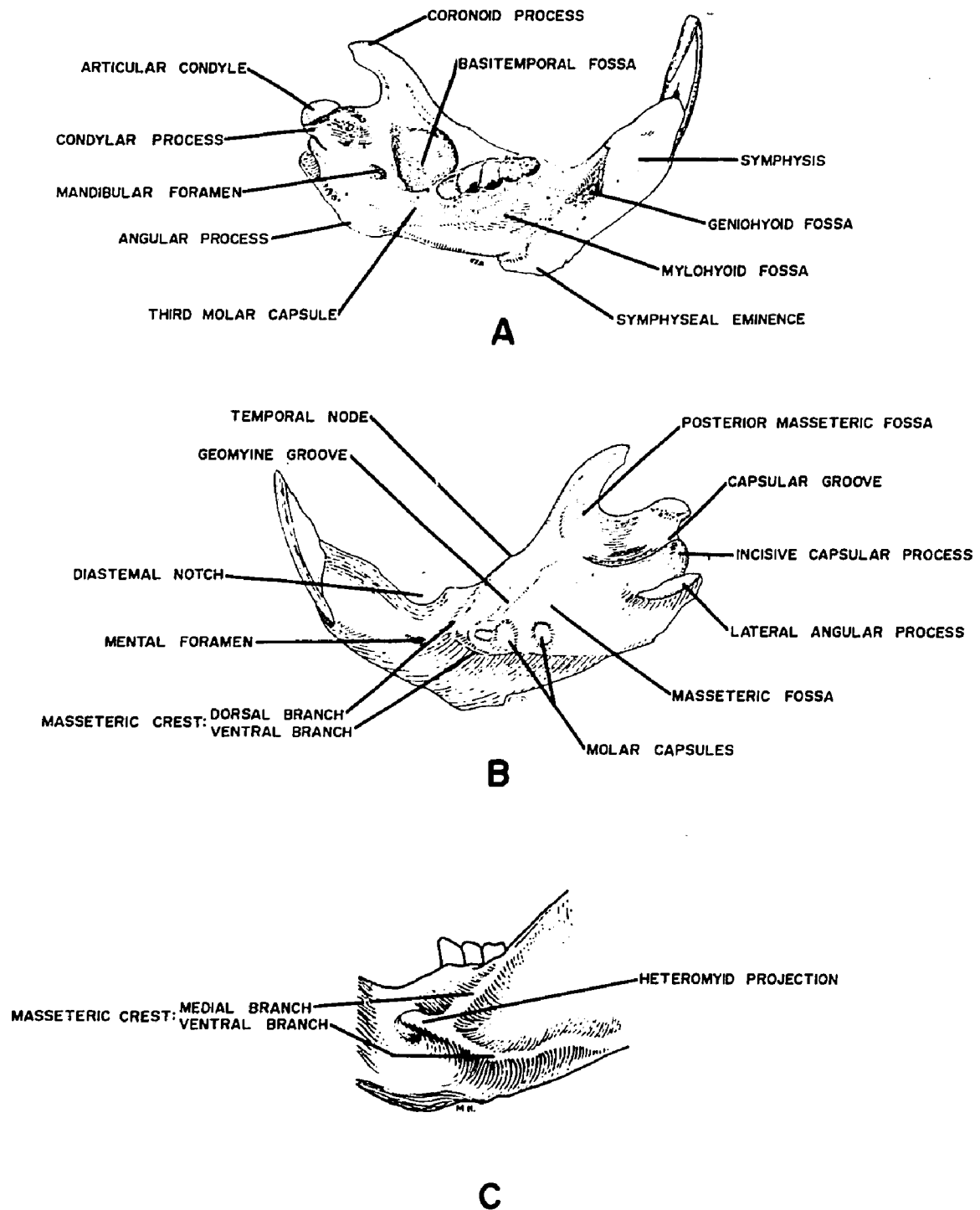
Upper molars.- The upper molars have an anterior protoloph and a posterior metaloph separated by an interloph valley (Text-fig. 3F). The protoloph bears three cusps which are usually almost in exact transverse alignment. These are, from labial to lingual: paracone, protocone, and protostyle. The ovoid metacone and hypocone are connected to each other on the metaloph. The hypostylar ridge joins these cusps at their point of confluence, runs linguad along the posterior margin of the tooth, turns anteriad along the lingual margin, and terminates at the hypostyle which varies in position from adjacent to the protostyle to adjacent to the hypocone. Various interloph connections extending across the interloph valley may occur. The strongest is usually the one through the protostyle and hypostyle. The lophids are not termed connected until the entire surface connecting them shows wear. Dentine tracts occur on the lingual and labial sides of the teeth in advanced forms and the  $M^3$  of very advanced forms commonly has posteromedial dentine tracts. The posterior enamel plates of  $M^1$  and  $M^2$  and the posterolingual enamel plates of  $m^3$  may be reduced or absent in advanced forms. Encrusting cuspules are rare on the  $M^1$  and  $M^2$  but common on advanced  $M^3$ 's.

Mandible.- Text-figure 6 illustrates the mandibular

terminology. Features named for the insertion of various muscles were verified by dissection of a recent Geomys pinetus.

On the internal surface (Text-fig. 6A), the most anterior portion of the mandible is occupied by a large symphysis. This extends posteriorly to form the symphyseal eminence which provides the area of insertion for the digastric muscle. The geniohyoid fossa, posterior to the symphysis, is the area of insertion for the muscle of the same name. The mylohyoid muscle originates on the large mylohyoid fossa, ventral to the alveoli for the cheek teeth. The basitemporal fossa, named by Russell (1968a), serves as the area of insertion for part of the deeper portion of the temporalis muscle. The mandibular foramen lies posterior to the basitemporal fossa. Dorsal to the basitemporal fossa is the coronoid process which serves as the area of insertion for the remainder of the deeper portion of the temporalis muscle along its lingual side and as the area of insertion for the shallow part of the temporalis along its anterior margin. The condylar process, posterior to the coronoid process, terminates in the articular condyle. The external pterygoid muscle attaches to a small fossa just anterior to the articular condyle. The internal pterygoid inserts on the lingual side of the angular process which is on the posteroventral margin of the mandible. The third molar capsule occurs just posteroventrad to the alveolar opening for that

Text-fig. 6- Mandibular nomenclature. A, medial surface of left mandible in advanced type (Geomys). B, lateral surface of left mandible in advanced type (Geomys). C, lateral surface of left mandible in primitive type (Pliogeomys).



Text-figure 6.

tooth.

In lateral view (Text-fig. 6B), beginning from the posteroventral part of the mandible, the lateral angular process serves as the area of insertion for a portion of the posterior part of the deep lateral masseter. The rest of this muscle inserts on the incisive capsular process, just dorsal to the lateral angular process. The capsular groove lies between the incisive capsular process and the condylar process. Much of the depressed semicircular region outlined by a rim extending from the tip of the coronoid process to the dorsal margin of the incisive capsular process, and including the condylar process, is the area of attachment for the posterior part of the medial masseter. A strong ridge extends from the angular process to a point about midway of the dorsal and ventral mandibular margins and about even with the anterior margin of the  $P_4$ . It then turns posterodorsad to the anterior margin of the ascending ramus and toward the coronoid process. The two parts of this ridge are termed the ventral and dorsal branches of the masseteric crest. The area between these ridges and extending posterior to the temporal node, posterior masseteric fossa, incisive capsular process, and lateral angular process serves as the area of insertion for several muscles of the masseter group and is termed the masseteric fossa. The superficial masseter inserts on the ventral and posterior margins of the mandible. Several features occur within the masseteric

fossa. Molar capsules are present for the bases of the first and second molars. A small capsule may be present for the lateral margin of the  $P_4$ 's posterior column. A shallow groove, the geomyine groove, occurs just ventral to the dorsal branch of the masseteric crest and is the primary insertion for the anterior part of the medial masseter. A similar groove-insertion for the anterior part of the medial masseter was described by Repenning (1968) in the microtine rodents. Secondary insertion for the anterior part of the medial masseter is provided by the surface between the geomyine groove and the dorsal branch of the masseteric crest anterior to the temporal node. The mental foramen is anterior to the anterior margin of the masseteric crest. A premolar capsule occurs just ventral to the anterior margin of the masseteric crest. The long diastema has a deep diastemal notch.

A different configuration of the anterior region of the masseteric crest (Text-fig. 6C), considered to be primitive, was present in the Nerterogeomyini and, presumably, in the ancestors to all the Geomyinae. The dorsal branch of the masseteric crest was absent and the geomyine groove was a ridge, termed the medial branch of the masseteric crest in these forms. The medial branch met the ventral branch to form a sharp anterodorsal projection, termed the heteromyid projection because it is typical of most heteromyids, extending anterior to the  $P_4$ . In forms which possessed the heteromyid projection, the mental

foramen usually occurred partially or wholly ventral to the projection. Advanced members of the Nerterogeomyini may possess other features, such as molar capsules, also present in advanced members of other lineages.

### Classification

Convenience, rather than estimates of degrees of relationships, dictated grouping all geomyoid rodents at the superfamily level rather than the family level. There have been recent suggestions that all geomyoid rodents should be grouped at the family level (e.g. Shotwell, 1967b). However, the use of the superfamily allows one more lower taxonomic level to indicate relationships. Where possible, suprageneric groups reflect lineages through time rather than evolutionary grades. The tribe Dikkomyini of Russell (1968a) is excluded with Dikkomys which is not a geomyine. Pliosaccomys sensu stricto (the other genus included in the Dikkomyini by Russell) is considered to be a member of the Geomyini. A new tribe, Nerterogeomyini, is erected to include the members of a separate lineage: Brachygeomys drewseyensis n. gen. and sp., Pliogeomys, and Nerterogeomys.

Russell (1968a) synonymized Nerterogeomys and Zygogeomys. Although the exact relationships of Zygo-  
geomys remain obscure, it certainly does not belong to even the tribe Nerterogeomyini. Russell's (1968a,b) synonymy of

Cratogeomys with Pappogeomys and of Heterogeomys and Macrogeomys with Orthogeomys is not followed here because examination of deciduous teeth and nearly unworn permanent teeth of these genera indicates that their relationships are probably more complex, although the former synonymy may well be correct.

### Systematic Descriptions

#### Family Geomyidae

Emended diagnosis.— Fossorial forms and their ancestors of the superfamily Geomyoidea. Members of the various lineages show increasing adaptation to a fossorial existence. Dental trends include a tendency to develop upper incisor grooves, to increase hypsodonty of cheek teeth, and to develop dentine tracts and reduce enamel plates on cheek teeth. Dental formula  $\frac{1}{1}, \frac{0}{0}, \frac{1}{1}, \frac{3}{3}$ . Known geologic range: late Oligocene? or early Miocene (Rensberger, 1971) to Recent. Restricted to North and Central America and northernmost South America.

#### Subfamily Geomyinae

Emended diagnosis.— Most recent group of geomyids to develop fossorial adaptations and the only one with living representatives.  $DP_{\frac{1}{4}}$  usually with bicusate anterior and posterior cingular lophids, protolophid and hypolophid well separated with neoconid between metaconid and entoconid, mesial lophid present.  $P_{\frac{1}{4}}$  bicolumnar with tri-

radiate ridge pattern on anterior column, medial connection between columns.  $M_1$  and  $M_2$  with cingular ridge connecting protostyle to entoconid and hypoconid, primitively with labial lophid connection. Upper incisors primitively smooth, usually strongly bisulcate in advanced forms except unisulcate in Thomomys (see Akersten, 1973).  $DP^4$  normally with multicusate anterior cingular loph, lingual ridge connecting protoloph and metaloph.  $P^4$  bicolumnar, anterior column bicusate, never with medial enamel lake, when unworn with lingual connection between columns, connection becoming medial with wear.  $M_1$  and  $M_2$  lack anterior cingulum, with cingular ridge connecting hypostyle to metacone and hypocone, primitively with lingual loph connection. Advanced  $M_3$ 's with extreme development and complication of posterior cingulum. Formation of dentine tracts on increasingly hypsodont cheek teeth with reduced numbers of roots and reduction of enamel plates characteristic of evolutionary sequences. The most advanced forms have evergrowing cheek teeth and a tendency to reduce or lose enamel on anterior surfaces of lower molars and on posterior surfaces of  $P^4$ ,  $M_1$ , and  $M_2$ . Mandible with tendency to develop arcuate ventral margin and to dorsally expand ascending ramus with advancing evolutionary grade. Modern forms with skull and body highly adapted to fossorial existence. Known geologic range: Clarendonian (early Pliocene) to Recent. Fossil and Recent forms known from North and Central America and extending into northern South

America.

### Tribe Geomyini

Emended diagnosis.-- Geomyines with basically lophodont  $DP_{\frac{4}{4}}$ 's in all but the most advanced forms, posterolophid of  $DP_{\frac{4}{4}}$  usually reduced. Advanced forms usually with strongly bisulcate upper incisors. All but most primitive genus, Pliosaccomys, with dentine tracts on hypsodont or evergrowing cheek teeth and with reduction or loss of enamel on anterior surface of lower molars and posterior surface of  $P_{\frac{4}{4}}$ , except in early wear stages. Some advanced forms with reduction of enamel on posterior surface of upper molars, many with elongate  $M^3$  caused by elaboration of posterior cingulum. Mandible shows tendency through time to expand ascending ramus dorsally and to develop arcuate ventral border. Except in primitive forms, mandible lacks heteromyid projection and has a geomyine groove instead of a medial branch of the masseteric crest. Mandible has a well developed dorsal branch of the masseteric crest and has the mental foramen anterior to the anterior margin of the masseteric crest. Primitive genera retain part of the medial branch of the masseteric crest and the heteromyid projection and develop the dorsal branch of the masseteric crest only slightly. They may have the mental foramen near or, rarely, just under the anterior margin of the masseteric crest. Known geologic range: Hemphillian (middle Pliocene) to Recent. Extinct genera:

Pliosacomys and Parapliosacomys. Extant genera: Geomys, Cratogeomys, Pappogeomys, Zygogeomys, Heterogeomys, Orthogeomys, and Macrogeomys. Known from North and Central America. Probably polyphyletic.

Genus Pliosacomys Wilson, 1936

Emended diagnosis.- Genotypic species Pliosacomys dubius Wilson (1936). Most primitive genus assigned to the Geomyini.  $DP_4$  basically lophodont with reduced posterolophid. Cheek teeth moderately hypsodont, rooted, lacking true dentine tracts, and without reduction of enamel plates. Occlusal patterns primitive.  $P_4$  with single root on each column.  $M_1$  and  $M_2$  with a large angular root, extending from the posterolabial corner through the posterolingual corner to the anterolingual corner, and a small anterolabial root.  $P_4$  with a large anterior root and two smaller posterior ones. Root pattern of upper molars unknown. Upper incisor without regular pattern of grooving. Mandible without arcuate ventral margin and with combination of primitive and advanced characters in area of masseteric crest. Symphyseal eminence small, angular process apparently relatively large, no true basitemporal fossa.

This diagnosis is taken from the genotypic species and Pliosacomys magnus (Kellogg) because none of the other forms which have been assigned to this genus by other writers can definitely be demonstrated to belong to it.

Pliosaccomys cf. P. dubius of Green (1956) and Pliosaccomys wilsoni of James (1963) are not geomyines. Brachygeomys drewseyensis n. gen. and sp. (= Pliosaccomys magnus (Kellogg), Shotwell, 1967b, in part) is herein assigned to the Nerterogeomyini. Pliosaccomys sp. of Shotwell (1967b) from UOloc. 2322 and 2323 (herein considered as gen. and sp. indet.) apparently possesses more hypsodont cheek teeth with moderately developed dentine tracts. Pliosaccomys? shotwelli n. sp. (= Pliosaccomys sp. of Shotwell, 1967b, from UOloc. 2500) and Pliosaccomys? sp. (= Pliosaccomys sp. of Shotwell, 1967b, from UOloc. 2347) may belong to this genus; the known material falls within the generic concept but the critical DP-<sup>4</sup>'s and mandibles are unknown. Pliosaccomys is known only from the Hemphillian of the Great Basin in North America.

Pliosaccomys dubius Wilson

Figure 1, A-N.

Pliosaccomys dubius Wilson, 1936, p. 20-29.

Pliosaccomys dubius Wilson, MacDonald, 1959, p. 875.

Pliosaccomys dubius Wilson, Russell, 1968a, p. 517.

Occurrence.- Smiths Valley local fauna, CIT locality 174, Lyon County, Nevada. Early Hemphillian (early middle Pliocene).

Materials studied.- (All CIT unless designated otherwise) Holotype: partial right mandible with  $P_4 - M_3$ , 1796;

partial right mandible with incisor,  $DP_4^-$ , partial  $M_1^-$ , 1810; partial left mandible with  $DP_4^- - M_3^-$ , 1807; partial left mandible with  $P_4^- - M_2^-$ , 1809; partial right mandible with  $P_4^- - M_2^-$ , 1804; partial right mandible with  $P_4^- - M_3^-$ , 1805; partial right mandible with  $M_1^- - M_3^-$ , 1806; partial left mandible with  $P_4^-$ , 1808; partial right mandible with  $M_1^- - M_3^-$ , 1803; partial palate with  $RP_4^- - RM_2^-$ ,  $LP_4^- - LM_1^-$ , 1798; partial palate with  $RP_4^- - RM_1^-$ ,  $LP_4^- - LM_2^-$ , 1799; partial right maxillary with  $P_4^- - M_2^-$ , fragment of  $M_3^-$ , 1800; partial left maxillary with  $P_4^- - M_1^-$ , 1801; partial rostrum with partial L incisor, partial  $P_4^-$ 's, 1797;  $P_4^-$ 's, LACM 33848-54;  $M_1^-$ 's or  $M_2^-$ 's, LACM 33855-56; R premaxillary fragment with incisor fragment, LACM 33857; miscellaneous skull fragments, LACM 17232.

Emended diagnosis.— As for the genus.

Lower incisor: The anterior surface of the lower incisor in CIT 1810, a very immature specimen, is slightly rounded at the tip and bears a faint longitudinal groove on its anterior surface. However, before the point where the tooth emerges from its alveolus, the anterior surface has become smooth and flat. I doubt that more than three mm of the incisor tip have been lost from wear. In all specimens which show part of the incisor, the lingual portion of the enamel band is relatively broader than in advanced geomyines.

Lower deciduous premolar: A partial left mandible, CIT 1807, bears a  $DP_4^-$  which is too worn to show any diagnostic

features but it agrees in size and general morphology with a slightly worn  $DP_{\frac{7}{4}}$  in CIT 1810. The arrangement of the occlusal pattern in this latter specimen is very similar to that of the  $DP_{\frac{7}{4}}$ , UO 24979, assigned to Brachygeomys drewseyensis n. gen. and sp. but the differences in detail are significant.

The most obvious difference is that the  $DP_{\frac{7}{4}}$  of Pliosacomys dubius is more lophodont while that of Brachygeomys drewseyensis n. gen. and sp. is more cusate. This difference continues in younger members of both lineages. The posterolophid is smaller in P. dubius than in B. drewseyensis and PC II is much lower in the former. The smaller posterolophid does not add appreciably to the posterior outline of the tooth so that there is no posterolabial notch as in B. drewseyensis. There is a low ridge in P. dubius instead of a pit in the valley separating the posterolophid and hypolophid. The rest of the cusps on the  $DP_{\frac{7}{4}}$  are lower than in B. drewseyensis. The medial lophid and its connecting ridges are relatively better developed in P. dubius. The anteroconid is well developed and the protoconid is anteroposteriorly elongate. AC I and AC II appear to be less well separated than in the  $DP_{\frac{7}{4}}$  of B. drewseyensis but this is not certain due to wear in the area. A low ridge connects AC I to the medial part of the protolophid. The labial portion of AC II is posteriorly elongate, approaching the protoconid. The features separating the  $DP_{\frac{7}{4}}$  of P. dubius and that of B. drewseyensis

seem rather minor compared to their similarities but some of these differences represent the early stages of differentiation into two separate lineages.

Lower fourth premolar: One specimen, CIT 1809, contains an unworn  $P_4$ . The anterior column has the typical triradiate occlusal pattern of ridges connecting to one another just anterior to the isthmus. The valleys which separate the ridges extend only a short distance down the anterior surface of the column. The valley separating the protoconid ridge from the anterostylid ridge is better developed than the one separating the metaconid ridge from the protoconid ridge; the anteroconid being closer to the metaconid than to the anterostylid. The anteroconid and metaconid show up as distinct cusps at the anterior ends of their respective ridges. The isthmus is very short in this specimen. The posterior column bears a laterally elongate entoconid and hypostylid and a prominent, circular hypoconid occurs where the isthmus joins the hypolophid. A small cusp, perhaps accessory, occurs on the posteromedial surface of the column. There is no trace of a posterior cingulum or of paired posterior projections, such as occur in several other slightly worn  $P_4$ 's. A few tiny bumps of enamel may represent the beginning development of the accessory cuspules which are so prominent on the  $P_4$ 's of advanced geomyines.

Considerable variation is present within the sample of  $P_4$ 's assigned to Pliosacomys dubius and, also, within any

sample of a particular tooth where more than a few specimens are known. The general occlusal outline of the posterior column in the worn  $P_4$ 's resembles a flattened oval in early wear, becoming broader and posteriorly rounded with advanced wear. The reentrants are generally squared U-shaped in early wear stages becoming V-shaped in later wear stages. Cement never occurs in the reentrants. Traces of the triradiate ridge pattern remain on the anterior column until wear is considerably advanced. A groove on the anterior surface of the tooth often persists until late wear stages. This groove is an extension of the valley between the protoconid ridge and the anterostylid ridge. After this groove is worn away, the anterior column becomes almost circular in outline, slightly longer than wide.

In the holotype, CIT 1796, the triradiate pattern is still present on the anterior column but a labial pit is present, apparently in the middle of the anterostylid ridge. The posterior column bears a pair of posterior projections as does the  $P_4$  of CIT (the information regarding CIT 1802 is taken from Wilson (1936, pl. 2, fig. 1) as the specimen apparently cannot be located.) These paired projections may represent an early stage in the development of a posterior cingulum. The sample shows considerable variation in the shape of the reentrants, shape and width of the isthmus, and the development of the groove on the anterior surface of the anterior column.

No true dentine tracts are present, but, where the

basal margin of the enamel cap is visible, there are small dorsal inflections on the lingual and labial sides of the columns, the places at which dentine tracts form in more advanced geomyines. On the lingual side of the posterior column in CIT 1805, a small and sharp flexure of the enamel cap could be termed a dentine tract. Since no isolated  $P_4$ 's are available and it is impossible to remove them from the known mandibles without causing serious damage, I am unable to determine the root pattern. However, all other known geomyines with rooted cheek teeth possess two roots on the  $P_4$ , one per column.

Lower molars: The  $M_1$  and  $M_2$  of Pliosaccomys dubius have the basic geomyine pattern but they display considerable variation in the development and sequence of lophid connections. The three cusps of the hypolophid occur in almost exact alignment. No known specimens are unworn enough to definitely show the relative sizes of the cusps except that the hypostylid is the smallest. The hypoconid and entoconid appear to have been subequal with, perhaps, the former slightly larger. In the  $LM_1$  of CIT 1807, a large cusp is present anterolabial to the hypostylid and contiguous with it. The protolophid consists of a large oval protoconid and metaconid, joined anterointernally with each other and with a very prominent protostylid ridge. The protostylid ridge curves posterolabial and ends at the protostylid which varies from very prominent to almost indistinguishable from the ridge. In many specimens, the

posterolabial portion of the protoconid connects to the protostylid ridge with moderate wear, forming a shallow enamel lake.

The proximity of the protostylid to the hypostylid varies from almost connected to as far apart as the remainder of the lophids. There is a trend within each lower dentition that the stylids are closer together in the  $M_1$  than in the  $M_2$ . Teeth in which the stylids are close to one another develop a very early labial lophid connection with a medial connection developing much later. The farther apart the stylids, the later the labial connection; hence, some specimens have a medial connection occurring almost simultaneously with (or even slightly earlier than) the labial one. A strong groove, the remains of the interlophid valley, persists on the lingual side of the teeth until very late wear stages. This groove results in a sharp inflection of the occlusal enamel outline on the lingual side. In final wear stages, the occlusal outline becomes approximately oval but somewhat lingually pointed. The base of the enamel cap shows variously developed inflections on the lingual and labial sides. The best developed of these, the lingual inflections on the  $M_1$  and  $M_2$  of CIT 1804, appear to be large enough to merit the term "dentine tracts" but it is slightly possible that they are artifacts of abrasion. At any rate, the occlusal enamel pattern is definitely interrupted on the lingual side in these two teeth. All lower molars have the ventral margin

of the enamel cap higher anteriorly than posteriorly. The two isolated lower molars in LACM 17232 show that the root pattern for the  $M_1$ 's and  $M_2$ 's consists of a small antero-labial root and a large root extending along the margins of the tooth from the posterolabial corner through the posterolingual corner to the anterolingual corner. It is not certain whether these isolated teeth are  $M_1$ 's or  $M_2$ 's but it is probably safe to assume that both have the same root pattern.

The known  $M_3$ 's have an occlusal pattern very similar to that of the  $M_1$  and  $M_2$  except that the stylids are always well separated and there is no discrete labial lophid connection. The  $M_3$ 's are also considerably smaller. The initial lophid connection is medial, gradually widening with wear until the lophids are completely connected. Both lingual and labial grooves, remnants of the interlophid valley, remain on the surface of the teeth until late wear stages. Both result in enamel flexures of the occlusal pattern, the lingual persisting in later wear stages than the labial. In very late wear stages both flexures disappear and the occlusal outline becomes a lingually pointed oval. No definite trace of dentine tracts or basal flexures of the enamel cap are known in the  $M_3$  but the anterior, labial, and lingual portions of the enamel cap are thinner than the posterior portion. The root pattern cannot be determined.

Upper incisor: Only two partial incisors in premaxillaries, CIT 1797 and a specimen included in LACM 17232, can

be assigned to Pliosaccomys dubius. The anterior surface of the former bears three faint grooves, that of the latter is smooth. The enamel of both is quite thin. Both are broken just beyond the premaxillaries, making further comparisons and descriptions very difficult. In neither specimen is it possible to measure the radius of curvature or angle subtended.

Upper deciduous premolar: Unknown.

Upper fourth premolar: The only known unworn  $P_4^4$  occurs in CIT 1800. The details of the occlusal pattern are somewhat obscured, especially on the metaloph, by encrusting cuspules. The protoloph appears to consist of a large paracone and a smaller protocone, indistinctly separated. The prominent entostyle is separated from the medial portion of the protoloph by a narrow valley and connects to the lingual end of the metaloph. The hypocone is larger in diameter than, but equal in height to, the metacone. A very irregular posterior cingulum connects to the metaloph between the metacone and hypocone and, lingually, between the hypocone and entostyle. On the posterior column, only the metacone is free of encrusting cuspules.

Considerable variation exists among the worn  $P_4^4$ 's. Some have a single groove on their anterior surfaces, probably resulting from a stronger separation of the protocone and paracone than in CIT 1800. Several even have two anterior grooves, giving an apparent three-fold division to the protoloph. Except for enamel inflections caused by the

anterior grooves, the occlusal outline of the anterior column varies from a flattened oval to a slightly rounded triangle. The posterior column is posteriorly convex with a flat anterior margin. The isthmus occurs at the lingual margin in early wear stages and moves mediad with advancing wear, becoming just lingual of medial in the most-worn specimens available. Reentrants vary from V- to U-shaped and have no trace of cement. Viewed from the side, the anterior margins of the  $P_4$ 's vary from straight through straight with an anterior basal projection to strongly concave. Incipient dentine tracts occur at the base of each column at the lingual and labial sides and are better developed than on the  $P_4$ 's. The enamel on the posterior surface of the posterior column does not extend as far basally as it does on the anterior surface. The basic root pattern consists of one large anterior root and two small posterior roots. These may be connected or fused in various ways.

Upper molars: The sample of upper molars is too small to give an indication of variation. Only one specimen, CIT 1800, retains an almost unworn occlusal pattern on the  $M_1^1$  and  $M_2^2$ . These are almost exact mirror images of the  $M_1^-$  and  $M_2^-$ . The cusps of the protoloph occur in transverse alignment with the protocone being the largest and the paracone and protostyle, apparently subequal. The metacone and hypocone are oval enamel loops joined at their postero-internal margins. They appear to be more anteroposteriorly

flattened than the protoconid and metaconid on the lower molars. The hypostylar ridge connects to the metacone and hypocone at their point of juncture and terminates at a prominent hypostyle at the lingual end of the interloph valley. The lingual end of the hypocone with wear connects to the hypostylar ridge, isolating a small enamel lake. The interloph valley is deep. The first loph connection occurs lingually because the hypostyle and protostyle are very close to each other. A labial connection would appear just before the obliteration of the interloph valley by wear. The right  $M_2^2$  of CIT 1798 shows this condition. A pronounced groove on the labial margin of each tooth represents the remains of the interloph valley and persists until the tooth is worn to the roots. An inflection of the base of the enamel cap is present on the lingual margin of each tooth. The labial groove extends too far toward the base of the tooth to permit a labial inflection of the enamel cap. The posterior portion of the enamel cap does not extend basally as far as does the anterior portion. The root pattern of the upper molars cannot be determined from the known material.

A fragment of an  $M_3^3$  is present in CIT 1800. It only shows that this tooth is more nearly circular in outline than  $M_1^1$  or  $M_2^2$ .

Mandible: The preserved portions of the mandibles also exhibit a high degree of variability. Starting from the posterior portion of the medial side, the coronoid and

condylar processes are not preserved in any specimen. A true basitemporal fossa is not present but there is a variably developed, shallow depression on the internal surface of the ascending ramus opposite the posterior molars and extending posterior to the  $M_3$ . The mandibular foramen occurs ventral to the posterior portion of this depression. This is relatively ventral and anterior to the position of the mandibular foramen in living Geomys. In CIT 1803, a second depression, possibly the attachment for the external pterygoid, occurs posterior to the first-mentioned depression. The angular process is missing from all specimens, but the traces which remain indicate that it was probably better developed than in Geomys and extended anterior to under the posterior margin of the  $M_3$ . The mylohyoid and geniohyoid fossae are very well developed. The symphysis is large and massive but the symphyseal eminence is small.

On the external surface, only CIT 1803 has much of the area posterior to the masseteric fossa preserved. The lateral angular process is missing but it must have been very small at best. The capsular process and capsular groove are only partially preserved but are well developed. Presence or absence of a temporal node cannot be determined. No trace exists of molar or premolar capsules, as would be expected in a relatively brachydont form. The diastemal notch is shallow. The configuration of the masseteric crest shows a variable blend of primitive and advanced

characteristics. The ventral branch is well developed while the medial varies from a well developed ridge to a ridge anteriorly and a groove posteriorly. A heteromyid projection is present but the mental foramen occurs from just anterior to well anterior of it. The dorsal branch of the masseteric crest is poorly to moderately developed. It shows up best in CIT 1804 and 1808, where it attaches to the anterior end of the heteromyid projection, extends dorsad to the base of the  $P_{\overline{4}}$ , then turns posteriad. A shallow fossa occurs just dorsal to the heteromyid projection. The above blending of primitive and advanced characteristics suggests that Pliosacomys dubius is in the early stages of developing an advanced geomyine mandible.

Discussion.- Much has been written about the relationships of Pliosacomys dubius with the rest of the Geomyoidea. In the type description, Wilson (1936) concluded that it probably represented a structural stage through which the ancestral geomyine passed, but that it could not be in the direct line of ancestry because of its late appearance in the geologic record. Hibbard (1954) considered Pliosacomys to be related to Thomomys but possibly not in the main evolutionary stock. He also noted similarities between the  $DP_{\overline{4}}$ 's of Pliosacomys dubius, Pliogeomys, and Nerterogeomys. Black (1961) suggested that Pliosacomys and Dikkomys represented two distinct lines of geomyine evolution, one of which may have led to the living geomyines. He also noted similarities between Pliosacomys

and Thomomys. Russell (1968a) concluded that Pliosacomys was an offshoot of the stock leading to Thomomys.

The cusp morphology of the cheek teeth, particularly of the  $DP_{\frac{1}{4}}$ ,  $DP_{\frac{1}{2}}$ , and the triradiate anterior column on the  $P_{\frac{1}{4}}$ , show conclusively that P. dubius should be included within the Geomyinae and that it has no close relationship with the Dipodomyinae or with any other heteromyid. Figure 8R shows a  $DP_{\frac{1}{4}}$  of Prodipodomys cf. P. centralis (P. centralis = Prodipodomys rexroadensis (Skinner and Hibbard, et al., 1972)) from the early Blancan for comparison with geomyine  $DP_{\frac{1}{4}}$ 's. Wood (1935b) illustrates the occlusal patterns of permanent and deciduous premolars from many fossil and recent heteromyids, none of which are close to the occlusal patterns found in geomyines. The preserved portions of the mandible also indicate a closer relationship to the Geomyinae than to any heteromyid. Additional confirmation is present in the characters of the rostrum and palate (see Wilson, 1936, for a discussion of these elements). As shown elsewhere in this paper, Dikkomys is not even a geomyine, much less related to Pliosacomys.

Pliosacomys dubius does provide an almost ideal structural ancestor for subsequent geomyines except for members of the Nerterogeomyini. The dentitions and mandibles of known late Pliocene and early Pleistocene Geomyini can easily be derived from P. dubius. The Thomomyini might also be derived from P. dubius; no known characteristic of either obviate this possibility, but structural inter-

mediates are lacking. For this reason, P. dubius is assigned to the Geomyini rather than to the Thomomyini. If P. dubius is not directly ancestral to some or all of the later Geomyine, it must be very close to the main stock. The argument that P. dubius occurs too late in time to be ancestral to later geomyines is rejected until more advanced forms are discovered in equivalent or older deposits.

Unfortunately, no postcranial material is known for this taxon so that its mode of life is difficult to determine. The only apparent clues are in the relatively stout construction of the mandible and the large, strong symphysis. These indicate that the mandible was subject to great stress, such as the stress developed in the digging activities of the modern, fossorial geomyines.

The great variability exhibited in this taxon lends itself to two interpretations since the material was collected from a single locality. The specimens either represent a single, highly variable species or they represent more than one species. As Wilson (1936) points out, if any taxonomic splitting were to be done on this material, too many new taxa would result, almost one for each specimen. Therefore, this material is herein considered to represent one highly variable species.

As noted in the discussion of Pliosacomys magnus, this species may prove to be a senior synonym of Pliosacomys dubius when additional material of both are known.

Pliosacomys magnus (Kellogg)

Figure 1, 0; 2, A-H.

Diprionomys magnus Kellogg, 1910, p. 434-435.Cupidinimus magnus (Kellogg), Wood, 1935b, p. 145.Dipodomys or Prodipodomys magnus (Kellogg), James, 1963, p. 106.Pliosacomys magnus (Kellogg) Shotwell, 1967b, p. 30-33, in part.Occurrence.- Thousand Creek local fauna, UCMPlocs 1103 and V69114, Humboldt County, Nevada. Early Hemphillian (early middle Pliocene).Materials studied.- (All UCMP) Holotype: fragmentary left mandible with  $P_4 - M_2$ , 12567. Paratype: partial left mandible with  $P_4$ , 12568;  $RP_4$ 's - 99193-94;  $P_4$ 's - 99195-200;  $M_1$ 's or  $M_2$ 's - 99522-23;  $M_3$ , 99524;  $2P_4^1$ 's, 84686;  $P_4^1$ 's - 99525-30, 99601-04;  $M_1^1$  or  $M_2^1$ , 99605.Emended diagnosis.- Known material not significantly different from Pliosacomys dubius except that  $P_4$  may have a weak posterior cingulum. May be conspecific with P. dubius but not enough material is available to make a judgment.Lower incisor: Unknown.Lower deciduous premolar: Unknown.Lower fourth premolar: Two  $P_4$ 's, UCMP 99193 and 99194, remain unworn. The differ somewhat from each other and could represent different taxa. UCMP 99193 has an occlusal

pattern very similar to the unworn  $P_4$  of Pliosacomys dubius with a prominent anteroconid closely appressed to, but distinct from, the anterostylid. It differs from P. dubius in that the posterior cingulum is present, although very weak. The anteroconid of UCMP 99194 is reduced and connected to the anterostylid. This occlusal pattern could easily develop into that shown in the least worn known  $P_4$  of Brachygeomys drewseyensis n. gen. and sp. UCMP 99194 also differs from UCMP 99193 in lacking any trace of a posterior cingulum, in being more hypsodont, and in having sharper reentrants. None of the worn  $P_4$ 's has enough of the occlusal pattern remaining to determine if the differences between the unworn specimens are the result of variation or the presence of two taxa. There do appear to be intermediate forms as far as hypsodonty and sharpness of reentrants are concerned. The  $P_4$  in the holotype mandible resembles UCMP 99193 in being relatively brachydont and having broader reentrants.

Lower molars: All  $M_1$ 's or  $M_2$ 's are so worn that the occlusal cusp pattern has disappeared. Their root patterns and the outlines of their occlusal surfaces are similar to those of Pliosacomys dubius. The  $M_3$  is too worn to yield useful information.

Upper incisor: Unknown.

Upper deciduous premolar: Unknown.

Upper fourth premolar: None of the  $P_4$ 's retains any of the original occlusal pattern. The observable characteris-

tics of these specimens do not distinguish them from comparably worn  $P_4$ 's of Pliosacomys dubius. They do appear to differ from the  $P_4$ , UO 24436, of Brachygeomys drewseyensis n. gen. and sp. illustrated by Shotwell (1967b, fig. 18, A, B). To judge from the illustrations (I did not see the specimen), the  $P_4$  of B. drewseyensis is very angular in occlusal outline and possesses a broader anterior column.

Upper molars: The only upper molar is too worn to have any diagnostic value. It does not differ significantly from worn upper molars of Pliosacomys dubius.

Mandible: The preserved portions of the holotype and paratype mandibles compare favorably to known mandibles of Pliosacomys dubius with one exception. An irregular mass of bone extends between the anterior termination of the masseteric crest and the anterior of the  $P_4$  alveolus in the paratype. I believe that this mass is pathogenic. In both specimens, the anterior of the heteromyid projection does not extend anterior to the  $P_4$ , the mental foramen is anterior to the heteromyid projection, and the dorsal branch of the masseteric crest is very faint.

Discussion.-- Shotwell (1967b) was entirely correct in assigning the specimens named Diprionomys magnus by Kellogg (1910) to the genus Pliosacomys but incorrect in assigning his material from the Bartlett Mountain local fauna to Pliosacomys magnus (see the discussion of Brachygeomys drewseyensis n. gen. and sp.). In the few instances when directly comparable specimens of both Pliosacomys dubius

and P. magnus are available, they are so similar as to indicate that P. dubius may prove to be a junior synonym of P. magnus. The only definite statement which can now be made is that these two nominal species are at least closely related.

Genus Parapliosacomys Shotwell, 1967b

Emended diagnosis.-- Monotypic genus, most advanced of rooted geomyines assigned to the Geomyini. Cheek teeth very hypsodont and with well developed dentine tracts but forming roots in very old individuals.  $DP_4$  lophodont, with moderately developed posterolophid, slightly more hypsodont than in Pliosacomys dubius, cusps rather blade-like.  $P_4$  two-rooted in old age, with hypoconid reduced or absent, encrusting cuspules on anterior column, small posterior cingulum.  $M_1$  and  $M_2$  with pronounced labial curvature; cusps, except protostylid, very anteroposteriorly compressed to form thin, sharp, transverse lophids; first lophid connection labial; teeth roughly triangular in outline, becoming ovoid in late wear stages; single root in older specimens; anterior enamel plate thin, becoming reduced or absent in very late wear.  $M_3$  with strong posterior curvature and medial lophid connection, often with labial lophid connection, ovoid occlusal outline, anterior enamel plate becoming thin and reduced with wear, poorly developed single root in old age.  $DP_4^{4/}$  typically geomyine with notch midway of lingual margin.  $P_4^{4/}$  without separation of proto-

cone and paracone; with scattered encrusting cuspules; posterior enamel plate thin and disappearing, except for two thin enamel streaks, when about one-half worn; single, trilobate root in older specimens.  $M^1$  and  $M^2$  posteriorly curved, with reduced metacone and hypostylar ridge, all cusps except hypostyle anteroposteriorly compressed to form thin and sharp lophs, lingual loph connections present in unworn teeth, posterior enamel plate thins and becomes reduced in very late wear, single root forms in older specimens.  $M^3$  with labial and lingual loph connections, subtriangular to subcircular in outline, thin posterior enamel plate with beginning of posterolabial dentine tract, single root in very old age. Mandible with ascending ramus less dorsally expanded than in Geomys, basitemporal fossa poorly developed but present, symphyseal eminence small and angular process moderately developed, ventral margin of mandible starting to approach arcuate outline of Geomys, lateral angular process well developed, mixture of primitive and advanced characteristics in masseteric crest morphology. Palate and rostrum definitely geomyine in character. Known only from the Hemphillian of the Great Basin.

Parapliosacomys oregonensis Shotwell

Figure 2, I-S; 3, A-V; 4, A-B.

Pliosacomys dubius Wilson, Shotwell, 1956, p. 730.

Parapliosacomys oregonensis Shotwell, 1967b, p. 34-46, in part.

Occurrence. - McKay Reservoir local fauna, UOloc. 2222, Umatilla County, Oregon. Middle or late Hemphillian (middle or late middle Pliocene).

Materials studied. - (All UO) Holotype: left mandible with incisor,  $P_4 - M_1$ , 3631; partial right mandible with  $P_4 - M_2$ , 3130; edentulous partial left mandible, 9300; edentulous partial right mandible, 9301; fragmentary right mandible with incisor, 3495; partial rostrum and edentulous palate, 27005;  $LDP_4$ 's - 24624, 26088, 26089;  $LP_4$ 's - 9326, 25349, 25367, 25371, 25386, 26081-84, 26087;  $RP_4$ 's - 25351, 26080, 26085, 26092;  $LM_1$ 's or  $LM_2$ 's - 24926, 25391, 26101, 26132-34, 26146, 26149, 26154, 26159, 26166;  $RM_1$ 's or  $RM_2$ 's - 25334, 25357, 26106-07, 26111, 26125, 26136, 26140-42, 26147, 26150, 26153, 26156, 26164, 26170;  $LM_3$ 's - 25363, 25368, 25388, 26103-04;  $RM_3$ 's - 25369, 26108, 26112, 26119, 26122; R upper incisors - 2222-18, 2222-20, 2222-21;  $LDP_4$ 's - 24623 (in a maxillary fragment), 26100; partial  $RDP_4$ , 26099;  $LP_4$ 's - 25344, 25358, 25361, 25366, 26094;  $RP_4$ 's - 24918, 25315, 25340, 25342, 25364, 25370, 26090, 26095-98, 26109;  $LM_1$ 's or  $LM_2$ 's - 24921, 25356, 25359, 26115-16, 26118, 26138, 26152, 26163, 26169;  $RM_1$ 's or  $RM_2$ 's - 25329, 25362, 25393, 26151, 26162, 26174;  $M_1$ 's or  $M_2$ 's - 24914, 25372, 25375, 26105, 26121, 26144, 26158, 26165, 26167-68;  $M_1$ 's or  $M_2$ 's or  $M_1$ 's or  $M_2$ 's - 24924, 25353, 26155, 26160;  $LM_3$ 's - 26131, 26139;  $RM_3$ 's - 25387, 26127-30;  $M_2$  - 26124.

Emended diagnosis. - As for the genus.

Lower incisor: The only well-preserved lower incisor assigned to this taxon is in the holotype, UO 3631. The labial and lingual portions of the enamel band on this specimen are relatively much broader than in living Geomys. The wear facet on its anterodorsal surface is unusually long.

Lower deciduous premolar: Two of the DP<sub>4</sub>'s, UO 24624 and 26088, are only slightly worn; the other, UO 26089, is heavily worn. Their occlusal patterns can easily be derived from the basic primitive pattern. The teeth are slightly more hypsodont than the DP<sub>4</sub>'s of Pliosaccomys dubius and Brachygeomys drewseyensis n. gen. and sp. and are lophodont. Two poorly separated cusps occur on the prominent posterolophid with PC I being much the larger. The posterolophid of UO 24624 is slightly smaller than that of UO 26088. The hypoconid and entoconid appear to have been rather bladelike and extend anteromedially from the tooth margins to connect with the mesial lophid. With wear, the posterolophid would first connect to the hypolophid at the lingual and labial margins, isolating a rather large enamel lake. The neoconid, protoconid, and metaconid are all well developed and probably were all rather bladelike. The connection between the neoconid and mesial lophid is oriented transversely and that between the metaconid and mesial lophid slants anterolinguad. The protoconid slants strongly posteriad from the mesial lophid, more so in UO 26088 than in UO 24624. The mesial lophid is labially

concave and slightly lower than the cusps which connect to it. The valley separating these cusps are very deep. The valley between the hypoconid and protoconid would close at its labial margin with wear, isolating an enamel lake. There is no trace of an anteroconid on either specimen. The anterolophid slants obliquely anterior from the lingual to the labial margins. Although it is blade-like, a faint division between AC I and AC II can be discerned. AC II connects to the protoconid but a deep valley separates the remainder of the anterolophid from the protolophid. The occlusal pattern of the worn DP<sub>4</sub>, UO 26089, retains four lingual projections representing, from posterior to anterior: the combined entoconid and PC I, neoconid, metaconid, and AC I. An anterolabial projection marks AC II, the remainder of the labial margin being almost straight. A labial enamel lake just anterior to the transverse axis of the tooth marks the remains of the valley between the protoconid and hypoconid. Shotwell (1967b, fig. 21, K) figured a posteromedial enamel lake on this specimen. There is no enamel lake in this area, just a slight discoloration of the dentine. Where the root region is preserved, there is a broad posterior root and a narrower anterior one.

Lower fourth premolar: I have removed two specimens, UO 25377 and 24904, figured by Shotwell (1967b, fig. 21, C, D, E, F) as Parapliosacomys oregonensis, to another taxon (see Thomomysini? indet.). Of the remaining specimens, UO 26080 is unworn, UO 26081 shows very slight wear, and

UO 25349 and 26083 are slightly worn. The posterior columns of the first two bear well developed, laterally elongate entoconids and hypostylids, but the hypoconids are very reduced or absent. Both have small posterior cingula. UO 26080 bears small accessory cuspules on the posterior cingulum and in the region where the hypoconid should be. UO 26081 is worn in these areas and all occlusal details on the posterior columns of UO 25349 and 26083 have been worn away. The anterior columns of all specimens show the basic triradiate pattern of ridges. All have the anteroconid distinct from the protoconid and the anterostylid fused with the protostylid. The metaconid ridge is close to the protoconid ridge but separated by a deep valley. The anterostylid and protoconid ridges are more widely separated but the intervening valley is partially filled with irregular cuspules and masses of enamel. In UO 26080 and 25349, the protoconid ridge appears to be longitudinally divided into two ridges. With advancing wear, the occlusal outline of the anterior column bears two anterior grooves, then becomes rounded to slightly elongate. The posterior column remains approximately a laterally elongate oval. Dentine tracts are present on the lingual and labial sides of both columns. The tracts on the anterior column are wider than those on the posterior column and become much wider toward the base. The posterior dentine tracts widen only slightly toward the base. Generally speaking, the labial tracts are of equal height and would

interrupt the occlusal enamel pattern first, closely followed by the posterior lingual tract, and much later by the anterior lingual tract. Reentrants are usually V-shaped in early wear, often becoming U-shaped to squared-U shaped in later wear stages. No cement occurs in the reentrants. Two roots, one on each column, develop during later wear stages. In lateral view, the anterior margin of the  $P_4$ 's is almost straight and the posterior margin is slightly convex and the labial, slightly concave.

Lower molars: The numerous isolated upper and lower first and second molars are difficult to sort out because of the presence of at least two geomyines in the fauna and differences in pattern and curvature in first and second molars from the same dental quadrant; all complicated by individual variation. Therefore, assignment of these isolated molars to taxon or to position may be partially in error, particularly in the case of very worn specimens. I believe, however, that these assignments represent a very close approximation to reality. UO 2411 (Shotwell, 1967b, fig. 21, M, N, O), which he considered to be an  $M_1$  or  $M_2$  of Parapliosacomys oregonensis, is herein assigned as an  $M_1^1$  or  $M_2^2$  of Thomomyini? ident. UO 26153 (Shotwell, 1967b, fig. 21, S, T, U), called an  $M_3$  of P. oregonensis, is herein considered to be an unworn enamel cap of an  $M_1$  or  $M_2$  of that species.

In most cases, the worn lower first and second molars can be distinguished from the uppers by having a moderate to

strong labial curvature with little or no anterior or posterior curvature. Unworn uppers and lowers of Parapliosacomys oregonensis can easily be distinguished by their occlusal patterns. Lower third molars are very strongly posteriorly curved with the occlusal surface very oblique to the radius of the tooth. Lower molars assigned to Thomomyini? indet. are larger, differ in occlusal pattern, and the  $M_2$ 's? are more strongly posteriorly curved than the  $M_2$ 's of P. oregonensis.

The occlusal pattern is preserved on a dozen unworn or slightly worn  $M_1$ 's or  $M_2$ 's. The cusps of the hypolophid are strongly compressed anteroposteriorly, forming a sharp transverse ridge which is usually straight except where the labial end of the protoconid bends slightly posteriad. The thin, sharp protostylid ridge forms a prominent anterolabial loop before terminating at a small to obscure protostylid. The position of the protostylid varies from just anterior to the labial end of the hypolophid to just labial of the protoconid. With wear, the protoconid connects to the protostylar ridge or the protostylid, isolating an enamel lake. This lake is better developed in those teeth which have the protostylid adjacent to the protoconid. In these same specimens, a labial lophid connection develops at a later wear stage than in those which have the protostylid adjacent to the hypolophid. The interlophid valley is deep, often with a small pit at its labial end. By analogy with Pliosacomys dubius, those specimens with the protostylid

adjacent to the hypolophid are probably  $M_1^-$ 's; those with the protostylid adjacent to the protoconid are probably  $M_2^-$ 's.

After the labial lophid connection has been formed, the occlusal outline of the teeth resembles a squared-U with the open end lingual. The anterior limb of the U thickens labially because of the protostylid ridge. Later, the lophids in some specimens merge medially, with an enamel lake marking the pit in the interlophid valley. A lingual enamel inflection persists for a short while longer. After the inflection disappears, the teeth are roughly triangular in outline with a blunt lingual apex. At this stage, a broad labial and a narrow lingual dentine tract interrupt the occlusal pattern and the anterior enamel plate becomes noticeably thinner than the posterior plate. In very worn specimens, the occlusal outline becomes oval and the anterior enamel plate is reduced or, occasionally, absent. Shotwell's (1967b, fig. 19, A, C) figures of the holotype are inaccurate in that he shows a thin anterior enamel plate on the  $M_1^-$ ; it is completely absent. Also, his figure (fig. 21, L) of UO 3630 shows the anterior enamel plates on  $M_1^-$  and  $M_2^-$  to be equal in thickness to the posterior plates; actually, they are much thinner. In old age, the bases of the molars close off to form a single root.

The occlusal pattern of the  $M_3^-$  differs in only minor details from that of the  $M_1^-$  and  $M_2^-$ . The labial end of the interlophid valley may or may not be closed off by an enamel ridge extending from the protolophid to the meta-

lophid. It is not clear that the portion of this ridge posterior to the protoconid is part of the protostylid ridge. In several specimens, e.g., UO 26108, the protostylid appears to occur adjacent to the protoconid and the ridge extending from this point to the hypolophid appears to be a neomorph. Most specimens have a low but definite medial lophid connection. Those lacking a labial lophid connection, e.g., UO 25369, form an H-shaped occlusal pattern after moderate wear; otherwise the patterns develop as in the  $M_1$  and  $M_2$ . Just after complete loss of the occlusal cusp pattern, the occlusal outline is almost oval with the lingual margin pointed. The outline becomes more regularly oval in the final wear stages. Dentine tracts are present with the labial tract broader than the lingual. As in the  $M_1$  and  $M_2$ , the anterior enamel plate becomes thinner and reduced from the labial end with wear. A single root, less well developed than in the  $M_1$  and  $M_2$  forms in very late wear stages. The  $M_3$  is very strongly curved posteriorly but lacks the lingual torsion found in the  $M_3$  of geomyines with evergrowing teeth.

Upper incisor: Three upper geomyine incisors are known from the fauna. I cannot find any significant characteristics which would divide them into two groups. As Parapliosaccomys oregonensis is the most common geomyine in the fauna, all of the incisors are assigned to it. All three have an almost flat anterior surface with a fine, sharp lingual groove. UO 2222-18 also has a very shallow labial

groove. The labial margin of each incisor is much more rounded than in modern geomyines. The radius of curvature of all three is 6.0 to 6.5 mm. UO 2222-21 is missing much of the basal part, but the others are almost complete and have subtended angles of  $140^{\circ}$  each. These rather low subtended angles indicate that P. oregonensis was probably very proodont.

Upper deciduous premolar: Of the three specimens known, UO 24623 is the least worn but it has already lost many cusp details. Wear has progressed to the point that all lophs are connected in an E-shaped pattern. A medial bulge of the protoloph marks the protocone and a large bulge on the anterolingual side of the metaloph marks the hypocone. No other traces of cusps can be found. The anteroloph is relatively broad and possesses a strongly developed lingual connection to the protoloph. A lower connection between the labial margins of the anteroloph and protoloph would close off the anterior interloph valley with advanced wear to form a large enamel lake. The protoloph, hypostylar ridge, and metaloph form a continuous arc. A labial connection between the metaloph and protoloph would close off the posterior interloph valley to form a large, very deep enamel lake with only a little more wear. A notch in the outline of the tooth occurs about midway of the lingual margin, about opposite of the posterior interloph valley. The specimen possesses a broad anterior root and two posterior roots, a broad lingual one and a narrower

labial one. The other two DP<sup>4</sup>'s yield very little information. UO 26100 is worn to the point that the posterior interloph valley is represented by an enamel lake. The anterior interloph valley would not close off. The anteroloph of UO 26099 is missing. Its posterior interloph valley is about to be closed off labially. One DP<sup>4</sup>, UO 26091, described and figured by Shotwell (1967b, fig. 23, 0) as belonging to Parapliosacomys oregonensis, is herein assigned to Thomomyini? indet.

Upper fourth premolar: Only one specimen, UO 26096, retains the occlusal cusp pattern and it shows slight wear anteriorly. The protoloph consists of a short, transverse ridge with a posterior bulge to meet the isthmus. The only surface irregularities are due to a medial mass of cuspules, slightly flattened by wear. No trace of a division into protocone and paracone can be seen. The isthmus attaches to the proterolingual corner of the bulge on the protoloph and extends posterolingual to the triangular entostyle. The metacone is smooth and small. Encrusting cuspules cover the large hypocone. An irregular but prominent posterior cingulum attaches to the lingual margin of the metacone and to the juncture of hypocone and entostyle.

The isthmus is lingual in early wear stages, becoming almost exactly medial in very late wear stages. The anterior column assumes the outline of a rounded triangle early in wear and maintains this shape throughout wear. Reentrants are V-shaped early, becoming nearly U-shaped later

and never contain cement. The posterior margin of the posterior column is convex in occlusal view until the posterior enamel plate disappears, then it becomes more or less flat, becoming slightly rounded in some very worn specimens. The lingual end of the long axis of the posterior column is often slightly anterior to the labial end. In lateral view, the  $P^4$ 's are straight or slightly concave anteriorly. In posterior view, they are very slightly concave labially. Slender dentine tracts occur on the labial and lingual sides of both columns. Those on the anterior column interrupt the occlusal enamel pattern later than those on the posterior column. The dentine tracts on each side of the same column, whether anterior or posterior, are of approximately equal height. The posterior enamel plate extends about one-third to one-half the distance from the unworn occlusal surface to the root, with two sharp V's of enamel extending even farther basally. These V's of enamel may be remnants reflecting the primitive root pattern. The posterior enamel plate does not thin noticeably until near its basal margin. A single, irregular root develops in old age. It is trilobed, reflecting the primitive condition of one anterior and two posterior roots.

Upper molars: Seven of the  $M^1$ 's or  $M^2$ 's assigned to taxon are unworn or nearly so. I did not see UO 25374 (Shotwell, 1967b, fig. 23, E). Even in the unworn specimens, the lingual loph connection is complete, forming a basically C-shaped occlusal pattern. The labial end of the

metaloph on unworn specimens does not extend as far labial as does the end of the protoloph because the metacone has become reduced. The metacone and hypocone are fused into a long, straight, slender ridge extending across the width of the posterior margin. The cusps are not differentiated on this ridge but their position is inferred from the point of juncture with the hypostylar ridge. The hypostylar ridge also connects with the lingual end of the hypocone to form a posteromedial pit. That part of the hypostylar ridge between its labial end and its connection with the lingual end of the hypocone is relatively reduced and could easily be interpreted as a simple posterior cingulum if the ancestral pattern were not known. The part of the hypostylar ridge anterior to the hypocone is well developed and connects to the protoloph. Either the protostyle or the hypostyle is missing or they have become fused into a single cusp on the lingual end of the protoloph. The protoloph is a straight, thin ridge with the protocone and paracone only slightly differentiated but with the protostyle and/or hypostyle fairly well set off by a shallow notch. The interloph valley is sharp with several low connections variably developed across it, one of which is usually labial. These usually lead to the development of an enamel lake with wear and the possibility of a second short-lived enamel lake. Unworn teeth are conspicuously expanded anteroposteriorly at the occlusal surface so that, as wear proceeds, the anteroposterior diameter of the teeth decreases

markedly. The last trace of the occlusal cusp pattern with increasing wear is a labial enamel flexure which may be accompanied by a medial enamel lake. After these are worn away, the tooth becomes ovoid with pointed lingual and labial margins. The lingual and labial dentine tracts are either of equal height or the lingual one may be slightly higher. The posterior enamel plate appears to be in the process of being reduced because it is conspicuously thinner than the anterior enamel plate and does not extend quite as far basally as the latter does. In lateral view,  $M^1$  and  $M^2$  vary from almost straight to strongly concave posteriorly. The more strongly curved ones are probably  $M^2$ 's (see Merriam, 1895, figs. 18, 26). In old age, the bases of the teeth close off to form single roots.

The cusp pattern of  $M^3$  is somewhat variable. The metaloph, including that portion of the hypostylar ridge posterior to the hypocone, is generally similar to the metalophs of  $M^1$  and  $M^2$  except that the metacone tends to be directed anterolabial from its juncture with the hypostylar ridge. The hypostylar ridge is more or less reduced anterior to its juncture with the lingual margin of the hypocone. In UO 26130, the hypostyle is a separate cusp at the lingual end of the interloph valley and a low loph connection exists just labial to it. In all other specimens which have the occlusal pattern preserved, the hypostyle cannot be distinguished, the hypostylar ridge connects to the protoloph, and a semicircular ridge originating from the approximate mid-

point of the protocone connects to the hypostylar ridge at about the midpoint of its lingual portion. The addition of this latter ridge results in the formation of a small but deep pit. The protoloph is nearly straight with slight posterior projections marking the apices of the protocone and paracone. The protostyle is difficult or impossible to see. A labial loph connection occurs by means of a small ridge connecting the anterolabial corner of the metacone to the apex of the paracone. This results in a deep pit, derived from the middle portion of the interloph valley, which persists into moderately worn stages. The outline of the  $M_3$  after the occlusal cusp pattern has been worn away is a sort of a compromise between a rounded triangle and a semicircle. The anterior margin is slightly convex anteriorly. The remainder of the outline approaches a hyperbola. Moderately wide lingual and labial dentine tracts interrupt the worn occlusal enamel pattern with the former usually a little more strongly developed. The posterior enamel plate becomes very thin in worn specimens with the beginning of a posterolabial dentine tract at its very base. A single root forms in very old age.

Mandible: The holotype mandible of Parapliosaccomys oregonensis, UO 3631, is nearly complete. It lacks only the tip of the coronoid process and part of the posterior alveolar rim for the  $M_3$ . Other mandibles assigned to this species range from moderately complete to fragmentary. None have any characters which would allow them to be separated

off and assigned to *Thomomyini?* indet., but the possibility exists that one or more of the edentulous mandibles may actually belong to it.

When a gross comparison is made between UO 3631 and modern Geomys mandibles, several differences are very evident. The ventral margin of the mandible in Parapliosaccomys oregonensis has not attained the arcuate outline of Geomys but shows a tendency toward doing so. The ascending ramus is not as dorsally expanded nor does it extend as far anteriorly as in the living genus.

In medial view, the symphysis is well developed but the symphyseal eminence is relatively small and terminates under the anterior of the  $P_4$  rather than extending to under the  $M_1$  or  $M_2$  as in Geomys. The mylohyoid fossa is well developed, the geniohyoid fossa only moderately so. The angular process, better developed than in Geomys, is much smaller than in Perognathus or Dipodomys. The condylar process and coronoid process appear very similar to Geomys but occur more ventral relative to the toothrow. The articular condyle faces more posteriad than in Geomys. The fossa for the external pterygoid is poorly developed. The basitemporal fossa is advanced over the simple depression found in Pliosaccomys dubius but it is still far more primitive than in modern Geomys. The ascending ramus is only slightly to moderately excavated but a definite trough has formed between the ascending ramus and the alveoli for  $M_2$  and  $M_3$ . There is no capsule for the  $M_3$ . A large

mandibular foramen, completely preserved only in UO 3631, occurs in a depression about midway between the  $M_3$  alveolus and the articular condyle. A smaller foramen occurs just posterodorsal to it. This area is not preserved in other specimens except that the anterior margin of the mandibular foramen is present in UO 9300 and 9301.

In labial view of UO 3031, the lateral angular process is less developed than in Geomys and its dorsal surface slants more anterodorsad-posteroventrad. The incisive capsular process appears well developed but part of it is missing. It probably extended dorsad to or above the level of the articular condyle. Consequently, the capsular groove is deep and prominent. The previous observation that the ascending ramus is not as dorsally expanded as in Geomys explains the fact that the posterior masseteric fossa is relatively narrower dorsoventrally in Parapliosaccomys than in Geomys. The rim marking the anterior margin of this fossa is absent or indistinct. The temporal node is very small but definitely present. The region of the masseteric fossa is obscured by a heavy layer of paint, used for numbering, in UO 9300 and 9301. No true capsules exist for the cheek teeth but the labial margins of the  $M_1$  and, occasionally, of the  $M_2$  are marked by elongate rounded ridges. A mixture of primitive and advanced characteristics occurs in the anterior masseteric crest region. These are quite similar to the mixtures found in Pliosaccomys dubius except that the anterior margin of the masseteric crest has

migrated posteriorly to under the  $P_4^1$ , providing a better separation between it and the mental foramen. Another difference is that the dorsal branch of the masseteric crest is stronger and reaches the dorsal margin of the mandible a little more posteriorly than in P. dubius. Development of the heteromyid projection varies from strong to very weak and development of the medial branch of the masseteric crest varies from strong to approaching the geomyine groove condition. The diastemal notch is weaker than in Geomys and slightly stronger than in Pliosacomys dubius.

Discussion.- Parapliosacomys could easily have been derived from Pliosacomys or a similar, very generalized geomyine. All details of dentition, mandible, and known skull elements conform to the Geomyinae. Shotwell (1967b) suggested that it might be ancestral to Thomomys. This relationship is ruled out by the reduction and loss, in maturity or old age, of the anterior enamel plates on lower molars and the posterior enamel plate on the  $P_4^1$  in Parapliosacomys; these plates are never reduced or lost in Thomomys. I doubt very much that the reduction of these plates in Parapliosacomys could have been reversed by evolutionary processes in order to attain the condition found in Thomomys. The possibility exists that Parapliosacomys is an offshoot of the main Thomomyini stock, as the larger form in the McKay Reservoir local fauna is tentatively considered to be. However, the lack of con-

firming evidence in the features of Parapliosacomys and the presence of another form in the same fauna with more Thomomysini-like features make this only a distant possibility.

Other possibilities include relationships with the Nerterogeomyini or with the Geomyini or a separate lineage without living descendants. The last possibility cannot be evaluated at the present state of knowledge of the group. Nothing in the occlusal patterns argues against relationships with the Geomyini or the Nerterogeomyini. The lophodont character of the  $DP_{\frac{7}{4}}$  is more like that of the condition found in the Geomyini, but the moderate development of the posterolophid on the  $DP_{\frac{7}{4}}$  is similar to that in the Nerterogeomyini. The variable mixture of primitive and advanced characters in the masseteric crest region of the mandibles of Parapliosacomys could allow assignment to either tribe. However, Pliogeomys from the late Hemphillian of Oklahoma and Kansas appears to be the ancestral stock giving rise to Nerterogeomys. The  $DP_{\frac{7}{4}}$  of Pliogeomys is almost identical to the  $DP_{\frac{7}{4}}$  of Brachygeomys drewseyensis n. gen. and sp., considered to be ancestral to Pliogeomys. Parapliosacomys is more primitive than Pliogeomys and more advanced than Brachygeomys, but the morphology of the  $DP_{\frac{7}{4}}$  does not fit a position between these forms on the main stock of evolution in the Nerterogeomyini. Parapliosacomys could be related to the Nerterogeomyini, but not part of the primary lineage leading to Nerterogeomys.

The  $M_1^1$  and  $M_2^2$  of Parapliosacomys exhibit a trend to

reduction of the posterior enamel plates from the base of the teeth but not as much as in the anterior enamel plates of the lower molars. This reduction could possibly be more subject to evolutionary reversal than in the lower molars. I still doubt very much that any such reversal could and did occur. Reduction of these enamel plates also occurs in three extant genera of the Geomyini: Zygogeomys, Pappogeomys, and Cratogeomys. Parapliosacomys is accordingly referred to the Geomyini.

Zygogeomys (not including Nerterogeomys) retains a reduced posterior enamel plate on the lingual half of the  $P_4^4$  and on the lingual two-thirds of  $M_1^1$  and  $M_2^2$ . This condition is almost impossible to derive from the condition found in Parapliosacomys where reduction is proceeding from the base of the teeth and not from the labial margin of the teeth. Only one species of Pappogeomys, P. alcorni, shows consistent reduction of these enamel plates (Russell, 1968a), and it retains the lingual portion of the posterior plate on  $M_1^1$  and a complete posterior plate on  $M_2^2$ . This condition is also difficult to derive from that of Parapliosacomys. Recent Cratogeomys have the posterior enamel plates completely missing from both  $M_1^1$  and  $M_2^2$ , making it the only living genus which could reasonably be derived from Parapliosacomys, providing that the type of enamel plate reduction found in the latter genus continued as it started.

Only two fossil occurrences of Cratogeomys are known from pre-Wisconsin deposits. Cratogeomys sp. is known from

an incisor and a jaw fragment from late Blancan deposits in Trans-Pecos Texas (Akersten, 1972). Cratogeomys bensoni Gidley (1922) is known from several specimens found in early Blancan deposits of southern Arizona. New material, including an  $M_1^1$  which lacks any trace of enamel on its posterior surface, confirms the generic assignment of this taxon (Lammers, 1970). Unfortunately, no deciduous or unworn permanent teeth are known from either of these occurrences.

I have been unable to locate any specimens of Recent Cratogeomys with unworn cheek teeth except for those which erupt last: namely,  $P_4^4$ ,  $P_3^4$ ,  $M_3^2$  and  $M_2^2$ . Several specimens do have deciduous premolars and first and second molars in very early wear stages. Most teeth, except the  $DP_4^4$ , appear to be fairly close in pattern and in posterior curvature of  $M_1^1$  and  $M_2^2$  to the teeth of Parapliosacomys. Although quite different in occlusal pattern, the  $DP_4^4$  of Cratogeomys is derivable from that of Parapliosacomys and, in light of the time span separating them, could easily have been derived from it. Geomys has had the occlusal pattern of the  $DP_4^4$  altered as much or more between the early Blancan and Recent. Without any knowledge of the dentitions in intermediate forms, it is not possible to definitely demonstrate any relationship between Parapliosacomys and extant Cratogeomys. However, the available material indicates that a relationship of some sort, possibly ancestor-descendant, is very likely between these genera.

Shotwell (1967b) assigned a rather long, large geomyoid tibia-fibula, UO 3140, to Parapliosacomys, apparently because this genus was the most common and considered to be the largest geomyoid known from the fauna. He also noted some minor differences between this tibia-fibula and that of Dipodomys ordii. On the basis of this assignment, Shotwell decided that Parapliosacomys was a saltatorial rodent.

Some isolated teeth of Dipodomys? are present in the McKay Reservoir local fauna, but Shotwell considered that they were too small to belong to the same form as the large tibia-fibula. He also assigned a distal fragment of a tibia-fibula to this Dipodomys? but neither figured it nor compared it to UO 3140. Relative tooth size between two different rodents is not always a reliable indicator of relative body size. An  $M_3$ , UO 26137, and an  $M_3$ , UO 26126, of a dipodomysine were included in the loan of Parapliosacomys from the University of Oregon. These teeth are larger than the corresponding teeth of Recent Dipodomys deserti but the tibia-fibula of D. deserti is larger than UO 3140. Therefore, size does not form a good basis for assigning UO 3140 to Parapliosacomys. The assignment of the only complete limb element to a particular taxon because this taxon is the most common in the fauna is not good paleontologic practice. Although UO 3140 cannot be perfectly matched with the tibia-fibula of living Dipodomys, it is amazingly close when one considers the span of time between them. It is also so different from that of any known

geomyine that no basis exists for assigning it to Parapliosacomys. If Parapliosacomys is ancestral to any later fossorial geomyine, which it seems to be, it could not be saltatorial. It seems impossible for a form which is highly adapted for a saltatorial habitus to evolve into a form highly adapted for a fossorial habitus.

The calcanea and astraguli assigned to Parapliosacomys by Shotwell (1967b) were not studied. Since Shotwell's assignment of the long tibia-fibula to Parapliosacomys is herein rejected, I can only base an assessment of the habitus of Parapliosacomys on dental, mandibular, and skull morphology. The similarity of all these elements to those of modern geomyines strongly suggests similar habits. The relatively robust mandible with a large, strong symphysis implies a habitus, such as fossorial, in which the mandible is subject to severe strain (see the discussion of Pliosacomys dubius). As discussed elsewhere (Akersten, 1973), lingual upper incisor grooves in geomyines probably developed to reinforce the lingual margins of the incisors against wear and chipping caused by the forces brought to bear on them in a fossorial environment. Although inconclusive, the foregoing indicates a good probability of a fossorial habitus for Parapliosacomys.

#### Tribe Thomomyini

Emended diagnosis.-- (Excluding Thomomyini? indet. which is very tentatively assigned to this tribe.) Known forms

with rooted cheek teeth cannot be assigned to the Thomomyini with any confidence. Members possess evergrowing cheek teeth with dentine tracts on both the labial and lingual sides but show no reduction of anterior enamel plates on  $M_1$  through  $M_3$  and no reduction of posterior enamel plates on  $P_4^4$  through  $M_2^2$  as found in forms having evergrowing cheek teeth in other tribes.  $DP_4^-$  and  $DP_4^4$  very hypsodont,  $DP_4^-$  being rather microtine-like. Upper incisor with fine lingual groove, often with faint medial groove. Mandible with poorly developed basitemporal fossa, advanced characters in masseteric crest region. Recent forms highly adapted to a fossorial existence. Known geologic range: early Blancan (late Pliocene) to Recent. Contains only the genus Thomomys.

Thomomyini? indet.

Figure 4, C-M.

Parapliosacomys oregonensis Shotwell, 1967b, p. 34-46, in part.

Occurrence.— McKay Reservoir local fauna, UOloc. 2222, Umatilla County, Oregon. Middle or late Hemphillian (middle or late middle Pliocene).

Materials studied.— (All UO)  $RDP_4^-$ , 24622;  $LP_4^-$ 's - 25377, 24904;  $RP_4^-$ , 26086;  $RM_1^-$ 's or  $RM_2^-$ 's - 25360, 25376, 25385, 26143;  $LM_1^-$ 's or  $LM_2^-$ 's - 25394, 26102, 26114;  $RM_3^-$ , 25378;  $LDP_4^4$ , 26091;  $LP_4^4$ , 26173;  $RP_4^4$ 's - 25352, 26093;  $RM_1^1$ 's

or  $RM^2$ 's - 2411, 26120;  $M^1$ 's or  $M^2$ 's - 26110, 26161;  $LM^3$ , 26113;  $M^3$ , 25354.

The following are a number of teeth which do not appear to be consistent with the material assigned to Parapliosacomys oregonensis. There is not enough material available for a coherent diagnosis or taxonomic designation. Although I doubt it very strongly, some or all of these specimens may simply represent aberrant individuals of P. oregonensis. It is also possible that they may belong to more than one species.

Lower deciduous premolar: UO 24622 is moderately worn but can easily be separated from the McKay Reservoir material assigned to Parapliosacomys oregonensis. The anterolophid is not connected to the protolophid and would become connected only in extremely late wear stages through AC I and the metaconid. In P. oregonensis the anterolophid connects very early to the protolophid through AC II and the protoconid. The valley between the protoconid and hypoconid of UO 24622 does not close off to form an enamel lake as it does in P. oregonensis. The size and configuration of the posterolophid and hypolophid, combined by wear, in UO 24622 indicate that the posterolophid must have been much smaller than in P. oregonensis. This specimen very closely resembles moderately worn  $DP_{\frac{4}{4}}$ 's of living Thomomys.

Lower fourth premolar: Two specimens figured by Shotwell (1967b, fig. 21, C, D, E, F), UO 25377 and 24904, and another, UO 26086, were separated from Parapliosacomys

oregonensis primarily because they have strongly concave posterior margins in lateral view. The  $P_4$ 's assigned to P. oregonensis have straight anterior margins in lateral view. In addition, UO 25377 is virtually unworn but already has two well-developed roots. These teeth do not differ significantly from the  $P_4$ 's assigned to P. oregonensis in any other way, but I find it difficult to assign strongly curved and almost straight  $P_4$ 's to the same taxon in the light of variation shown in other fossil and recent samples, especially when intermediates are missing. Strongly curved  $P_4$ 's are not inconsistent with a relationship to Thomomys.

Lower molars: The primary differences between these specimens and those assigned to Parapliosacomys oregonensis include greater size, occlusal details, greater posterior curvature of  $M_2$ 's, and less reduction of the anterior enamel plate. The two least worn specimens, UO 25376 and 26102, show strong labial curvature but little posterior curvature; accordingly, I consider them to be  $M_1$ 's. The posteriorly convex hypolophids show no differentiation into cusps and are continuous with the protostylid ridges to form unbroken, sharp ridges from the posterolingual corners of the teeth to the juncture of the protoconid and metaconid. There is a very small notch in this ridge about opposite of the interlophid valley in UO 26102. The metaconid is very elongate, thin, and directed linguad or slightly posteriad. The protoconid is shorter and directed posterolabiad. The protoconid would connect to the protostylar ridge with wear,

and form an enamel lake. Early wear, just after loss of cusp detail, would result in a squared-U occlusal pattern as in P. oregonensis. Two other specimens, UO 26143 and 25385, are more worn but retain some details of the cusp pattern. They are strongly curved posteriad and I consider them to be  $M_2$ 's. The primary difference in occlusal pattern between these and the  $M_1$ 's is that the former have a definite separation between the protostylid and the hypolophid. The first lophid connection with wear would be labial, a second one would occur later just lingual to the midline of the tooth. In all  $M_1$ 's and  $M_2$ 's, the occlusal outline would be roughly triangular in moderate wear stages, becoming more oval in the final wear stages. They do not appear to become as oval as do the  $M_1$  and  $M_2$  of P. oregonensis. The dentine tracts are well developed with the labial ones broader than the lingual. The anterior enamel plate is less reduced than in P. oregonensis but it is still noticeably thinner than the posterior plate in advanced wear stages. It does become progressively narrowed from the labial margin but would rarely, if ever, be completely absent. A single root forms in very late wear.

Only one specimen can be definitely assigned as an  $M_3$ , although it is possible that one or more of the specimens considered to be  $M_2$ 's may actually be  $M_3$ 's. This definite  $M_3$ , UO 25378, is heavily worn and can only be distinguished from the  $M_3$  of Parapliosacomys oregonensis by size. It is ovoid in occlusal outline, possesses a single root, and has

a thick posterior enamel plate. A thin enamel plate occurs on the lingual half of the anterior margin.

Upper incisor: Unknown.

Upper deciduous premolar: One specimen, UO 26091 (Shotwell, 1967b, fig. 23, N), was separated from the DP<sup>4</sup>'s assigned to Parapliosacomys oregonensis because it possessed a narrower anteroloph, dentine tracts, a broader anterior interloph valley, a low lingual connection between the protoloph and metaloph, and a lingual notch opposite the anterior interloph valley rather than opposite the posterior interloph valley. The specimen is very hypsodont and only slightly worn. It is almost identical to the DP<sup>4</sup> of a recent Thomomys bottae, AMNH 127161; the only difference being that the latter has a slightly narrower anterolophid and lacks dentine tracts.

A small labial cusp can be distinguished on the anteroloph of UO 26091. The remainder of the anteroloph has been worn to form a uniform, anteriorly convex ridge. No labial connections exist across either interloph valley. A small paracone and a larger protocone are still evident on the protoloph. The protoloph, hypostylar ridge, and metaloph are connected to form a roughly C-shaped ridge. Two styles, probably the entostyle and hypostyle, are represented by bulges along the lingual margin of this ridge. The hypocone is a large loop of enamel directed anterolinguad with a deep pit posterior to it. The hypocone would connect with wear to the hypostylar ridge, isolating the pit as an enamel

lake. The posterolabial corner of the specimen is missing; only the anterior tip of the metacone remains. Dentine tracts occur opposite the labial and lingual margins of the protoloph. I have not seen dentine tracts on the  $DP^4$  of any other geomyine. The roots have not yet formed.

Upper fourth premolar: Three worn  $P^4$ 's were separated from those assigned to Parapliosacomys oregonensis because they had very strong anterior curvatures. No other diagnostic characters are apparent, but unworn material may show something useful. The posterior enamel plate of UO 26093 is rounded basally, the others possess two basal V's of enamel as in P. oregonensis. None are old enough to show more than the beginnings of root development.

Upper molars: The four specimens herein assigned as  $M^1$ 's or  $M^2$ 's are a rather mixed lot. One, UO 26102, is very slightly worn and another, UO 2411, is slightly worn. The latter specimen was figured by Shotwell (1967b, fig. 21, M, N, O) as a lower molar of Parapliosacomys oregonensis. Both resemble the lowers assigned to Thomomyini? indet. but show no lateral curvature. They are almost straight in lateral view and slant slightly anterior relative to their occlusal surfaces. Straight  $M^1$ 's, although unusual, do occur in some modern forms (see Merriam, 1895, fig. 26-3, Geomys tuza). In UO 26120, the protoloph is a straight, slender ridge showing no division between the paracone and protocone and only a minor one between the protocone and protostyle. The long metacone is initially directed

slightly anterolabial from its juncture with the hypocone then turns slightly posterolabial. The hypocone is directed anterolingual from its juncture with the metacone. The hypostylar ridge terminates well posterior of a prominent hypostyle. A low ridge connects the hypocone to the hypostyle and a shallow notch separates the hypostyle from the protostyle. The interloph valley is deep with a very faint lophid connection near its labial end. The cusp pattern of UO 2411 appears to have been similar except that the hypostylar ridge was continuous with the hypostyle. It is worn to the stage of having a squared C-shaped occlusal pattern. The lingual dentine tract is broader than the labial and a little closer to the occlusal surface. The posterior enamel plate does not reach the base of the tooth. The occlusal outline would be subtriangular in early and moderate wear stages, becoming ovoid later. The two worn specimens, UO 26110 and 26161, were separated from P. oregonensis because they are larger. They slant slightly posteriad relative to their occlusal surfaces and possess oval occlusal outlines. Their posterior enamel plates are thinner than the anterior ones and lack only a little of reaching the base of the tooth.

Only one of the two large  $M^3$ 's (UO 26113) assigned to this form retains any traces of the occlusal pattern and it is worn to the point that almost all cusp details are obliterated. Although it appears to be similar to the  $M^3$ 's assigned to Parapliosacomys oregonensis, detailed compari-

sons are impossible. The medial pit is large and deep. An anterolingual pit appears to be present but damage in this area makes it uncertain. The posterior part of the hypostylar ridge appears to have had a similar configuration to that of P. oregonensis because there is an appropriate posteromedial enamel lake. Both specimens possess posterior enamel plates which thin rapidly and disappear before reaching the base of the tooth, broad labial and narrower lingual dentine tracts, and only the faintest traces of posterolingual inflections at the bases of the posterior enamel plates. The occlusal outline of UO 25354, moderately worn, is that of a rounded triangle, relatively shorter anteroposteriorly than similar specimens of P. oregonensis. A single root forms in old age.

Mandible: Unknown.

Discussion.-- Assuming that all of the material included here belongs to a single taxon, it may have had some sort of a relationship with the Thomomyini. The  $DP_{4}^{-}$  and  $DP_{4}^{4}$  closely resemble those of living Thomomys. The reduction of posterior enamel plates in the  $P_{4}^{4}$ 's and of the anterior enamel plates in the lower molars eliminates this form from being in the main evolutionary stock leading to Thomomys. Until more and better material is available, it seems best to very tentatively consider this form as an offshoot of the Thomomyini which underwent some reduction of enamel plates in the cheek teeth. Habitus cannot be determined.

## Tribe Nerterogeomyini (New Name)

Type: Nerterogeomys Gazin, 1942.

Diagnosis.— Geomyines with basically cusate  $DP_{\frac{4}{4}}$ 's, becoming more lophodont in the genus Nerterogeomys. Known mandibles retain primitive features with well developed medial branch of masseteric crest, well developed heteromyid projection, and mental foramen under heteromyid projection; except some specimens of Pliogeomys buisi which may have dorsal branch of masseteric crest faintly developed and mental foramen very slightly anterior to heteromyid projection. Only one known primitive form, Brachygeomys drewseyensis n. gen. and sp. with relatively brachydont cheek teeth lacking true dentine tracts. Advanced forms parallel the Geomyini closely in the development of hypsodont cheek teeth which loose roots to become evergrowing, bisulcate upper incisors, dentine tracts on lingual and labial margins of the cheek teeth, reduction of enamel on the posterior face of  $P_{\frac{4}{4}}$  and anterior face of lower molars, and general configuration of the mandible. No known forms with elongation of  $M^3$ . Known geologic range: Hemphillian (middle Pliocene) through late Blancan (early Pleistocene). Genera included: Brachygeomys n. gen., Pliogeomys, and Nerterogeomys. Known only from North America.

Genus Brachygeomys n. gen.Diagnosis.— Monotypic genus, primitive, very similar

to other primitive geomyines which have moderately hypsodont, rooted cheek teeth lacking dentine tracts. Differs from Pliosacomys in the very cusped  $DP_4$  with a strong posterolophid, greater labial curvature of lower molars, molars with straighter lophs and lophids, lingual connection of lophs in  $M_1^1$  and  $M_2^2$  virtually simultaneous with medial connection. Differs from Pliosacomys? shotwelli n. sp. in being more advanced in a number of characters, including more hypsodont cheek teeth and roots in alignment with crown in all known permanent cheek teeth. The generic name is a combination of brachy or short, referring to the relatively low crowned cheek teeth, and geomys or earth-mouse, the generic name used for some extant gophers.

Brachygeomys drewseyensis n. sp.

Figure 4, N-X; 5, A-F.

Pliosacomys magnus (Kellogg), Shotwell, 1967b, p. 30-33, in part.

Occurrence.— Bartlett Mountain local fauna, UOloc. 2357, Harney County, Oregon. Early Hemphillian (early middle Pliocene).

Materials studied.— (All UO) Holotype:  $RP_4$ , 26058. Rest Paratypes:  $RDP_4$ 's - 24978, 24979; anterior column of  $LP_4$ , 27009;  $P_4$ , 24943;  $LM_1$ 's or  $LM_2$ 's - 2239-B, 26046;  $RM_1$ 's or  $RM_2$ 's - 2239-A, 25229, 25258, 26063, 27010;  $LM_3$ 's - 24987, 26043;  $RM_3$ 's - 2239-A, 24952, 26037;  $LM_1^1$ 's or  $LM_2^2$ 's -

2239-D-5, 24960, 25250, 26195; RM<sup>1</sup>'s or RM<sup>2</sup>'s - 2239-B-2, 25233, 25246; RM<sup>3</sup>, 25252.

Diagnosis. - As for the genus. Specific name derived from the Drewsey Formation.

Lower incisor: Unknown.

Lower deciduous premolar: Two right DP<sub>4</sub>'s, UO 24979 and 24978, display the primitive pattern of the Geomyinae. The former is complete except for roots and has only the slightest traces of wear on the highest cusps. The latter is lacking most of the anteroloph and is a little more worn. Another DP<sub>4</sub>, UO 2239-3, labelled Pliosaccomys magnus clearly belongs to Diprionomys. It is practically identical to but smaller than UMMP 42196 which was assigned to D. agrarius by Klingener (1968).

The DP<sub>4</sub>'s of Brachygeomys drewseyensis appear to have been two-rooted with a broad posterior root and a narrower anterior root. The cusps are very high in contrast to the low mesial lophid and connecting ridges. The posterolophid is highly developed and prominent, forming an addition to the posterior outline of the tooth. A posterolabial notch in the tooth outline results from this addition. PC I is very laterally elongate and makes up most of the posterolophid. PC II is at the labial end of the posterolophid. Its labial margin is directed slightly anteriorly, toward the hypoconid. The first connection, with wear, between the posterolophid and hypolophid occurs between PC II and the hypoconid. A much later connection occurs between the

entoconid and PC I. The deep valley between these lophids has a pit about midway of its length. The entoconid and hypoconid are laterally elongate with the labial margin of the hypoconid curving slightly posteriorly. The connection between them is very low. The rounded neoconid occurs about half way between the metaconid and entoconid. The metaconid is rounded as is the top of the protoconid, but the protoconid would become posteriorly elongate with wear. The ridge connecting these cusps is very low, almost absent. The mesial lophid is low throughout its length in comparison to the height of the cusps. The only sign of an anteroconid is a minute projection where the mesial lophid meets the protolophid. A low ridge connects the anteroconid to AC II. There is no connection between AC I and the protolophid. AC I and AC II are very distinct and slightly transversely elongate.

Lower fourth premolar: The slightly worn anterior column of a left  $P_4$ , UO 27009, bears the basic cusp pattern of the geomyines: a triradiate pattern of metaconid ridge, protoconid ridge, and anterostylid ridge. The small anterostylid and anteroconid occur at the anterior margin. Two small enamel pits are present; the labial pit is surrounded by the protostylid, anterostylid, and protoconid; the lingual pit occurs between the protoconid, metaconid, and anteroconid. No dentine tracts are present, though lower margins of enamel on the lingual and labial sides of the column are higher, suggesting incipient tracts. A right  $P_4$ , UO 26058,

is slightly more worn and the cusp details have been obliterated. However, the anterior groove between the anterostylid and anteroconid remains and an anterolabial projection marks the position of the anterostylid. The enamel on the top of the isthmus has not yet been worn. The reentrants are broad and U-shaped with no trace of cement. The hypoconid and entoconid occur as large, prominent cusps; the hypostylid is small and low. No trace of a posterior cingulum exists. Again, no dentine tracts are present but inflections of the lower margin of the enamel cap mark their positions. A large, well-developed root occurs in alignment with each column.

UO 24943 is so worn that it cannot be assigned to either side of the jaw. No dentine tracts are present on either the round anterior column or the oval posterior column. The reentrants are slightly narrower than in UO 26058 but they retain the U-shape. Characteristics of the roots and the base of the enamel cap are the same as in the other  $P_4$ 's.

Lower molars: Shotwell's (1967b) description of the molars he assigned to Pliosacomys magnus is confused by the misassignment of numerous specimens. Eight of the molars he included in his concept of this taxon belong to one or two other species of geomyoid rodents, including the two (UO 26068, fig. 17, L and UO 26067, fig. 17, M of Shotwell, 1967b) on which the description of the  $M_3$  was based. UO 26037 (fig. 17, F, G, and H of Shotwell, 1967b),

described as an  $M_1^-$  or  $M_2^-$ , is an  $M_3^-$ . UO 27010 (fig. 18, C of Shotwell, 1967b), described as an  $M_1^1$  or  $M_2^2$ , is an  $M_1^-$  or  $M_2^-$ .

The lower molars are distinguished from the uppers by root pattern and by having a pronounced labial curvature whereas the uppers are straight-sided. Lower molars, in which wear has obliterated the occlusal pattern, can be further oriented by the posterior enamel plate which extends more ventrad than the anterior. None of the known  $M_1^-$ 's or  $M_2^-$ 's are completely unworn; the least worn retain separate lophids but lack cusp details. The configuration of these teeth indicates that they were virtually identical to the lower molars of Pliosaccomys dubius except that the lophids are straighter and slightly thinner in Brachygeomys drewseyensis. Moderately worn molars show that a labial connection between the lophids appears before a medial connection. Until very late wear stages, the position of the interlophid valley is marked by a shallow, vertical groove on the labial margin and a deeper groove on the lingual margin of the molar. The occlusal surface is oval at a very late wear stage. No dentine tracts are present but the lower margin of the enamel cap rises at the labial and lingual margins of the teeth. The root pattern consists of a large root extending across the posterior and lingual margins of the teeth, from under the hypostylid to under the metaconid, and a smaller, anterolabial root.

Three of the  $M_3^-$ 's are unworn or very slightly worn. In

addition to the labial curvature they curve strongly posteriorly. The protolophid is higher than the hypolophid. The thin, sharp metaconid and protoconid occur almost in lateral alignment. The protostylid ridge is well developed and ends at a small protostylid, the posterior portion of which curves linguad. The thin, straight hypolophid consists of a small hypostylid and a larger hypoconid and entoconid. An exception occurs in UO 24987 in which the entoconid and hypoconid have merged to form a single, large cusp. The labial and medial connections between the lophids would occur about simultaneously. There is no trace of dentine tracts. One of the worn  $M_3$ 's, UO 26043, shows the pattern of connections with the labial connection slightly weaker than the medial. This specimen is in about the same stage of wear as the  $M_3$  in the holotype of Pliosaccomys dubius. They appear very similar except that the lophids are more slender and the cusp pattern disappears at an earlier stage of wear in Brachygeomys drewseyensis. The other worn  $M_3$ , UO 2239-A, has developed a good labial lophid connection but the medial connection is very low and would not develop until just before the entire interlophid valley was worn away. This specimen is also the only one which has well-developed roots. Two transverse roots, separated by a narrow valley, occur across the anterior and posterior basal margins of the tooth.

Upper incisor: Unknown.

Upper deciduous premolar: Unknown.

Upper permanent premolar: I have not seen this tooth reported by Shotwell (1967b).

Upper molars: None of the  $M_1^1$ 's or  $M_2^2$ 's of Brachygeomys drewseyensis is unworn enough to determine cusp details. The shape of the lophs indicates, however, that cusp morphology and placement is probably quite similar to that of Pliosaccomys dubius. One difference is that the strong tendency of the  $M_1^1$  and  $M_2^2$  in P. dubius to form a lingual connection between the lophs prior to any medial connection does not exist in the material of B. drewseyensis. Instead, the lingual connection forms at the same time as, or a little later than, the medial connection. In one specimen, UO 25233, the medial connection is well developed but the lingual connection is still a little over one-tenth of a millimeter below the occlusal surface. The basal margin of the enamel caps on the anterior surfaces of the  $M_1^1$ 's or  $M_2^2$ 's is more dorsal than on the other surfaces. Very slight to moderate indentations of the enamel margin on the lingual and labial sides of the teeth mark the positions of the dentine tracts present in more advanced geomyines. The root pattern consists of two labial roots and one lingual root. A shallow, lingual, vertical groove and a deeper labial one mark the position of the interloph valley until very late wear stages when the occlusal pattern becomes smoothly oval.

The  $M_2^3$  is moderately worn and probably was very similar in cusp pattern to the other upper molars, to judge from the configuration of the worn lophs. The  $M_2^3$  is more rounded in

outline with a greater length to width ration than in the  $M_1$ 's or  $M_2$ 's. The lingual loph connection is about to develop, a labial connection would develop later. The root pattern consists of a large lingual root and two smaller labial ones.

Mandible: Unknown.

Discussion.— Shotwell (1967b) equated this material with that of Diprionomys magnus Kellogg (1910) but assigned it to the genus Pliosaccomys. He was correct in that D. magnus should be placed in the genus Pliosaccomys but the Bartlett Mountain local fauna specimens are here considered to be distinct from Pliosaccomys at the generic level.

The known material of Brachygeomys drewseyensis is very similar to Pliosaccomys dubius except for a few minor details and the cusp morphology of the  $DP_{\frac{1}{4}}$ 's. These  $DP_{\frac{1}{4}}$ 's can only be differentiated from the  $DP_{\frac{1}{4}}$  of Pliogeomys buisi on the basis of size and are not closely similar to the  $DP_{\frac{1}{4}}$ 's of any other known geomyine. For this reason, Brachygeomys drewseyensis is placed in the tribe Nerterogeomyini and is considered to be either the form which gave rise to Pliogeomys or close to the form which did. One other interesting difference noted between the material of Pliosaccomys dubius and Brachygeomys drewseyensis is that a high percentage of the known teeth of the former (but a low percentage of the known teeth of the latter) are unworn or nearly so. This may simply reflect accident of sampling the biocoenose or of preservation, or it may point to some more basic

difference such as relative durability of the occlusal cusp pattern. The habitus of B. drewseyensis cannot be determined from the available material.

Genus Pliogeomys Hibbard, 1954

Emended diagnosis.-- Most advanced of all geomyines with rooted cheek teeth. Upper incisors bisulcate. Cheek teeth very hypsodont, with well-developed dentine tracts, forming roots in very old age with possible exception of  $M_3$  which may be evergrowing. Only known  $DP_4$ , of Pliogeomys buisi, very cusate with prominent posterior cingulum; morphologically indistinguishable from  $DP_4$ 's of Brachygeomys drewseyensis. Cusp patterns of molars lost early in life. Those few with cusp patterns can easily be derived from the primitive geomyine condition. Enamel plates reduced on the posterior of the  $P_4$  and the anterior of the lower molars. Permanent premolars lacking cement in reentrants except for  $P_4$  of Pliogeomys transitionalis n. sp. Mandible with moderate to strong symphyseal eminence and with reduction of angular process approaching that of recent Geomys. Ventral margin of mandible quite arcuate. Basitemporal fossa only slightly to moderately developed. Ascending ramus, where known, more dorsally expanded than in other geomyines with rooted cheek teeth but less so than in recent Geomys. Masseteric crest region with primitive configuration and mental foramen under heteromyid projection except for several specimens of P. buisi which have mixture of primi-

tive and advanced characteristics. Geologic range: late Hemphillian (late middle Pliocene) to middle Blancan (late Pliocene). Three recognized species, one of which, P. parvus, may be generically separable.

Pliogeomys buisi Hibbard

Figure 5, G-P; 6, A.

Pliogeomys buisi Hibbard, 1954, p. 353-357.

Pliogeomys buisi Hibbard, Russell, 1968a, p. 522-523.

Occurrence.— Buis Ranch local fauna, Beaver County, Oklahoma. Ogallala Formation, late Hemphillian (late middle Pliocene).

Materials studied.— (All UMMP) Holotype: right mandible with incisor,  $P_4 - M_2$ , V29147. Paratypes:  $RP_4$ ,  $LP_4$ ,  $LM_1$  or  $LM_2$ ,  $M_1^1$  or  $M_2^2$ , V30195. Paratype:  $LDP_4$  (termed a right by Hibbard, 1954), V30194; Rest new material: edentulous right mandible, V33446; left mandible with incisor,  $P_4 - M_3$ , V56274; edentulous partial left mandible, V60465; edentulous partial palate, V60466; 7 upper incisors, V60463, 3 lower incisors, V60465; partial right  $P_4$ , V 60468.

Emended diagnosis.— Only species of this genus known to show faint development of advanced characters in masseteric crest region of some specimens. Much larger than Pliogeomys parvus and differs from it in lacking molar capsules for  $M_1$  and  $M_2$ . Cheek teeth develop roots earlier in life than in Pliogeomys transitionalis n. sp.  $P_4$ 's lack cement in re-

entrants, have shorter dentine tracts and are less hypsodont than those of P. transitionalis.

Lower incisor: The lower incisor is typically geomyine except that the lingual portion of the enamel band is wider than in living Geomys.

Lower deciduous premolar: The  $DP_{\frac{1}{4}}$  of Pliogeomys buisi is virtually identical to, but larger than, the  $DP_{\frac{1}{4}}$  of Brachygeomys drewseyensis. The only qualitative differences are that, in the former, AC I is larger than AC II, the anteroconid is more prominent, and the portion of the mesial lophid anterior to the mesoconid is better developed. Otherwise, the description of the  $DP_{\frac{1}{4}}$  of Brachygeomys drewseyensis is applicable to that of Pliogeomys buisi.

In all of Hibbard's publications (1954, 1956, 1967) in which he discusses or figures geomyine  $DP_{\frac{1}{4}}$ 's, the fossil  $DP_{\frac{1}{4}}$ 's are assigned to the wrong side of the jaw. Hibbard (personal communication, 1971) informed me that, to orient the specimens, he had used Stehlin and Shaub (1951, fig. 532) who had refigured the  $DP_{\frac{1}{4}}$  of Pliosaccomys dubius. Examination of this figure shows that it was reversed without being noted in the text that such was the case.

Lower fourth premolar: The  $P_{\frac{1}{4}}$ 's are hypsodont and two rooted, one root on each column. Dentine tracts are present on the lingual and labial edges of each column but do not interrupt the occlusal enamel pattern until wear is considerably advanced. Only in one specimen, the left  $P_{\frac{1}{4}}$  of V30195, do the dentine tracts interrupt the occlusal pattern

and then only on the posterior column. The dentine tracts extend slightly higher on the labial sides of the teeth than on the lingual sides. The unworn pattern of the  $P_4$  is unknown but in the least worn specimen, V56274, there is a suggestion of the triradiate pattern on the anterior column. The enamel reentrants between the anterior and posterior columns are sharply V-shaped in the less worn specimens and become more rounded with wear. The lingual reentrant is slightly deeper than the labial. There is no cement present in the reentrants.

Lower molars: The only known unworn permanent tooth is a left  $M_1$  or  $M_2$ , V30195. The crown pattern of this tooth is slightly advanced from that in Pliosacomys dubius. The lophids are more sharply divided and the proto-lophid is more anteroposteriorly compressed. This compression has resulted in the alignment of the protoconid and metaconid into an almost straight, slender, sharp ridge. The protoconid is closely appressed to the parastylid ridge and its labial end connects to the ridge with only a slight demarcation. This would result in a small, temporary enamel lake with a little wear. The protoconid and metaconid are not as clearly differentiated as in Pliosacomys. The proto-stylid is reduced and well separated from the metalophid. The interlophid valley is of fairly uniform depth throughout and there probably would not be any pronounced "first connection" between the lophids. The metalophid is thin, straight, and sharp and not much narrower than the proto-

lophid. There is little differentiation between the entoconid and hypoconid. The hypostylid is still distinct but very reduced and lower than the rest of the metalophid. The labial edge of the tooth is concave in posterior view which confirms its assignment as a lower tooth. The tip of a dentine tract is present on the anterior portion of the labial side about 2 mm. below the crown and there appears to be the tip of a lingual dentine tract. No roots are present at this stage of development.

The  $M_1$  through  $M_3$  of V56274 were removed from the jaw so that they could be studied in greater detail. The  $M_1$  is strongly curved labially and tapers to a single root at the base. A strong concavity exists on the anterior surface, just above the root. The labial dentine tract has reached the occlusal surface at the anterolabial corner of the tooth. The lingual dentine tract remains just below the occlusal surface. The labial third of the anterior enamel plate is absent at the occlusal surface and the remainder of it would disappear with another 1 1/2 mm. of wear. The region of the dentine tracts bears a thin, irregular cover of a material resembling cement.

The  $M_2$  is very similar to the  $M_1$  except that the labial curvature is weaker, about the labial one-half of the anterior enamel plate is absent, and only about 1 mm. of additional wear would result in the disappearance of the remainder of the anterior enamel plate. The single root is well developed but less so than that of the  $M_1$ .

The  $M_3$  possesses a torsion toward the labial side and is strongly curved posteriorly. The enamel pattern on the occlusal surface is uninterrupted but the enamel on the anterior, lingual, and labial sides is very thin. The cement-like substance covers much of the tooth except for the posterior enamel plate. Because of it, the pattern of the dentine tracts and the lower edge of the anterior enamel plate are very difficult to discern. It appears as though the anterior enamel plate would disappear after about 1 1/2 to 2 mm. of wear. This tooth tapers slightly toward the base, but, as yet, there is no root development. As the  $M_3$  is the last molar to erupt, the root may simply not have formed yet or the tendency to develop evergrowing cheek teeth may be first showing up in the  $M_3$ .

No other isolated lower molars are available but the alveoli for these teeth in the known jaws show that they were hypsodont and single rooted. In the known  $M_1$ 's and  $M_2$ 's the labial dentine tracts interrupt the occlusal enamel pattern at an earlier stage of wear than do the lingual tracts. In the holotype, V29147, both the lingual and labial tracts interrupt the occlusal enamel pattern. The lingual tracts are narrow and interrupt the enamel pattern only at the extreme lingual portion of the teeth but the labial tracts are quite broad. The  $M_1$  has all the enamel missing from the labial side and the labial one-fourth to one-third of the anterior margin. In the  $M_2$ , very little enamel is missing from the anterior margin and

there is still a little enamel present on the postero-labial corner. Both teeth are roughly oval in outline but slightly pointed lingually.

Upper incisor: The upper incisors are sharply bisulcate with the medial groove slightly lingual to the midline. The radius of curvature of the five most complete specimens is from 8 to 8 1/2 mm. The maximum arcs subtended (two specimens) are  $190^{\circ}$ , indicating probable opisthodonty.

Upper deciduous premolar: Unknown.

Upper fourth premolar: The only known  $P_4$  lacks approximately the posterolingual one-half and is moderately worn. It is very hypsodont and slightly concave anteriorly. An anterior root fragment can be discerned but the area where the posterior portion of the root would be located is missing. Alveoli for the  $P_4$ 's, in a specimen with partial maxillaries, show that only a small vestige remains of the posterior portion of the root. The labial reentrant between the anterior and posterior columns appears to be deeper than the lingual one; neither one shows any development of cement. The labial dentine tract on the anterior column is narrow, sharp-pointed and reaches only about half way to the occlusal surface. Only the anterior portion of the posterior labial dentine tract remains. It is broader and higher than the anterior and may have reached the occlusal surface. The area which would bear the lingual tracts and posterior enamel plate is missing. Reentrants are V-shaped.

Upper molars: Only one upper molar has been collected, an M<sup>1</sup> or M<sup>2</sup> which cannot be assigned to side. It is moderately worn and a small chip is missing from a posterior corner. The tooth tapers suddenly at the base to a single root and is slightly concave posteriorly. Narrow lingual and labial dentine tracts interrupt the occlusal enamel pattern. The posterior enamel plate tapers to a point and disappears before reaching the base of the tooth.

Mandible: The one partial and three nearly complete mandibles of Pliogeomys buisi are more similar to modern Geomys than are the known mandibles of Hemphillian forms from the Great Basin region. The variability exhibited in so few specimens leads me to suspect that more than one taxon is present. However, different similarities and various differences occur between any pair of specimens so that, if any taxonomic separation were made, each of the four would have to be considered a different taxon. The simplest solution is to consider them all as individuals from a highly variable population. No specimen possesses more than the base of the coronoid process and all have the incisive capsular process broken. The outline of the ventral margin approaches the arcuate condition of modern Geomys.

In medial view, the condylar process is slightly narrower than in Geomys. The articular condyle faces dorsad and the fossa for the external pterygoid is poorly developed. Most of the closer approach to an arcuate ventral margin comes from the reduction of the slightly variable

angular process, almost to its condition in living Geomys. The basitemporal fossa ranges from slightly to moderately developed. The excavation of the ascending ramus is conspicuous in all specimens but the depression between the ascending ramus and the alveolar row varies from a shallow trough in UMMP V60465 to a moderately sized pit in the holotype, UMMP V29147. The mandibular foramen is just posterior to the basitemporal fossa and about midway between its dorsal and ventral margins. In UMMP V29147, a faint depression with a single small foramen to the incisive capsular process occurs posterior to the mandibular foramen. In UMMP V33446, this depression is slightly deeper with three small foramina and a larger one but in UMMP V56274 this depression is very deep and bears four larger foramina. The geniohyoid and mylohyoid fossae appear well developed and the latter is very deep posteriorly. The symphysis is large and massive. The symphyseal eminence is better developed than in Parapliosaccomys oregonensis and less so than in recent Geomys, extending posteriorly to under the  $P_4$ . The diastemal notch compares to that of Geomys. The capsular process for the  $M_3$  is present but variably developed and usually broken. The alveoli for the  $M_3$ 's in different mandibles vary considerably in width with UMMP V33446 having the narrowest. In all specimens, the alveolus is conspicuously narrower than the  $M_2$  alveolus. The  $M_3$  of UMMP V56274 and the  $M_3$  alveolus of UMMP V33446 lie dorsal and only slightly lingual of the incisor. In UMMP V29147,

the  $M_3$  alveolus is more lingual and in UMMP V60465, the incomplete  $M_3$  alveolus appears to extend almost vertically from the alveolar surface along the lingual margin of the incisor, causing a similar orientation of the  $M_3$  capsule.

In lateral view, the lateral angular process is prominent with a nearly horizontal dorsal surface. The incisive capsular process, when complete, would have extended dorsad close to the level of the articular condyle, resulting in a strong capsular groove. The posterior masseteric fossa, while not as dorsoventrally expanded as in Geomys, is more expanded and possesses a better defined anterior margin than in Parapliosacomys oregonensis. The small temporal node is more ventral in position along the anterior margin of the ascending ramus in UMMP V29147 than in the other specimens. No molar or premolar capsules exist on the lateral surface of any of the mandibles but a slight swelling just posterior to the anterior margin of the masseteric crest in UMMP V56274 marks the posterior column of the  $P_4$ . UMMP V60465 lacks the anterior portion of the mandible. All other specimens have strong ventral branches of the masseteric crest and well-developed heteromyid projections. The holotype, UMMP V29147, has a medial branch of the masseteric crest which, anteriorly, is a low ridge with a faint groove dorsal to it. About midway of its length, the ridge fades out and only the groove remains to its termination at the temporal node. The mental foramen is just anterior to the heteromyid projection which ends just under the anterior

margin of the  $P_4$ . The dorsal branch of the masseteric crest is very faint, attaching to the anterior of the heteromyid projection. UMMP V33446 has a very similar configuration except that the medial branch of the masseteric crest retains a faint ridge farther posteriorly and the posterior margin of the mental foramen is just under the anterior margin of the heteromyid projection. In UMMP V56274, the heteromyid projection extends slightly anterior to the  $P_4$  and above the mental foramen, the medial branch of the masseteric crest maintains a faint ridge and groove along its entire length, and the dorsal branch of the masseteric crest is extremely faint. The diastemal notch is well developed in all three.

Discussion.- Hibbard (1954, 1964) and Zakrzewski (1969) suggested that Pliogeomys buisi gave rise to the genus Geomys. Russell (1968a) considered it to be an offshoot of the Geomyini. However, the retention of largely primitive characters in the mandibles and the cusped nature of the  $DP_4$  place P. buisi in the Nerterogeomyini. It could be derived from almost any of the primitive forms lumped under Pliosaccomys but the strong similarity of the  $DP_4$  with that of Brachygeomys drewseyensis indicates at least a close relationship between them, if not a phylogenetic one. There is little doubt that P. buisi gave rise to the slightly more advanced Pliogeomys transitionalis n. sp. found in slightly younger deposits of the same area. It is probable that P. buisi represents a different line of the Nertero-

geomyini from Pliogeomys parvus Zakrzewski but that they shared a common ancestor.

The partial palate of Pliogeomys buisi is geomyine in its preserved features. A number of post-cranial elements, including a partial skeleton, UMMP V60752, closely resemble those of living Geomys on cursory inspection. Pliogeomys buisi can definitely be considered to have had a fossorial habitus.

Pliogeomys transitionalis n. sp.

Figure 6, B-I.

Family Geomyidae Hibbard, 1953, p. 392.

Pliogeomys sp. Hibbard, 1954, p. 356.

Pliogeomys cf. P. buisi Hibbard, Hibbard, 1964, p. 124.

Occurrence.- Saw Rock Canyon local fauna, KU loc. 6, Seward County, Kansas. XI Member of Rexroad Formation, late Hemphillian (upper middle Pliocene). The holotype was found by Carl Sanders July 5, 1969, in Saw Rock Canyon, near the center of the west section line of Sec. 36, T. 34S., R. 31W., XIT Ranch (west part of old XI Ranch), Seward County, Kansas. This is also the type locality of Marmota sawrockensis (Hibbard, 1964) and is just a short distance up the canyon from the main quarry which yielded all of the paratypes.

Materials studied.- (All UMMP) Holotype: partial left mandible with  $P_4 - M_2$ , V60474. Paratypes: associated upper

incisors,  $LP_1^4$ ,  $RP_1^4$ ,  $M_3$ , V28286; associated upper R incisor,  $LP_1^4$ , partial  $LM_1$  or  $LM_2$ , V29719; partial  $RP_4$ , V41401; upper L incisor, V60469; 2  $M_3$ 's, V60470;  $LM_1$  or  $LM_2$ , V60471;  $M_1^1$  or  $M_2^2$ , V60472; 2 unworn posterior columns of  $P_1^4$ 's, V60473.

Diagnosis.-  $P_4$  with cement in reentrants, more hypsodont with higher dentine tracts than Pliogeomys buisi. Cheek teeth form roots later in growth than in P. buisi. Only known mandible has mental foramen under heteromyid projection and has dorsal branch of masseteric crest faintly developed. No other significant demonstrable differences exist between Pliogeomys transitionalis and P. buisi. Differs from Pliogeomys parvus in same ways as P. buisi does. Specific name derived from its apparant transitional position between P. buisi and Nerterogeomys.

Lower incisor: The lingual portion of the enamel band is slightly narrower than in Pliogeomys buisi. There is no significant difference between the lower incisor of Pliogeomys transitionalis and those of living Geomys.

Lower deciduous premolar: Unknown.

Lower fourth premolar: From the available material, the  $P_4$  of Pliogeomys transitionalis is more hypsodont, has higher dentine tracts, has cement in the reentrants, and has poorly developed roots which form at a later growth stage in comparison to the  $P_4$  of Pliogeomys buisi.

The  $P_4$  of the holotype, V60474, was removed from the mandible. It is rather poorly preserved with a corroded

surface and ferruginous stains. The occlusal surface is typically geomyine in outline, having a rounded anterior column and an oval posterior column. The reentrants are V-shaped and filled with an iron-stained deposit which is probably cement. The dentine tracts have not yet interrupted the occlusal enamel pattern, but both lingual tracts and the posterolabial tract are very close to the occlusal surface. The anterolabial tract appears to be farther from the occlusal surface but this is not certain because the area is very corroded. In lateral view, the anterior margin of the tooth is slightly convex and the posterior margin is slightly concave. It also shows a distinct labial curvature. The anterior and posterior columns merge near the base and the indistinct beginnings of two small roots occur at the very base.

The posterior portion of the posterior column of V41401 is missing. It appears to be considerably more worn than the  $P_4$  of V60474; all dentine tracts interrupt the occlusal enamel pattern to produce a pattern of enamel plates indistinguishable from that of modern Geomys. The anterolabial tract is much broader than the others. The reentrants are squared U-shaped and are filled with cement.

Lower molars: The  $M_1$  and  $M_2$  of the holotype, V60474, are so severely damaged that little information can be gotten from them. The occlusal surface of the only complete  $M_1$  or  $M_2$ , V60471, is roughly oval with a flat anterior margin and a pointed lingual margin. A broad labial dentine tract and

a narrower lingual one separate the enamel into a thick posterior plate and a thinner anterior plate. The anterior plate disappears 2 mm. below the crown. The tooth is labially concave and tapers toward the base. This taper suggests the beginning of root development but no definite root exists. V29719 is broken parallel to the occlusal surface with only about the basal half remaining. It lacks the anterior enamel plate and has the same basal taper with no definite root as does V60471. The  $M_1$  of the holotype lacks most of the anterior half at the occlusal surface. Damage to the specimen is so extensive that it is impossible to be certain of anything but the tooth appears to be complete where it enters the alveolus and no trace of an anterior enamel plate is present. The posterior enamel plate is almost complete and thick. The  $M_2$  of the holotype, also damaged, bears traces of a thin anterior enamel plate at the occlusal surface but none where it enters the alveolus. The posterior enamel plate is complete and thick.

The two  $M_3$ 's of V60470 are in early stages of wear. They were not recovered in association. The right is worn to the stage that the details of the cusps are lost but the lophids remain separated. The first lophid connection would be labial but a complete connection would soon follow. The entire specimen is twisted lingually. Both lateral dentine tracts lack less than 1 mm. of reaching the occlusal surface and the thin anterior enamel plate would disappear after about 1 1/2 mm. of additional wear. The left  $M_3$  is slightly

more worn but an indentation marking the last vestiges of the interlophid valley remains on the lingual margin. This specimen lacks the anterior portion except for the basal one-third. No observations are possible regarding the height of the dentine tracts or the anterior enamel plate. The left  $M_3$  of V28286 is still more worn, the labial dentine tract has just reached the occlusal surface and the lingual tract is about to do so. The very thin anterior enamel plate still extends about 1.5 mm. below the occlusal surface.

All three specimens have thick posterior enamel plates. All have a torsion to the lingual side so that the posterior margin at the occlusal surface becomes the posterolingual margin at the base of the tooth. All are tapered toward the base but show no definite root development. This tapering of the basal portions suggests that roots might develop in old age.

Upper incisors: The upper incisors differ slightly from those of Pliogeomys buisi in that the lingual groove is slightly better developed and the medial groove has steeper sides. Only two were complete enough to measure the radius of curvature, 7.5 and 8.0 mm. None is complete enough to estimate the subtended angle.

Upper deciduous premolar: Unknown.

Upper fourth premolar: The unworn left and right enamel caps from the posterior columns of  $P_4$ 's, V60473, are the only unworn dental specimens known from this species. Neither

has any encrusting cuspules and both possess a very prominent posterior cingulum. The posterior cingulum of the right is a simple ridge, higher mesially than labially or lingually. The posterior cingulum of the left  $P_4^4$  bears a cusp at the labial end. The metacones of both are large and vaguely divided into three cusps. The anterior ends of the metacones curve anterolingual ending anterior to the labial margins of the hypocones. The laterally elongate hypocones make up most of the metaloph and small entostyles occur just posterior to where the teeth are broken.

The left  $P_4^4$  of V28286 is slightly less worn than the right. The connection between the columns is near the lingual margin in the former and just lingual to the midline in the latter. Neither have any cement in the V-shaped reentrants. In both, the dentine tracts lack 1 to 2 mm. of reaching the occlusal surface with the lingual tracts slightly higher than the labial. The posterior enamel plate is still fairly thick at the occlusal surface but after about 2 mm. of wear, it would be completely absent from the occlusal pattern. Both teeth taper toward the base and appear as though they would develop roots later in the life of the individual. The left  $P_4^4$  of V27919 is virtually identical to the left  $P_4^4$  of V28286.

Upper molars: The only known  $M_1^1$  or  $M_2^2$ , V60472, lacks a small chip on one corner, probably the labial. A slight curvature probably indicates the labial side but the specimen displays no criteria which would serve to distinguish

between the anterior and posterior margins. It is moderately worn, the lingual dentine tract has not quite interrupted the occlusal surface. Because of the missing chip, it cannot be determined whether or not the wider labial tract had reached the occlusal surface. Neither enamel plate shows any reduction. The basal taper is greater than on the lower molars and a true root appears to be forming.

Mandible: The only known mandible is badly damaged but it does not appear to differ significantly from the mandibles of Pliogeomys buisi. The mental foramen is under the heteromyid projection, the dorsal branch of the masseteric crest is faintly developed, and the diastemal notch is well developed.

Discussion.— Pliogeomys transitionalis represents an evolutionary stage more advanced than Pliogeomys buisi and, apparently, leading to Nerterogeomys. It is the most advanced of all known geomyines having rooted cheek teeth in that roots form only in very old age and may not form at all in some posterior molars, and in having cement occurring in the reentrants of the  $P_4$ . The mandible and  $DP_4$  of Nerterogeomys can be more easily derived from P. buisi and P. transitionalis than from any other known geomyine. There is nothing in the known material of either form which would argue against developing Nerterogeomys from P. transitionalis.

A few fragments of limb bones in the UMMF collections from the Saw Rock Canyon local fauna closely resemble

specimens of Pliogeomys buisi and recent Geomys. Pliogeomys transitionalis undoubtedly had a fossorial habitus.

Pliogeomys parvus Zakrzewski

Figure 6, J-M; 7, A-J.

Pliogeomys parvus Zakrzewski, 1969, p. 8-11.

Occurrence.-- Hagerman local fauna, Twin Falls County, Idaho. Glenns Ferry Formation, early Blancan (late Pliocene).

Materials studied.-- (All UMMP) Holotype: partial right mandible with incisor,  $P_4 - M_2$ , V55185. Paratypes: partial left mandible with  $M_2 - M_3$ , V54366; partial left mandible with  $P_4 - M_2$ , V53562; partial left mandible with incisor,  $P_4 - M_1$ , partial right mandible with  $P_4$ , fragment of right mandible with  $P_4 - M_1$ , V55957;  $LP_4$ 's - V56017, V51578;  $LM_1$  or  $LM_2$ , V53450; anterior skull fragment with L incisor,  $LP_4^4 - M_2^2$ ,  $RP_4^4$ , V55184; R upper incisor, V53495;  $LP_4^4$ , V55031. Rest new material: fragment of edentulous right mandible, V60803; isolated upper incisors - V60753-54, V60755 (2), V60756-60, V60761 (2), V60762 (2), V60763-65, V60791-97, V60798 (3), V60799, V60800 (6), V60801, V60802 (2).

Emended diagnosis.-- Only geomyine with rooted cheek teeth known from post-Hemphillian deposits. Very small, possesses mixture of advanced and primitive characteristics. Morphology of anterior masseteric crest region completely primitive, no trace of a dorsal branch of the masseteric

crest. Enamel reduced on anterior of lower molars and posterior of  $P_4^4$  through  $M_2^2$ . Reduction of anterior enamel plate on  $P_4$  greater than in any other known geomyine. Upper incisor with lingual groove fainter than in other species of Pliogeomys. Smaller than other species of Pliogeomys or any other geomyine with hypsodont cheek teeth. Molar and premolar capsules present in masseteric fossa. Basitemporal fossa moderately developed but rather posterior to the usual position.

Lower incisor: The lower incisors are similar to those of recent Geomys except for the lingual enamel band being relatively broader.

Lower deciduous premolar: Unknown.

Lower fourth premolar: The least worn specimen, UMMP V56017, lacks cusp details on the anterior column but retains them on the posterior column. The outline of the slightly worn anterior column is more anteroposteriorly compressed than in similarly worn  $P_4$ 's of other geomyines which have rooted cheek teeth. Anterolingual and anterolabial enamel inflections appear to mark the valleys between the three ridges of the anterior column. Accordingly, the anterostylid and metaconid ridges seem to have been directed labiad and linguad, respectively, from their point of junction. The protoconid ridge was directed approximately anteriad and may have been quite broad. The common junction of all three ridges is marked by some remaining enamel and was probably cusplate, extending posteriorly onto the short

isthmus. The hypostylid and entoconid are laterally elongate, thin, and sharp. A pit occupies the position of the hypoconid, just posterior to the isthmus. The low posterior cingulum attaches about midway of the hypostylid and midway of the entoconid. It has an irregular surface but is not cusate. The occlusal patterns of the slightly more worn  $P_4$ 's in UMMP V55957 and UMMP V53562 indicate that they probably had similar cusp patterns. The occlusal outline of the anterior column becomes more rounded, then slightly elongate as wear continues. The posterior column becomes anteroposteriorly expanded with very rounded labial and lingual margins as wear progresses. The shape changes of the reentrants with increasing wear are: narrow and V-shaped, broader and U-shaped, and squared U-shaped in late wear stages. Cement is never present. Dentine tracts on the labial and lingual sides of the posterior column are sharp and thin but only interrupt the occlusal enamel outline late in wear. The dentine tracts on the labial and lingual sides of the anterior column are usually slightly lower and broader and would only interrupt the occlusal pattern in pre-final wear. The anterior enamel plate extends only a short distance basally from the highest parts of the anterior dentine tracts and would disappear in extreme old age. None of the known specimens has reached this stage. There is no sign of roots in the almost unworn specimen, UMMP V56017. The other isolated  $P_4$ , UMMP

V51578, in a pre-final wear stage, has a single root on each column. These roots approximate the outline of their respective columns. The  $P_4$  in a right mandible fragment in UMMP V55957 is in early wear stages but two well-developed roots are exposed by breakage of the mandible.

Lower molars: The only known slightly worn  $M_1$  or  $M_2$ , UMMP V53450, preserves much of the occlusal pattern which closely resembles the primitive geomyine pattern. The hypolophid is basically straight with small irregularities. The cusp pattern on it cannot be made out. The thin metaconid is straight and lies along the lingual portion of the anterior tooth margin. The broader protoconid trends posterolabial from its junction with the metaconid and is well separated from the protostylid ridge. The protostylid ridge follows the anterior and labial margins of the tooth from its juncture with the protoconid and metaconid to the protostylid. The elongate protostylid occurs just anterior to the labial end of the hypolophid and is slightly separated from the protostylid ridge. Just a little more wear would result in a complete labial lophid connection and a squared C-shaped occlusal pattern. Another lophid connection would occur just lingual to the midline of the specimen just before the interlophid valley was obliterated by wear. A lingual enamel flexure would remain for a while. Labial and lingual dentine tracts are almost non-existent because the anterior enamel plate only extends a maximum of 1 1/2 mm. basally from the occlusal surface, even less on

the labial portion. There is no sign of root development in this specimen. The occlusal outline of  $M_1$  and  $M_2$ , after the last vestige of the interlophid valley is removed by wear, becomes a rather fat oval with the labial margin much broader than the lingual. With additional wear, the outline becomes more regularly oval but the labial margin remains slightly broader than the lingual. Younger specimens retain a complete rim of enamel around the occlusal surface which soon thins anteriorly, becomes interrupted, and then the anterior plate disappears. Small enamel lakes mark the labial portion of the interlophid valley in some younger specimens. The base of the  $M_2$  in UMMP V53562, a young specimen, is exposed by breakage of the mandible and shows no root development. However, the alveolus for the  $M_2$  in the left mandible of UMMP V55959 and the alveolus for the  $M_1$  in UMMP V54366 show that a single root forms in old age.

An  $M_3$ , UMMP V54366, is in an early wear stage. The occlusal ring of enamel is uninterrupted and a faint lingual flexure remains. This tooth is slightly narrower than the  $M_2$  but has a greater anteroposterior diameter. The basal portion is not visible.

Upper incisor: The upper incisor bears two grooves, a faint lingual one and a deep one just labial to the midline of the tooth. The left incisor is present in the skull fragment, UMMP V55184. Numerous other isolated incisors have been recovered from various localities in

the Hagerman fauna. The seven most complete specimens have radii of curvature from 5 to 5 1/2 mm. The maximum angle subtended by the most complete specimen is 180°. This rather large subtended angle agrees with the opisthodont condition of the upper incisor remaining in the skull fragment.

Upper deciduous premolar: Unknown.

Upper fourth premolar: All of the three known  $P_4^4$ 's are at least moderately worn. All have subtriangular occlusal outlines of the anterior column, ovoid posterior columns with flattened anterior margins, V-shaped reentrants without cement, and the isthmuses lingual to the midlines of the teeth. The  $P_4^4$ 's in UMMP V55184 have uninterrupted occlusal enamel outlines. The occlusal outline in UMMP V55031 is interrupted at the labial margins of both columns; the lingual dentine tracts do not quite reach the occlusal surface. The posterior enamel plates of UMMP V55031 and the  $RP_4^4$  of UMMP V55184 would disappear with a little additional wear except for a lingual strip of enamel which extends to near the root. The posterior surface of the  $LP_4^4$  of UMMP V55184 is not visible. UMMP V55031 is forming a single, trilobate root at its base.

Upper molars: The only known upper molars are the  $M_1^1$  and  $M_2^2$  in the skull fragment, UMMP V55184. Zakrzewski's (1969, fig. 4, A) figure of these molars is misleading because it does not show enamel on their posterior margins. Both show lingual and labial dentine tracts interrupting

the occlusal pattern. The  $M_1^1$  has a thin posterior enamel plate across the labial three-quarters of the tooth. If a large chip were not missing from the posterolingual corner, the posterior plate may have been complete. The posterior plate on the  $M_2^2$  is just slightly thinner than the anterior plate and is complete. The  $M_2^2$  was removed to expose the posterior surface of the  $M_1^1$ . The posterior enamel plate on the  $M_1^1$  would be completely absent after less than 1 mm. of additional wear. The posterior enamel plate of the  $M_2^2$  tapers basally to a medial point just above the root. Both upper molars have ovoid occlusal surfaces and taper to single roots which are not too well differentiated from the body of the teeth.

Mandible: None of the available material retains the posterior portion of the mandible. Only the very anterior-most part of the angular process remains, extending to under the  $M_3$ . The basal portion of the basitemporal fossa appears to have been moderately developed but occurs posterior to the  $M_3$  in UMMP V54366. The mandibular foramen is not preserved in any specimen nor does any specimen retain enough of the ascending ramus to determine if it is excavated dorsal to the basal portion of the basitemporal fossa. The geniohyoid and mylohyoid fossae are well-developed. The symphysis is large and heavy with only a moderate to small symphyseal eminence.

In external view, only the area anterior to the posterior masseteric fossa is preserved. The posterior portion

of the masseteric fossa is somewhat excavated. Capsules for the  $P_4$  and  $M_2$  may or may not be present in the masseteric fossa but the capsule for the  $M_1$  is present in all known specimens. The dorsal branch of the masseteric crest is never present and the medial branch is always well developed. The mental foramen occurs ventral to the very strong heteromyid projection which extends well anterior to the  $P_4$ . The diastemal notch is poorly developed.

Discussion.— The known material of Pliogeomys parvus presents an interesting combination of primitive and advanced characteristics. The configuration of the masseteric crest region and the occlusal pattern of the lower molar are very primitive. The development of the basitemporal fossa is relatively advanced but posterior to its usual position in other geomyines. The hypsodonty of the cheek teeth and reduction of the anterior enamel plates on the lower molars and the posterior plate of the  $P_4$  is advanced. The reduction of the posterior enamel plates on the  $M_1$  and  $M_2$  has previously been considered to be one of the most advanced dental features in the Geomyinae. This species clearly illustrates some of the convergence and parallelism which is very common among the pocket gophers. The extreme reduction of the anterior enamel plate on the  $P_4$  is unique among the Geomyinae.

Zakrzewski (1969) suggested that Pliogeomys parvus may have been a late survivor of the line which gave rise to Nerterogeomys but, as shown elsewhere, Pliogeomys transi-

tionalis more nearly fits the ancestral role for Nerterogeomys. The peculiar specializations and late appearance of P. parvus show that it could not be directly ancestral to any known later geomyine. Pliogeomys parvus can best be regarded as the last survivor of a line separate from, but having a common ancestor with, the line which gave rise to Pliogeomys buisi, P. transitionalis, and Nerterogeomys. It may well prove to be generically separable from the other species of Pliogeomys when more material of all is available.

Although there is not any post-cranial material known for Pliogeomys parvus, the strongly geomyine aspect of the skull and mandible indicate that it was at least semi-fossorial.

Reexamination of the UMMP Hagerman collections turned up 36 isolated incisors from various localities at different stratigraphic levels. These extend the known range of Pliogeomys parvus within the Hagerman localities down to the 2950' elevation (locality UM-Ida 14-64) from the 3050' elevation given by Zakrzewski (1969, text-fig. 13) as the lowest occurrence.

#### Tribe indeterminate

The known material of the following taxa is not sufficient for assignment to a tribe.

Pliosaccomys? shotwelli n. sp.

Figure 7, K-M; 8, A-P.

Cupidinomys sp. (= Cupidinimus sp.) Shotwell and Russell,  
1963, p. 47.

Pliosaccomys sp. Shotwell, 1967b, p. 26-30.

Occurrence.— Black Butte local fauna, UOloc. 2500 (type locality) and UOloc 2337, Malheur County, Oregon. Late Clarendonian (late early Pliocene).

Materials studies.— (All UO and UOloc. 2500 unless otherwise noted) Holotype:  $LP_{\frac{7}{4}}$ , 24478. Paratypes:  $LP_{\frac{7}{4}}$ , 24466;  $RP_{\frac{7}{4}}$ , 24477;  $LM_1$ 's or  $LM_2$ 's - 24461, 24470;  $LM_3$ 's - 24467, 24482;  $RM_1$ 's 24873, 24891;  $RP_{\frac{4}{4}}$ 's - 6301-15, 24474, 24475;  $LP_{\frac{4}{4}}$ , 24462;  $LM_1$ 's or  $LM_2$ 's - 24460, 24463, 24481, 25270;  $RM_1$ 's or  $RM_2$ 's - 24458, 24464, 24468, 24480;  $M_3$ , 25269. Referred specimen:  $LP_{\frac{7}{4}}$  (UOloc. 2337), F-18236.

Diagnosis.— Oldest and most primitive of known geomyines. Occlusal patterns of cheek teeth typically geomyine. Cheek teeth hypsodont, but less so than any other geomyine.  $P_{\frac{4}{4}}$  with large anterior root and two smaller posterior ones.  $M_1$  and  $M_2$  with two labial roots and one lingual root.  $P_{\frac{7}{4}}$  with anterior root long and strongly convex anteriorly. Named for J. Arnold Shotwell whose work on the Pliocene faunas of the northern Great Basin region resulted in much of the fossil material on which this paper is based.

Lower incisor: Unknown.

Lower deciduous premolar: Unknown.

Lower fourth premolar: The holotype, UO 24478, is the least worn  $P_{\frac{4}{4}}$  from this locality but almost all cusp details are missing. The posterior column is rounded posteriorly and has a smaller width/length ratio than more advanced forms. The posterior margins of the reentrants are straight and at right angles to the longitudinal axis of the tooth. The anterior reentrant margins, also straight, trend antero-laterally from sharp apices. The anterior column bears a deep groove on its anterior margin, extending from the occlusal surface about half way to the base of the enamel cap. By analogy with more advanced forms, this groove probably separates the anterostylid and anteroconid. A trace of the anterostylid exists labial to the groove. The base of the enamel cap bears inflections on the labial and lingual sides of each column. These mark the positions where dentine tracts develop in more advanced geomyines. The posterior root is broken off, but appears to have been broad. The anterior root is long and anteriorly convex.

The referred specimen, UO F-18236 from UOloc. 2337, is almost identical to the holotype except that it is less worn and has both roots preserved. The anterostylid forms a prominent loop anterior to the protostylid and lingual to the anterior groove. A small, probably secondary, cuspsule occurs at the base of the groove. Lingual to the groove is the anteroconid. The posterior root is broad, long, and straight. The other two  $P_{\frac{4}{4}}$ 's are more worn and UO 24477 has the anterior root missing. The remaining traces of the

occlusal pattern agree with the holotype except that the reentrants are slightly more open.

Lower molars: Only the partial specimen, UO 24470, is relatively unworn of the  $M_1$ 's or  $M_2$ 's. Most of the hypolophid is broken off and only the anterior margins of the hypostylid and hypoconid remain. The sharp, oval protoconid and metaconid extend posterolabial and posterolingual, respectively, from their point of juncture. The protostylid is well developed and a large, prominent cusp occupies most of the protostylid ridge. A deep interlophid valley separates the protostylid and hypostylid as well as the remainder of the lophids. Labial and lingual lophid connections would be virtually simultaneous with wear. UO 24461 is moderately worn, just enough to remove all cusp details. A lingual lophid connection is present but the dentine is not yet continuous across it. A medial connection would occur with a little more wear, creating a shallow enamel lake. The root pattern consists of a large root across the posterior and lingual margins and a small root at the anterolabial corner. The posterior margin of the enamel cap extends just slightly more basal than do the lateral and anterior margins. There is no trace of dentine tract development.

Of the  $M_3$ 's, only UO 24467 retains the occlusal cusp pattern. The hypolophid bears a small, low hypostylid, a larger and higher hypoconid, and the entoconid, largest and highest of the cusps. The interlophid valley is shallowest

medially, so that the first lophid connection would be medial, between the labial margins of the entoconid and metaconid. There would be no other separate connection; the medial connection would simply become broader until it extended across the width of the tooth. A small chip is missing from the anterolingual margin of the metaconid. The large metaconid and protoconid are almost in transverse alignment. Posterior to the point where they connect to each other and to the protostylid ridge, they are separated by a narrow, straight-sided valley. The labial part of the protostylid ridge is moderately worn and terminates in a large loop with a center of dentine. It cannot be determined whether or not this resulted from wear of a single, large protostylid or wear of a small protostylid and a larger anterior cusp such as exists in the unworn  $M_1$  or  $M_2$  described previously. In all  $M_3$ 's, a broad posterior root and two narrower anterior roots are present. All have the posterior margin of the enamel cap extending farther ventrally than on the rest of the enamel margins. The other  $M_3$ 's are essentially the same but more worn. UO 24482 has two unconnected transverse lophids with no details preserved except for an enamel lake on the anterolabial corner of the protolophid. Lophid connection would be the same as in UO 24467. The other two specimens are worn to the point that a broad medial lophid connection exists.

Upper incisor: Unknown.

Upper deciduous premolar: Unknown.

Upper fourth premolar: Only UO 5301-15 retains any trace of the occlusal pattern but little information can be gotten from it. The protoloph does not retain any traces of the cusps. The entostyle is represented by a conspicuous bulge at the anterolingual corner of the metaloph but all features of the metaloph have been obliterated; only an irregular oval of enamel remains. A posterior bulge of this enamel oval suggests that a posterior cingulum may have been present. The connection to the isthmus occurs at the posterolingual corner of the protoloph. This connection moves more mesial with wear but in the most worn specimen, UO 24474, it is still conspicuously lingual of the medial axis. There is no cement in the V-shaped reentrants. The enamel cap extends more dorsally on the anterior surface, rising ventrally along the sides to the posterior margin where it is closest to the occlusal surface. Slight inflections of the base of the enamel occur at the lingual and labial margins of each column, marking the points of formation of dentine tracts in more advanced geomyines. All P<sup>4</sup>'s possess V- to broadly U-shaped reentrants, a large anterior root, and two smaller posterior ones. I did not examine UO 24472 (Shotwell, 1967b, fig. 16, J) but, to judge from the figure, it appears to be from a heteromyid rather than a geomyine.

Upper molars: Two left upper molars, UO 24463 and 24460, are almost unworn. UO 24463 has a tricusate protoloph with a protostyle and paracone, which are about equal

in size and height, and a larger and higher protocone. The hypocone is the largest and highest cusp on the metaloph, the metacone being small and irregular. The low hypostylar ridge is closely appressed to the posterior margin of the hypocone and terminates in a small hypostyle, well separated from the protostyle. In UO 24460, the protocone and paracone are about equally developed with the protostyle much smaller and lower. The hypocone is smaller than in UO 24463, but is still the largest cusp on the metaloph. The metacone is small and appears to have had a constriction dividing it into two roughly equal parts. The hypostylar ridge is better separated from the hypocone and the hypostyle is more prominent. The available material is not sufficient to allow a determination of whether these differences indicate two different taxa or variation within a single taxon. I favor the latter explanation. Both specimens would develop lingual and medial loph connections almost simultaneously. One moderately worn molar, UO 24458, considered to be an upper because of root pattern and configuration of the basal edge to the enamel cap, has developed a broad medial loph connection without any separate lingual connection. All  $M^1$ 's and  $M^2$ 's have two labial roots and a single lingual root. The basal margin of the enamel extends slightly farther toward the roots anteriorly than on the other sides. Again, very slight enamel inflections mark the position of future dentine tracts.

One badly worn tooth, UO 25269, is tentatively consid-

ered to be an  $M_3^2$ . It lacks any occlusal detail and is nearly round in occlusal outline. The basal margin of the enamel cap shows no inflections. I cannot definitely orient this specimen but a large root may be approximately posterior and a smaller one anterior.

Mandible: Unknown.

Discussion.— A number of changes were made in the previous identifications of these specimens. UO 24467 (fig. 16, C, D, E of Shotwell, 1967b) is a  $LM_3$  not a  $LM_1$  or  $LM_2$ , UO 24461 (fig. 16, P, Q of Shotwell, 1967b) is a  $LM_1$  or  $LM_2$  not a  $RM_1$  or  $RM_2$ , UO 24458 and 24468 (fig. 16, R, S of Shotwell, 1967b) are  $RM_1$ 's or  $RM_2$ 's not  $LM_1$ 's or  $LM_2$ 's.

The known material of Pliosaccomys? shotwelli constitutes an ideal structural ancestor for all later geomyines. It is possible to derive any geomyine from this taxon by slightly altering the occlusal cusp pattern of the cheek teeth, increasing their hypsodonty, and reducing the number of roots on the cheek teeth. Pliosaccomys? shotwelli is considered to be, if not the direct ancestor, at least near the ancestor of all later geomyines.

The  $DP_4$  and mandible, the most useful material for tribal assignment, are unknown. Also, if Pliosaccomys? shotwelli is near the common ancestor of the various tribes, it may prove to be impossible to assign it to any of them. The generic designation is questioned because of the differences which exist between this material and the genotypic species of Pliosaccomys. The available material sheds no

light on the habitus of this species.

Pliosaccomys? sp.

Pliosaccomys dubius Wilson, Shotwell, 1963, p. 73.

Pliosaccomys sp. Shotwell, 1967b, p. 33-44.

Occurrence.-- Otis Valley local fauna, UOloc. 2347, Harney County, Oregon. Early Hemphillian (early middle Pliocene).

Materials studied.-- None.

A  $P_{\overline{4}}^4$  from the Otis Valley local fauna was assigned to Pliosaccomys dubius and figured by Shotwell (1963, fig. 110) without description. Shotwell (1967b) mentioned an additional  $P_{\overline{4}}^4$  and a calcaneum from the same locality and figured the  $P_{\overline{4}}^4$  (fig. 19, A, B, C). The figures of the  $P_{\overline{4}}^4$  and  $P_{\overline{4}}^4$  indicate that they are probably related to one or more of the other Hemphillian forms referred to Pliosaccomys by Shotwell (1967b).

Gen. and sp. indet.

Pliosaccomys sp. Shotwell, 1967b, p. 44-45.

Occurrence.-- Krebs Ranch local fauna, UOloc. 2322, Gilliam County, Oregon. Middle or late Hemphillian (middle or late middle Pliocene).

Materials studied.-- None.

Shotwell (1967b, fig. 19, D, E, F) figured a  $P_{\overline{4}}^4$ ,

UO 26948, which is more advanced than Pliosacomys but less advanced than Parapliosacomys in crown height and development of dentine tracts. He mentions this specimen and a lower molar from another Krebs Ranch local fauna locality (UOloc. 2323) on pages 44 and 45 but gives no definitive descriptions. These specimens appear to represent an intermediate stage of evolution between the Pliosacomys type and more advanced geomyines such as Parapliosacomys. They do not readily fit any of the generic diagnoses used here and do not represent sufficient material on which to base a new generic concept.

Notes on forms incorrectly assigned to the Geomyinae

#### Dikkomys

Two species of Dikkomys have been described: D. matthewi Wood (1936), the genotypic species, and D. woodi Black (1961). Galbreath (1948) described an additional mandible which he assigned to D. matthewi, apparently with some doubt as to the specific assignment. The few known specimens are all from the early and middle Miocene. Wood (1936) assigned Dikkomys to the Geomyinae and considered it to be the ideal ancestor for later geomyines. Galbreath (1948) did not discuss the relationships of the genus. Black (1961) included Dikkomys in the Geomyinae but pointed out several problems in its relationships with Pliosacomys and later geomyines. Russell (1968a) considered it to be

the ancestral stock of the Geomyinae and to be close to the ancestral stock of all the Geomyidae.

In my opinion, the very feature, strong medial lophid connections and weak or absent labial lophid connections in the lower molars, which led the above researchers to place Dikkomys in the Geomyinae, precludes its inclusion within that group. Although I have not seen any of the specimens, Black's figure (1961, fig. 5, B) of the holotype of D. woodi is very instructive. There are two well-developed cusps on the hypolophid of  $P_4$ , there appear to be three well-developed cusps along the anterior margin of  $P_4$ , the hypolophid of the  $M_4$  is triangular, and the metaconid of the  $M_1$  is directed posterolingual. None of these characteristics is present in any form certainly assigned to the Geomyinae but all are present in Lignimus montis Storer (1970). For these reasons, I consider Dikkomys to be a member of the Lignimus group of the Geomyinae. J. E. Storer (personal communication, 1972) shares this opinion.

#### Horatiomys montanus Wood

A mandible with one anterior tooth, AMNH 22714, from the late middle Miocene Deep River Formation of Montana was described by Wood (1935a) as the holotype of Horatiomys montanus. He assigned this taxon to the Cricetidae but could not show affinities with any other cricetid. Black (1969) restudied the holotype and noted that the anterior tooth possessed characteristics of a deciduous premolar and

that the mandible and incisor possessed features common to juvenile rodents. He also found general similarities between the tooth of H. montanus and  $DP_{\overline{4}}$  of Gregorymys. Because of these similarities and the presence of deep alveoli for  $M_{\overline{1}}$  and  $M_{\overline{2}}$  in H. montanus, he concluded that Horatiomys was a geomyid. Dikkomys woodi Black (1961) is the only geomyid known from the Deep River Formation, so Black decided that H. montanus was probably an immature D. woodi. Previously, he (Black, 1961), in the type description of D. woodi, had assigned Dikkomys to the Geomyinae (but see the discussion of Dikkomys in this paper). Therefore, although not directly stated in his 1969 paper, H. montanus was assigned to the Geomyinae by inference.

I examined the holotype of Horatiomys montanus and there is no question that the mandible is immature and the tooth is a  $DP_{\overline{4}}$ . However, in spite of gross similarities, the detailed cusp morphology of the  $DP_{\overline{4}}$  does not compare favorably with the  $DP_{\overline{4}}$  of any known geomyid. Moreover, the rounded anterior surface of the lower incisor, the position of the mental foramen far anterior to the  $DP_{\overline{4}}$ , the termination of the masseteric crest posterior to the  $DP_{\overline{4}}$ , and the configuration of the preserved portions of the angular process and the ascending ramus are unlike the corresponding elements in any known geomyid. I decided that H. montanus could not be a geomyid and considered it to be either a juvenile aplodontid or a juvenile eomyid with unusually hypsodont cheek teeth, probably the latter. After I had

returned the specimen, Mr. Donald L. Rasmussen showed me a fragmentary mandible of a juvenile aplodontid with  $DP_{\overline{4}}$  and  $M_{\overline{1}}$  he had collected from the Cabbage Patch area of western Montana. Although the  $DP_{\overline{4}}$  was slightly damaged, its preserved portions agree very well with the  $DP_{\overline{4}}$  of H. montanus. One aplodontid, Niglarodon koerneri Black (1961) is known from the early Miocene Fort Logan Formation in the same area from which H. montanus was collected. Comparison of Black's figure (1961, fig. 1, B) with the holotype of H. montanus indicates great similarities in the preserved portions of the back end of the mandible, position of the mental foramen, and configuration of the masseteric crest. Aplodontids also often have hypsodont cheek teeth. My conclusion is that Horatiomys is an aplodontid and not a geomyid.

"Pliosacomys" wilsoni James

James (1963) assigned a new species of geomyoid rodent from late Clarendonian deposits in the Cuyama Valley Badlands of California to the genus Pliosacomys. Only UCMF 50351, the holotype right mandible with partial  $DP_{\overline{4}}$ ,  $M_{\overline{1}}$ ,  $M_{\overline{2}}$ , and unerupted  $P_{\overline{4}}$ , is known. The characters of the teeth are different from those of Pliosacomys and from those of all other known geomyids.

Most of the  $DP_{\overline{4}}$  is preserved, except for the portion anterior to the anterior root. James believed that the anterior one-third was missing but I know of no heteromyid

or geomyid in which this much of the  $DP_{\frac{1}{4}}$  extends anterior to the anterior root. The position of the existing cusps does not correspond very well to cusp positions in Pliosacomys. There is a posterior lophid and a cusp which occupies the position of the entoconid in Pliosacomys but there is no cusp which corresponds to the hypoconid of Pliosacomys. A mesial lophid exists but it extends to the posterior lophid unlike the case in the geomyines. Cusps exist in the apparent positions of the protoconid and the neoconid. The latter extends posteriad from its connection with the mesial lophid, unlike geomyines in which it projects labiad. The portion missing from the anterior end of the  $DP_{\frac{1}{4}}$  in "Pliosacomys" wilsoni is not large enough to account for the missing cusps which would be present in the  $DP_{\frac{1}{4}}$  of a geomyine.

The  $P_{\frac{1}{4}}$  of this specimen is not fully developed. It is not as sharply bicolumnar as are most geomyines and the hypolophid is bicusate rather than tricusate as in primitive geomyines. The protoloph bears the usual three major cusps but shows no sign of an anteroconid or anterostylid.

The lower molars differ from Pliosacomys and other geomyines in having no well-developed connections between the lophids, a very strong and large protostylid ridge which extends more anteriorly, and more strongly developed cusps.

The characteristics of "Pliosacomys" wilsoni are not at all geomyine except in the most superficial manner. I

consider it to be a member of the Heteromyidae. J. A. Storer (personal communication, 1972) also considers this form to probably be a heteromyid.

Pliosaccomys cf. P. dubius of Green (1956)

Green (1956, text-fig. 5, B, C) figured two  $P_4$ 's, both numbered SDSM 5264, from the Ogallala - Wolf Creek local fauna of South Dakota. He assigned them and an " $M_2$ ", SDSM 5269, to Pliosaccomys cf. P. dubius without any definitive description. The fauna is now considered to be from the Ash Hollow Formation, probably the lower part (Green, personal communication to C. W. Hibbard, 1972).

One of the  $P_4$ 's (Green's text-fig. 5, C) is apparently lost. According to the illustration, the anterior column of this tooth is much narrower than the posterior column and only very slightly wider than the isthmus. These proportions are unlike the proportions found in any geomyine and are similar to those found in several heteromyids. Green (personal communication to C. W. Hibbard, 1972) has re-identified this specimen as a heteromyid since the original description.

I consider the " $M_2$ " to be an upper molar, probably a left  $M_2^2$ . It and the other, right,  $P_4$  belong to a single taxon. They appear strongly geomyine in general aspect but the details of their occlusal patterns exclude them from the Geomyinae. Both are very hypsodont and show no signs of closing off to form terminal roots, although they may do so

in later growth stages.

The slightly worn  $P_{\frac{1}{4}}$  bears very short and narrow dentine tracts on both sides of the posterior column but none on the anterior column. Three cusps are arranged along the labial margin of the tooth and a single, elongate cusp occurs on the lingual margin. A deep, anteromedial pit connects to another deep pit on the isthmus by means of a trough. The original occlusal pattern of the posterior column is somewhat obscured by wear but probably consisted of strong lingual and labial cusps connected by a short posterior cingulum.

The upper molar is moderately curved posteriorly and bears well-developed dentine tracts on its labial and lingual sides. As in the molars of geomyines with very hypsodont cheek teeth, the cusp pattern is relatively suppressed in the formation of anterior and posterior lophs which are connected labially in a C-shaped pattern. The protostyle and paracone are connected by an anterior ridge (anterior cingulum?) which passes anterior to the protocone. At this stage of wear, the protocone has a narrow, anterolingual connection to the anterior ridge but it would have been well-separated from the ridge before wear began. The hypocone is almost isolated from the rest of the meta-loph. With additional wear, the paracone and metacone would connect to isolate a large, central enamel lake.

These two teeth cannot be geomyine; their occlusal patterns are completely unlike the patterns found in any of

the Geomyinae but are similar to patterns which exist in the Entoptychinae, particularly Lignimus and Dikkomys. Similar materials from Clarendonian deposits of the Great Plains have been assigned to Lignimus by Storer (1973). I do not know of any specimens from pre-late Hemphillian deposits in the Great Plains which can be assigned to the Geomyinae.

Some of the early records of Geomys and Thomomys from the Clarendonian of the Great Plains (see Russell, 1968a, p. 485-486) may have been based on similar, pseudo-geomyine teeth. An incident which happened to me might show how other of these records came about. While on a field party led by Claude W. Hibbard of the University of Michigan, I was dry screening, with the aid of Earl Brown of Ainsworth, Nebraska, for microvertebrates in Clarendonian deposits at a roadcut northeast of Valentine, Nebraska. Several Pleistocene fossils, including a Geomys upper incisor, turned up in the screen. Morris Skinner of the American Museum of Natural History subsequently informed me that a Pleistocene channel, now partially hidden by slumpage, was present at the top of the section. The Pleistocene specimens were the result of slope wash from this channel.

## PALEOZOOGEOGRAPHY

All records of the Geomyinae prior to the late Hemphillian are from the Great Basin region (including the Columbia Plateau). Even though many faunas are known from the Clarendonian through middle Hemphillian of the Great Plains, none contains any geomyines. They are also unknown from west of the Sierra Nevada although well studied deposits belong to this time span. No data are available about faunas of this age from Mexico.

The known pre-Blancan distribution of geomyines in the Great Basin region is restricted to Nevada and Oregon, the only areas where microvertebrate faunas of appropriate ages have been well studied. The range of pre-Blancan geomyines could easily have extended throughout the Great Basin and into the Colorado Plateau, Sonoran Desert, and Mexican Plateau because the physiographic barriers were not too great. If geomyines were present in much of the Mexican Plateau during this time span, it does seem as though they could have easily have invaded the southern Great Plains in the southern New Mexico - Trans-Pecos, Texas area, where physiographic barriers were less developed than to the north.

The known distributional pattern, combined with areas in which data are lacking, allows three possibilities for the origin and early diversification of the geomyines. One is that they originated and diversified to the north of the

Great Basin region and colonized it with successive waves of more advanced forms. This is highly improbable because of the mountainous topography north of the Great Basin region. Only forms well adapted to a montane existence could accomplish such a feat and they would have been able to move into the Great Plains as easily as into the Great Basin region.

A second, somewhat more tenable, hypothesis is that the origin and center of diversification was in Mexico with waves of colonization from that area. If the center of diversification were the Mexican Plateau, any form able to migrate from that region into the Great Basin region would easily, perhaps more easily, have been able to penetrate the southern Great Plains and rapidly colonize the entire Great Plains. If the center of diversification were the Sierra Madre Occidental, the ancestral geomyines would be montane forms and could have as easily penetrated other regions than the Great Basin. If the Sonoran Desert were the center of diversification, then the spread of geomyines into the Great Basin region would be relatively unhindered while mountain barriers would prevent their spread into other areas. This would involve the geomyines developing in a relatively small area having only a moderate diversity of landforms and environments, then invading a larger area with a greater diversity of landforms and environments.

Although none of the foregoing hypotheses can be disproved, the simplest way of explaining the origin and

early diversification of the geomyines is to accept the known paleontological evidence at face value and postulate that the origin and early diversification occurred in the Great Basin region, the third possibility. As it exists today, this area is an ideal region for the diversification of fossorial and semi-fossorial mammals. The variety of terrain creates a diversity of ecologic niches and the alternation of basins and mountain ranges provides barriers which strongly restrict gene flow between populations preferring either a basin or submontane habitat. The proliferation of nominal subspecies of geomyines in such areas is notorious, but geomyines are much less variable in areas of more homogeneous terrain such as the Great Plains (see the distribution maps of Hall and Kelson, 1959). Similar patterns of variation can be found in Eutamias minimus and Dipodomys ordi (Hall and Kelson, 1959).

The sequence of events in the early evolution and dispersion of the geomyines appears to follow a relatively simple pattern. The main stock was present in the Great Basin area by late Clarendonian and probably much earlier. Diversification was well underway by early Hemphillian and probably initiated in the Clarendonian or even the Barstovian. Stocks of the two tribes, Nerterogeomyini and Geomyini, which are known to be present in the early Hemphillian were relatively primitive. By the late Hemphillian, representatives of these tribes were considerably advanced with extremely hypsodont cheek teeth. Presumably, the Thomomini

and representatives of the other lineages now included in the Geomyini were developing in other portions of the Great Basin. At least one representative of the Nerterogeomyini was able to invade the Great Plains by late Hemphillian. The time and sequence of the invasion of other areas outside the Great Basin cannot be determined but, by early Blancan, geomyines with evergrowing cheek teeth are present in faunas throughout much of the Great Plains and the northern part of the Mexican Plateau.

The apparent rapid evolution and diversification of the geomyines during the Hemphillian deserves some discussion. As noted above, the present physiography of the Great Basin is highly conducive to diversification among populations of fossorial and semi-fossorial mammals. The tectonism and vulcanism which produced the present physiography probably had its inception during the middle Miocene and has continued until the present with the strongest episode of tectonism during the Pliocene (King, 1959; Osmond, 1960). The coincidence of this tectonic activity with the early diversification of the Geomyinae indicates a possible causal relationship. The tectonism and vulcanism may have disrupted the distribution of one or several fairly homogeneous, widespread populations of primitive geomyines, restricting gene flow between adjacent segments of the same population. Another possibility is that one or several more restricted populations gradually spread across the area, diversifying as they went, after the topography had

already become somewhat irregular. Further tectonic activity restricted gene flow to the point that new species and lineages developed rapidly. Under these conditions, parallelism and convergence were probably common and evolution probably took place rapidly.

## GENERAL EVOLUTIONARY TRENDS

Root reduction, hypsodonty, and development of ever-growing cheek teeth.- The increase of crown height, development of dentine tracts, and reduction of roots in the cheek teeth of geomyine rodents are interrelated. The basic evolutionary trend is to increase crown height while developing dentine tracts and reducing the roots. An estimate of the details in the evolution of root reduction and hypsodonty, leading to evergrowing cheek teeth, can be gotten from assuming that it was similar in the several lineages and combining them to show the trends. No single lineage demonstrates more than several structural stages in some of the cheek teeth. In order to simplify the description, dentine tracts will be considered separately. Text-figure 7 outlines the known stages of root reduction.

Although White (1959) recognized three types of tooth hypsodonty, namely cusp, tooth-base, and root, he did not interpret their modes of development. In this discussion, no distinction is made between the first two which are simply lumped as hypsodonty of the crown. White (1959) assigned the Geomyidae to his type 3, root hypsodonty. I agree with him that most of the molar and premolar growth in the more recent Geomyinae takes place below the crown, but growth of the crown portion was important in the early stages of development of a hypsodont dentition. A recent study by Phillips and Oxberry (1972) contains some data

Text-fig. 7- Root patterns of some fossil Geomyini. Anterior is to the top and labial is to the right.

| Taxon \ Tooth                      | $P_4$ | $M_1 \& M_2$                                                                        | $M_3$                                                                                | $P^1$                                                                                 | $M^1 \& M^2$                                                                          | $M^3$                                                                                 |
|------------------------------------|-------|-------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------|
| <i>Parapliosacomys oregonensis</i> | :     |  |  |  |  |  |
| <i>Brachygeomys drewseyensis</i>   | :     |  |  |                                                                                       |  |  |
| <i>Pliosacomys dubius</i>          | :     |  |                                                                                      |  |                                                                                       |                                                                                       |
| <i>Pliosacomys? shotwelli</i>      | :     |  |  |  |  |                                                                                       |

Text-figure 7.

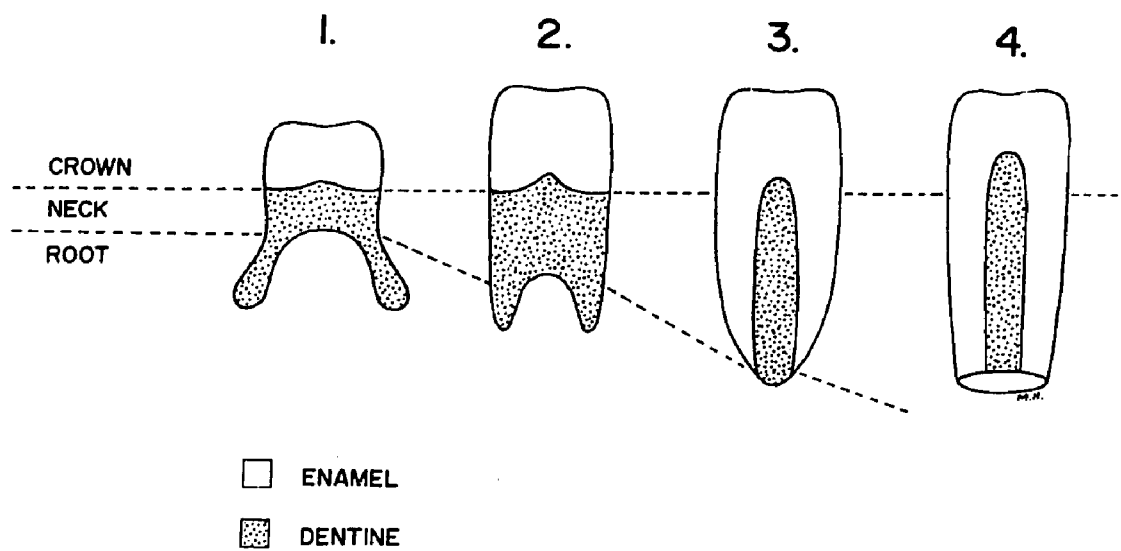
which suggest that evergrowing microtine cheek teeth may be a result of root hypsodonty.

The development of evergrowing cheek teeth from brachydont, firmly rooted cheek teeth in geomyines appears to have gone through the following stages, illustrated in text-figure 8.

Stage 1: Relatively brachydont teeth possessing curved roots which may have terminal bulges or hooks to provide solid, permanent anchorages for the teeth.

Stage 2: More hypsodont teeth with roots which may or may not be reduced in number but which are in alignment with the crown. The increase in height of the enamel covered portions of the teeth in this stage appears to be the result of an increase in the hypsodonty of the crown. In advanced forms belonging to this stage, the portion of the main root between the crown of the tooth and the division into the terminal roots, hereafter termed the neck, is often elongate with an outline approaching that of the crown. The stage 2 condition allows the roots to grow and increase in length for a while so that the crown of the tooth is moved distally as it wears down. This prevents the tooth from wearing down to the gums while useable portions are still present below the gum line. In the Geomyinae assigned to this stage, the continuance of root growth can be observed only in a general, qualitative way. With one exception, the samples of complete teeth assignable to a particular jaw position are so small that quantitative measurements are

Text-fig. 8- Stages in development of evergrowing cheek teeth and dentine tracts in the Geomyini. See text for explanation.



Text-figure 8.

meaningless. The largest sample is the seven isolated  $P_4$ 's of Pliosacomys dubius, only four of which are complete enough to be measured. The measurements in mm. of these specimens with crown height first and root length second are: 2.78, 1.70; 2.73, 1.30; 1.83, 1.77; 1.73, 2.12. Although they are not completely consistent, a general trend can be observed in which the lengths of the roots increase as the crown is worn down. Outside of the Geomyinae, this stage is exemplified by a large sample of the fossil microtine, Pliophenacomys finneyi (Hibbard and Zakrzewski, 1972), from the upper Pliocene of Kansas. In the cheek teeth of this species, there is a strong inverse correlation between the lengths of the roots and the crown heights of the teeth, showing that the roots are growing as the crowns are being worn down (unpublished data).

Stage 3: Only a single root is present on the molars. Premolars in early stage three may form two terminal roots which are reduced to a single root before stage 4 is attained. The neck region is greatly extended and continues to grow in the outline of the crown until old age when it closes off to form one or two terminal roots. As the neck grows, the enamel organ remains active, depositing enamel on the outside of the neck so that it represents an extension of the crown. The so-called high-crowned condition of advanced geomyine cheek teeth is not due as much to elongation of the crown as to elongation of the neck which is subsequently covered with enamel.

Stage 4: In the final stage the neck never closes off but continues to grow while enamel is being deposited on the external surface. Half a dozen supposedly rooted geomyine cheek teeth (UMMP V60837) reported from the Fox Canyon local fauna by Zakrzewski (1969) illustrate an early variant of this stage in which the base of the tooth repeatedly constricts as if to form a terminal root, then continues to grow while a heavy ring of enamel is deposited. Several of these teeth are broad at the occlusal surface, narrow considerably, and broaden again toward the base. None of these teeth has a true root.

The  $P_{\bar{4}}$  of Pliosacomys? shotwelli is moderately hypsodont with a single root on each column. Two roots appear to be the primitive number on the geomyine  $P_{\bar{4}}$ . The anterior root is strongly convex anteriorly forming the good, solid anchorage typical of stage 1. In the slightly more hypsodont  $P_{\bar{4}}$  of Brachygeomys drewseyensis, both roots are aligned with the tooth column and are fused distally to form a longer neck, devoid of enamel as in stage 2. The  $P_{\bar{4}}$  of Parapliosacomys oregonensis is in stage 3 with a long period of neck growth and activity of the enamel organ before small anterior and posterior roots close off from their respective columns. The  $P_{\bar{4}}$  of Pliogeomys is still in stage 3 but with growth ceasing later than in Parapliosacomys.

The  $M_{\bar{1}}$  and  $M_{\bar{2}}$  appear to follow patterns identical to one another. The primitive number of roots probably was four, one on each corner of the tooth. In the most primi-

tive known form, Pliosacomys? shotwelli, the roots are already reduced to a small anterolabial one and a large root extending posteriad from the anterolingual corner to the posterolingual corner then labiad to the posterolabial corner. This latter root appears to have resulted from the combination of separate roots on the three corners which it encompasses. The roots are moderately divergent and somewhat curved, representing stage 1. The root pattern in Brachygeomys drewseyensis and Pliosacomys dubius is the same but in stage 2 with roots in alignment with the crown and a longer neck between the base of the enamel cap and the area of root division. In Parapliosacomys and Plio-geomys, except Pliogeomys transitionalis, the neck continues to grow and is covered with enamel until old age when it closes off, stage 3. The  $M_2$  and/or  $M_1$  of P. transitionalis may be in stage 4, evergrowing, but good specimens in advanced wear stages are lacking.

The  $M_3$  root pattern in Pliosacomys? shotwelli consists of a broad posterior root and two smaller anterior roots, one at each anterior corner. Apparently, the primitive root pattern was the same for the  $M_1$  and  $M_2$  but the sequence of root connection has been different. The roots in P.? shotwelli are already in alignment with the crown, placing the  $M_3$ 's in stage 2. The  $M_3$  of Brachygeomys drewseyensis is also in stage 2 but with the two anterior roots combined to form a single, broad anterior root in addition to the posterior root. In Parapliosacomys the  $M_3$  is in stage 3,

closing off only in old age, but in Pliogeomys it appears to be in stage 4, evergrowing.

The primitive root pattern of the  $P^4$  appears to be that found in Pliosacomys? shotwelli, a single large root on the anterior column and two smaller roots on the labial and lingual margins of the posterior column. They are in stage 1 with the anterior root curved and all roots slightly divergent. The same basic pattern is found in Pliosacomys dubius except that connections are variably developed between the roots, which are in alignment with the crown, and a longer neck is present; this represents stage 2. The  $P^4$ 's of Parapliosacomys and Pliogeomys parvus are in stage 3 with a single trilobate root developing in old age. The root regions of the  $P^4$  in specimens of Pliogeomys buisi and P. transitionalis are not preserved.

The primitive root pattern of  $M^1$  and  $M^2$  appears to be a single lingual root and two labial roots such as found in Pliosacomys? shotwelli. The divergent roots of these teeth place them in stage 1. In Brachygeomys drewseyensis, the root pattern is the same but they are in alignment with the crown and there is a relatively long neck between the crown and the terminal division into roots, as is typical of stage 2. The  $M^1$ 's and  $M^2$ 's of Parapliosacomys and Pliogeomys are in stage 3 with a single root forming in old age.

$M^2$ 's are relatively rare in the fossil record. The oldest known with well preserved roots, of Brachygeomys

drewseyensis, is in stage 2. The single lingual root and the two labial ones are in alignment with the crown. The only other known  $M_3^2$ 's with roots are from Parapliosaccomys. As in the other molars of this genus, they are in stage 3 with the neck closing off in old age.

Two interesting observations from these descriptions are that the  $M_3$ 's are usually one developmental stage ahead of the rest of the cheek teeth and that the  $M_1$  and  $M_2$  of Pliogeomys transitionalis may be in stage 4 while the upper cheek teeth and  $P_4$  are in stage 3. A possible explanation for these anomalies lies in the maximum space available for the growth of each tooth. In all geomyines with hypsodont or evergrowing cheek teeth, the  $M_3$  has a relatively shorter crown height because it lies close to the incisor and to the ventral margin of the mandible. Since it would tend to wear out faster than the other lower cheek teeth if it were in the same developmental stage, there would be an advantage in being a stage ahead. The  $M_1$  and  $M_2$  have more space available for growth than does the  $M_3$  but less than that of the  $P_4$ . If the  $M_1$  and  $M_2$  of P. transitionalis are evergrowing, it may be for the same reason as suggested for the  $M_3$ . Similar factors may play a part in the antero-posterior elongation of the  $M_3^2$ .

Hypsodont or evergrowing cheek teeth are characteristic of many fossorial rodents other than geomyines, e.g., Aplodontia, Ctenomys, Myospalax, and bathyergids. The occurrence of hypsodont cheek teeth is undoubtedly related

to the abrasive effects of sand introduced into the oral cavity while digging or feeding in a subterranean environment. At the present time, it is impossible to demonstrate a correlation between the evolution of hypsodonty in geomyines and their degree of adaptation to a fossorial habitus but there is probably a causal relationship between the two.

Dentine tracts and enamel plate reduction.- The scheme described above for the development of very hypsodont and evergrowing cheek teeth from brachydont, firmly rooted teeth is also useful to explain the accompanying development of dentine tracts in the Geomyinae. In the more primitive geomyines with cheek teeth in stage 1 or stage 2, true dentine tracts are lacking. However, small inflections of the base of the enamel cap do occur at the positions where true dentine tracts form in more advanced geomyines. If it is assumed that these small inflections resulted from enamel deposition ceasing earlier at these places than on the rest of the enamel cap, the following relationships between the development of dentine tracts and the stages of cheek tooth evolution can be interpreted.

Stage 1: The crowns of the cheek teeth are relatively brachydont and the roots form solid attachments to the jaw. Dentine tracts are absent, but small inflections in the bases of the enamel caps mark the positions where they will develop in more advanced forms. The taxon representative of this stage is Pliosaccomys? shotwelli.

Stage 2: The crowns of the cheek teeth are higher and a

longer neck is present but the enamel has not yet begun to extend over the neck. The enamel inflections are only slightly, if at all, better developed than in stage 1 except for several specimens in which they appear to approach small dentine tracts. True dentine tracts have not yet developed in this stage because the increase in height of the enamel-covered portions of the teeth is the result of hypsodonty of the crowns and not the result of enamel deposition on an elongate-neck. Typical examples of this stage are Pliosacomys dubius and Brachygeomys drewseyensis.

Stage 3: The cheek teeth in this stage have necks which continue to grow until relatively late in the life of the individual. They are largely covered with enamel, produced by an enamel organ which remains active until growth ceases. If the above mentioned inflections present at the bases of the enamel caps on more brachydont geomyine teeth are the result of some tendency of the enamel organ to cease deposition earlier at these places, the mode of dentine tract development can easily be explained. The continued activity of the enamel organ which produced the enamel covered necks simply did not extend to the places where the inflections exist. Parapliosacomys and Pliogeomys are examples of this stage.

Stage 4: Further development of dentine tracts in forms with evergrowing cheek teeth is just an extension of the stage 3 condition. There is a trend for earlier cessation of enamel deposition at the position of the dentine tracts

so that the apices of the dentine tracts become progressively closer to the occlusal surface of unworn teeth. This also accounts for differences in height between dentine tracts on opposite sides of a tooth.

There appear to be two mechanisms for the reduction and loss of enamel plates. One is similar to that of the dentine tracts because plates in advanced forms are lost by basal reduction from those portions of the teeth where the plates extended less basally in primitive geomyines. The lost plates include the anterior plates of the lower molars and the posterior plates of  $P^4$  through  $M^2$ . This type of enamel-plate loss typically occurs prior to the teeth becoming evergrowing and involves the total cessation of enamel deposition on that plate before deposition stops on the other plate or plates from the same tooth. The cheek teeth of Parapliosacomys exemplify this mode of plate loss.

A second type of enamel-plate reduction, possibly leading to eventual plate loss, occurs in the upper dentition after the teeth have become evergrowing. In this type, the enamel plate is transversely shortened from the labial end as if the labial dentine tract were being widened. Examples of this type occur in the posterior plates of the  $P^4$ 's in Zyrogeomys and Heterogeomys and the posterior plate of the  $M^1$  in Pappogeomys alcorni. Transverse plate reduction was the only type recognized by Russell (1968a). It led him to believe that reduction of enamel plates in the upper dentition did not begin until it was complete in the

lower dentition. That this is not true in all lineages is shown by Parapliosacomys oregonensis.

The adaptive significance of dentine tracts and enamel plate loss has been adequately discussed by Merriam (1895) and Russell (1968a). Briefly, it increases the efficiency of shearing action between the lower and upper dentitions.

Cement.— As discussed by White (1959) and Phillips and Oxberry (1972), cement on mammalian teeth serves as attachment for the periodontal ligaments which support the teeth. A very thin layer of cement may be present on the roots of primitive geomyines and on the enamel of hypsodont forms but it usually cannot be seen under the dissecting microscope. The only cement which can readily be detected on geomyine teeth is in the reentrants of the fourth premolars. Among the Geomyinae with rooted cheek teeth, none have visible cement in the reentrants of the  $P_4^4$  and only Pliogeomys transitionalis has visible cement in the reentrants of the  $P_4$ . Some molars of Pliogeomys buisi appear to have cement covering the dentine tracts. Most modern geomyines have a heavy deposit of cement in the reentrants of the fourth premolars except Thomomys, which has little or none. In the forms with heavy cement, it probably has a secondary function to reinforce the relatively narrow and weak isthmuses of the fourth premolars.

Peyer (1968) and many others have pointed out that cement covers only the roots (including the neck) of brachydont mammal teeth. Deposition of the heavy layer of cement

on the fourth premolars of geomyines starts well below the unworn occlusal surface of the teeth. This is consistent with the hypothesis concerning the development of hypsodonty. Deposition of cement appears to begin at a position approximately homologous to the juncture of the enamel cap and neck in primitive geomyines.

Lower incisor.-- The only noticeable evolutionary trend in the lower incisor is a gradual reduction of the lingual portion of the enamel band.

Upper incisor.-- The evolution and function of grooves on the upper incisor has been discussed elsewhere (Akersten, 1973).

I cannot find a definite trend in the amount of recurvation in the upper incisor. Only two genera with rooted cheek teeth include upper incisors which are complete enough for measurement of the subtended angle. Parapliosacomys is proodont with a maximum subtended angle of  $140^{\circ}$ . Pliogeomys buisi is opisthodont with a maximum subtended angle of  $190^{\circ}$ . Pliogeomys parvus is opisthodont with a maximum subtended angle of  $180^{\circ}$ . The opisthodont condition of P. parvus is confirmed by a skull fragment which contains the left incisor. The conclusion of White and Downs (1961), that the opisthodont condition is primitive in Geomys and the proodont condition is advanced, can neither be supported or negated by these few data.

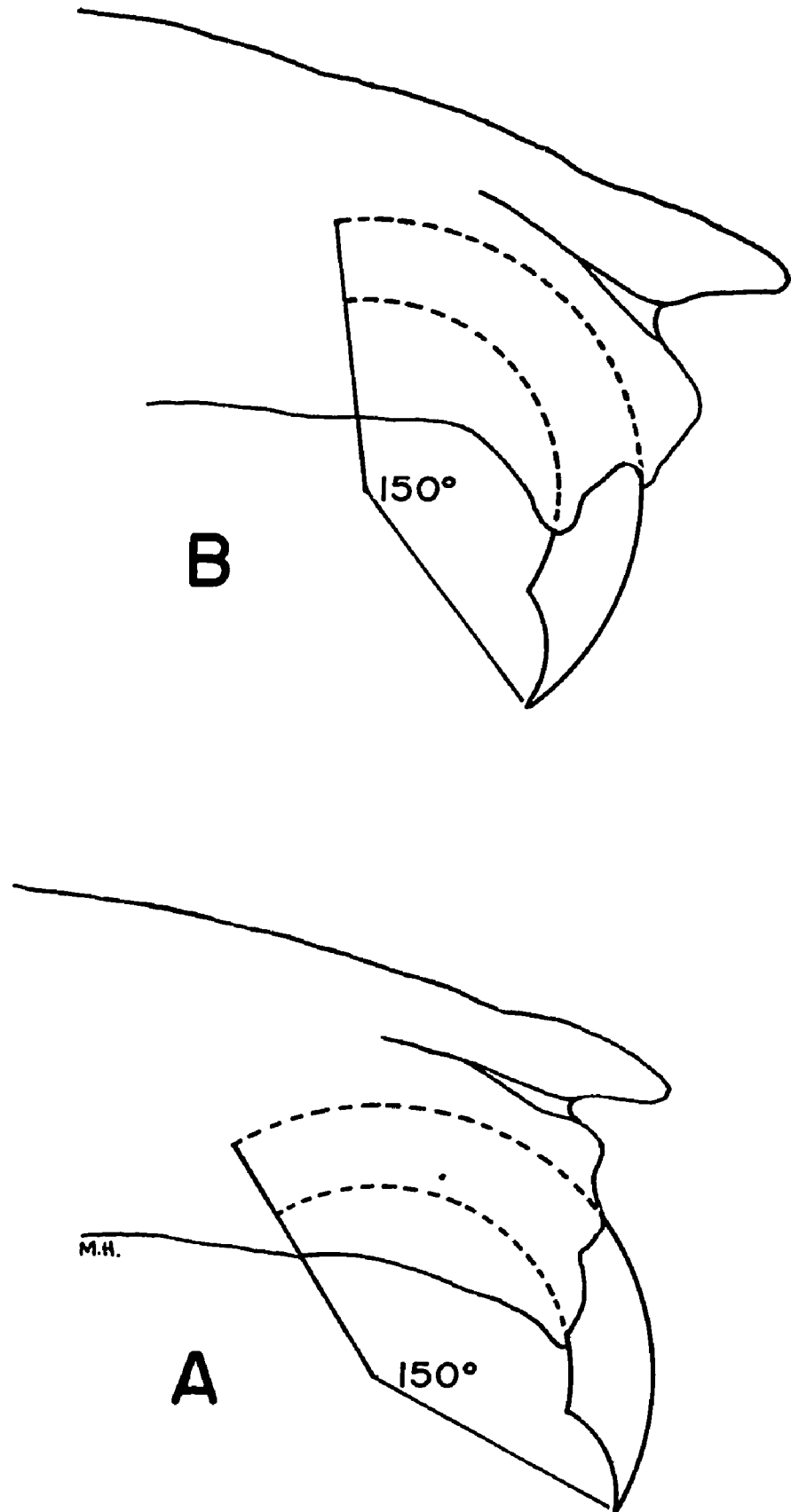
The boundary between proodonty and opisthodonty lies somewhere between subtended angles of  $140^{\circ}$  and  $180^{\circ}$ . A

complication arises in that proodonty and opisthodonty depend not only on the angle subtended by the incisor but also on the attitude of the incisor in its supporting bones. In advanced geomyines, the upper incisor originates dorsal to the  $P_4^4$  and its initial direction of growth is very strongly dorsad. An incisor with a subtended angle such that it would be proodont under these conditions could be opisthodont if it were to originate more anteriorly and have a less dorsad initial component of growth (Text-fig. 9). It may well prove impossible to clearly designate a particular subtended angle as the point of division between proodont and opisthodont incisors.

Occlusal patterns of cheek teeth.— In general, the occlusal patterns of the cheek teeth do not undergo any great modification until after the permanent teeth become evergrowing.

The primitive condition of the  $DP_4$  appears to have been cusate, similar to that of Brachygeomys drewseyensis. This type persisted in the tribe Nerterogeomyini until the late Hemphillian genus Pliogeomys and gradually became more lophodont in Nerterogeomys, a genus with evergrowing cheek teeth. Lophodont  $DP_4$ 's also developed earlier in geomyine history, perhaps more than once. Pliosacomys dubius, a contemporary of B. drewseyensis, possesses a lophodont  $DP_4$  with a reduced posterior cingulum. A later form, Parapliosacomys oregonensis also has a lophodont  $DP_4$  but with a moderately well-developed posterior cingulum. The unique,

Text-fig. 9- How identical incisors may be opisthodont or  
proodont. A, opisthodont. B, proodont.



Text-figure 9.

prismatic  $DP_4$  of Holocene Thomomys cannot be traced into the rooted geomyines with the possible exception of the one assigned to Thomomyini? indet. The cusp arrangements on the  $DP_4$ 's of many Holocene geomyines are so radically changed from the primitive condition that homologies are often difficult to draw.

The basic pattern of triradiating ridges on the anterior column of the  $P_4$  persists throughout known geomyine history. With advancing evolutionary grade the valleys separating the ridges become shallower, the anteroconid and anterostylid become indistinguishable from the ridges upon which they are located, and irregular encrusting cuspules obscure the primary pattern. In geomyines with evergrowing cheek teeth, and possibly in Pliogeomys parvus, the metaconid ridge and anterostylid ridge become nearly transversely oriented. There is no visible evolutionary trend in the shape of the reentrants except that advanced forms tend to have narrower reentrants which are squared U-shaped in later wear stages. On the posterior column, the entoconid and hypostylid become more prominent and transversely elongate with advanced evolutionary grade. The hypoconid is reduced, lost, or replaced by a pit in advanced forms. The tendency toward development of encrusting cuspules is less pronounced than on the anterior column.

The cusps of the lower molars tend to become antero-posteriorly compressed, transversely elongated, and aligned to produce thin, sharp, transverse ridges. As crown height

increased, there is a tendency, except in Pliogeomys parvus, for the cusps to blend together as the notches separating them become shallower. The protoconid and metaconid progress from oval, discrete cusps connected anterointernally to being fused into a thin transverse ridge. That part of the protostylid ridge anterior to the protoconid becomes reduced and closely appressed to the protoconid. The labial lophid connection in the  $M_1$  and  $M_2$  usually occurs prior to, or almost simultaneous with, the medial lophid connection. Generally speaking, the labial lophid connection of the  $M_1$  in any individual is better developed than in the  $M_2$ . In some modern forms, such as Heterogeomys, the medial connection may form slightly before the labial one in the  $M_2$ . Russell (1968a, pp. 551-552, fig. 5-E) described and figured a recent Geomys, KU 2948, in which the medial connection of the  $M_2$  was supposedly complete but the labial one had not yet formed. Careful examination of this specimen reveals that neither has formed yet and that the labial would form just before the medial. Normally, only a medial lophid connection occurs in the  $M_3$ 's because the protostylid ridge becomes extremely reduced. Lingual lophid connections are rare and appear to be inconsistent.

Upper deciduous premolars are rare in the fossil record. Among the geomyines with rooted cheek teeth, they are only known for Parapliosacomys oregonensis and Thomomyini? indet., both from the McKay Reservoir local fauna. The  $DP^{44}$  of P. oregonensis does not differ signifi-

cantly from specimens assigned to fossil and living Geomys and Cratogeomys. The  $DP^4$  of Thomomyini? indet. is similar to that of P. oregonensis but more hypsodont as in living Thomomys. Not enough material is available to show evolutionary trends in this tooth, but the lack of any major differences in known geomyine  $DP^4$ 's and their general similarity with the  $DP^4$ 's of living and fossil heteromyids would seem to indicate that the occlusal configuration of this tooth is relatively stable. The occlusal pattern of the  $DP^4$  is much like that of the  $M^1$  and  $M^2$  with the addition of an anterior cingulum.

The most primitive known unworn  $P^4$ , of Pliosacomys dubius, has an indistinctly bicusate anterior column. This appears to be advanced over a truly primitive condition and may have been derived from a condition similar to that of Entoptychus, where the anterior column is tricusate with the protocone slightly anterior to the paracone and proto-style (Rensberger, 1971). In more advanced geomyines, the anterior column loses all traces of cusps to become a simple transverse ridge. The occlusal configuration of the posterior column in Pliosacomys dubius, where the labial end of the posterior cingulum attaches to the metaloph near the juncture of metacone and hypocone and its lingual end attaches between the hypocone and entostyle, may have been derived from a configuration similar to that of the  $M^1$  and  $M^2$ . In these teeth, the hypostylar ridge attaches to the metacone at the juncture of the metacone and hypocone,

trends linguad along the posterior margin of the tooth, then anteriad along the lingual margin to pass very close to the lingual end of the hypocone. A few minor changes would yield the basic pattern found on the posterior column of the  $P_4^4$ . The only evolutionary change in the occlusal pattern of the posterior column is an increasing complication due to the development of irregular accessory cuspules, a few of which were already present in Pliosacomys dubius. One observable evolutionary trend is for the isthmus to shift closer to a medial position in the worn  $P_4^4$ 's of more advanced forms. No definite trend is visible in the shape of the reentrants in forms with rooted cheek teeth. Most specimens have V-shaped reentrants, but some may have rounded apices. Most forms with evergrowing cheek teeth, except Thomomys, have squared U-shaped reentrants.

Evolutionary changes in the occlusal patterns of the  $M_1^1$  and  $M_2^2$  essentially parallel those of the lower molars. The cusps and lophs tend to become anteroposteriorly compressed with a tendency for the cusps to become less well separated. An early lingual loph connection remains throughout the evolutionary history while a labial lophid connection becomes better developed in advanced forms. Medial loph connections are well developed in primitive forms but disappear in advanced forms. The hypostylar ridge in some living forms becomes reduced to the point of becoming a small posterior cingulum.

The  $M_3^3$  is relatively rare in the fossil record. The

known specimens indicate that the same evolutionary trends occurred in it as did in the  $M^1$  and  $M^2$  with the exception of the posterior portion of the hypostylar ridge. In taxa which show a strong posterior "lobe" as discussed by Russell (1968a), the posterior portion of the hypostylar ridge has become very elaborated to produce the posterior lobe. Russell believed that the lobe was a remnant of a primitive bilophate condition rather than the result of an advanced evolutionary character which could easily have developed parallel in more than one lineage.

Mandible.— A number of striking changes have occurred in the geomyine mandible. Presumably, the primitive, generalized condition was rather like that of living Perognathus, Heteromys, or Liomys. The functions of the various muscles which attach to the mandible are primarily from Merriam (1895) supplemented by Turnbull (1970).

Starting with the anterior portion of the medial surface, the symphysis has progressively become more massive reflecting the greater stress placed on the mandible in a fossorial habitus. The symphyseal eminence has also become more pronounced, apparently to provide a larger attachment area for a stronger digastric muscle. The digastric functions to open the mandible and to shift it posteriorly in propalinal, anterior-posterior, mastication. Enhancement of the symphyseal eminence correlates with the development of very hypsodont to evergrowing cheek teeth. Propalinal mastication probably developed at an evolutionary grade about

equivalent to that of Parapliosacomys oregonensis.

The mylohyoid and geniohyoid fossae are well developed in all known geomyines. The third molar capsule becomes better developed as the hypsodonty of the  $M_3$  increases.

Another major change occurring with an increase of evolutionary grade is the development of a basitemporal fossa. It can more or less be divided into two parts, excavation of the ascending ramus and development of a depression between the ascending ramus and the alveolar row. The ascending ramus has become slightly excavated but no depression has yet formed between it and the alveolar row in Pliosacomys dubius, the most primitive taxon for which this region of the mandible is known. In Parapliosacomys oregonensis, the ramus is slightly more excavated and a trough has formed between it and the alveolar row. Pliogeomys buisi has both portions of the fossa well developed but somewhat variable. No specimen of Pliogeomys parvus retains the ascending ramus, but a moderately developed depression occurs between the ascending ramus and the alveolar row, posterior to its position in other species. This may indicate some parallelism in the development of a basitemporal fossa. The prominence of this fossa in advanced forms reflects the increasing role played by the deeper portion of the temporalis muscle in closing the mandible and in aiding posteriad movements during propalinal mastication.

The available material exhibits a progressive reduction

of the angular process. As it becomes reduced, the ventral outline of the mandible approaches a more uniformly arcuate condition except for the symphyseal eminence. Reduction of the angular process results in a reduction of the attachment area for the internal pterygoid muscle. Its function in closing the jaws is apparently partially taken over by other muscles, especially the temporalis. The insertion for the external pterygoid muscle is not preserved in any form more primitive than Parapliosacomys. No significant changes are indicated in the available material. The articular condyle is more posteriorly directed in Parapliosacomys than in more recent geomyines, indicating a change in the lever systems of the masticatory apparatus. The coronoid process is too rarely preserved to yield information about any possible changes.

In lateral view, the lateral angular process becomes better developed in forms more advanced than Parapliosacomys, increasing the attachment area for the posterior part of the deep lateral masseter muscle. Only fragments of the lateral angular process are preserved in forms more primitive than Parapliosacomys but the unknown generalized ancestral form probably possessed an angular process similar to that now found in generalized heteromyids. This evolutionary trend in mandibular morphology also appears to be tied to a shift toward propalinal mastication since the deep lateral masseter serves to pull the mandible anteriorly.

Although evidence from forms more primitive than Parapliosaccomys is missing, there also appears to be a trend toward dorsoventral expansion of the posterior masseteric fossa, between the incisive capsular process and the coronoid process. This would increase the area of attachment for the posterior part of the medial masseter, another muscle which appears to play a major part in moving the mandible posteriorly. The capsular groove tends to become shallower in more advanced forms as the articular condyle moves more dorsad relative to the capsular process. Changes in the attachment area for the temporalis muscle and the posterior part of the deep masseter cannot be determined because the coronoid process is so rarely preserved.

The insertion for the superficial masseter, primarily along the ventral margin of the mandible, is very strong and elongate in advanced geomyines. It appears to be smaller and slightly less stout in more primitive forms. This muscle plays a very major part in moving the mandible anteriorly.

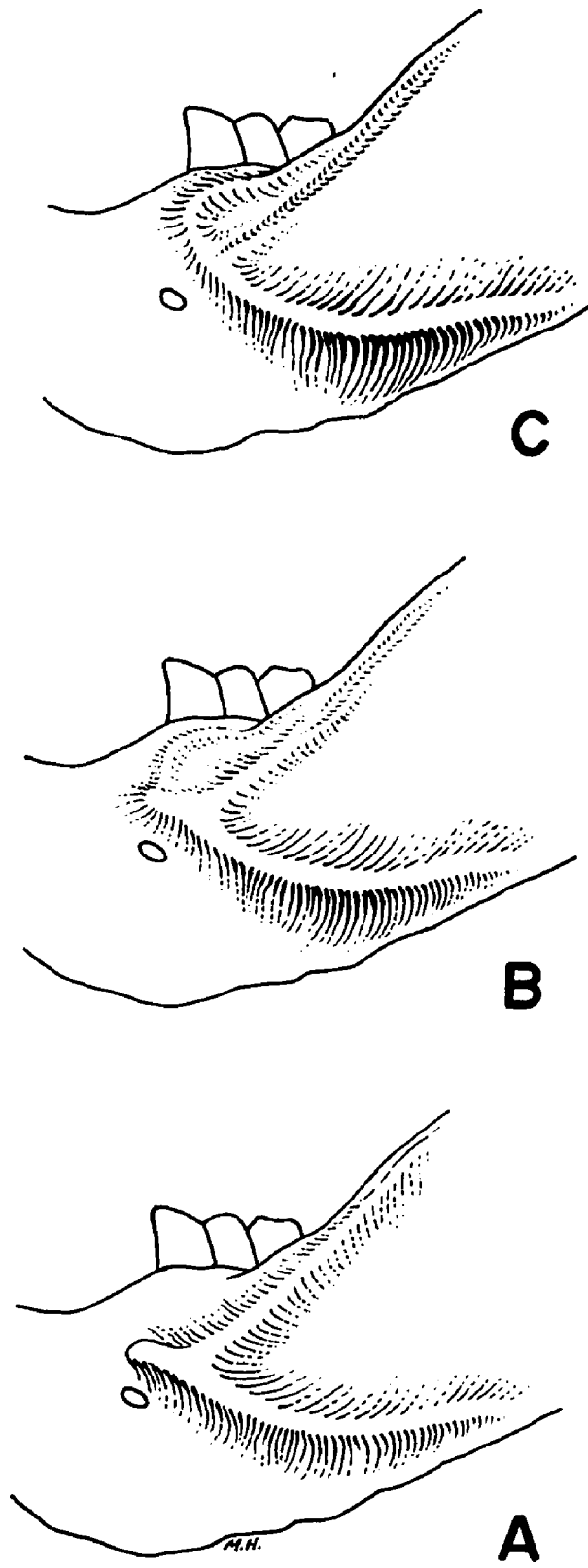
A number of changes occur during the evolutionary history of the geomyines to provide a larger and stronger area of attachment for the remainder of the masseteric complex. The posterior portion of the mandible expands dorsally to increase that part of the masseteric fossa. The addition of the dorsal branch of the masseteric crest expands the anterior portion of the masseteric fossa to provide additional insertion for the anterior part of the

medial masseter. The ventral branch of the masseteric crest becomes far more pronounced and the area between it and the geomyine groove becomes rugose in advanced forms. This forms a better attachment area for the anterior part of the deep lateral masseter. The anterior masseteric complex functions to hold the jaws closed and the anterior part of the deep lateral masseter aids in anterior shifts of the mandible.

My interpretation of the mode of evolutionary development of the anterior region of the masseteric fossa (Text-fig. 10) assumes that the ancestral configuration for all the Geomyinae was that found in the Nerterogeomyini. This assumption is based on the fact that almost all other geomyoid rodents possess similar configurations. The primitive condition includes a well-developed medial branch of the masseteric crest, a heteromyid projection extending anterior to the mental foramen, and the lack of a dorsal branch of the masseteric crest. In at least one geomyine stock, the fibers of the anterior part of the medial masseter secondarily began to attach in the region dorsal to the medial branch of the masseteric crest. As this progressed, the area of secondary attachment became outlined by the dorsal branch of the masseteric crest, the heteromyid projection disappeared, and the medial branch of the masseteric crest became the geomyine groove.

Molar and premolar capsules develop on the lateral surface of the mandible as the teeth become very hypsodont.

Text-fig. 10- Evolution of the geomyine masseteric crest region. A, Primitive or Nerterogeomyini condition with well-developed heteromyid projection extending dorsal to the mental foramen, well-developed medial branch of the masseteric crest and no dorsal branch of the masseteric crest. B, Intermediate condition, with reduced heteromyid projection, medial branch of masseteric crest weakening and becoming a groove posteriorly, and a dorsal branch of the masseteric crest beginning to develop. C, Advanced or Geomyini condition with heteromyid projection lost, geomyine groove rather than medial branch of the masseteric crest, and well developed dorsal branch of the masseteric crest.



Text-figure 10.

The reason for the diastemal notch becoming better developed in advanced geomyines is not evident.

Most of the evolutionary trends found in early geomyine mandibles reflect the result of increasingly heavy stress being placed on the mandible and of better adaptation for a propalinal type of mastication. The latter correlates with the evolution of increasingly hypsodont cheek teeth, which wear to flat-surfaced columns progressively earlier in the ontogeny of the individual.

## PHYLOGENY

Perhaps the best introduction to this section is the following quote from Wood (1935b, p. 250-251) concerning heteromyid rodents but which is also very applicable to the geomyine rodents.

"The most important point to be emphasized is that 'Parallelism, parallelism, more parallelism and still more parallelism' is the evolutionary motto of the rodents in general and of the heteromyids in particular. This extends to all parts of the body. It makes the task of determining interrelationships particularly difficult, and renders exceptionally dangerous any postulates as to what the relationships of a given form may really be, if full evidence does not exist to clear the maze of parallel adaptations for us. This shows the insuperable difficulties awaiting anyone who attempts a classification based on a single character or on a group of characters with a common cause. The parallelism is so great that there is no justification for believing two apparently identical structures to be the same, unless the apparent identity is supported by apparent identity of many other structures, or unless the development of the two characters can be traced through and proven to be identical at every step. As it has not been possible to trace the complete sequence of heteromyid evolution, there are undoubtedly many errors of interpretation in the present work."

The tremendous amount of parallelism among the geomyines renders any effort to decipher their evolutionary history inconclusive and subject to modification whenever additional material becomes available. As this study progressed, each new sample of fossil geomyines I examined caused me to alter my hypotheses regarding the phylogeny of the group. Future collecting will undoubtedly yield material which will further alter such hypotheses. I suspect that the actual evolutionary history of the geomyines is so complex that it will never be possible to decipher it com-

pletely.

The basic stock of the Geomyidae was probably some generalized geomyoid which would more closely resemble living heteromyines than living geomyines. Many living heteromyines spend much of their lives in extensive burrow systems with entrances that they plug during the daytime. This habitus in a rather generalized form would provide an ideal starting point for the development of forms specialized for a fossorial existence.

The morphology of all the geomyoid rodents indicates that they form a coherent group of taxa. Although there is much similarity in the configuration of the occlusal surfaces in unworn molars in all geomyoid rodents, the morphology of the deciduous and permanent premolars separates the geomyids from the heteromyids. As many as four different groups may be distinguished within the geomyids: the Geomyinae, the Entoptychinae (sensu Rensberger, 1972), the Dikkomys-Lignimus group, and the Pleurolicus group. The latter two groups are being studied by several researchers to determine their relationships and status. Shotwell's (1967b) inclusion of the dipodomyines within the Geomyinae is not consistent with the available evidence. Dipodomyine deciduous and permanent premolars are more heteromyid than geomyid in nature. Separation of the dipodomyines from the Geomyinae is also supported by a recent study of penal morphology (Kelly and Starrett, in manuscript).

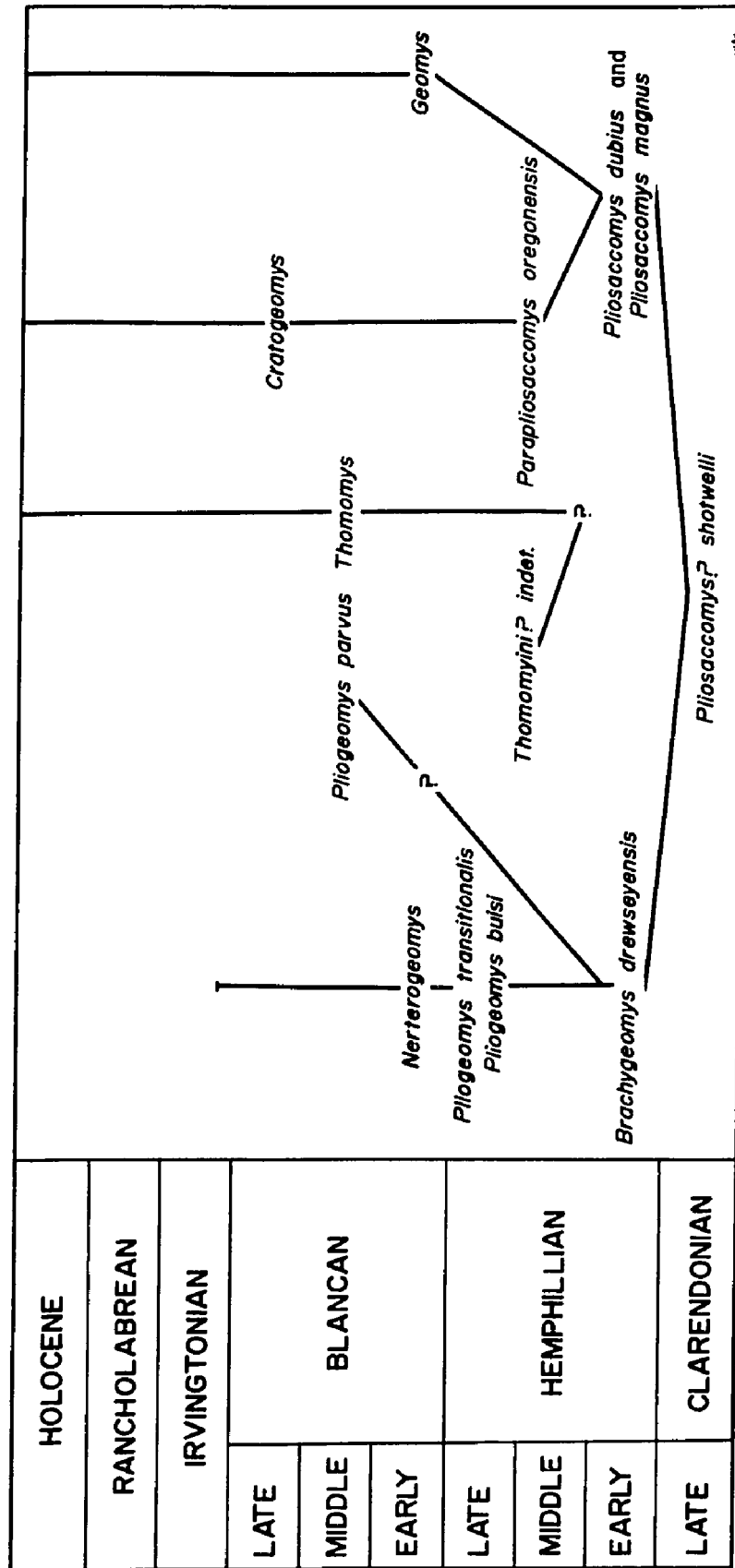
The history of the geomyid rodents appears to have

involved a number of groups which separately evolved from the same generalized stock toward a fossorial habitus. The last and most successful of these groups became the Geomyinae who appear to have developed independently of any earlier, highly fossorial group of geomyids. The most primitive known geomyine, Pliosaccomys? shotwelli, is relatively generalized with brachydont cheek teeth. It cannot be derived from any known member of the other groups of geomyids.

Pliosaccomys? shotwelli provides the ideal structural ancestor for the rest of the known Geomyinae. It may eventually prove to be a member of one of the individual lineages rather than ancestral to all lineages when more material of it and other primitive geomyines becomes available. However, a form which, if not ancestral, was very close to the ancestor for all subsequent geomyines existed during the Clarendonian. By early Hemphillian, the two lineages of Neterogeomyini and Geomyini were well separated (Text-fig. 11).

Members of the Tribe Nerterogeomyini retain the heteromyid projection, do not develop a dorsal branch of the masseteric crest, and possess a basically cusped  $DP_4$ . The early Hemphillian representative of the Nerterogeomyini was Brachygeomys drewseyensis from the Bartlett Mountain local fauna of Oregon. It was only moderately advanced over Pliosaccomys? shotwelli. The next known occurrences of the Nerterogeomyini are Pliogeomys buisi and Pliogeomys transi-

Text-fig. 11- Interpretation of geomyine phylogeny.



Text-figure 11.

tionalis from the latest Hemphillian of the Oklahoma Panhandle and southwestern Kansas. Pliogeomys has very hypsodont cheek teeth, some of which may be evergrowing in P. transitionalis, and is the most advanced of known geomyines with rooted cheek teeth. Pliogeomys transitionalis gave rise to Nerterogeomys which retains the heteromyid projection and never develops a dorsal branch of the masseteric crest but has evergrowing cheek teeth and gradually develops a more lophodont  $DP_4$ . Nerterogeomys ranged from the early Blancan to the end of the Blancan and probably into the Irvingtonian before becoming extinct without any descendants.

Pliogeomys parvus, the only known Blancan geomyine with rooted cheek teeth, shows a peculiar mixture of primitive, advanced, and unique characteristics. It was an evolutionary dead-end and may be generically distinct from the other species assigned to Pliogeomys. Pliogeomys parvus appears to have been the last remnant of an isolated primitive population in the northern Great Basin region.

The Geomyini are characterized by the reduction and loss of the heteromyid projection, development of the dorsal branch of the masseteric crest and a more lophodont, but not prismatic,  $DP_4$ . Pliosaccomys dubius and Pliosaccomys magnus, which may be conspecific, are the known early Hemphillian representatives of the Geomyini. Both lived in the Great Basin region of Nevada and represent a developmental stage equivalent to that of Brachygeomys drewseyen-

sis. The next more advanced known form, Parapliosacomys oregonensis, occurs in the Bartlett Mountain local fauna from Oregon near the boundary between middle and late Hemphillian and appears to possibly be ancestral to Cratogeomys. It is not as advanced as Pliogeomys buisi, especially in mandibular characteristics. The grade of development equivalent to P. buisi and Pliogeomys transitionalis is not known for the Geomyini. Geomys and Cratogeomys, distinguished by evergrowing cheek teeth, first appeared in the early Blancan and survive today. Pappogeomys, Heterogeomys, Macrogeomys, Orthogeomys, and Zygogeomys are other living genera with evergrowing cheek teeth usually included in the Geomyini. I have followed this practice here, but with reservations. None of these genera has any fossil record. Contrary to Russell (1968a) Nerterogeomys has no relationship to Zygogeomys. Examination of juvenile dentitions shows that these recent genera have some dental characteristics widely divergent from either recent Geomys or known fossil genera of the Geomyini. A careful comparative study of the occlusal patterns of both deciduous and permanent teeth of recent geomyines would shed much light on their interrelationships.

With the possible exception of the Thomomyini? indet. from the Bartlett Mountain local fauna, the fossil history of Thomomyini with rooted cheek teeth is unknown.

The history of the geomyines appears to consist of at least three different lineages developing separately but with considerable parallelism.

## APPENDIX

Each of the following tables of measurements is internally arranged in order of the taxonomic sequence used in the section on systematics. Single asterisks prior to designation as L or R indicate specimens which are unworn or only slightly worn. An "I" indicates that the specimen is not complete enough to provide a particular measurement. A "B" indicates that some part of the specimen needed for a particular measurement is probably present but obscured by bone, another tooth, or by being glued to a pin. An "a" directly preceding a measurement indicates that the measurement is approximate.

Measurements of maximum length and maximum width were made at the occlusal surface by aligning the apparent axes of each specimen with cross-hairs in the measuring microscope. I was not able to devise a truly uniform method of specimen orientation because of the highly variable occlusal outlines of the teeth. Enamel height and base height were measured on the portion of the tooth bearing the most phylogenetically persistent enamel plate. This is the posterior enamel plate on the lower permanent cheek teeth. The teeth were oriented with the occlusal surfaces parallel to the vertical cross-hair. Enamel height is measured from the occlusal surface to the most basal part of the enamel plate. Base height is from the base of the enamel plate to the base of the tooth. Total height equals the sum of the enamel and base heights. In most cases, if either the base height or

the enamel height could not be measured, the other height measurements were not taken.

Table 1. Measurements of lower incisors.

| Taxon                              | Specimen<br>Number | Side | Width |
|------------------------------------|--------------------|------|-------|
| <u>Pliosacomys dubius</u>          | CIT 1804           | R    | 1.35  |
| "                                  | CIT 1805           | R    | 1.47  |
| "                                  | CIT 1808           | L    | 1.40  |
| "                                  | CIT 1810           | R    | 0.85  |
| "                                  | CIT 1796           | R    | 1.31  |
| <u>Parapliosacomys oregonensis</u> | UO 3631            | L    | 1.46  |
| "                                  | UO 9301            | R    | 1.58  |
| <u>Pliogeomys buisi</u>            | UMMP V29147        | R    | 1.90  |
| "                                  | UMMP V56274        | L    | 1.99  |
| <u>Pliogeomys transitionalis</u>   | UMMP V60474        | L    | 1.99  |
| <u>Pliogeomys parvus</u>           | UMMP V55185        | R    | 1.28  |
| "                                  | UMMP V53562        | L    | 1.14  |

Table 2. Measurements of lower deciduous premolars.

| Taxon                              | Specimen<br>Number | Side | Max.<br>Length | Max.<br>Width |
|------------------------------------|--------------------|------|----------------|---------------|
| <u>Pliosacomys dubius</u>          | CIT 1807           | *L   | a1.90          | 1.28          |
| "                                  | CIT 1810           | R    | 2.03           | 1.15          |
| <u>Parapliosacomys oregonensis</u> | UO 26088           | L    | 2.12           | 1.24          |
| "                                  | UO 24624           | *L   | 2.03           | 1.23          |
| "                                  | UO 26089           | L    | 2.23           | 1.28          |
| Thomomyini? indet.                 | UO 24622           | R    | 2.02           | 1.25          |
| <u>Brachygeomys drewseyensis</u>   | UO 24978           | *R   | I              | 1.19          |
| "                                  | UO 24979           | *R   | 1.89           | 1.19          |
| <u>Pliogeomys buisi</u>            | UMMP V30194        | *L   | 2.65           | 1.60          |

Table 3. Measurements of lower fourth premolars.

| Taxon                              | Specimen Number | Side | Max. Length | Width       |              | Enamel Height | Base Height | Total Height |
|------------------------------------|-----------------|------|-------------|-------------|--------------|---------------|-------------|--------------|
|                                    |                 |      |             | Ant. Column | Post. Column |               |             |              |
| <u>Pliosacomys dubius</u>          |                 |      |             |             |              |               |             |              |
| "                                  | CIT 1809        | *L   | 1.28        | 1.14        | 1.22         | B             | B           | B            |
| "                                  | CIT 1804        | R    | 1.82        | 1.14        | 1.52         | B             | B           | B            |
| "                                  | CIT 1805        | R    | 1.74        | 1.21        | 1.75         | B             | B           | B            |
| "                                  | CIT 1808        | L    | 1.93        | 1.07        | 1.55         | B             | B           | B            |
| "                                  | CIT 1796        | *R   | 1.38        | 1.06        | 1.33         | B             | B           | B            |
| <u>Pliosacomys magnus</u>          |                 |      |             |             |              |               |             |              |
| "                                  | UCMP 12567      | L    | 1.73        | 1.08        | 1.55         | B             | B           | B            |
| "                                  | UCMP 12568      | L    | 1.51        | 1.04        | 1.54         | B             | B           | B            |
| "                                  | UCMP 99193      | *R   | 1.10        | 1.04        | 1.19         | 1.97          | I           | I            |
| "                                  | UCMP 99194      | *R   | 0.99        | 0.92        | 1.25         | 2.41          | I           | I            |
| <u>Parapliosacomys oregonensis</u> |                 |      |             |             |              |               |             |              |
| "                                  | UO 26092        | R    | 2.08        | 0.90        | 1.37         | 2.10          | 1.45        | 3.55         |
| "                                  | UO 26080        | *R   | 1.30        | 1.18        | 1.29         | 3.54          | 0.51        | 4.05         |
| "                                  | UO 26085        | R    | 1.98        | 1.16        | 1.52         | 2.93          | 1.17        | 4.10         |
| "                                  | UO 25351        | R    | I           | I           | 1.48         | I             | I           | I            |
| "                                  | UO 25349        | *L   | 1.28        | 0.99        | 1.15         | 3.73          | 0.28        | 4.01         |
| "                                  | UO 26081        | *L   | 1.34        | 1.15        | 1.19         | 3.59          | 0.21        | 3.80         |
| "                                  | UO 26083        | *L   | 1.17        | 0.84        | 1.21         | 3.75          | 0.42        | 4.18         |
| "                                  | UO 25371        | L    | 2.35        | 1.17        | 1.60         | I             | I           | I            |
| "                                  | UO 9236         | L    | 1.48        | 1.08        | 1.39         | B             | B           | B            |

Table 3. (continued)

| Taxon                               | Specimen<br>Number | Side | Max.<br>Length | Width<br>Ant.<br>Column | Width<br>Post.<br>Column | Enamel<br>Height | Base<br>Height | Total<br>Height |
|-------------------------------------|--------------------|------|----------------|-------------------------|--------------------------|------------------|----------------|-----------------|
| <u>Parapliosaccomys oregonensis</u> | UO 26084           | L    | 1.64           | 1.20                    | 1.50                     | I                | I              | I               |
| "                                   | UO 26082           | L    | 1.63           | 1.11                    | 1.52                     | I                | I              | I               |
| "                                   | UO 26087           | L    | 1.83           | 1.06                    | 1.48                     | I                | I              | I               |
| "                                   | UO 25367           | L    | 1.74           | I                       | I                        | 3.71             | 0.61           | 4.28            |
| "                                   | UO 3631            | L    | 2.17           | 1.12                    | 1.63                     | B                | B              | B               |
| "                                   | UO 3630            | R    | 1.79           | 1.19                    | 1.47                     | B                | B              | B               |
| Thomomyini? indet.                  | UO 25377           | *L   | 1.39           | 1.02                    | 1.27                     | 5.03             | 0.04           | 5.07            |
| "                                   | UO 24904           | L    | 1.61           | 1.20                    | 1.47                     | 4.50             | 0.36           | 4.86            |
| "                                   | UO 26086           | R    | 2.20           | 0.98                    | 1.44                     | 1.54             | 1.98           | 3.52            |
| <u>Brachygeomys drewseyensis</u>    | UO 27009           | *L   | I              | 1.10                    | I                        | I                | I              | I               |
| "                                   | UO 26058           | *R   | 1.33           | 1.08                    | 1.27                     | 2.28             | 1.27           | 3.55            |
| "                                   | UO 24943           | ?    | 1.65           | 1.04                    | 1.53                     | I                | I              | I               |
| <u>Pliogeomys buisi</u>             | UMMP V29147        | R    | 2.39           | 1.62                    | 2.05                     | B                | B              | B               |
| "                                   | UMMP V56274        | L    | 2.09           | 1.81                    | 2.09                     | B                | B              | B               |
| "                                   | UMMP V30195        | R    | 2.12           | 1.37                    | 1.96                     | I                | I              | I               |
| "                                   | UMMP V30195        | L    | 2.46           | 1.54                    | 1.93                     | 4.41             | 0.78           | 5.19            |
| <u>Pliogeomys transitionalis</u>    | UMMP V60474        | L    | 2.29           | 1.66                    | 2.13                     | B                | B              | B               |
| "                                   | UMMP V41401        | R    | I              | 1.58                    | I                        | I                | I              | I               |

Table 3. (continued)

| Taxon                          | Specimen<br>Number | Side | Max.<br>Length | Width          |                 | Enamel<br>Height | Base<br>Height | Total<br>Height |
|--------------------------------|--------------------|------|----------------|----------------|-----------------|------------------|----------------|-----------------|
|                                |                    |      |                | Ant.<br>Column | Post.<br>Column |                  |                |                 |
| <u>Pliogeomys parvus</u>       | UMMP V55185        | R    | 1.53           | 0.88           | 1.21            | B                | B              | B               |
| "                              | UMMP V53562        | *L   | 1.14           | 0.93           | 1.05            | B                | B              | B               |
| "                              | UMMP V56017        | *L   | 0.92           | 0.83           | 0.95            | I                | I              | I               |
| "                              | UMMP V51578        | L    | 1.63           | 0.95           | 1.29            | 2.31             | 0.63           | 2.94            |
| <u>Pliosaccomys? shotwelli</u> | UO 24478           | *L   | 1.23           | 0.84           | 1.25            | I                | I              | I               |
| "                              | UO 24466           | L    | 1.39           | 0.97           | 1.22            | I                | I              | I               |
| "                              | UO 24477           | R    | 1.18           | 0.90           | 1.23            | I                | I              | I               |
| "                              | UO F-18236         | *L   | 1.36           | 0.85           | 1.09            | 1.43             | 1.54           | 2.96            |

Table 4. Measurements of lower first and second molars.

| Taxon                              | Specimen<br>Number | Side | M <sub>1</sub><br>or M <sub>2</sub> | Max.<br>Length | Max.<br>Width | Enamel<br>Height | Base<br>Height | Total<br>Height |
|------------------------------------|--------------------|------|-------------------------------------|----------------|---------------|------------------|----------------|-----------------|
| <u>Pliosacomys dubius</u>          | CIT 1806           | R    | 1                                   | 1.26           | 1.73          | B                | B              | B               |
| "                                  | CIT 1806           | R    | 2                                   | 1.18           | 1.85          | B                | B              | B               |
| "                                  | CIT 1803           | *R   | 2                                   | 1.30           | 1.51          | B                | B              | B               |
| "                                  | CIT 1809           | *L   | 1                                   | 1.21           | 1.60          | B                | B              | B               |
| "                                  | CIT 1809           | *L   | 2                                   | 1.27           | 1.64          | B                | B              | B               |
| "                                  | CIT 1804           | R    | 1                                   | 1.09           | I             | B                | B              | B               |
| "                                  | CIT 1804           | R    | 2                                   | I              | 1.52          | B                | B              | B               |
| "                                  | CIT 1805           | R    | 1                                   | 1.26           | 1.86          | B                | B              | B               |
| "                                  | CIT 1805           | R    | 2                                   | I              | 1.78          | B                | B              | B               |
| "                                  | CIT 1807           | *L   | 1                                   | 1.15           | 1.60          | B                | B              | B               |
| "                                  | CIT 1807           | *L   | 2                                   | 1.26           | 1.51          | B                | B              | B               |
| "                                  | CIT 1796           | R    | 1                                   | 1.26           | 1.63          | B                | B              | B               |
| "                                  | CIT 1796           | R    | 2                                   | 1.22           | 1.59          | B                | B              | B               |
| "                                  | LACM 33855         | *R   | ?                                   | 1.28           | 1.61          | 2.37             | 1.52           | 3.89            |
| "                                  | LACM 33856         | *L   | ?                                   | 1.06           | 1.49          | I                | I              | I               |
| <u>Pliosacomys magnus</u>          | UCMP 12567         | L    | 1                                   | 1.07           | 1.48          | B                | B              | B               |
| "                                  | UCMP 12567         | L    | 2                                   | 1.12           | 1.58          | B                | B              | B               |
| <u>Parapliosacomys oregonensis</u> | UO 26134           | *R   | ?                                   | 1.07           | 1.45          | I                | I              | I               |

Table 4. (continued)

| Taxon                              | Specimen<br>Number | Side | M <sub>1</sub><br>or M <sub>2</sub> | Max.<br>Length | Max.<br>Width | Enamel<br>Height | Base<br>Height | Total<br>Height |
|------------------------------------|--------------------|------|-------------------------------------|----------------|---------------|------------------|----------------|-----------------|
| <u>Parapliosacomys oregonensis</u> | UO 26136           | *R   | ?                                   | 1.01           | 1.55          | I                | I              | I               |
| "                                  | UO 26133           | *L   | ?                                   | 0.88           | 1.23          | I                | I              | I               |
| "                                  | UO 26132           | *L   | ?                                   | 1.02           | 1.47          | I                | I              | I               |
| "                                  | UO 26153           | *R   | ?                                   | 1.02           | 1.57          | I                | I              | I               |
| "                                  | UO 26107           | *R   | ?                                   | 1.08           | 1.46          | I                | I              | I               |
| "                                  | UO 24926           | *L   | ?                                   | 0.95           | 1.52          | I                | I              | I               |
| "                                  | UO 25357           | *R   | ?                                   | 1.13           | 1.45          | I                | I              | I               |
| "                                  | UO 26149           | *L   | ?                                   | 0.93           | 1.49          | I                | I              | I               |
| "                                  | UO 26154           | L    | ?                                   | 0.98           | 1.68          | 3.97             | 0.48           | 4.45            |
| "                                  | UO 26147           | R    | ?                                   | 0.85           | 1.54          | I                | I              | I               |
| "                                  | UO 26150           | R    | ?                                   | 1.11           | 1.66          | B                | B              | B               |
| "                                  | UO 26141           | R    | ?                                   | 1.02           | 1.71          | 3.74             | 0.61           | 4.35            |
| "                                  | UO 25391           | L    | ?                                   | 0.89           | 1.47          | I                | I              | I               |
| "                                  | UO 26159           | L    | ?                                   | 0.84           | 1.68          | 2.73             | 0.81           | 3.54            |
| "                                  | UO 26156           | R    | ?                                   | 0.89           | 1.71          | 3.71             | 0.60           | 4.31            |
| "                                  | UO 26140           | R    | ?                                   | I              | 1.66          | B                | B              | B               |
| "                                  | UO 26146           | L    | ?                                   | 0.86           | 1.55          | B                | B              | B               |
| "                                  | UO 26142           | R    | ?                                   | 0.91           | 1.58          | I                | I              | I               |

Table 4. (continued)

| Taxon                              | Specimen<br>Number | Side | M <sub>1</sub><br>or M <sub>2</sub> | Max.<br>Length | Max.<br>Width | Enamel<br>Height | Base<br>Height | Total<br>Height |
|------------------------------------|--------------------|------|-------------------------------------|----------------|---------------|------------------|----------------|-----------------|
| <u>Parapliosacomys oregonensis</u> | UO 26101           | *L   | ?                                   | 1.08           | 1.47          | I                | I              | I               |
| "                                  | UO 26111           | R    | ?                                   | 1.01           | 1.77          | B                | B              | B               |
| "                                  | UO 25334           | R    | ?                                   | 0.98           | 1.52          | I                | I              | I               |
| "                                  | UO 26164           | R    | ?                                   | 0.89           | 1.60          | 2.35             | 0.77           | 3.11            |
| "                                  | UO 26125           | R    | ?                                   | 1.04           | 1.51          | 4.06             | 0.51           | 4.57            |
| "                                  | UO 26106           | R    | ?                                   | 0.81           | 1.70          | 1.07             | 1.46           | 2.53            |
| "                                  | UO 26170           | R    | ?                                   | 1.01           | 1.55          | B                | B              | B               |
| "                                  | UO 26166           | *L   | ?                                   | 1.00           | 1.52          | 3.90             | 0.16           | 4.05            |
| "                                  | UO 3631            | L    | 1                                   | 1.05           | 1.80          | B                | B              | B               |
| "                                  | UO 3630            | R    | 1                                   | 1.11           | 1.74          | B                | B              | B               |
| "                                  | UO 3630            | R    | 2                                   | 1.04           | 1.76          | B                | B              | B               |
| Thomomyini? indet.                 | UO 25360           | *R   | ?                                   | 1.05           | 1.69          | I                | I              | I               |
| "                                  | UO 26102           | *L   | ?                                   | 1.07           | 1.75          | I                | I              | I               |
| "                                  | UO 25376           | *R   | ?                                   | 0.92           | 1.38          | I                | I              | I               |
| "                                  | UO 25385           | *R   | ?                                   | 1.19           | 1.63          | I                | I              | I               |
| "                                  | UO 25394           | L    | ?                                   | 0.98           | 1.72          | I                | I              | I               |
| "                                  | UO 26114           | L    | ?                                   | 1.15           | 1.87          | 1.88             | 1.12           | 3.00            |
| "                                  | UO 26143           | *R   | ?                                   | 1.08           | 1.63          | I                | I              | I               |

Table 4. (continued)

| Taxon                            | Specimen<br>Number | Side | M <sub>1</sub><br>or M <sub>2</sub> | Max.<br>Length | Max.<br>Width | Enamel<br>Height | Base<br>Height | Total<br>Height |
|----------------------------------|--------------------|------|-------------------------------------|----------------|---------------|------------------|----------------|-----------------|
| <u>Brachygeomys drewseyensis</u> |                    |      |                                     |                |               |                  |                |                 |
| "                                | UO 26036           | R    | ?                                   | 1.18           | 1.68          | I                | I              | I               |
| "                                | UO 25258           | R    | ?                                   | 1.28           | 1.69          | 1.20             | 1.91           | 3.10            |
| "                                | UO 2239-A          | *R   | ?                                   | 1.21           | 1.54          | I                | I              | I               |
| "                                | UO 27010           | R    | ?                                   | 1.15           | 1.77          | 0.80             | 1.69           | 2.49            |
|                                  | UO 2239-B          | L    | ?                                   | 1.04           | 1.47          | I                | I              | I               |
| <u>Pliogeomys buisi</u>          | UMMP V29147        | R    | 1                                   | 1.17           | 2.37          | B                | B              | B               |
| "                                | UMMP V29147        | R    | 2                                   | 1.31           | 2.33          | B                | B              | B               |
| "                                | UMMP V56274        | L    | 1                                   | 1.34           | 2.26          | B                | B              | B               |
|                                  | UMMP V56274        | L    | 2                                   | 1.26           | 2.32          | B                | B              | B               |
| <u>Pliogeomys transitionalis</u> | UMMP V60471        | L    | ?                                   | 1.22           | 2.03          | 5.41             | 0.53           | 5.94            |
| <u>Pliogeomys parvus</u>         | UMMP V55185        | R    | 1                                   | 0.91           | 1.38          | B                | B              | B               |
| "                                | UMMP V55185        | R    | 2                                   | 0.84           | 1.39          | B                | B              | B               |
| "                                | UMMP V54366        | L    | 2                                   | 0.81           | 1.41          | B                | B              | B               |
| "                                | UMMP V53562        | L    | 1                                   | 1.04           | 1.35          | B                | B              | B               |
| "                                | UMMP V53562        | *L   | 2                                   | 1.04           | 1.39          | B                | B              | B               |
| "                                | UMMP V53450        | *L   | ?                                   | 0.89           | 1.33          | I                | I              | I               |
| <u>Pliosaccomys? shotwelli</u>   | UO 24461           | L    | ?                                   | 1.05           | 1.49          | 1.38             | 1.08           | 2.47            |

Table 5. Measurements of lower third molars.

| Taxon                               | Specimen<br>Number | Side | Max.<br>Length | Max.<br>Width | Enamel<br>Height | Base<br>Height | Total<br>Height |
|-------------------------------------|--------------------|------|----------------|---------------|------------------|----------------|-----------------|
| <u>Pliosaccomys dubius</u>          | CIT 1806           | R    | 1.22           | 1.50          | B                | B              | B               |
| "                                   | CIT 1805           | R    | 1.20           | I             | B                | B              | B               |
| "                                   | CIT 1807           | *L   | 1.02           | 1.39          | B                | B              | B               |
| "                                   | CIT 1796           | *R   | 1.14           | 1.45          | B                | B              | B               |
| <u>Parapliosaccomys oregonensis</u> | UO 26108           | *R   | 0.90           | 1.48          | I                | I              | I               |
| "                                   | UO 26104           | *L   | 0.97           | 1.54          | I                | I              | I               |
| "                                   | UO 26119           | *R   | 0.91           | 1.46          | I                | I              | I               |
| "                                   | UO 26112           | *R   | 1.02           | 1.54          | 2.97             | 0.34           | 3.31            |
| "                                   | UO 26103           | *L   | 1.07           | 1.51          | 2.71             | 0.41           | 3.12            |
| "                                   | UO 25363           | *L   | 1.13           | 1.55          | I                | I              | I               |
| "                                   | UO 25369           | *R   | 0.97           | 1.51          | I                | I              | I               |
| "                                   | UO 25368           | *L   | 0.92           | 1.36          | I                | I              | I               |
| "                                   | UO 25388           | L    | 1.03           | 1.55          | I                | I              | I               |
| "                                   | UO 26122           | R    | 0.99           | 1.45          | I                | I              | I               |
| Thomomyini? indet.                  | UO 25378           | R    | 0.91           | 1.53          | 1.86             | 0.89           | 2.75            |
| <u>Brachygeomys drewseyensis</u>    | UO 24987           | *L   | 0.99           | 1.22          | I                | I              | I               |
| "                                   | UO 26037           | *R   | 1.03           | 1.42          | I                | I              | I               |
| "                                   | UO 2239-A          | *R   | 1.00           | 1.31          | 1.10             | 0.83           | 1.93            |
| "                                   | UO 26043           | L    | 1.14           | 1.61          | I                | I              | I               |

Table 5. (continued)

| Taxon                            | Specimen<br>Number | Side | Max.<br>Length | Max.<br>Width | Enamel<br>Height | Base<br>Height | Total<br>Height |
|----------------------------------|--------------------|------|----------------|---------------|------------------|----------------|-----------------|
| <u>Pliogeomys buisi</u>          | UMMP V56274        | L    | 1.23           | 1.99          | B                | B              | B               |
| <u>Pliogeomys transitionalis</u> | UMMP V60470        | *L   | 1.20           | 1.66          | I                | I              | I               |
| "                                | UMMP V28286        | L    | 1.33           | 1.99          | I                | I              | I               |
| <u>Pliogeomys parvus</u>         | UMMP V 54366       | L    | 0.80           | 1.15          | B                | B              | B               |
| <u>Pliosaccomys? shotwelli</u>   | UO 24891           | H    | 0.98           | 1.37          | 0.63             | 0.91           | 1.54            |
| "                                | UO 24873           | R    | 1.05           | 1.34          | I                | I              | I               |
| "                                | UO 24482           | L    | 0.92           | 1.18          | 1.35             | 0.64           | 1.99            |
| "                                | UO 24467           | *L   | 0.87           | 1.14          | 1.40             | 0.60           | 2.00            |

Table 6. Measurements of upper incisors.

| Taxon                              | Specimen<br>Number | Side | Width |
|------------------------------------|--------------------|------|-------|
| <u>Pliosacomys dubius</u>          | CIT 1797           | L    | 2.06  |
| "                                  | LACM 33857         | R    | 1.71  |
| <u>Parapliosacomys oregonensis</u> | UO 2222-20         | R    | 1.61  |
| "                                  | UO 2222-21         | R    | 1.59  |
| "                                  | UO 2222-18         | R    | 1.49  |
| <u>Pliogeomys buisi</u>            | UMNP V60463        | L    | 2.14  |
| "                                  | UMNP V60463        | L    | 2.07  |
| "                                  | UMNP V60463        | L    | 2.07  |
| "                                  | UMNP V60463        | L    | 2.36  |
| "                                  | UMNP V60463        | R    | 2.08  |
| <u>Pliogeomys transitionalis</u>   | UMNP V60469        | L    | 2.11  |
| <u>Pliogeomys parvus</u>           | UMNP V53495        | R    | 1.31  |
| "                                  | UMNP V60799        | L    | 1.26  |
| "                                  | UMNP V60791        | R    | 1.26  |
| "                                  | UMNP V60795        | L    | 1.24  |
| "                                  | UMNP V60758        | L    | 1.30  |
| "                                  | UMNP V60757        | L    | 1.21  |
| "                                  | UMNP V60801        | R    | 1.31  |
| "                                  | UMNP V60763        | L    | 1.36  |
| "                                  | UMNP V55184        | L    | 1.30  |

Table 7. Measurements of upper deciduous premolars.

| Taxon                              | Specimen<br>Number | Side | Max.<br>Length | Max.<br>Width |
|------------------------------------|--------------------|------|----------------|---------------|
| <u>Parapliosacomys oregonensis</u> | UO 24623           | L    | 2.15           | 1.47          |
| "                                  | UO 26099           | R    | I              | 1.39          |
| "                                  | UO 26100           | L    | 1.98           | 1.44          |
| Thomomyini indet.                  | UO 26091           | *L   | a2.14          | I             |

Table 8. Measurements of upper fourth premolar.

| Taxon                              | Specimen<br>Number | Side | Max.<br>Length | Width<br>Ant.<br>Column | Width<br>Post.<br>Column | Enamel<br>Height | Base<br>Height | Total<br>Height |
|------------------------------------|--------------------|------|----------------|-------------------------|--------------------------|------------------|----------------|-----------------|
| <u>Pliosacomys dubius</u>          |                    |      |                |                         |                          |                  |                |                 |
| "                                  | CIT 1800           | *R   | 1.24           | 0.89                    | 1.16                     | B                | B              | B               |
| "                                  | CIT 1798           | L    | 1.78           | 1.18                    | 1.74                     | B                | B              | B               |
| "                                  | CIT 1798           | R    | 1.78           | 1.22                    | 1.85                     | B                | B              | B               |
| "                                  | CIT 1799           | L    | 1.27           | 0.83                    | 1.38                     | B                | B              | B               |
| "                                  | CIT 1799           | R    | 1.38           | 0.83                    | 1.39                     | B                | B              | B               |
| "                                  | CIT 1797           | L    | I              | 1.12                    | I                        | B                | B              | B               |
| "                                  | CIT 1801           | L    | 1.81           | 1.26                    | 1.64                     | B                | B              | B               |
| "                                  | LACM 33848         | L    | 1.93           | 1.24                    | 1.95                     | 1.86             | 1.92           | 3.78            |
| "                                  | LACM 33849         | L    | 1.35           | 1.22                    | 1.48                     | 3.09             | 1.64           | 4.72            |
| "                                  | LACM 33850         | L    | 1.85           | 1.24                    | 1.81                     | 1.78             | 2.23           | 4.01            |
| "                                  | LACM 33851         | L    | 1.28           | 0.74                    | 1.37                     | 3.26             | 1.08           | 4.33            |
| "                                  | LACM 33852         | L    | 1.54           | 1.06                    | 1.58                     | I                | I              | I               |
| "                                  | LACM 33853         | L    | 1.25           | 0.85                    | 1.40                     | I                | I              | I               |
| "                                  | LACM 33854         | R    | 1.60           | 1.11                    | 1.64                     | I                | I              | I               |
| <u>Parapliosacomys oregonensis</u> | UO 25340           | R    | 1.61           | 1.22                    | 1.61                     | 3.10             | 1.02           | 4.13            |
| "                                  | UO 25370           | R    | 1.45           | 1.08                    | 1.49                     | B                | B              | B               |
| "                                  | UO 25364           | R    | 1.70           | 1.31                    | 1.59                     | 2.54             | 1.47           | 4.01            |
| "                                  | UO 25342           | R    | 1.44           | 1.09                    | 1.49                     | 4.17             | 0.36           | 4.53            |

Table 8. (continued)

| Taxon                               | Specimen<br>Number | Side | Max.<br>Length | Width<br>Ant.<br>Column | Width<br>Post.<br>Column | Enamel<br>Height | Base<br>Height | Total<br>Height |
|-------------------------------------|--------------------|------|----------------|-------------------------|--------------------------|------------------|----------------|-----------------|
| <u>Parapliosaccomys oregonensis</u> | UO 24918           | R    | 1.90           | 1.40                    | 1.83                     | 3.46             | 0.38           | 3.84            |
| "                                   | UO 26090           | R    | 1.63           | 1.32                    | 1.80                     | I                | I              | I               |
| "                                   | UO 25315           | R    | 1.88           | 1.33                    | 1.71                     | 3.23             | 1.22           | 4.44            |
| "                                   | UO 25361           | L    | 1.65           | 1.20                    | 1.54                     | I                | I              | I               |
| "                                   | UO 26097           | R    | 1.77           | 1.35                    | 1.78                     | 4.39             | 0.89           | 5.27            |
| "                                   | UO 26095           | *R   | 1.37           | 0.82                    | 1.56                     | I                | I              | I               |
| "                                   | UO 26096           | *R   | 1.16           | 0.66                    | 1.27                     | I                | I              | I               |
| "                                   | UO 26098           | R    | I              | 1.34                    | I                        | 4.61             | 0.65           | 5.26            |
| "                                   | UO 25358           | L    | 1.58           | 1.37                    | 1.60                     | I                | I              | I               |
| "                                   | UO 25344           | L    | R              | B                       | B                        | 2.43             | 2.19           | 4.62            |
| "                                   | UO 26094           | L    | 1.68           | 1.44                    | 1.75                     | 4.46             | 0.53           | 5.01            |
| "                                   | UO 26109           | R    | 1.63           | 1.38                    | 1.44                     | 1.30             | 1.91           | 3.21            |
| Thomomyini? indet.                  | UO 25352           | R    | 1.63           | 1.34                    | 1.72                     | 3.97             | 0.47           | 4.44            |
| "                                   | UO 26093           | R    | 1.64           | 1.25                    | 1.70                     | I                | I              | I               |
| "                                   | UO 26173           | L    | 1.34           | 1.02                    | 1.54                     | 4.41             | 0.06           | 4.47            |
| <u>Plioeomys transitionalis</u>     | UMMP V28286        | L    | 2.02           | 1.71                    | 2.13                     | 6.79             | 0.48           | 7.27            |
| "                                   | UMMP V28286        | R    | 1.93           | 1.80                    | 2.26                     | I                | I              | I               |
| "                                   | UMMP V29719        | L    | 1.95           | 1.54                    | 2.07                     | 7.05             | 0.48           | 7.53            |

Table 8. (continued)

| Taxon                          | Specimen<br>Number | Side | Max.<br>Length | Width          |                 | Enamel<br>Height | Base<br>Height | Total<br>Height |
|--------------------------------|--------------------|------|----------------|----------------|-----------------|------------------|----------------|-----------------|
|                                |                    |      |                | Ant.<br>Column | Post.<br>Column |                  |                |                 |
| <u>Pliogeomys parvus</u>       | UMMP V55184        | L    | 1.37           | 1.09           | 1.43            | B                | B              | B               |
| "                              | UMMP V55184        | R    | 1.37           | 1.05           | 1.47            | B                | B              | B               |
| "                              | UMMP V55031        | L    | 1.37           | 0.98           | 1.44            | I                | I              | I               |
| <u>Pliosaccomys? shotwelli</u> | UO 6301-15         | *R   | 1.23           | 0.70           | 1.22            | 2.11             | 1.32           | 3.43            |
| "                              | UO 24462           | L    | 1.37           | 0.85           | 1.53            | 1.73             | 1.42           | 3.15            |
| "                              | UO 24474           | R    | 1.39           | 0.95           | 1.61            | I                | I              | I               |
| "                              | UO 24475           | R    | 1.54           | 0.85           | 1.44            | I                | I              | I               |

Table 9. Measurements of upper first and second molars.

| Taxon                               | Specimen<br>Number | Side | M <sup>1</sup> -<br>or M <sup>2</sup> | Max.<br>Length | Max.<br>Width | Enamel<br>Height | Base<br>Height | Total<br>Height |
|-------------------------------------|--------------------|------|---------------------------------------|----------------|---------------|------------------|----------------|-----------------|
|                                     |                    |      |                                       |                |               |                  |                |                 |
| <u>Pliosaccomys dubius</u>          |                    |      |                                       |                |               |                  |                |                 |
| "                                   | CIT 1800           | *R   | 1                                     | 1.04           | 1.37          | B                | B              | B               |
| "                                   | CIT 1800           | *R   | 2                                     | 0.88           | 1.33          | B                | B              | B               |
| "                                   | CIT 1798           | R    | 1                                     | 1.13           | 1.85          | B                | B              | B               |
| "                                   | CIT 1798           | R    | 2                                     | 0.95           | 1.77          | B                | B              | B               |
| "                                   | CIT 1798           | L    | 1                                     | 1.00           | 1.72          | B                | B              | B               |
| "                                   | CIT 1799           | L    | 1                                     | 1.14           | 1.52          | B                | B              | B               |
| "                                   | CIT 1799           | L    | 2                                     | 0.92           | 1.34          | B                | B              | B               |
| "                                   | CIT 1799           | R    | 1                                     | 1.13           | 1.55          | B                | B              | B               |
| "                                   | CIT 1801           | L    | 1                                     | 1.00           | 1.84          | B                | B              | B               |
| <u>Parapliosaccomys oregonensis</u> |                    |      |                                       |                |               |                  |                |                 |
| "                                   | UO 26174           | R    | ?                                     | 0.85           | 1.54          | 4.29             | 0.36           | 4.65            |
| "                                   | UO 26162           | R    | ?                                     | 0.81           | 1.42          | 4.00             | 0.24           | 4.24            |
| "                                   | UO 25359           | *L   | ?                                     | 0.94           | 1.45          | I                | I              | I               |
| "                                   | UO 26151           | *R   | ?                                     | 0.88           | 1.51          | I                | I              | I               |
| "                                   | UO 25362           | R    | ?                                     | 0.84           | 1.56          | I                | I              | I               |
| "                                   | UO 26152           | L    | ?                                     | 0.92           | 1.66          | 4.58             | 0.46           | 5.04            |
| "                                   | UO 26163           | L    | ?                                     | 0.98           | 1.64          | I                | I              | I               |
| "                                   | UO 26118           | *L   | ?                                     | 0.82           | 1.55          | I                | I              | I               |
| "                                   | UO 25356           | *L   | ?                                     | 1.15           | 1.47          | 3.78             | 0.31           | 4.08            |

Table 9. (continued)

| Taxon                               | Specimen<br>Number | Side | M <sup>1</sup><br>or M <sup>2</sup> | Max.<br>Length | Max.<br>Width | Enamel<br>Height | Base<br>Height | Total<br>Height |
|-------------------------------------|--------------------|------|-------------------------------------|----------------|---------------|------------------|----------------|-----------------|
| <u>Parapliosaccomys oregonensis</u> | UO 26138           | *L   | ?                                   | 0.71           | 1.46          | I                | I              | I               |
| "                                   | UO 24914           | ?    | ?                                   | 0.88           | 1.57          | I                | I              | I               |
| "                                   | UO 26105           | ?    | ?                                   | 0.84           | 1.63          | I                | I              | I               |
| "                                   | UO 26169           | *L   | ?                                   | 0.77           | 1.21          | I                | I              | I               |
| "                                   | UO 25393           | *R   | ?                                   | 0.91           | 1.34          | I                | I              | I               |
| "                                   | UO 26115           | *L   | ?                                   | 0.79           | 1.37          | B                | B              | B               |
| "                                   | UO 26116           | *L   | ?                                   | 0.93           | 1.40          | I                | I              | I               |
| "                                   | UO 24921           | *L   | ?                                   | 0.86           | 1.43          | I                | I              | I               |
| "                                   | UO 26105           | ?    | ?                                   | 0.92           | I             | I                | I              | I               |
| "                                   | UO 25375           | ?    | ?                                   | 0.83           | 1.53          | B                | B              | B               |
| "                                   | UO 26158           | ?    | ?                                   | 0.87           | 1.72          | 2.25             | 1.11           | 2.96            |
| "                                   | UO 26157           | ?    | ?                                   | 0.71           | 1.45          | 2.97             | 0.35           | 3.32            |
| "                                   | UO 26121           | ?    | ?                                   | 0.89           | 1.77          | I                | I              | I               |
| "                                   | UO 25372           | ?    | ?                                   | 0.86           | 1.60          | 3.09             | 0.54           | 4.63            |
| "                                   | UO 26167           | ?    | ?                                   | 0.87           | 1.44          | 2.10             | 0.73           | 2.83            |
| "                                   | UO 26168           | ?    | ?                                   | 0.69           | 1.44          | I                | I              | I               |
| "                                   | UO 26165           | ?    | ?                                   | 0.84           | 1.72          | I                | I              | I               |
| "                                   | UO 26144           | ?    | ?                                   | 0.78           | 1.61          | 2.54             | 1.02           | 3.55            |

Table 9. (continued)

| Taxon                            | Specimen<br>Number | Side | M <sup>1</sup><br>or M <sup>2</sup> | Max.<br>Length | Max.<br>Width | Enamel<br>Height | Base<br>Height | Total<br>Height |
|----------------------------------|--------------------|------|-------------------------------------|----------------|---------------|------------------|----------------|-----------------|
| Thomomyini? indet.               |                    |      |                                     |                |               |                  |                |                 |
| "                                | UO 2411            | *R   | ?                                   | 1.09           | 1.61          | I                | I              | I               |
| "                                | UO 26161           | ?    | ?                                   | 0.86           | 1.73          | I                | I              | I               |
| "                                | UO 26120           | *R   | ?                                   | 0.90           | 1.28          | I                | I              | I               |
| "                                | UO 26110           | ?    | ?                                   | 0.87           | 1.78          | B                | B              | B               |
| <u>Brachygeomys drewseyensis</u> | UO 25250           | L    | ?                                   | 1.06           | I             | 1.05             | 1.30           | 2.35            |
| "                                | UO 25246           | *L   | ?                                   | 1.04           | 1.44          | I                | I              | I               |
| "                                | UO 24960           | *L   | ?                                   | 1.05           | 1.68          | I                | I              | I               |
| "                                | UO 2239-B-2        | R    | ?                                   | 1.13           | 1.72          | I                | I              | I               |
| "                                | UO 25233           | *R   | ?                                   | 1.10           | 1.59          | I                | I              | I               |
| <u>Pliogeomys buisi</u>          | UMMP V30195        | ?    | ?                                   | 1.34           | 2.06          | 3.48             | 1.18           | 4.66            |
| <u>Pliogeomys parvus</u>         | UMMP V55184        | L    | 1                                   | 0.74           | 1.38          | B                | B              | B               |
| "                                | UMMP V55184        | L    | 2                                   | 0.77           | 1.40          | B                | B              | B               |
| <u>Pliosacomys? shotwelli</u>    | UO 24463           | *L   | ?                                   | 0.92           | 1.06          | I                | I              | I               |
| "                                | UO 24460           | *L   | ?                                   | 0.90           | 1.16          | 1.56             | 0.81           | 2.37            |
| "                                | UO 25270           | L    | ?                                   | 1.04           | 1.30          | I                | I              | I               |
| "                                | UO 24464           | R    | ?                                   | 0.99           | 1.49          | I                | I              | I               |
| "                                | UO 24480           | R    | ?                                   | 0.97           | 1.47          | 0.82             | 1.28           | 2.10            |
| "                                | UO 24468           | R    | ?                                   | 0.94           | 1.50          | I                | I              | I               |
| "                                | UO 24458           | R    | ?                                   | 1.07           | 1.45          | I                | I              | I               |
| "                                | UO 24481           | L    | ?                                   | 1.00           | 1.53          | I                | I              | I               |

Table 10. Measurements of upper third molars.

| Taxon                               | Specimen<br>Number | Side | Max.<br>Length | Max.<br>Width | Enamel<br>Height | Base<br>Height | Total<br>Height |
|-------------------------------------|--------------------|------|----------------|---------------|------------------|----------------|-----------------|
| <u>Parapliosaccomys oregonensis</u> | UO 26139           | *L   | 1.09           | 1.29          | I                | I              | I               |
| "                                   | UO 26130           | *R   | 1.04           | 1.36          | B                | B              | B               |
| "                                   | UO 26128           | *R   | 1.09           | 1.36          | I                | I              | I               |
| "                                   | UO 26131           | *L   | 1.03           | 1.31          | I                | I              | I               |
| "                                   | UO 25387           | *R   | 1.14           | 1.34          | I                | I              | I               |
| "                                   | UO 26124           | ?    | 1.16           | 1.26          | 0.75             | 1.93           | 2.68            |
| "                                   | UO 26127           | *R   | 0.94           | 1.33          | I                | I              | I               |
| "                                   | UO 26129           | R    | 1.09           | 1.30          | a2.46            | a0.52          | 2.98            |
| Thomomyini? indet.                  | UO 26113           | *L   | a1.25          | 1.41          | I                | I              | I               |
| "                                   | UO 25354           | ?    | 1.24           | 1.46          | 1.99             | 0.34           | 2.33            |
| <u>Brachygeomys drewseyensis</u>    | UO 25252           | R    | 1.14           | 1.41          | B                | B              | B               |

Table 11. Measurements of mandibles.

(O) indicates measurement taken at occlusal surface and (A) indicates measurement taken on alveoli. \*\* indicates  $DP_{\overline{4}} - M_{\overline{3}}$ . Total length measured parallel to the base of mandible not including the incisor. Depth of the mandible under the  $P_{\overline{4}}$  measured perpendicular to the base of the mandible. Symphysis length measured in a straight line from the posterior of the symphyseal eminence to the anterodorsal termination of the symphysis.

| Taxon                              | Specimen Number | Side | Length $P_{\overline{4}} - M_{\overline{3}}$ | Total Length without Incisor | Length Diastema | Depth Under $P_{\overline{4}}$ | Length Symphysis |
|------------------------------------|-----------------|------|----------------------------------------------|------------------------------|-----------------|--------------------------------|------------------|
| <u>Pliosacomys dubius</u>          | CIT 1804        | R    | I                                            | I                            | I               | 5.1                            | I                |
| "                                  | CIT 1805        | R    | 5.8(O)                                       | I                            | I               | 5.1                            | I                |
| "                                  | CIT 1808        | L    | I                                            | I                            | I               | 4.7                            | I                |
| "                                  | CIT 1807        | L    | **5.3(O)                                     | I                            | I               | a5.3                           | I                |
| "                                  | CIT 1810        | R    | I                                            | I                            | a3.5            | 3.9                            | a5.9             |
| "                                  | CIT 1796        | R    | 4.9(O)                                       | I                            | I               | 4.9                            | I                |
| <u>Parapliosacomys oregonensis</u> | UO 3631         | L    | 6.6(A)                                       | 19.0                         | 4.7             | 5.1                            | 8.4              |
| "                                  | UO 9301         | R    | a6.3(A)                                      | I                            | 4.7             | 5.4                            | 8.1              |
| <u>Pliogeomys buisi</u>            | UMMP V29147     | R    | I                                            | I                            | a6.8            | 7.7                            | a11.7            |
| "                                  | UMMP V56274     | L    | 5.7(O)                                       | 22.6                         | 6.0             | 7.3                            | 11.4             |
| "                                  | UMMP V33446     | R    | I                                            | I                            | a6.2            | 7.7                            | 12.0             |

Table 11. (continued)

| Taxon                            | Specimen<br>Number | Side | Length<br>$P_4 - M_3$ | Total<br>Length<br>without<br>Incisor | Length<br>Diastema | Depth<br>Under<br>$P_4$ | Length<br>Symphysis |
|----------------------------------|--------------------|------|-----------------------|---------------------------------------|--------------------|-------------------------|---------------------|
| <u>Pliogeomys transitionalis</u> | UMMP V60474        | L    | I                     | a24.5                                 | 5.7                | I                       | I                   |
| <u>Pliogeomys parvus</u>         | UMMP V55185        | R    | I                     | I                                     | 3.6                | 4.3                     | 7.1                 |
| "                                | UMMP V53562        | L    | I                     | I                                     | 3.2                | 4.5                     | 6.9                 |

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Figure 1. A-N, Pliosaccomys dubius; O, Pliosaccomys magnus. A, CIT 1810, left mandible with  $DP_4^- - M_1^-$ , occlusal view X3. B, CIT 1796, Holotype, right mandible with  $P_4^- - M_3^-$ , lateral view X3. C, LACM 33855,  $RM_1^-$  or  $RM_2^-$ , root view X4. D, CIT 1796, Holotype, internal view X3. E, CIT 1796, Holotype, occlusal view X3. F, CIT 1803, right mandible with  $M_1^- - M_3^-$ , occlusal view X3. G, CIT 1805, right mandible with  $P_4^- - M_3^-$ , occlusal view X3. H, CIT 1805, internal view X3. I, CIT 1809, left mandible with  $P_4^- - M_2^-$ , occlusal view X3. J, CIT 1805, external view X3. K, CIT 1800, right maxillary with  $P_4^4 - M_2^2$ , occlusal view X3. L, CIT 1798, palate with  $RP_4^4 - M_2^2$  and  $LP_4^4 - M_1^1$ , occlusal view X3. M, LACM 33851,  $LP_4^4$ , labial view X4. N, LACM 33851, root view X4. O, UCMP 99193,  $RP^-$ , occlusal view X4.

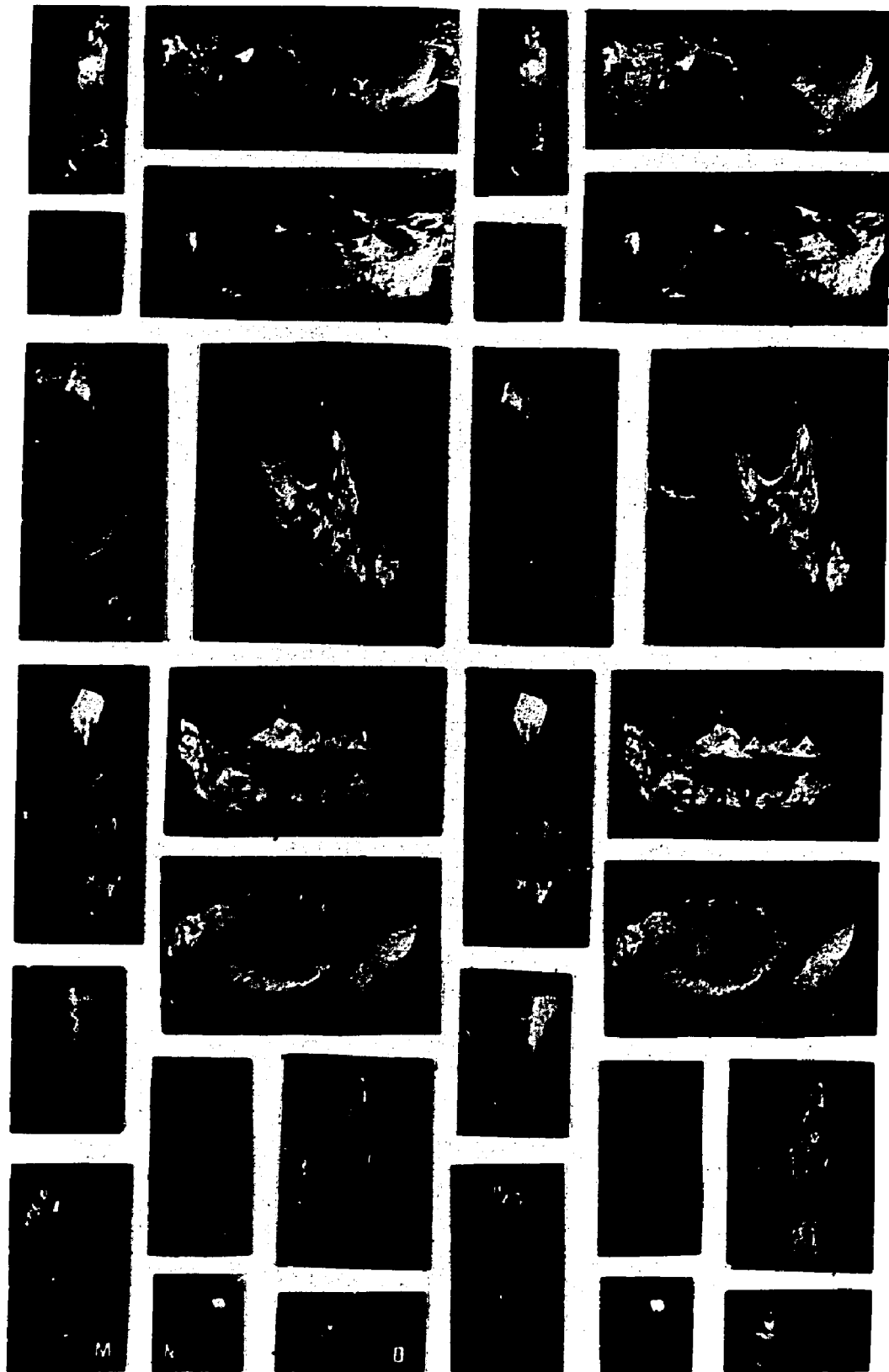


Figure 2. A-H, Pliosacomys magnus; I-S, Parapliosacomys oregonensis. A, UCMP 12567, Holotype, left mandible with  $P_4 - M_2$ , lateral view X3. B, UCMP 12568, left mandible with  $P_4$ , lateral view X3. C, UCMP 12567, Holotype, internal view X3. D, UCMP 12567, Holotype, occlusal view X3. E, UCMP 12568, occlusal view X3. F, UCMP 99193,  $RP_4$ , labial view X4. G, UCMP 99194,  $RP_4$ , labial view X4. H, UCMP 99194, occlusal view X4. I, UO 3631, Holotype, left mandible with  $P_4 - M_1$ , internal view X2. J, UO 3631, Holotype, lateral view X2. K, UO 3631, Holotype, occlusal view X2. L, UO 3630, right mandible with  $P_4 - M_2$ , occlusal view X2. M, UO 26088,  $LDP_4$ , occlusal view X4. N, UO 26088, lingual view X4. O, UO 26081,  $LP_4$ , occlusal view X4. P, UO 26084,  $LP_4$ , lingual view X4. Q, UO 26080,  $RP_4$ , lingual view X4. R, UO 26084, occlusal view X4. S, UO 25361,  $RP_4$ , occlusal view X4.

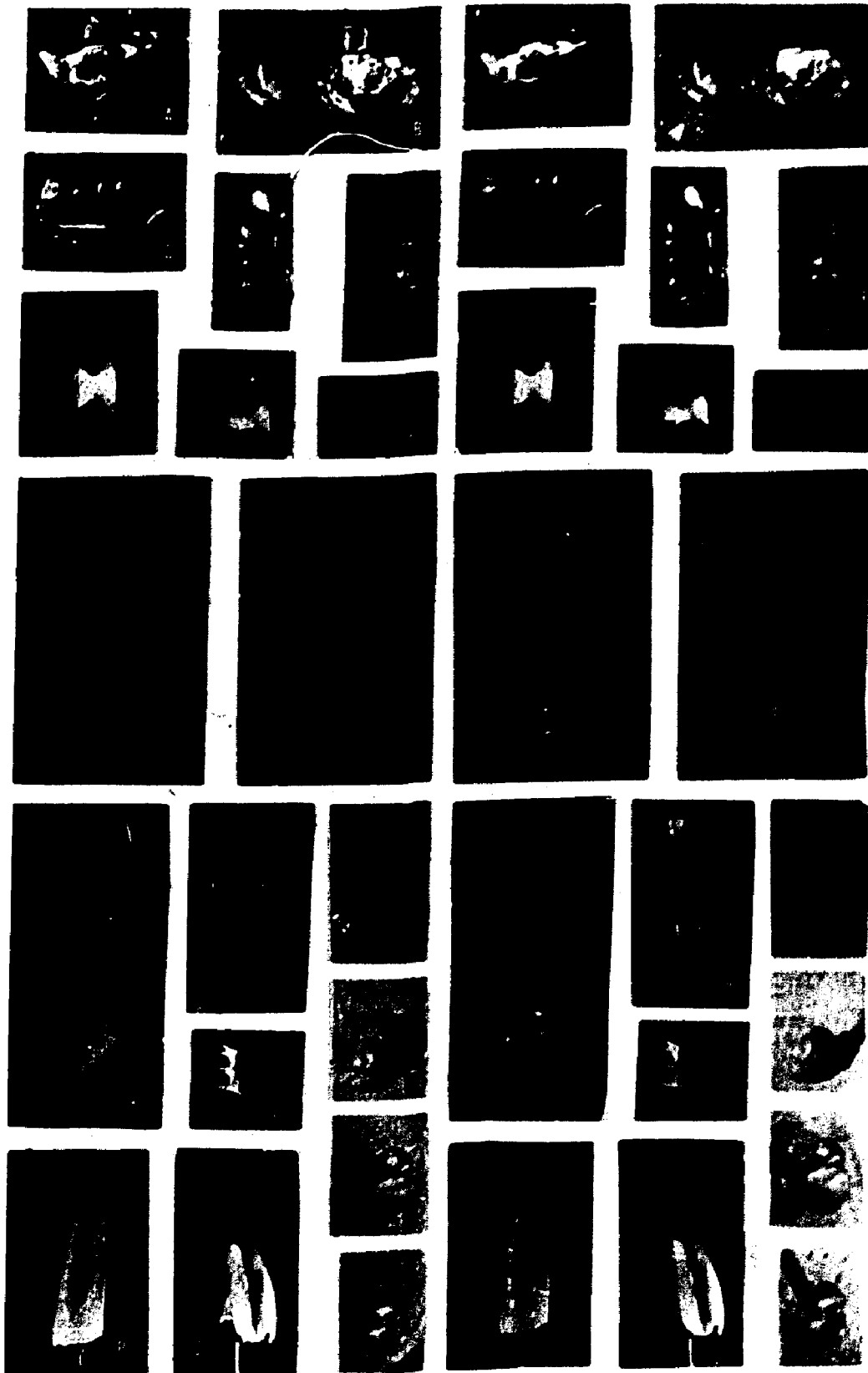


Figure 3. Parapliosacomys oregonensis. A, UO 24926, LM<sub>1</sub><sup>-</sup> or LM<sub>2</sub><sup>-</sup>, lingual view X<sup>4</sup>. B, UO 24926, occlusal view X<sup>4</sup>. C, UO 24149, LM<sub>1</sub><sup>-</sup> or LM<sub>2</sub><sup>-</sup>, occlusal view X<sup>4</sup>. D, UO 26147, RM<sub>1</sub><sup>-</sup> or RM<sub>2</sub><sup>-</sup>, occlusal view X<sup>4</sup>. E, UO 26147, anterior view X<sup>4</sup>. F, UO 26108, RM<sub>3</sub><sup>-</sup>, occlusal view X<sup>4</sup>. G, UO 25388, LM<sub>3</sub><sup>-</sup>, occlusal view X<sup>4</sup>. H, UO 25388, anterior view X<sup>4</sup>. I, UO 25388, lingual view X<sup>4</sup>. J, UO 27005, partial rostrum and edentulous palate, occlusal view X<sup>2</sup>. K, UO 2222-18, L upper incisor, labial view X<sup>3</sup>. L, UO 2222-18, anterior view X<sup>3</sup>. M, UO 24623, LDP<sub>1</sub><sup>4</sup> in maxillary fragment, occlusal view X<sup>4</sup>. N, UO 26096, RP<sub>1</sub><sup>4</sup>, occlusal view X<sup>4</sup>. O, UO 26097, RP<sub>1</sub><sup>4</sup>, lingual view X<sup>4</sup>. P, UO 26097, occlusal view X<sup>4</sup>. Q, UO 26115, LM<sub>1</sub><sup>1</sup> or LM<sub>2</sub><sup>2</sup>, lingual view X<sup>4</sup>. R, UO 26105, M<sub>1</sub><sup>1</sup> or M<sub>2</sub><sup>2</sup>, posterior view X<sup>4</sup>. S, UO 26115, occlusal view X<sup>4</sup>. T, UO 26097, posterior view X<sup>4</sup>. U, UO 26105, occlusal view X<sup>4</sup>. V, UO 26131, LM<sub>3</sub><sup>3</sup>, occlusal view X<sup>4</sup>.

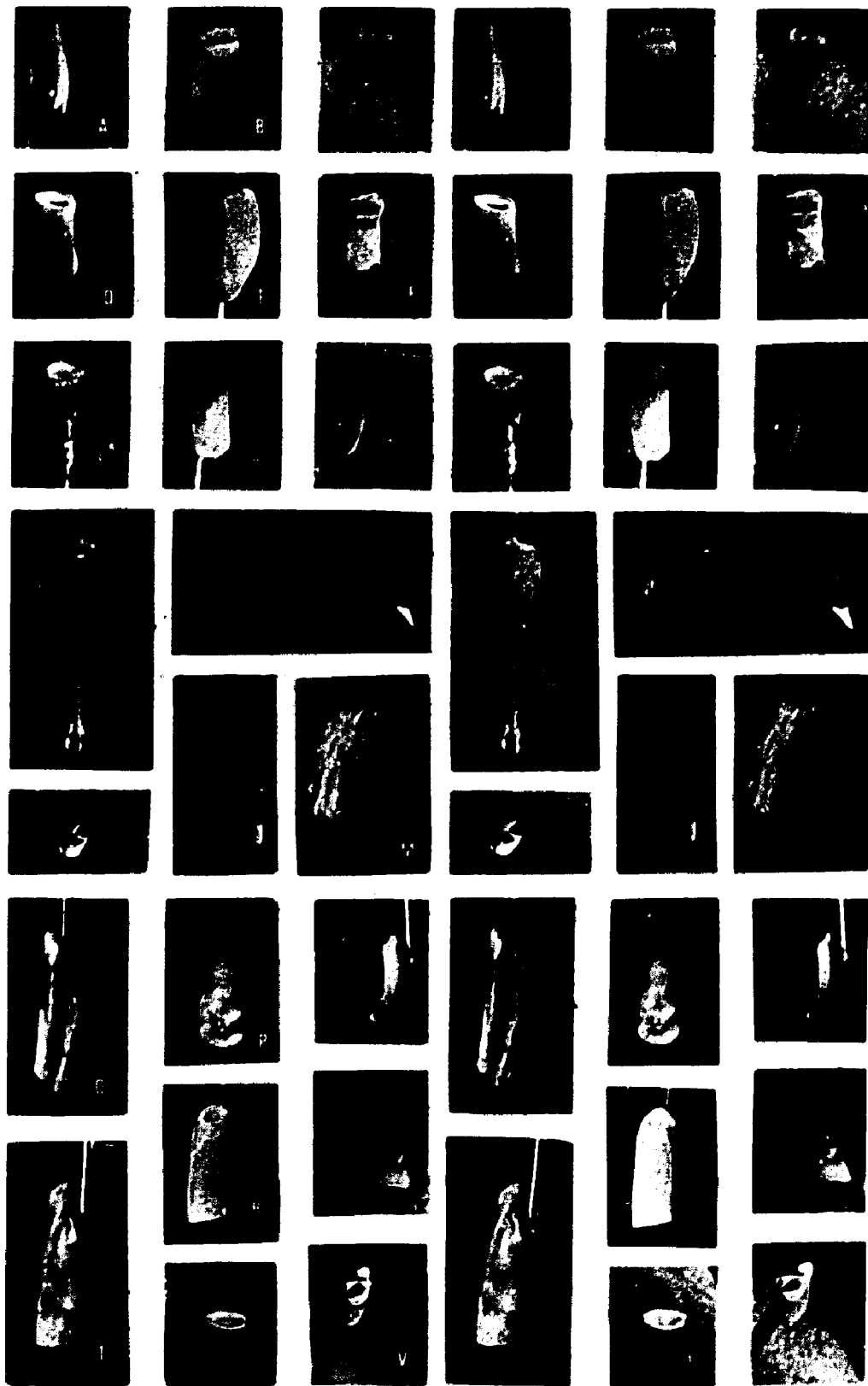


Figure 4. A-B, Parapliosacomys oregonensis; C-M, Thomomyini? indet.; N-X, Brachygeomys drewseyensis. A, UO 26129,  $RM_2^3$ , occlusal view X4. B, UO 26129, lingual view X4. C, UO 24622,  $RDP_{\overline{4}}$ , occlusal view X4. D, UO 24622, lingual view X4. E, UO 25377,  $LP_{\overline{4}}$ , occlusal view X4. F, UO 25377, labial view X4. G, UO 26102,  $LM_1$  or  $LM_2$ , occlusal view X4. H, UO 26091,  $LDP_{\overline{4}}$ , occlusal view X4. I, UO 26091, labial view X4. J, UO 26173,  $LP_{\overline{4}}$ , occlusal view X4. K, UO 26173, lingual view X4. L, UO 26120,  $RM_1$  or  $RM_2$ , occlusal view X4. M, UO 26113,  $M_2^3$ , occlusal view X4. N, UO 24979,  $RDP_{\overline{4}}$ , occlusal view X4. O, UO 24979, labial view X4. P, UO 26058, Holotype,  $RP_{\overline{4}}$ , occlusal view X4. Q, UO 26058, Holotype, lingual view X4. R, UO 26058, Holotype, labial view X4. S, UO 27009, anterior column of  $LP_{\overline{4}}$ , occlusal view X4. T, UO 24943,  $P_{\overline{4}}$ , occlusal view X4. U, UO 2239-A,  $RM_1$  or  $RM_2$ , occlusal view X4. V, UO 25258,  $RM_1$  or  $RM_2$ , occlusal view X4. W, UO 25258, labial view X4. X, UO 25258, lingual view X4.

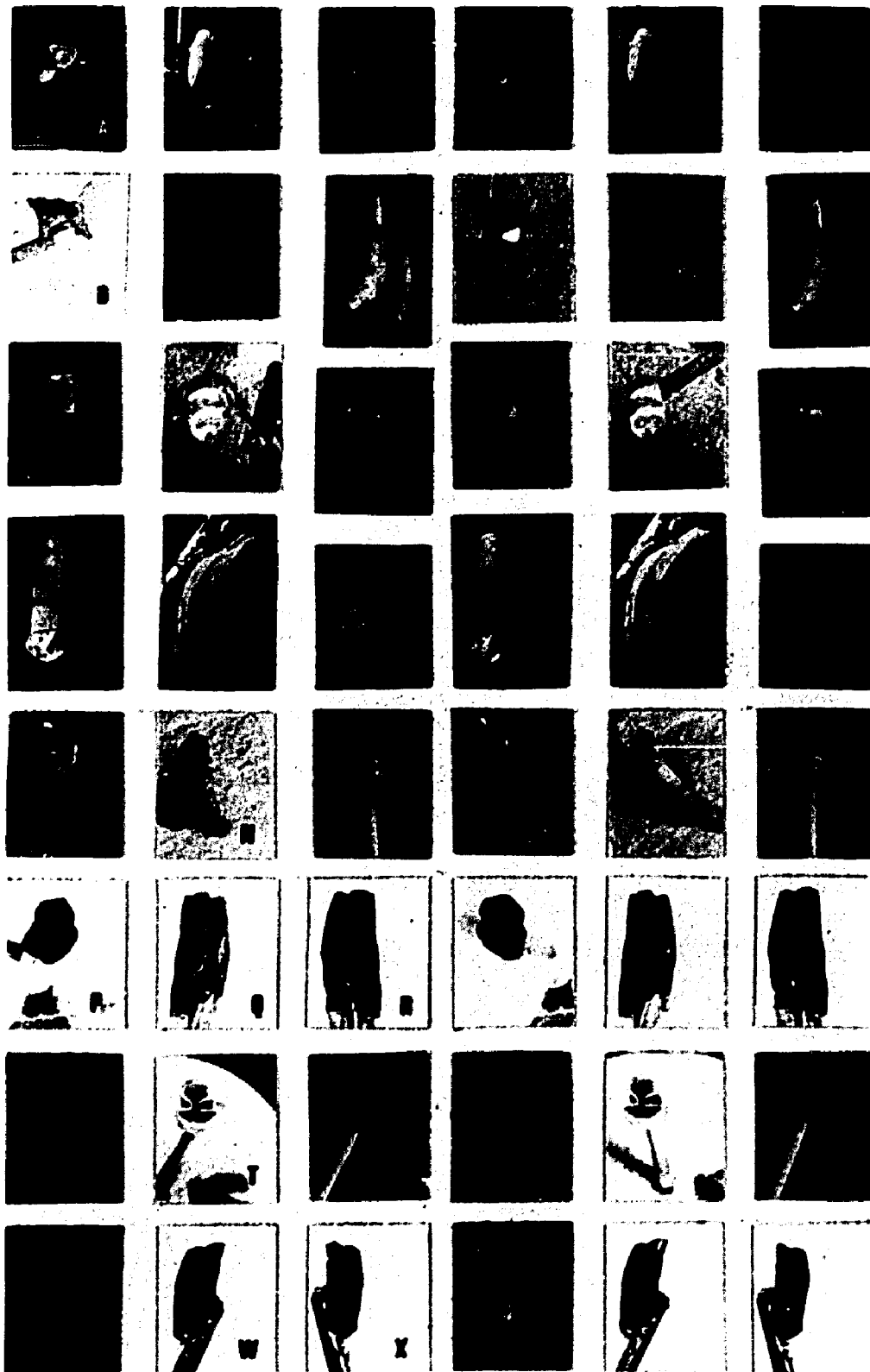


Figure 5. A-F, Brachygeomys drewseyensis; G-P, Plio-geomys buisi. A, UO 24987,  $LM_3$ , occlusal view X4. B, UO 25246,  $RM_1$  or  $RM_2$ , occlusal view X4. C, UO 24960,  $LM_1$  or  $LM_2$ , occlusal view X4. D, UO 24960, labial view X4. E, UO 25252,  $RM_3$ , occlusal view X4. F, UO 25252, lingual view X4. G, UMMP V29147, Holotype, right mandible with  $P_4 - M_2$ , occlusal view X2. H, UMMP V29147, Holotype, lateral view X2. I, UMMP V56274, left mandible with  $P_4 - M_3$ , occlusal view X2. J, UMMP V56274, internal view X2. K, UMMP V30194,  $LDP_4$ , occlusal view X4. L, UMMP V30194, labial view X4. M, UMMP V30195,  $LM_1$  or  $LM_2$ , occlusal view X3. N, UMMP V56274,  $LM_1$ , posterior view X3. O, UMMP V56274,  $LM_1$ , anterior view X3. P, UMMP V60470,  $RM_3$ , occlusal view X3.

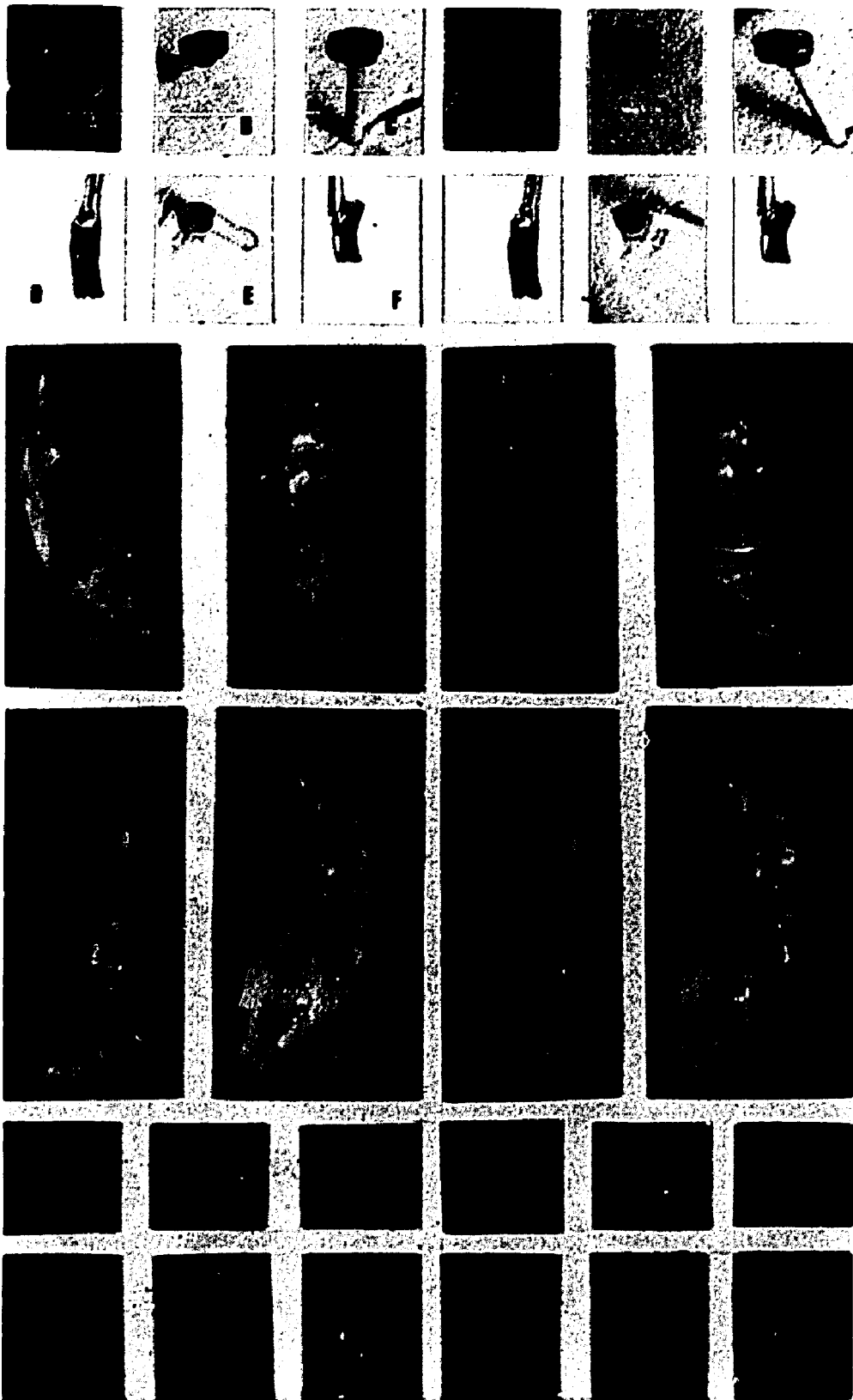


Figure 6. A, Pliogeomys buisi; B-I, Pliogeomys transi-  
tionalis; J-M, Pliogeomys parvus. A, UMMP V56274, left  
mandible with  $P_4 - M_3$ , occlusal view X2. B, UMMP V60474,  
Holotype, left mandible with  $P_4 - M_2$ , occlusal view X2.  
C, UMMP V60474, Holotype, lateral view X2. D, UMMP V41401,  
 $RP_4$ , occlusal view X3. E, UMMP V41401, labial view X3.  
F, UMMP V60469, L upper incisor, anterior view X3. G,  
UMMP V60469, labial view X2. H, UMMP V27919,  $LP_4$ , occlusal  
view X3. I, UMMP V27919, lingual view X3. J, UMMP V55185,  
Holotype, right mandible with  $P_4 - M_2$ , occlusal view X3.  
K, UMMP V56017,  $LP_4$ , occlusal view X4. L, UMMP V53450,  $LN_1$   
or  $LN_2$ , occlusal view X4. M, UMMP V53450, anterior view X4.



Figure 7. A-J, Pliogeomys parvus; K-M, Pliosaccomys? shotwelli. A, UMMP V55185, Holotype, right mandible with  $P_4^- - M_2^-$ , lateral view X3. B, UMMP V55185, Holotype, internal view X3. C, UMMP V53562, left mandible with  $P_4^- - M_2^-$ , occlusal view X3. D, UMMP V53562, lateral view X3. E, UMMP V60757, L upper incisor, lateral view X3. F, UMMP V55184, anterior skull fragment with L incisor,  $LP_4^4 - M_2^2$ ,  $RP_4^4$ , occlusal view X3. G, UMMP V55184, lateral view X3. H, UMMP V60757, anterior view X3. I, UMMP V55031,  $LP_4^4$ , occlusal view X4. J, UMMP V55031, posterior view X4. K, UMMP V24478, Holotype,  $LP_4^-$ , occlusal view X4. L, UMMP V24478, Holotype, lingual view X4. M, UMMP V24478, Holotype, labial view X4.

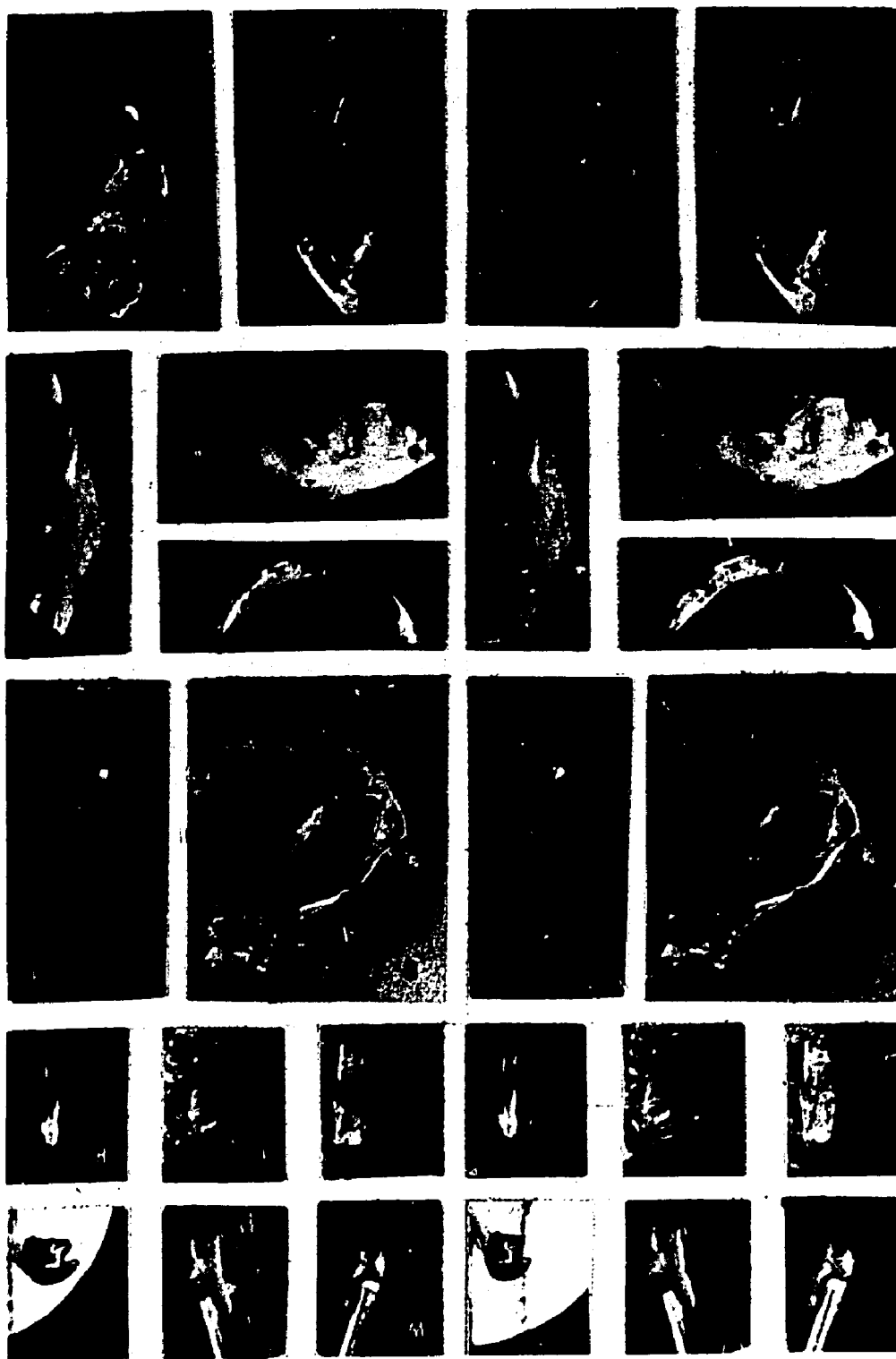


Figure 8. A-P, Pliosaccomys? shotwelli; Q, "Pliosaccomys" wilsoni; R, Prodipodomys cf. P. centralis; S, Geomys bursarius majusculus. A, UO F-18236,  $LP_{\bar{4}}^1$ , occlusal view X4. B, UO F-18236, labial view X4. C, UO 24461,  $LM_{\bar{1}}^1$  or  $LM_{\bar{2}}^2$ , occlusal view X4. D, UO 24461, labial view X4. E, UO 24461, lingual view X4. F, UO 24467,  $LM_{\bar{3}}^3$ , occlusal view X4. G, UO 24467, labial view X4. H, UO 24467, lingual view X4. I, UO 24462,  $LP_{\bar{4}}^4$ , occlusal view X4. J, UO 24462, lingual view X4. K, UO 24463,  $LM_{\bar{1}}^1$  or  $LM_{\bar{2}}^2$ , occlusal view X4. L, UO 24464,  $RM_{\bar{1}}^1$  or  $RM_{\bar{2}}^2$ , occlusal view X4. M, UO 24464, labial view X4. N, UO 24460,  $LM_{\bar{1}}^1$  or  $LM_{\bar{2}}^2$ , occlusal view X4. O, UO 24460, anterior view X4. P, UO 25269,  $M_{\bar{2}}^3$ , occlusal view X4. Q, UCMP 50351, Holotype, right mandible with  $DP_{\bar{4}}^4 - M_{\bar{2}}^2$ , occlusal view X4. R, UMMP V60711, right mandible with  $DP_{\bar{4}}^4$ , occlusal view X4. S, KU 2931, mandibles with incisors,  $LDP_{\bar{4}}^4 - M_{\bar{3}}^3$ ,  $RDP_{\bar{4}}^4 - M_{\bar{2}}^2$ , occlusal view X1.

