THE UNIVERSITY OF KANSAS

PALEONTOLOGICAL CONTRIBUTIONS

THE EARLY EVOLUTION OF THE CRICETIDAE
IN NORTH AMERICA[1]

LARRY D. MARTIN

Department of Systematics & Ecology and Museum of Natural History

University of Kansas, Lawrence, Kansas 66045

ABSTRACT

The early radiation of cricetid rodents in North America is discussed and a new classification based on incisor and molar morphology, infraorbital foramina, and other characters of the skull and skeleton is proposed. One new subfamily, the Nonomyinae, and two new tribes, the Leidymini and the Geringini, are proposed. A new genus and species of eumyine, *Coloradoeumys galbreathi*, and new genera *Wilsoneumys*, *Eoeumys*, and *Geringia* are created for *"Eumys" planidens*, *"Leidymys" vetus*, and *"Paciculus" mcgregori* respectively. *"Eumys" exiguus* is considered congeneric but not conspecific with *"Leidymys" vetus* and both are placed in the genus *Eoeumys*. *"Eumys" blacki* and *Cotimus alicae* are placed in *Leidymys*. *"Eumys" woodi* is placed in *Paciculus* and *"Eumys" gloveri* is considered congeneric with *Geringia mcgregori*. None of the North American Oligocene or early Miocene cricetids are thought to be ancestral to any living cricetids, and the modern North American cricetid radiation is thought to stem from a cricetid similar to *Copemys*.

INTRODUCTION

The highly diverse muroid rodents are distributed naturally on all continents except Antarctica and on many oceanic islands. In most places, they are the most abundant small herbivore. Their success is due to a remarkable ability to adapt to various environments, a generally high reproductive rate, and a natural capability for waif dispersal.

The stem group of the muroids, the Cricetidae, appeared at about the same time as the other "myomorph" rodents, including the eomyids and the sicistines. The earliest and most primitive known cricetid is *Nonomys* from lower Oligocene strata in North America; however, cricetids are also known from the lower Oligocene in Europe. If they

originated in North America, they were able quickly to disperse across the Bering land bridge. An alternative hypothesis is that they originated in Asia and dispersed from there to Europe and North America. Among the other myomorphs, the eomyids occur in North America in upper Eocene strata and probably originated in North America, whereas sicistines may be of Eurasian origin.

Although the early Cricetidae are among the most abundant small mammalian fossils, much is unknown about their morphology. No skeletal elements have been referred to North American Oligocene cricetids, and in only four species is any substantial part of the skull known. Of course, many other features used in the classification of living forms, including structure of the penis, are unavailable.

The early North American cricetid radiation appears to have been an important but ultimately dead-end affair. The center of the modern cricetid radiation almost certainly was in Eurasia. Early Eurasian cricetids are in general similar to North American cricetids, but during the Miocene they developed important adaptations that tend to unite them with the modern cricetines. The cricetids appear to have originated in mesic temperate or subtropical environments, but during the Miocene developed a fully tropical branch, the Muridae, which have low-crowned, lophate teeth. Although enormously successful in the Old World tropics, the Muridae apparently could not cross high latitudes without the artificial environment of human homes; however, the New World tropics were successfully colonized by cricetids. The source of these cricetids is unclear. Cricetids are extremely rare in the Hemingfordian of North America. The total record consists of only two dubious teeth from the Thomas Farm local fauna of Florida (Black, 1963), some fragmentary material from the Hemingfordian of South Dakota (Martin, 1976) and a form from the Hemingfordian of Nebraska (Martin & Corner, 1980). The Florida teeth are not similar to any known North American Oligocene or Arikareean cricetids. If correctly assigned, they might represent an otherwise unknown southern radiation of cricetids, which could be part of the ancestral stock of the South American cricetid radiation. Alter-

natively, the South American cricetids might have been derived from the Eurasian emigrant cricetid *Copemys,* which first appears in Barstovian strata. Not long after the arrival of *Copemys* in North America, the Central American filter bridge became operative and would have permitted easy access to South America. If the South American forms, with complex penes, are derived from *Copemys,* and if a complex penis is primitive in cricetids, then *Copemys* must have had a complex penis, and those cricetids with simple penes are probably narrowly monophyletic and developed in temperate North America during the Clarendonian. Kimballian climates were somewhat more severe and may have maintained forms with a complex penis in a southerly distribution; the warm, mesic Blancan that followed saw the northern migration of *Oryzomys* and *Sigmodon.*

During the Miocene, the Eurasian cricetids also developed a saltatorial desert branch, the Gerbillinae. In North America essentially the same adaptive zone is occupied by heteromyids, although the Arikareean cricetid *Paciculus* was an early experiment in this direction.

The murids and the South American cricetids represent the tropical cricetid radiation, but there was also a major radiation of grassland forms, the Arvicolidae (voles and lemmings), whose radiation was less extensive but comparable to that of the murids. I follow those workers (e.g., Repenning, 1968) who give them family rank. The arvicolids have their earliest fossil record in the Clarendonian of North America, but their complex penis and greater initial diversity in Europe may suggest an Eurasian origin. Whatever the case, they have a Holarctic distribution almost at the point of their first appearance in the fossil record. They are the last mammalian family to appear, with their earliest record only about 11 million years old.

Many of the most interesting events of cricetid history occurred in Eurasia. In part because of this, the early European cricetids have had much more intensive study than their American counterparts, and the most recent revision of the fossil cricetids (Mein & Freudenthal, 1971) is based almost wholly on European material. The present study is meant in part to complement their work and

to clarify the relationships of the cricetids in the two areas.

A moderate amount of work has been done on North American Oligocene and early Miocene cricetids since Leidy (1856) described *Eumys elegans.* Cope described a series of cricetids from the John Day beds of Oregon: *Hesperomys* (=*Peromyscus) nematodon, Paciculus insolitus* (Cope, 1879), and *Eumys lockingtonianus* (Cope, 1881b). Sinclair (1905) placed in *Peromyscus* another John Day form, *P. parvus.*

Most of the later work has been done by A.E. Wood (1936; 1937), who erected the genus *Leidymys* for *Hesperomys nematodon* and *Eumys lockingtonianus.* He also erected four new species of *Eumys,* one species of *Leidymys,* and a new genus, *Scottimus.* Since that time, White (1954) has proposed three new species of *Eumys;* Wilson (1949a) erected one; Black (1961a) erected one; and Macdonald (1963; 1970) has proposed two. Black (1961a, b, c) also described new species of *Scottimus* and *Paciculus* and erected a new genus *Cotimus* which he interpreted at the time to be late Miocene. Alker (1969) and Russell (1972) described new species of *Paciculus* and *Eumys,* respectively. In addition, the following genera have been thought to be cricetids by various authors: *Schaubeumys* (Wood, 1935; Alker, 1967) and *Megasminthus* (Alker, 1967), which are sicistines, and *Horatiomys* (Wood, 1935; Alker, 1967), which is based on the deciduous tooth of an aplondontid (D.L. Rasmussen, personal communication). The relationships of the enigmatic Oligocene rodent *Diplolophus* (Wood, 1937) are unclear, and it is not considered in this study. Alker (1967) attempted a comprehensive review of the North American fossil cricetids, but most of his work remains unpublished. He synonymized all of the described species of *Eumys* into *E. elegans* except *E. exiguus* (Alker, 1966), which he referred to the European early Oligocene *Paracricetodon* (Alker, 1968).

For the present study I have examined the holotypes or casts of the holotypes of the species of North American Chadronian through Arikareean cricetids, and many are refigured. I have also provided expanded descriptions of many taxa utilizing the types

and referred material, although I have tried to avoid duplicating descriptions of dental characters that are well discussed elsewhere. I have also examined referred specimens of most of the European cricetid genera and the Mongolian Oligocene collection housed in the American Museum of Natural History.

Most North American Oligocene and Miocene cricetid species have been assigned to the genus *Eumys.* This practice has hidden the true diversity of early cricetids in North America. Also as *Eumys* is by far the best known and most abundant Oligocene cricetid, it has often been placed as ancestral to later forms (see Clark, Dawson, & Wood, 1964). The present study examines their relationships and shows that the eumyine cricetids are a side branch of cricetid evolution. The ancestry and place of origin of the early cricetids is also addressed, and a revised classification of the North American forms is proposed.

BIOSTRATIGRAPHIC RELATIONSHIPS

In both Eurasia and North America, fossil

mammals have been useful in the correlation of Cenozoic continental deposits. In North America their most important application has been in the "land mammal ages" of the Wood Committee (Wood & others, 1941). I agree with Tedford (1970) that these "land mammal ages" are defined by the temporal span of a unique suite of mammalian genera and are not bound to any lithostratigraphic units nor to an absolute time scale.[1] First and last appearances are stressed in the definition of "land mammal ages," and ordinarily these are thought to be expressions of immigration and extinction. However, some appearances may express changes due to progressive evolution. Nonetheless, I regard such changes as useful and incorporate them into my biostratigraphic scheme.

The oldest North American land mammal age that certainly contains cricetids[2] is the Chadronian. Major Chadronian local faunas include the Titus Canyon local fauna in California; the McCartys Mountain and Pipestone Springs* local faunas in Montana; the Little Egypt, Airstrip*, and Ash Springs local faunas in Texas; the Cypress Hills local fauna in Saskatchewan; the Horsetail Creek* local fauna in Colorado; the Yoder, Cameron Springs, and Bates Hole* local faunas in Wyoming; the Conglomerate Creek Valley* fauna in Canada, and the Chadron Formation local faunas in South Dakota and Nebraska*. The Chadronian is characterized in North America by the first appearance of sabertoothed cats (*Dinictis* and *Hoplophoneus*); amphicyonid dogs (*Daphoenocyon, Daphoenictis,* and *Daphoenus*); cricetid rodents (*Nonomys, Eumys,* and *Eoeumys*), and beavers (*Agnotocastor*), and by the last appearance of titanotheres, oreonetine oreodonts, specialized eomyid rodents (*Yoderimys, Centimanomys,* and *Namatomys*), and cylindrodontid rodents.

The Orellan Land Mammal Age includes part of the Canyon Ferry* fauna in Montana; Scenic* faunas in South Dakota; Cedar Creek* faunas in Colorado; and lower Brule*

faunas in Nebraska. The Orellan is marked by the first appearance of leptauchenine oreodonts; flat-incisored beavers (*Palaeocastor*); and the shrew, *Trimylus.* It probably also contains the last appearance of *Ischyromys.*

The Whitneyan Land Mammal Age is considered here to include Whitney* faunas in Nebraska; the Vista* faunas in Colorado; the Blue Ash* local fauna, Poleslide* and lower Sharps* faunas in South Dakota, and the Cedar Ridge* local fauna in Wyoming. Whitneyan faunas contain the first appearances of the cricetid genera *Scottimus, Leidymys,* and *Paciculus.* They are also characterized by the first appearances of *Eumys brachyodus, Leptauchenia,* and *Pithecistes,* and the last appearances of lepticid insectivores, the sabertoothed cat *Hoplophoneus,* and miniochoerine oreodonts.

The Arikareean and Hemingfordian land mammal stages are not comparable to other land mammal ages but are more nearly equivalent to series. Their subdivision into a number of new provincial "ages" seems advisable. This has already been undertaken by Wilson (1960) with the proposal of the provincial "ages" Harrisonian and Marslandian. I concur with Wilson on the usefulness of these new terms, although the Marslandian is clearly Hemingfordian rather than Arikareean as Wilson (1960, p. 16, fig. 7) originally suggested (McKenna, 1965). Unfortunately, Wilson did not designate a type section or list a fauna for his Harrisonian. A suitable type section and local fauna would be that from the Agate Springs National Monument, which is the most important single Harrisonian locality. The Harrisonian presently includes the first appearance of *Moropus, Promerycochoerus, Phenacocoelus,* and *Merychyus.* It includes the last appearance of *Nimravus,* the Entoptychinae, the Promerycochoerinae, and Eporeodontinae, the Desmatochoerinae, and the flat-incisored, fossorial beavers (*Palaeocastor, Euhapsis, Capacicala*) in North America.

In the Central Great Plains, the Gering, Sharps, and Monroe Creek faunas also form a natural grouping separated from the Whitneyan faunas by the absence of *Hoplophoneus, Miniochoerus,* and lepticid insectivores, and the first appearance of *Amphechinus,* talpine moles, and *Plesiosminthus.* They are

---

[1]The use of land mammal ages in this paper is that current in vertebrate paleontology and does not necessarily conform to use of the term age in the *Code of Stratigraphic Nomenclature.* A thorough discussion of this problem can be found in Tedford (1970).

[2]In the discussion that follows, faunas known to contain cricetids are marked with an asterisk.

separated from the Harrisonian faunas by the presence of leptauchenine oreodonts, *Hypisodus, Geolabis,* and *Ekgmowecheshala.* For these faunas and their biochron correlatives in North America, I have proposed a new provincial "age," the Geringian (Martin, 1975).

The fauna of the lower Sharps is probably Whitneyan and should be excluded from the Geringian. At Redington Gap both the Helvas Canyon and Mitchell Pass members of the Gering Formation as well as the Monroe Creek Formation are fossiliferous. This provides an almost complete suite of Geringian faunas at its type section. The Whitney Member of the Brule Formation is also well exposed and fossiliferous at Redington Gap, and thus provides direct comparisons between the Whitneyan and the Geringian at its type locality. Outside of the Central Great Plains, the Upper Sespe* faunas in California, John Day* faunas in Oregon, and Cabbage Patch*, Fort Logan*, and Deep River* faunas in Montana are partly Geringian and partly Harrisonian in age.

Correlation of continental deposits between North America and Eurasia has always been a difficult task that is not simplified by the fact that for both areas workers use a common terminology largely based on the marine sequence in Europe. Certainly the boundaries of series in North America should correspond reasonably well to boundaries of their type sections in Europe, but we have had little real success in correlating continental rocks in North America with the marine sequence in Europe. Hopefully, this problem can be alleviated by the introduction of a matrix of radiometric dates into which the vertebrate faunas can be positioned (Wilson, 1975).

The Chadronian has been dated as early as 37.5 m.y. (Evernden & others, 1964) and a few earlier dates have been reported (Wilson & others, 1968). The latest dates that may be associated with Chadronian faunas are around 31 m.y. (Evernden & others, 1964). The earliest Geringian may be as early as 28.0 ± 0.7 m.y. (Obradovich, Izett, & Naeser, 1973), and the Harrisonian has a later date of about 21 m.y. (Evernden & others, 1964). Berggren (1972) used these and other dates to show that the Orellan, Whitneyan, and most

of the Arikareean are equivalent to the marine Chattian. Presumably the Arikareean and especially the Geringian are Oligocene, an interpretation that agrees with that of Osborn (1921) but disagrees with those of most recent workers (Macdonald, 1963; Martin, 1972), who have regarded faunas now included in the Geringian to be early Miocene.

Although new techniques may ultimately give a stable subdivision of the Tertiary sequence in North America, a more detailed review of the radiometric dates and biostratigraphic correlations is needed to establish this. I have therefore treated Geringian faunas as early Miocene because this has been the conventional interpretation among North American paleontologists and should not result in confusion. Nevertheless, I have no objections to regarding these faunas as Oligocene, should Berggren's interpretation be substantiated.

MATERIALS AND METHODS

The following generic revision is based almost entirely on qualitative characters. Most of the cricetids studied are present in samples adequate for statistical analysis, and such an analysis is needed to resolve species-level problems. I have not provided additional measurements except for new taxa. Measurements were taken to the nearest 0.1 mm on an occular micrometer. The terminology for tooth morphology follows that of Wood and Wilson (1936) and Lindsay (1972).

The following abbreviations are used: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences of Philadelphia; CM, Carnegie Museum; F:AM, Frick American Mammals, Department of Vertebrate Paleontology, American Museum of Natural History; KUVP, University of Kansas Museum of Natural History, Division of Vertebrate Paleontology; LACM, Los Angeles County Museum (California Institute of Technology Collection); MCZ, Museum of Comparative Zoology, Harvard University; ROM, Royal Ontario Museum; SDSM, South Dakota School of Mines and Technology; TMM, Texas Memorial Museum; UCMP, University of California Museum of Paleontology; UNSM, University of Nebraska State Museum; USNM, United States National

Museum; and YPM, Peabody Museum of Natural History, Yale University.

The classification of the North American early cricetids proposed in this paper follows in part that offered by Mein and Freudenthal (1971), for European cricetids.

Superfamily Muroidea Miller and Gidley, 1918
  Family Cricetidae Rochebrune, 1883
  Subfamily Nonomyinae, new
    Genus *Nonomys* Emry and Dawson, 1973.
      Type species: *N. simplicidens* (Emry & Dawson), 1972
    Genus *Subsumus* Wood, 1974
      Type species: *S. candelariae* Wood, 1974
  Subfamily Eumyinae Stehlin and Schaub, 1951
    Genus *Eumys* Leidy, 1856
      Type species: *E. elegans* Leidy, 1856
      Other species: *E. brachyodus* Wood, 1937; *E. parvidens* Wood, 1937; *E. pristinus* Russell, 1972
    Genus *Coloradoeumys,* new
      Type species: *C. galbreathi,* new
    Genus *Wilsoneumys,* new
      Type species: *W. planidens* (Wilson),

1949
  Subfamily Eucricetodontinae Mein and Freudenthal, 1971
    Tribe Leidymini, new
      Genus *Eoeumys,* new
        Type species: *E. vetus* (Wood), 1937
        Other species: *E. exiguus* (Wood), 1937
      Genus *Scottimus* Wood, 1937
        Type species: *S. lophatus* Wood, 1937
        Other species: *S. kellamorum* Black, 1961
      Genus *Leidymys* Wood, 1936
        Type species: *L. nematodon* (Cope), 1879
        Other species: *L. blacki* (Macdonald), 1963; *L. alicae* (Black), 1961; *L. parvus* (Sinclair), 1905; *L. lockingtonianus* (Cope), 1881
    Tribe Geringini, new
      Genus *Geringia,* new
        Type species: *G. mcgregori* (Macdonald), 1970
        Other species: *G. gloveri* (Macdonald), 1970
      Genus *Paciculus* Cope, 1879
        Type species: *P. insolitus* Cope, 1879
        Other species: *P. montanus* Black, 1961; *P. woodi* (Macdonald), 1963; *P. nebraskensis* Alker, 1969

SYSTEMATIC PALEONTOLOGY

In the following accounts, I have tried to give an adequate diagnosis for each taxon, utilizing the original diagnosis and any additional data ascertained from restudy of the type or referred material. The original description of the taxon and important subsequent references to it are cited. I have also provided a detailed description of the known morphology of almost all taxa discussed and given their geographic and stratigraphic distributions.

Subfamily NONOMYINAE, new

Type genus.—Nonomys Emry and Dawson, 1973.
  *Geographic distribution.—*Wyoming.
  *Stratigraphic distribution.—*Lower Oligocene (Chadronian).
  *Diagnosis.—*Cricetid rodents with brachy-

dont and cuspidate molars (central areas of molars occupied by undivided basins); anteroconid and metaconid of M_1 closely associated (twinned); distinct hypoconulids on M_{1-2}, prominent buccal cingula on lower molars; M_3 relatively small and simple; masseteric lines meeting in a "V" under M_1.

NONOMYS Emry and Dawson, 1973

Nanomys Emry and Dawson, 1972 (preoccupied).

  Type species.—Nonomys simplicidens (Emry & Dawson), 1972.
  *Geographic distribution.—*As for subfamily.
  *Stratigraphic distribution.—*As for subfamily.
  *Emended diagnosis.—*Small cricetids with

low-crowned, simple, cuspidate teeth; lower incisor small, compressed laterally, flattened lingually, and rounded buccally; mental foramen high and anterior to M_1.

NONOMYS SIMPLICIDENS (Emry & Dawson), 1972

Figure 1A

Nanomys simplicidens Emry and Dawson, 1972.

Holotype.—F:AM 79304, right ramus with incisor and M_{1-3}.

Type locality.—North Fork of Lone Tree Gulch, in the SE¼, sec. 22, T. 31 N., R. 83 W., Natrona County, Wyoming.

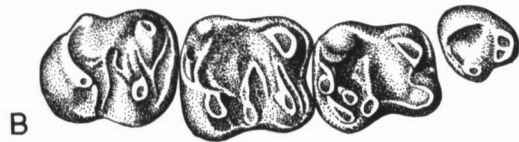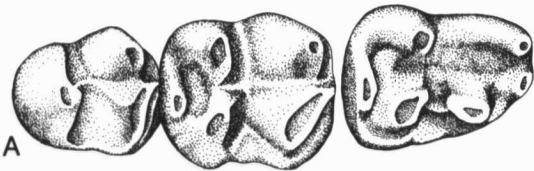*Horizon.*—Lower Oligocene (Chadronian).

Diagnosis.—As for genus.

A

B

Fig. 1. A. Right M_{1-3} of *Nonomys simplicidens* (after Emry & Dawson, 1972). B. Right P_4-M_3 of *Pauromys* (after Dawson, 1968). Not drawn to scale.

Discussion.—This is the most primitive and possibly the oldest cricetid known. Its presence is a strong argument for the origin of the cricetids in North America. It shows interesting similarities to certain North American late Eocene sciuravids, including *Pauromys* (Fig. 1B). In order to transform *Pauromys* into *Nonomys,* it would be necessary to further reduce and eventually lose P_4, and at the same time enlarge M_1 (trends already evident in the Sciuravidae). The M_3 would have to decrease in size and lose the entoconid, and the masseteric lines would have to move forward. *Pauromys* and

Nonomys share the same general molar shape, having large central basins crossed by only low lophs, large hypoconulids on M_{1-2}, buccal cingula on lower molars, M_1 with buccal anteroconid twinned with metaconid, protoconid rather posteriorly situated, and similar incisor shape. Emry and Dawson (1972) did not state whether the incisor is smooth or ridged, but their illustrations indicate that it is smooth. Dawson (1968) has described a maxilla of *Pauromys* with tendencies toward a myomorph zygomasseteric structure. All features one would expect in a cricetid ancestor occur in the Sciuravidae, and *Nonomys* makes an almost ideal connecting link.

SUBSUMUS Wood, 1974

Type species.—*Subsumus candelariae,* Wood, 1974.

Geographic distribution.—Texas.

Stratigraphic distribution.—Lower Oligocene (Chadronian).

Emended diagnosis.—Small cricetid with low-crowned cuspidate teeth that may be distinguished from those of *Nonomys simplicidens* by presence of small, centrally located anteroconid on M_1.

SUBSUMUS CANDELARIAE Wood, 1974

Holotype.—TMM 40504-244, left M_{1-2}.

Type locality.—TMM locality 40504, Presidio County, Texas.

Horizon.—Capote Mountain Tuff Formation, lower Oligocene.

Diagnosis.—As for genus.

Discussion.—The holotype and only known specimen of *Subsumus candelariae* is fragmentary and does not permit a sure identification of the anterior tooth as M_1. Because of this, Wood (1974) questioned his assignment of *Subsumus* to the Cricetidae. I share his reservation, but point out that the teeth of *Subsumus* are basically similar to those of *Nonomys,* from which they differ slightly in arrangement of the cusps.

Subfamily EUMYINAE Stehlin and Schaub, 1951

Type genus.—*Eumys* Leidy, 1856.

Geographical distribution.—Montana, Wyoming, Colorado, North Dakota, South Dakota, Nebraska, and Saskatchewan.

Stratigraphic distribution.—Lower Oligocene (Chadronian) to lower Miocene (Geringian).

Diagnosis.—Cricetid rodents with single sagittal crest; infraorbital foramina smaller than in most Eucricetodontinae; M^1 always with buccal anterocone; cusps on molars not strongly alternating; incisor enamel smooth.

EUMYS Leidy, 1856

Type species.—*Eumys elegans* Leidy, 1856.

Geographic distribution.—As for subfamily.

Stratigraphic distribution.—Lower Oligocene (Chadronian) to lower Miocene (Arikareean).

Diagnosis.—Rostrum broad; infraorbital foramina with distinct ventral slits; molars usually low and cuspidate, terraced; lower incisors rounded ventrally with enamel extending far labially; incisors large; M^1 with distinct buccal anterocone; anteroventral margin of ramus tending to become rounded.

Discussion.—Material referable to *Leidymys, Paciculus, Wilsoneumys* (n. gen.), and *Eoeumys* (n. gen.) have all been described as species of *Eumys*. Even with these taxa excluded, *Eumys* is still by far the most abundant and one of the most widely distributed of the Tertiary cricetid genera. Except for *"Eumys" asiaticus* Matthew and Granger, 1923, *Eumys* has been considered to be restricted to North America. *"Eumys" asiaticus* has a more square M_3, a large incisive foramen, a more distinct anterocone on M^1, and the lower incisors are ridged as in *Leidymys*. It is not a eumyine but may instead be referable to the Eucricetodontinae (Lindsay, 1978).

Eumys is highly variable, especially in its tooth crown patterns. Alker (1966) placed *Eumys obliquidens, E. parvidens, E. cricetodontoides, E. spokanensis, E. latidens, E. brachyodus, E. planidens, E. eliensis,* and *Cricetodon nebraskensis* in synonymy with *E. elegans.* This is an extreme action; however, some justification does exist for an extended

synonymy. The dental characters of most "species" of *Eumys* overlap each other to a remarkable degree. It may be that the question could be resolved by a multivariate study of the enormous samples of *Eumys* that are available. I have not conducted such a study, and follow Alker's (1966) synonymy except for the small *Eumys parvidens, E. brachyodus,* which can be defined on good qualitative characters, and *E. planidens,* which I place in *Wilsoneumys* (n. gen.). In samples from Nebraska and Colorado, *Eumys cricetodontoides* overlaps the large *Eumys elegans* in size and dental characters, and I presently include it in *E. elegans.* Certainly, the characters of the cingula used by White (1954, p. 410-411) to separate it from *E. latidens* and *E. spokanensis* are inadequate according to present knowledge of variation in these features. Galbreath (1953, p. 69-71) recognized the distinction of *Eumys obliquidens* from *E. elegans,* but also recognized the considerable overlap of characters. He placed *E. obliquidens* at the base of a morphocline leading up through *E. elegans* to *E. brachyodus.* I am unable to demonstrate this cline to my satisfaction and find the development of the lophids to be highly variable in this genus. In my opinion, both *Eumys obliquidens* and *Eumys nebraskensis* should be considered junior synonyms of *E. elegans.* There is, of course, no reason to maintain *Eumys nebraskensis* in the European genus *Cricetodon* where it was originally placed by Wood (1937). At present, a conservative course would be to regard the smallest species, *E. parvidens,* and the highly specialized *E. brachyodus* as valid, and I follow this course.

Chadronian representatives of *Eumys* are extremely rare, and Alker reported them to be absent from the lowermost Orellan (Orella A of Schultz & Stout, 1955); however, I have seen a few isolated teeth, which may be referred to *Eumys,* from the latter strata in the University of Nebraska collection. Wood (1969, p. 4) reported *Eumys* cf. *E. elegans* from the lower Oligocene, *Chadronia* Pocket local fauna in Sioux County, Nebraska. Also, there is an unreported specimen in the University of Kansas collection from the Chadronian of Weld County, Colorado, collected by R.W. Wilson. It is a member of the Horsetail Creek

fauna, which was discussed by Galbreath (1953, p. 28), who collected fragments of titanothere teeth, KUVP 9123, at the same locality in 1949. Galbreath (written communication, 1972) reaffirmed the Chadronian age of this locality. The *Eumys* specimen, KUVP 11173, is the anterior portion of a skull including the right M^{1-3} and the left M^2. It indicates a relatively large individual with a wide, robust rostrum. The incisive foramina are small, as are the palatine foramina. The upper molars are similar to *Eumys elegans,* although the anterocone on M^1 is relatively larger and more distinct than is usual in that species.

EUMYS ELEGANS Leidy, 1856
Figure 2

Eumys elegans Leidy, 1856.
Eumys obliquidens Wood, 1937.
Cricetodon nebraskensis Wood, 1937.
Eumys cricetodontoides White, 1954.
Eumys latidens White, 1954.
Eumys spokanensis White, 1954.

Holotype.—ANSP 11027, partial left ramus with part of M_1 and a complete M_2.
Type locality.—Bear Creek, Big Badlands, South Dakota.
Horizon.—Scenic Member, Brule Formation, White River Group; Oligocene.
Diagnosis.—Medium-sized *Eumys* with well-developed buccal anterocone on M^1; mesolophs and mesolophids fairly well developed; metalophid II detached on lower molars.
Description.—Skull short with rounded cranium and short broad muzzle; nasals broad anteriorly, even with incisors, pointed posteriorly, terminating near anterior edge of orbits; supraorbital area highly constricted and narrower than muzzle; saggital crest single; occipital region rounded and occipital crest indistinct; interparietal large; zygoma robust, horizontal, and well above tooth row; molars extending anteriorly almost to zygomatic plate; zygomatic plate inclined; infraorbital foramen constricted ventrally; incisive foramina variable in size and position (see Fig. 24); palate narrow, deep, terminating just posterior to posterior margin of M^3;

nasolacrimal canal (Fig. 2D) small and situated almost in infraorbital foramen; anterior ethmoid foramen prominent and just dorsal and anterior to relatively small optic foramen; sphenofrontal foramen about same size as optic foramen and immediately posterior to it; sphenopalatine foramen large; sphenoidal foramen just posterior to it. Basicranial region not preserved in my material nor is it described by Wood (1937). Bullae probably loosely attached. Upper incisor large, strongly recurved and opisthodont; anterior face rounded with smooth enamel extending half way up labial side. M^1 with distinct buccal anterocone. Lower jaw with distinct symphyseal flange; masseteric lines usually meeting in "V."
Discussion.—The highly variable dentition of *Eumys elegans* has been described in detail by Wood (1937) and Galbreath (1953).
Eumys elegans, as defined in this paper, is one of the most variable known cricetids. In this sense, it is similar to the contemporaneus Oligocene heteromyid, *Heliscomys vetus.*

EUMYS BRACHYODUS Wood, 1937
Figure 3

Eumys brachyodus Wood, 1937.
Eumys eliensis Black, 1961a.

Holotype.—MCZ 5062, ramus with M_{1-3}.
Type locality.—Chimney Rock, Morrill County, Nebraska.
Horizon.—From above the Upper Ash in the Whitney Member, Brule Formation, White River Group; Oligocene (Whitneyan).
Emended diagnosis.—M^1 with anterocone reduced; incisors large and strongly recurved; lower anterior margin of ramus strongly rounded; dorsal and ventral masseteric lines meeting in broad curve on ramus; lower molars short and wide, especially M_1; lower molars small in relation to ramus; mesolophids usually absent; lingual arm of anterior cingulum very short.
Description.—(Based on fragmentary skull, UNSM 66174). Saggital crest single, broad; skull not recessed above molars as in *E. elegans;* sphenopalatine foramen higher up on skull and more posterior than in *E. elegans.* M^1 rectangular with small buccal anterocone, attached centrally to anterior mure, parastyle

absent; protocone large and rounded, paracone smaller and directly across from protocone, mesoloph absent, hypocone large and rounded, metacone smaller and more compressed, parallel to and only slightly longer than posterior cingulum. M^2 resembling M^1 in absence of distinct mesoloph. M^3 relatively larger than in *E. elegans* but similar to M^2 in that species. Ramus thick and robust, rounded anteroventrally; masseteric lines meeting in curve; wear on upper and lower molars planar; lower molars short and broad.

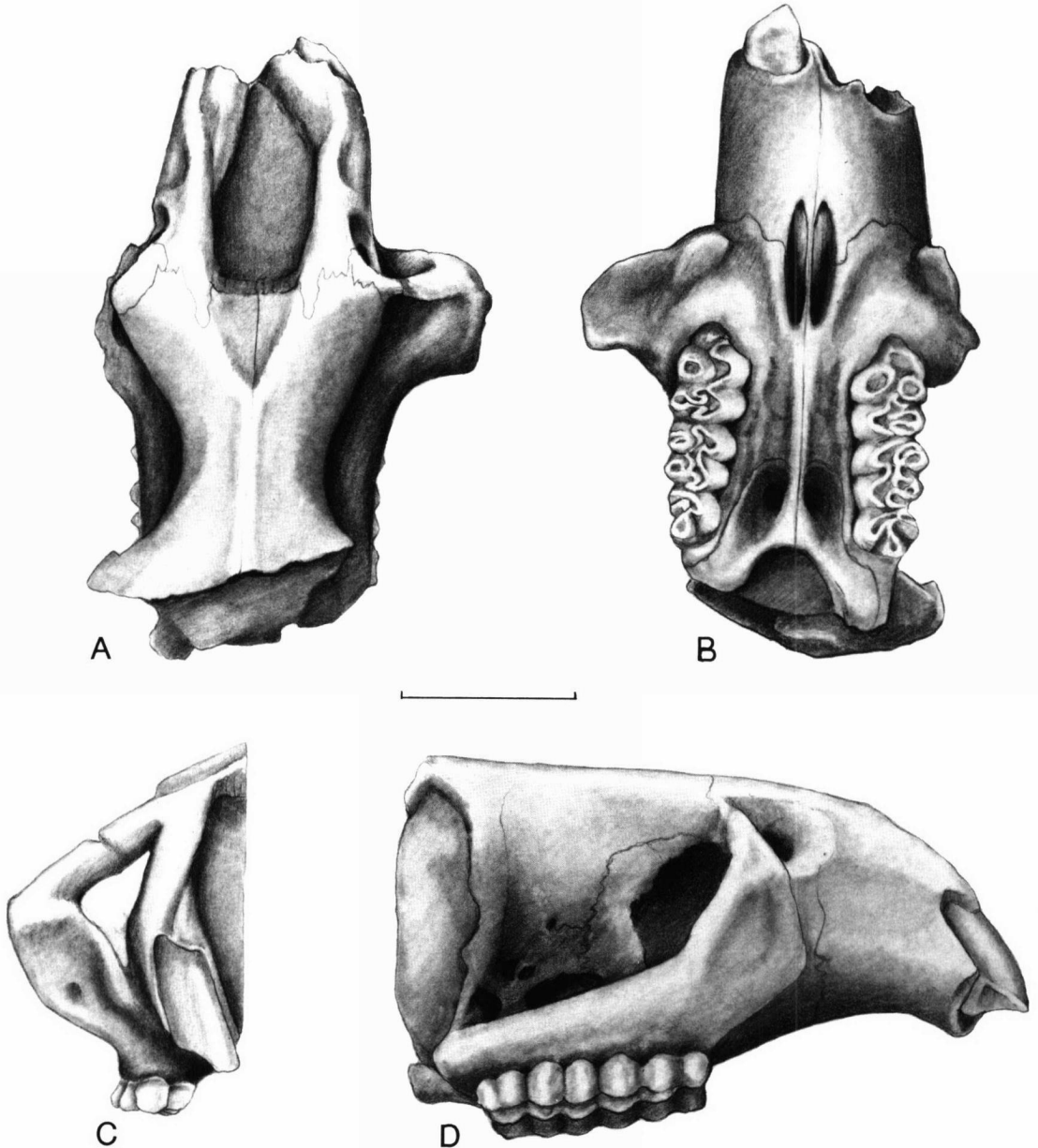(Based on referred lower jaws fairly common in collections.) M_1 smaller than M_2,

Fig. 2. Partial skull of *Eumys elegans,* UNSM 10779; A, dorsal view; B, ventral view; C, anterior view; D, lateral view; scale = 5 mm.

anteroconid small and united to protoconid but not necessarily to metaconid (*contra* Wood, 1937, p. 252), mesoconid small and mesolophid absent, entoconid and metaconid large and rounded. M_{2-3} rather square with mesolophids attaching to metaconids to enclose a basin in some individuals whereas in others (including type) mesolophids short; only labial moiety of anterior cingula present.

Fig. 3. *Eumys brachyodus,* M^{1-3}, UNSM 66174; scale = 5mm.

Discussion.—*Eumys brachyodus* occurs throughout the Whitney Member of the Brule Formation in Nebraska, but I have not observed it in older beds. It is the only eumyine that occurs in the Gering Formation and it is quite abundant in the Blue Ash local fauna (Martin, 1975). In Colorado it occurs in the Vista local fauna (Galbreath, 1953) and in Wyoming in the Cedar Ridge local fauna (Setoguchi, 1978).

Comparison of the holotype of *Eumys eliensis* with specimens of *E. brachyodus* from Whitney deposits in Nebraska showed that the following characters given in the diagnosis of *E. eliensis* (Black, 1961a, p. 7) also occur in some specimens of *E. brachyodus:* teeth large in relation to jaw size; teeth progressively longer from M^1 to M^3; lingual arm of anterior cingulum on M^1-M^3 present; mental foramen near inferior border of mandible below anterior root of M_1. As none of these or other recognized characters separate *Eumys eliensis* from *E. brachyodus,* I regard *E. eliensis* to be a synonym of *E. brachyodus.* The incisor on the holotype of *E. eliensis* is too large and too recurved posteriorly for the ramus. As no actual contacts existed between it and the ramus when the ramus was restored, it seems possible that it may actually be an upper incisor.

Eumys brachyodus is the largest species of *Eumys* and has large, highly curved incisors.

Although the skeleton of *Eumys* is presently unknown, the jaws suggest that *E. brachyodus* may have become fossorially adapted during the Whitneyan. The sagittal crest, which was probably primitively double in cricetids, is single and prominent; the skull is short and broad with the incisors highly recurved and the lower incisors recurved with the anteroventral margin of the ramus smoothly rounded.

EUMYS PARVIDENS Wood, 1937
Figures 4B, 5A, D

Type.—UNSM 10036, partial skull and mandible.

Type locality.—NW¼, sec. 35, T. 33 N., R. 56 W; 8 miles north and 1.5 miles east of Harrison, Sioux County, Nebraska.

Horizon.—Middle part of Orella Member (Orella C. of Schultz and Stout, 1955), Brule Formation, White River Group; Oligocene.

Emended diagnosis.—Smallest species of genus; mesolophs and mesolophids poorly developed; incisive foramina much anterior to M^1; palate shallow and palatine foramina small.

Description.—Supraorbital constriction narrow, saggital crest single; sphenopalatine foramen small and above M^2; optic foramen, sphenofrontal foramen, and sphenoidal fissure as in *Eumys elegans;* incisive foramina anterior to M^1; palate shallow and flat; palatine terminating anteriorly medial to posterior edge of M^1; palatal foramina medial to M^2; palate terminating just posterior to M^3. M^1 with distinct buccal anterocone connected lingually to protocone; paracones and metacones teardrop-shaped and narrowly attached to central mure; mesolophs essentially absent. M^3 with paracone attached to anterior cingulum and to central mure forming an isolated basin with ascending ramus just anterior to M_3; ramus with coronoid process wide, heavy, much higher than condyle (Fig. 4B); angle of ramus rounded and lower than symphysis; masseteric lines meeting in "V" below posterior edge of M_1; ventral line heavier than dorsal but not carried anteriorly as shelf; mental foramen anterior to M_1 and at level of conjunction of masseteric lines; Incisor of typical *Eumys* type, terminating posterior to M_3 on labial side. M_1 with small anteroconid con-
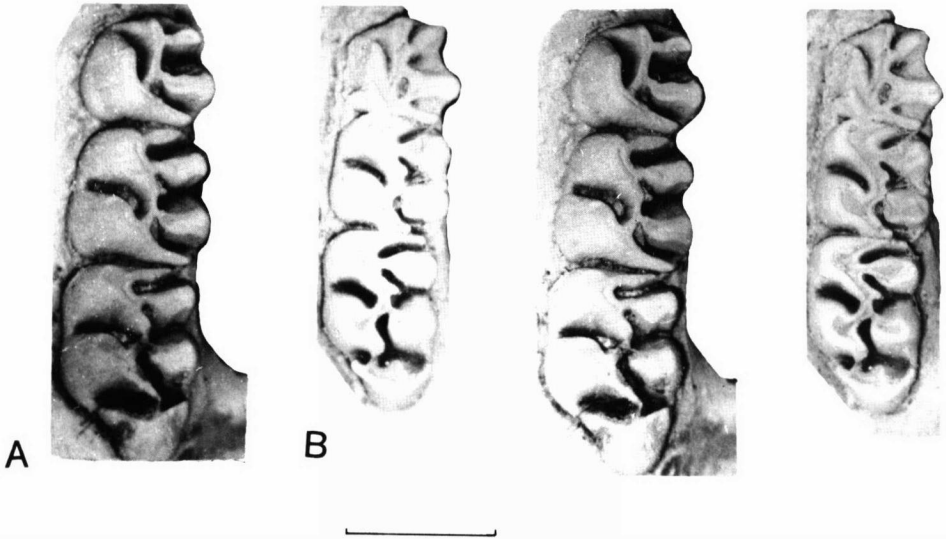
Fig. 4. A. Stereophotograph of *Coloradoeumys galbreathi*, M^{1-3}, KUVP 11132 (holotype). B. Stereophotograph of *Eumys parvidens*, M^{1-3}, UNSM 10036 (holotype). Scale = 2mm.

nected centrally to protoconid; posterior pro-toconid arm connecting with metaconid, mesolophid small (absent on other molars).

Molars described further by Wood (1937).

Discussion.—This small species of *Eumys* seems sufficiently distinct from *E. elegans* to
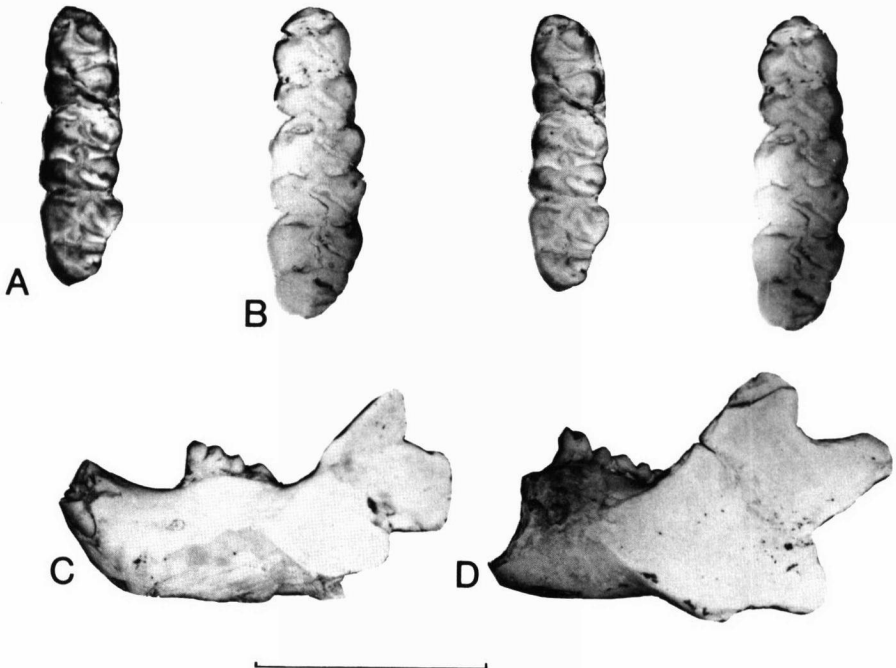

Fig. 5. A. Stereophotograph of *Eumys parvidens*, left M_{1-3}, occlusal view, UNSM 10036 (holotype); scale = 3.2 cm. B. Stereophotograph of *Coloradoeumys galbreathi*, left M_{1-3}, occlusal view, KUVP 11132 (holotype); scale = 3.2 cm. C. *Coloradoeumys galbreathi*, left ramus, lateral view; scale = 2.0 cm. D. *Eumys parvidens*, left ramus, lateral view; scale 1.6 cm.

warrant recognition.

EUMYS PRISTINUS Russell, 1972

Holotype.—ROM 6324; right M^1.

Type locality.—Conglomerate Creek Valley, Saskatchewan, Canada.

Horizon.—Cypress Hills Formation, lower Oligocene (Chadronian).

Discussion.—The diagnosis of Russell (1972, p. 41) is followed here. His material is too fragmentary to permit significant comparison with other *Eumys*.

COLORADOEUMYS, new genus

Etymology.—Named as a eumyine from Colorado.

Type species.—*Coloradoeumys galbreathi*, new.

Geographic distribution.—Colorado.

Stratigraphic distribution.—Middle Oligocene (Orellan).

Diagnosis.—Small eumyine with short and narrow snout; infraorbital foramen not constricted ventrally as in *Eumys*; incisive foramina much anterior to M^1; sphenoidal fissure large.

COLORADOEUMYS GALBREATHI, new species
Figures 4A; 5B, C; 6

Etymology.—Named in honor of Edwin C. Galbreath in recognition of his important work on Oligocene faunas.

Holotype.—KUVP 11132, skull and left mandible.

Type locality.—W½, sec. 21, T. 11 N. R. 54 W., Logan County, Colorado.

Horizon.—Cedar Creek Formation, middle Oligocene (Orellan).

Diagnosis.—As for genus.

Description.—About size of grasshopper mouse (*Onychomys*); skull short and broad with short narrow muzzle; cranium rounded with widest point across posterior zygomatic roots; nasals missing in holotype but probably short and widely flaring anteriorly; nasal-frontal suture nearly straight and across from anterior zygomatic root; zygomatic arches not
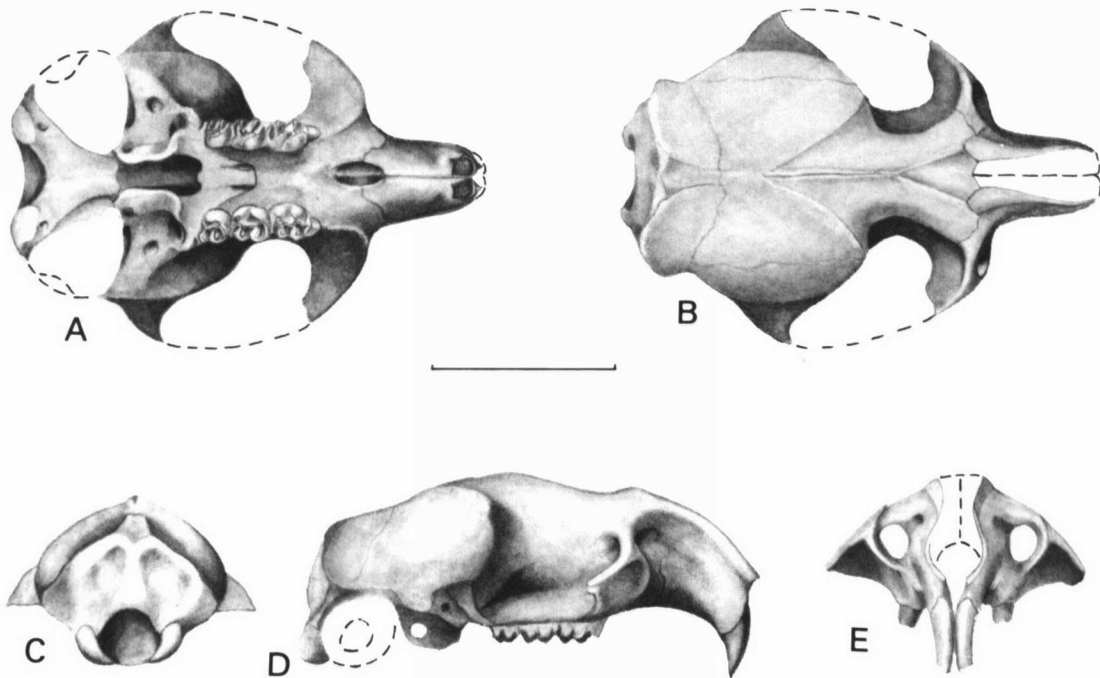

Fig. 6. *Coloradoeumys galbreathi*, reconstruction of the skull based on KUVP 11132 (holotype). A, ventral view; B, dorsal view, C, posterior view; D, lateral view; E, anterior view. Scale = 1 cm.

preserved but anterior and posterior roots suggesting that they were delicate; squamosal-parietal suture not clear but squamosal seemingly forming part of skull roof; parietals small; interparietal large; supraorbital constriction narrow; saggital crest single and low; infraorbital foramen large and circular (not constricted ventrally as in *Eumys*); incisive foramina small, mostly in maxilla, and posterior border much anterior to margin of M^1; anterior border of palatine maxillary suture opposite anterior margin of M^2; palatine foramina large and elongate; posterior palatal margin nearly "V" shaped; zygomatic plate not as inclined as in *Eumys*; sphenopalatine foramen more posterior in *Coloradoeumys* than in *Eumys* (in *Eumys* above M^2), foramina in *Coloradoeumys* appearing deeply recessed within sphenoidal fissure; basisphenoid broad and extending under palate; pterygoid rounded and extending further ventrally than tooth row; pterygoid fossa short and broad; small foramen ovale lying just above large ventral alisphenoid canal, alisphenoid canal just anterior to posterior lacerate foramen; large posterior maxillary foramen anterior to alisphenoid canal; auditory bulla not preserved but large and loosely attached. Upper incisors smaller than in *Eumys elegans* with smooth enamel extending up onto labial side of tooth. M^1 with large buccal anterocone connected centrally by mure to protocone, major cusps across from each other rather than alternating, no mesoloph, internal reentrant valley highly inclined, posterior cingulum long. M^2 similar to M^1 but with small mesoloph. M^3 protocone lophate and continuous with anterior cingulum; paracone, metacone, and hypocone joining with mure in trefoil pattern. All molars slightly terraced.

Ramus with slight symphyseal flange; mental foramen under M_1 and at edge of ascending ramus in front of M_3. M_1 with small anteroconid joined centrally by both paraconid and metaconid; posterior arm of protoconid joining paraconid; very small mesolophid present, as is a projection into external reentrant, posterior cingulum almost joining entoconid. M_{2-3} similar to M_1 but lacking mesolophid, posterior arm of protoconid not joining paraconid, posterior cingulum not joining entoconid, and anterior cingulum complete across anterior face of M_{2-3} with paraconids and protoconids attaching to it independently.

Measurements of holotype (KUVP 11132) in mm.—Length: M^1, 3.13; M^2, 2.00; M^3, 1.72; M^{1-3}, 6.69; M_1, 2.48; M_2, 1.73; M_3, 1.88; M_{1-3}, 6.85. Width: M^1, 2.00; M^2, 1.93; M^3, 1.78; M_1, 1.74; M_2, 2.04; M_3, 1.95.

Discussion.—*Coloradoeumys galbreathi* illustrates the danger in depending too much on dental characters in species of *Eumys*. Although it is a small species (most comparable in size with *E. parvidens*), its dental pattern is probably included in the many variations presently ascribed to *Eumys elegans*. However, characters of the skull, especially the short narrow snout, separate it from that species and support assignment to a different genus.

WILSONEUMYS, new genus

Type species.—*Wilsoneumys planidens* (Wilson), 1949a.

Geographic distribution.—Wyoming, Colorado, Nebraska, South Dakota, and North Dakota.

Stratigraphic distribution.—Middle Oligocene (Orellan) to upper Oligocene (Whitneyan).

Diagnosis.—Cricetid rodents similar in size to *Eumys elegans* but with crests of upper and lower molars highly compressed, their occlusal surfaces nearly planar, and their labial and lingual reentrants comparatively large, with "square" terminations; M^1 triangular with anterocone connecting buccally to anterior mure; protolophule and mesoloph absent on upper molars; lower incisor small, triangular, with flat ventral surface, enamel smooth, extending only slightly onto labial surface; anterior lingual cingulum absent on lower molars, and anteroventral flange distinct on ramus.

Etymology.—Named in honor of Robert W. Wilson in recognition of his important work on fossil rodents.

WILSONEUMYS PLANIDENS (Wilson), 1949

Figures 7, 8

Eumys planidens Wilson, 1949a.

Holotype.—University of Colorado Museum 19810, partial left ramus with M_{2-3}.

Type locality.—Middle $W\frac{1}{2}$, sec. 7, T. 11 N., R. 53 W., Logan County, Colorado.

Horizon.—Cedar Creek Member, Brule Formation, White River Group; Oligocene.

Diagnosis.—As for genus.

Description.—Palate shallow, terminating posteriorly just behind M^3; incisive foramina much anterior to M^1; all upper molars lacking protolophules and mesolophs; reentrant angles broad and square; cusps and lophs all thin with planar wear on both upper and lower molars. M^1 with anterocone centered, giving tooth triangular appearance, connected labially by diagonal mure to protocone. M^3 with trefoil pattern. Ramus with exceptionally prominent anteroventral flange; masseteric lines meeting in rounded curve below M_2; mental foramen fairly high; lower incisor small, triangular, ventral surface flat, enamel not extending so far labially as in *Eumys;* lower molars lacking anterior cingula, and with broad valleys between lophs. M_1 with anteroconid connected almost centrally (if connected at all) by an anterior mure to protoconid and metaconid; protoconid extending by central mure to posterior arm of protoconid; short buccal spur in reentrant angle; hypolophid extending into posterior cingulum. M_2 and M_3 relatively large.

Discussion.—*Wilsoneumys* occurs in Nebraska in the Orella D (upper Orellan) of Schultz and Stout (1955); however, the upper Orellan material and the Whitneyan *Wilsoneumys* from Wyoming are both larger than the Orellan material from Colorado. Because of its compressed cusps and thin connecting crests, Wilson (1949a, p. 48) suggested that *W. planidens* may be a forerunner of *Paciculus.* This is not the case as *Paciculus* is much closer to *Leidymys* than it is to any eumyine. The upper molars have been described recently by Setoguchi (1978).

Galbreath (1953, p. 74) suggested that *Eumys planidens* might be placed in a different genus. Examination of additional material from the Whitneyan (Setoguchi, 1978) demonstrated that it is a collateral lineage showing somewhat different evolu-
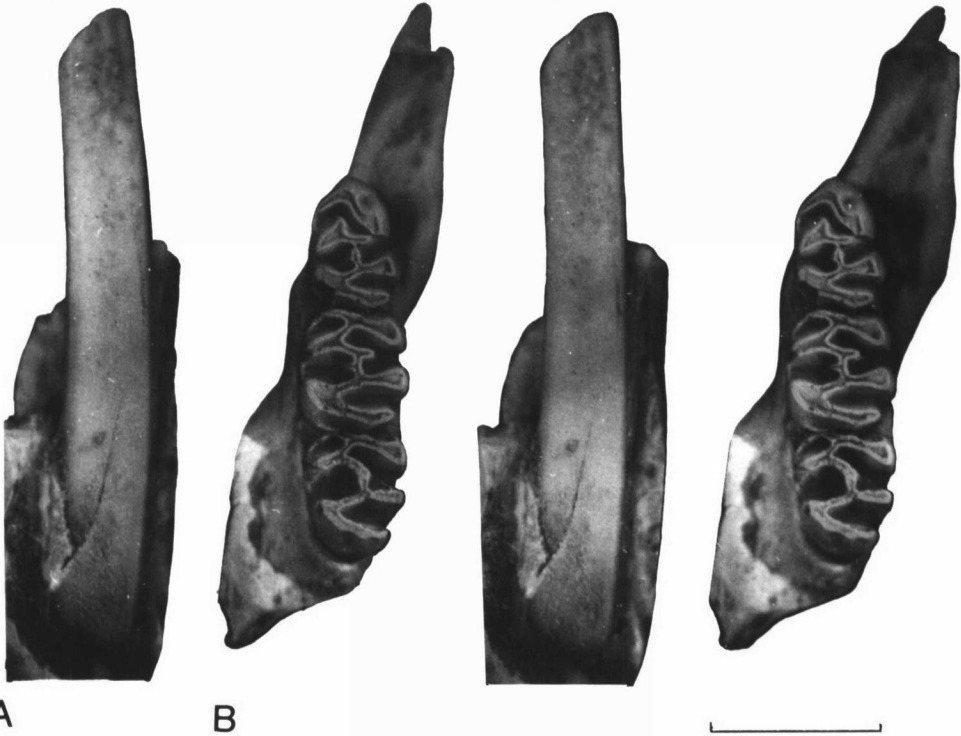

A B

Fig. 7. Stereophotographs of *Wilsoneumys planidens*. A. Incisor, ventral view, KUVP 8450. B. Left ramus with M_{1-3}, occlusal view, KUVP 8472. Scale = 3 mm.
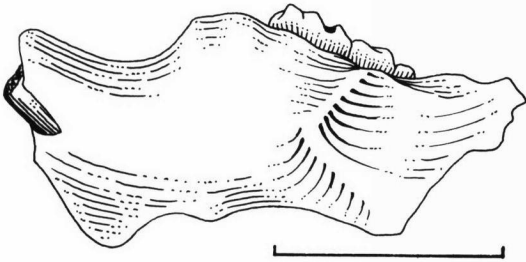
Fig. 8. *Wilsoneumys planidens*, left ramus, labial view, AMNH 98563; scale = 7 mm.

tionary trends from the *Eumys elegans* lineage. Primitively the anteroventral margin of the jaw in the Eumyinae bore a distinct dependent flange that has become highly accentuated in *Wilsoneumys planidens*.

Subfamily EUCRICETODONTINAE Mein and Freudenthal, 1971

Type genus.—*Eucricetodon* Thaler, 1966.
Geographic distribution.—Europe, Asia, and North America.

Tribe LEIDYMINI, new

Type genus.—*Leidymus* Wood, 1936.
Geographic distribution.—Oregon, Montana, Wyoming, South Dakota, and Nebraska.
Diagnosis.—Cricetid rodents with enlarged infraorbital foramina; molars tending to be low crowned; anterocone attached to the protocone near the midline of the tooth (except in *Eoeumys vetus.*).

EOEUMYS new genus

Etymology.—Greek, *eos*, early; *eumys*, true mouse.
Type species.—*Eoeumys vetus* (Wood), 1937.
Geographic distribution.—South Dakota, Nebraska, Colorado, Wyoming, and Montana.
Stratigraphic distribution.—Lower Oligocene (Chadronian to middle Oligocene (Orellan).
Diagnosis.—Differs from *Eumys* in not having anteroventral margin of ramus rounded; in having masseteric lines of ramus

meeting at a distinct angle; in having two saggital crests on skull; differing from *Leidymys, Paciculus, Geringia, Scottimus, Eucricetodon,* and *Cricetodon* in having pinnately ridged incisors (see Fig. 26); also differing from *Geringia, Scottimus* and most *Paciculus* in having distinct, buccally placed anterocone; differing from *Paracricetodon* in having shorter and more rounded M^3; similar to *Eucricetodon* but with a less complicated M^3 and, usually, a more quadrate M^1.

EOEUMYS VETUS (Wood), 1937
Figures 9, 10

Leidymys vetus Wood, 1937.
Eumys exiguus (Wood) Galbreath, 1953.

Type.—AMNH 8742, antorbital portion of skull with incisors and M^{1-3}.
Type locality.—Logan or Weld County, Colorado.
Type horizon.—Middle Oligocene (Orellan).
Emended diagnosis.—Lophs on molars more transverse than in *Eoeumys exiguus;* hypocone present on M^3; molars smaller than *E. exiguus.*
Description.—About size of deer mouse (*Peromyscus*); muzzle broad and not elongate; nasals broad, slightly convex dorsally, extending slightly past anterior surface of incisors, terminating posteriorly across from anterior orbital border; supraorbital constriction broad and flat with indications of double saggital crests; dorsal surface of maxilla faintly sculptured; infraorbital foramen large and not much constricted ventrally; anterior zygomatic root inclined about 45°; ventral premaxillary-maxillary suture straight, posteriorly located, most of incisive foramina posterior to it; incisive foramina large, elongate, with posterior border across from anterocone of M^1; palate wide, short, shallow, upper incisor small, enamel smooth, not extended labially, not much rounded anteriorly.

M^1 with large buccal anterocone attached labially to protocone by protoloph I, small central posterior spur off anterocone not connecting with paracone; paracone teardrop shaped and connecting to paraloph diagonal to main lingual reentrant; mesoloph short;

metacone similar to protocone with narrow connection at about center of hypocone; posterior cingulum well developed but not connecting with metacone. M^2 anterior cingulum short and leading diagonally into protocone; labially connecting with paracone to form anterior basin, paraloph connecting to center of mure, mesoloph practically absent, metaloph connecting to hypocone anteriorly, posterior cingulum well developed, lingual reentrant inclined. M^3 anterior cingulum leading diagonally into protocone and connecting buccally to paracone isolating small anterior basin, protolophules I and II developed to form small basin; metacone connected by metaloph to mure just anterior to hypocone; internal reentrant inclined.

Ramus with elongate diastemal regions and a slight symphyseal flange; mental foramen anterior to M_1 and at level of junction of masseteric lines; masseteric lines meeting in
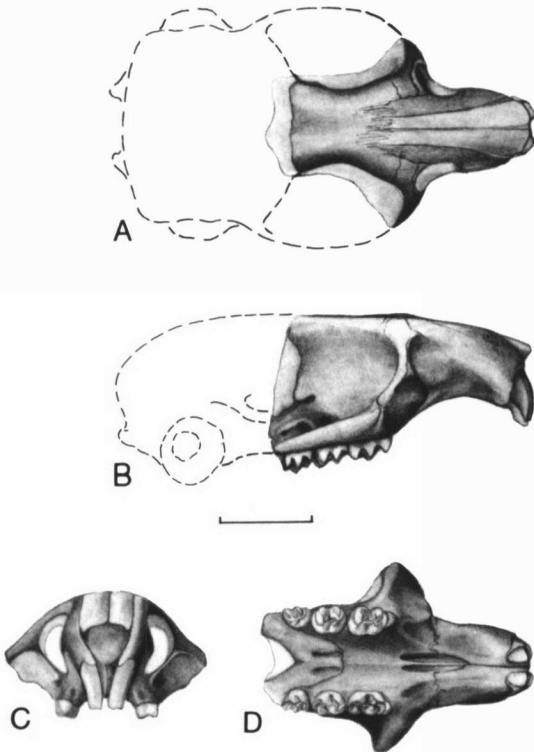
A

B

C

D

Fig. 9. *Eoeumys vetus*, skull, dashed lines represent reconstruction, AMNH 8742 (holotype); A, dorsal view; B, lateral view; C, anterior view; D, ventral view; scale = 5 mm.

"V"; ascending ramus just anterior to M_3. Incisor slender, compressed, and somewhat flattened with pinnately ridged enamel extending only short distance labially. M_{1-3} cuspidate and terraced; anterior cingula complete on M_{2-3}; external and internal reentrant broad, square, and not inclined in M_{1-3}; transverse lophs only barely developed.

Discussion.—The association of rami with the holotype and upper dentitions of *Eoeumys vetus* must be made on size. The rami used for the description of the lower dentition are from Colorado and are about as close to topotypes as we can hope to have. All lower incisors on jaws of the proper size and character to go with uppers of *E. vetus* are pinnately ridged, and it seems likely that the character is correctly associated. I have examined a cast generously given me by John Wahlert of a complete skull and lower jaws of a cricetid from the Chadronian of Wyoming presently in the Frick collection of the American Museum of Natural History. This skull is similar to *E. vetus* in having a double saggital crest, an enlarged infraorbital foramen not much constricted ventrally, and pinnately ridged lower incisors. It differs from *E. vetus* in having narrow, pinnately ridged upper incisors, a longer, narrower snout, and smaller molars. It is presently being described by Wahlert and E.H. Lindsay.

EOEUMYS EXIGUUS (Wood), 1937
Figures 10, 11

Eumys exiguus Wood, 1937
Scottimus exiguus (Wood) Black, 1961c.

Type.—AMNH 12261, partial palate and left ramus.

Type locality.—Sheep Mountain, probably Pennington or Shannon County, South Dakota.

Horizon.—Middle Oligocene, Rodent zones 4 to 7, Orella-equivalent ("Scenic Member," "Middle Oreodon Beds"), Brule Formation.

Emended Diagnosis.—Lophs elongated anteroposteriorly, hypocone reduced or absent on M^3.

Description.—Palate narrower than in *Leidymys*, and with small central ridge; palate shallow with no lateral walls; incisive fora-
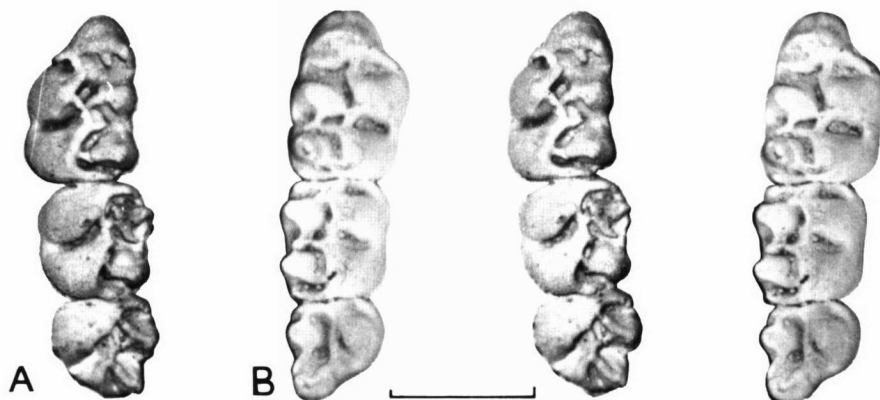
Fig. 10. Stereophotographs of M$^{1-3}$ of: A, *Eoeumys vetus,* AMNH 8742 (holotype); B, *E. exiguus,* AMNH 12261 (holotype); scale = 2mm.

mina terminating posteriorly just across from anterior edge of anterocone on M^1; distinct palatal spine present; maxillary-palatine suture across from anterior half of M^2; palatines depressed dorsally with large elongate palatal foramina present, palate terminating posterior to M^3.

M^1 with anterocone larger and more nearly centered than in *E. vetus;* anterior mure connecting near center of anterocone; small posterior spur sometimes present, directed toward but not connected to paracone; external reentrant not as inclined as in *E. vetus;* mesoloph long and sometimes connected to paracone by short mure; metacone connected by metaloph II to center of hypocone; posterior cingulum long and tending to be connected to metacone.

M^2 differing from that of *E. vetus* in having anterior cingulum across entire face of tooth and connected to posterior arm of paracone and anterior arm of metacone; metacone connected to hypocone by transverse metaloph; posterior cingulum long; external reentrant narrow and straight.

M^3 with anterior cingulum straight and connected lingually to mure and large protocone, labially to paracone; paracone connected posteriorly to anterior arm of metacone; metacone connecting directly to mure; mesoloph absent, central basin single and elongate; hypocone absent, external reentrant inclined.

Ramus with masseteric lines meeting in broad "V" under M$_1$, mental foramen low.

Lower incisor pinnately ridged. M$_1$ elongate with distinct anterior cingulum; cingulum connected lingually to metaconid and labially to protoconid, isolating an anterior basin; labial cingulum prominent and connecting anteroconid to protoconid; mesolophid long; central mure with spur directed into labial reentrant; hypoconid connected by two lophs to entoconid, forming posterior basin; posterior cingulum low, connecting hypoconid with entoconid. M$_{2-3}$ similar to M$_1$ although M$_2$ has much smaller mesolophid; M$_3$ relatively large, almost as long as M$_2$. All molars cuspidate and terraced.

Discussion.—Both Galbreath (1953, p. 72) and Black (1961c, p. 3) regarded *Eoeumys vetus* to be conspecific with *E. exiguus;* however, Clark, Dawson, and Wood (1964, pp. 42-43) and Alker (1967) separated the two species on the development of the hypocone on M^3. *Eoeumys exiguus* also has a greater amount of anteroposterior lophing on the molars. The anterior mure is connected centrally to the anterocone, and the anterior mure tends to be larger.

SCOTTIMUS Wood, 1937

Type species.—*Scottimus lophatus* Wood, 1937.

Geographic   distribution.—Nebraska, South Dakota, and Wyoming.

Stratigraphic   distribution.—Upper Oligocene (Whitneyan) to lower Miocene? (Geringian).

Emended diagnosis.—Posterior border of incisive foramina across from anterior border of M1; M1 with anterocone nearly centered and obsolete; molars elongated with strong longitudinal crests isolating central basins; incisors rounded and smooth.

Discussion.—*Scottimus* is clearly derived from *Eoeumys exiguus,* as suggested by Wood (1937) and Black (1961c).

SCOTTIMUS LOPHATUS Wood, 1937

Figures 11, 12

Type.—MCZ 5064, right maxilla with M1-3.

Type locality.—Jail Rock and not "Chimney Rock" (UNSM locality Mo-103), Morrill County, Nebraska (Alker, 1967).

Horizon.—From below Upper Ash, Whitney Member, Brule Formation, White River Group; upper Oligocene.

Description.—Palate shallow, posterior border of incisive foramina anterior to M1. M1 anterocone large, central, anteroposteriorly compressed with distinct buccal reentrant; protoloph I connected centrally to anterocone, and in some specimens with small labial spur; paraloph connecting to center of mure, long mesoloph connecting by spur to paracone thus isolating central lake, metacone connecting to mesoloph by anteroposterior spur isolating posterior lake; posterior cingulum unusually short and lingual reentrant perpendicular to long axis of tooth. M2 with anterior cingulum along entire anterior margin of tooth and connecting centrally to paraloph, mesoloph absent, and four major cusps compressed and connected transversely to form "Y"-shaped basin in center of tooth; posterior cingulum short. M3 relatively larger and more elongate than in *Eoeumys exiguus,* hypocone present, center of tooth occupied by central basin; ramus slender with the masseteric lines meeting in broad curve. Lower molars have been adequately described by Wood (1937).

Discussion.—*Scottimus lophatus* appears to have smooth enamel on its lower incisors. The lower incisors referred to *Eoeumys exiguus* are pinnately ridged and I have not followed Black (1961b) in assigning it to Scottimus.

SCOTTIMUS KELLAMORUM Black, 1961

Scottimus kellamorum Black, 1961c.

Type.—MCZ 7342, right maxillary with M1-2.
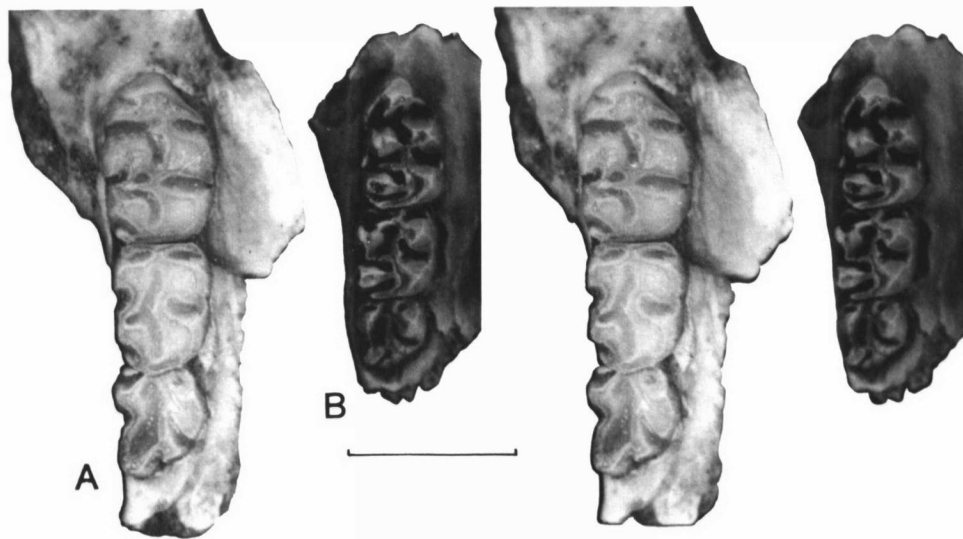
Type locality.—Sec. 11, T. 20 N., R. 61

Fig. 11. A. *Scottimus lophatus,* left maxillary with M1-3, UNSM 66168. B. *Eoeumys exiguus,* left maxillary with M1-3, UNSM 65910. Scale = 3 mm.
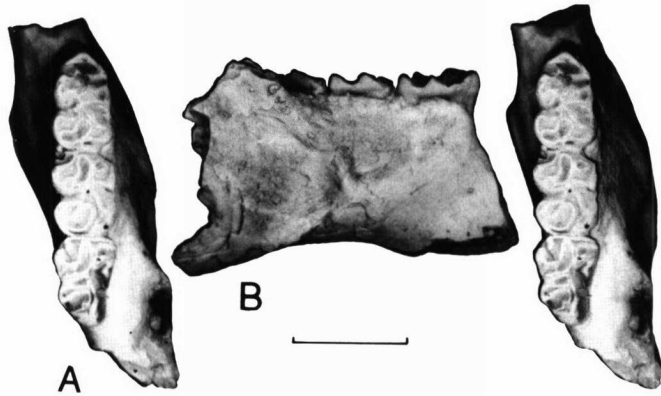
Fig. 12. *Scottimus lophatus,* right ramus, UNSM 66167; A, stereophotograph of M_{1-3}; B, lateral view; scale = 4 mm.

W., Goshen County, Wyoming.

Horizon.—?Gering Formation, Arkaree Group; Miocene.

Emended diagnosis.—Smaller than *S. lophatus;* more accessory transverse crests on M^{1-2}, anterocone relatively larger and more lingual than in *S. lophatus.*

Description.—M^1 with anterocone large and more labial than in *S. lophatus,* lacking prominent buccal reentrant found in that species; protoloph I long and with small paralophule; paracone nearly circular and connected by lophs to both mure and long mesoloph; mesoloph also connecting to metacone whereas posterior metacone arm passes posterolingually to join short posterior cingulum; lingual cingulum fairly well developed. M^2 similar to that of *Scottimus lophatus* except central basin not "Y" shaped but broken by two transverse lophs, the mesoloph and the metaloph; external reentrant broad and containing small lingual spur off mure.

Discussion.—*Scottimus lophatus* is known only from the Whitney Member of the Brule Formation (a loess deposit), whereas *S. kellamorum* is known from channel deposits. It seems reasonable that *S. kellamorum* was adapted for less xeric habitats than *S. lophatus.* The two species have never been found together.

LEIDYMYS Wood, 1936

Type species.—*Leidymys nematodon* (Cope), 1879.

Geographic distribution.—Oregon, Montana, South Dakota, Wyoming, and Nebraska.

Stratigraphic distribution.—Upper Oligocene (Whitneyan) and lower Miocene (Arkareean).

Emended diagnosis.—Ranging in size from about that of field mouse (*Peromyscus*) to that of woodrat (*Neotoma*); supraorbital region broad; sagittal crest double; infraorbital foramina very large (see Fig. 15); incisive foramina large and extending past anterior border of M^1; incisors small, compressed, with rounded enamel surfaces, which are usually ridged; lower incisors generally with two lingual and three labial ridges (see Fig. 26); lower diastema elongate; masseteric lines meeting in "V"; M^1 with distinct labial anterocone; molars terraced and cuspidate.

Discussion.—*Leidymys* might have been derived from *Eoeumys vetus.* It apparently became extinct at the end of the Arikareean and did not give rise to *Copemys,* as suggested by Clark, Dawson, and Wood (1964, p. 42), and Alker (1966). Alker placed *Leidymys* in synonomy with *Paracricetodon,* a view not accepted here.

Leidymys represents the more conservative lineage of Miocene cricetids. It retains lower-crowned teeth and a terraced dentition, both seemingly primitive cricetid features. The anterocone is still a large and distinct feature on M^1 and the cheek teeth remain elongate and cuspidate.

LEIDYMYS NEMATODON (Cope), 1879

Figure 13

Hesperomys nematodon Cope, 1879.

Eumys nematodon (Cope) Cope, 1881a.
Peromyscus nematodon (Cope) Wood, 1936.

Type.—AMNH 7018, partial skull.
Type locality.—"The Cove," John Day River, probably Grant County, Oregon.
Horizon.—Middle John Day beds, lower Miocene.

Emended diagnosis.—"Skull top with broad level area between temporal crests; cusps of molars rounded as in *Eumys*; two crests from protocone to anterocone of M^1; central cusp indistinct, with well-developed buccal crests, which do not, however, reach the buccal border of the tooth except on M^{2-3}; cingula complete on all teeth; slight dams
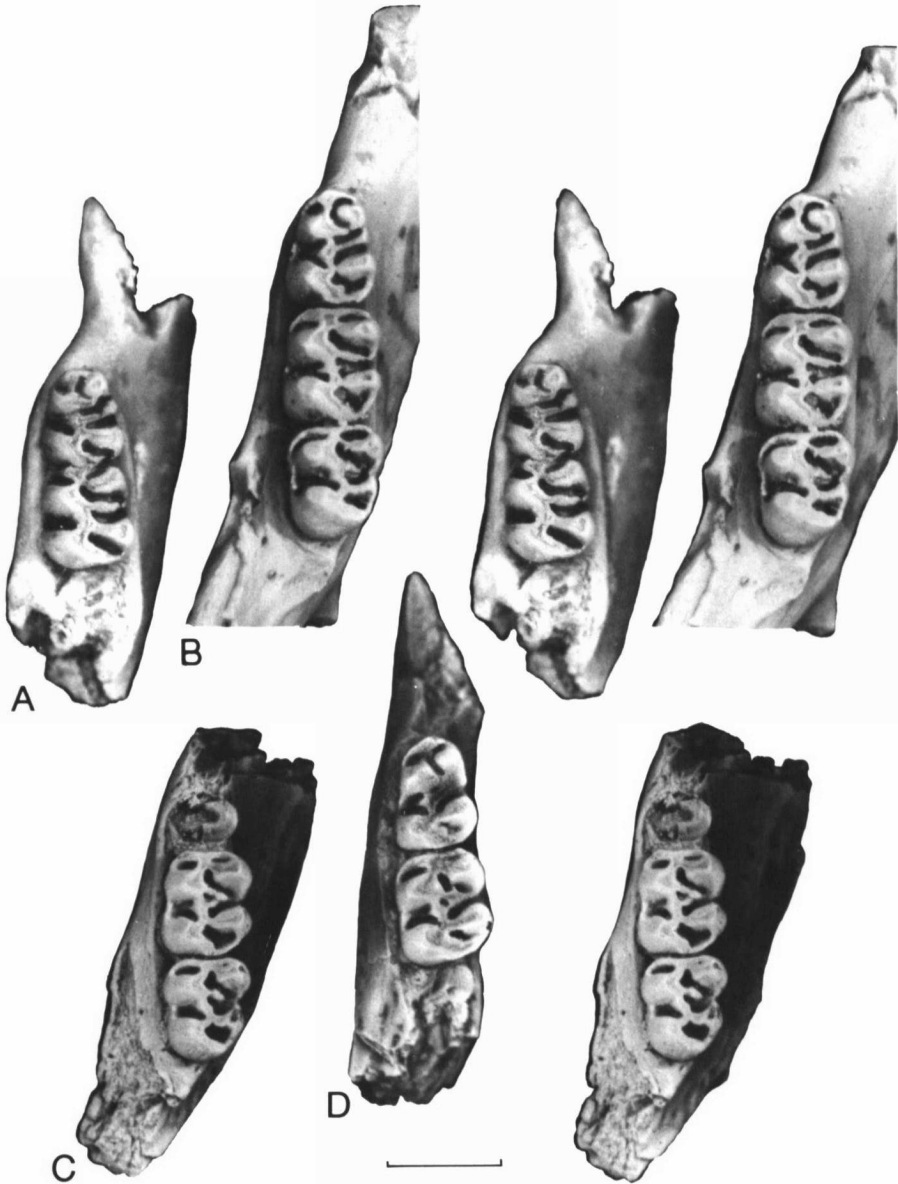

Fig. 13. Stereophotographs of: A, *Paciculus woodi*, left ramus with M_{1-2}, SDSM 54330 (holotype); B, *Leidymys blacki*, left ramus with M_{1-3}, SDSM 5362; C, *L. nematodon*, left ramus with M_{1-2}, AMNH 7025. D. *L. nematodon*, left ramus with M_{2-3}, AMNH 7027. Scale = 2 mm.

across median valleys of M^{2-3}" (Wood, 1936). Ramus lighter than in *L. lockingtonianus* and molars with less compressed cusps than other species of genus.

Description.—Nasals terminating posteriorly along maxillary-frontal suture just posterior to antorbital junction of zygomatics; supraorbital ridges appearing to lead into lyrate saggital crests; cranium expanded but skull long and narrow; zygomatic plate of maxilla inclined at about 45°, coming off just anterior to M^1; incisive foramina large with large posterior border medial to anterocone of M^1; palate broad and shallow, terminating immediately posterior to M^3; upper incisors not known; molars terraced; upper molars with straight lingual reentrants. M^1 with distinct buccal anterocone united at labial margin with protocone; mesoloph long; metacone and hypocone connected by metaloph; posterior cingulum long. M^2 with long anterior cingulum leading into hypocone, otherwise like M^1. M^3 large; posterior arm of protocone joining hypocone, forming small central lake with mure; metaloph long; distinct hypocone present. M_1 anteroconid small and connected labially to protoconid and lingually to metaconid; metaconid joining protoconid posteriorly by a metalophid, isolating "Y"-shaped anterior lake; anterior mure short with mesolophid long and joining metaconid lingually; labial reentrants straight and containing short labial spur off mure; entoconid joining hypoconid; posterior cingulum long and confluent with hypoconid; about same size as M_2. M_2 anterior cingulum confluent lingually with metaconid; metaconid connected by metalophid I to protoconid anteriorly; posterior arm of protoconid joining lingual margin of metaconid and, near its middle, joined by a short mesolophid from metaconid, forming small central lake; posterior cingulum large, confluent with the hypoconid. M_3 large and very similar to M_2 but with a very small entoconid.

LEIDYMYS BLACKI (Macdonald), 1963
Figures 13, 14

Eumys blacki Macdonald, 1963.

Holotype.—SDSM 5574, right ramus with M_{1-3}.

Type locality.—SDSM V5410, S½, secs. 11 and 12, E½, sec. 14, W½, sec. 13, T. 40 N., R. 44 W., South Dakota.

Horizon.—Sharps Formation, Arikaree Group; Miocene.

Emended diagnosis.—Smaller than *Leidymys lockingtonianus,* larger than *L. parvus;* cusps on molars more lophate than in *L. nematodon.*

Description.—Anterior root of zygomatic arch broad as in *Eumys;* incisive foramina large with posterior margin just anterior to M^1. M^1 with three roots; large distinct anterocone, anterior cingulum joining anterocone and protocone, paracone and metacone higher and more compressed anteroposteriorly than hypocone and protocone, paracone and protocone directly across from each other and narrowly connected, protocone connected to hypocone by an endoloph; mesoloph long and thin, metacone teardrop-shaped with narrow connection to hypocone, hypocone leading into strong posterior cingulum. M^2 lacking anterocone and having strong anterior cingulum, otherwise similar to M^1. Ramus somewhat robust, dorsal and ventral masseteric crests meeting in narrow "V" shape below posterior margin of M_1 and ventral crest extending at the same level as mental foramen anteriorly as shelf under anterior edge of M_1, mental foramen on about midline of ramus and just anterior to M_1, no pit between ascending ramus and M_1, diastema relatively short. Incisor slender with thin enamel, three ridges on ventral labial margin and faint ridge on ventral-lingual side. M_1 elongate; anteroconid of M_1 large and connected to metaconid; anteroconid connected by separate crest to protoconid; this crest separates anterior end of tooth into two deep pits enclosed by anterior cingulum; mesolophid long, extending to lingual border of tooth, at border of tooth meet a low crest extending to the metaconid; metaconid joined to hypoconid by hypolophids; small hypoconulid present; strong posterior cingulum joining hypoconid and entoconid, entoconid and hypolophid enclosing posterior basin, posterior cingulum in some specimens giving off small lingually directed crest, buccal valley relatively broad and square. M_2 with strong anterior and posterior cingula, small ante-

rocone connected by crests to metacone and protocone; mesolophid, entoconid, and hypoconid joined by hypolophid and pos-terior cingulum. M_3 similar to M_2 but shorter with narrow posterior end; posterior arm of protoconid and mesolophid not connecting as
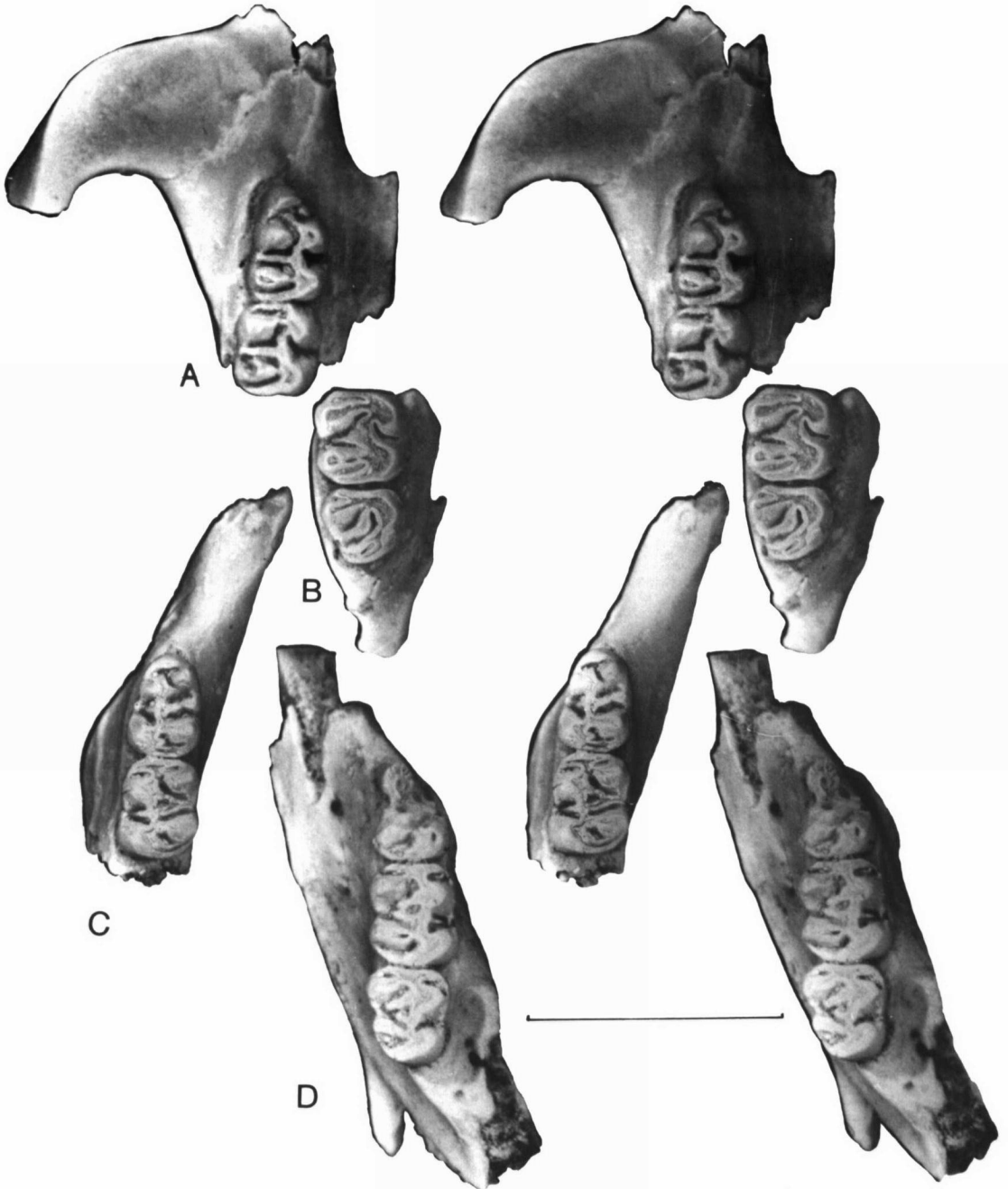

Fig. 14. *Leidymys blacki.* A. Right maxillary with M^{1-2}, UNSM 11669. B. Partial right maxillary with M^{2-3}, UNSM 11646. C. Partial left ramus with M_{1-2}, UNSM 11646. D. Partial right ramus with $M_{1(br)-3}$, UNSM 11624. All occlusal views; scale = 5 mm.

in M_2, not joining lingual border to produce three basins as in *Paciculus montanus.*

Discussion.—The description of *Leidymus blacki* is based on abundant material from the Gering Formation in Nebraska (Fig. 14A-D). It is the oldest and most primitive species of *Leidymys* described at the present time. The ancestors of both *Paciculus* and *Geringia* probably looked much like *Leidymys blacki*, as is well-evidenced by the extreme similarity between this species and the most primitive *Paciculus, P. woodi* (Fig. 13).

LEIDYMYS ALICAE (Black), 1961

Cotimus alicae Black, 1961b.

Holotype.—CM 8868, partial left ramus with M_{1-3}.

Type locality.—Several miles south of New Chicago, Granite County, Montana.

Horizon.—Cabbage Patch beds, early Miocene (D.L. Rasmussen, personal communication).

Emended diagnosis.—Small *Leidymys* with more compressed cusps than in *L. nematodon.*

Discussion.—Donald Rasmussen has made collections near the type locality of *Cotimus alicae* and has found new material including upper dentitions. Associated material shows that *Cotimus alicae* is early Miocene (Arikareean) in age rather than lower middle Miocene (Barstovian) as originally reported (D.L. Rasmussen, personal communication). The upper dentition also demonstrates that *Cotimus* Black is congeneric with *Leidymys* Wood. The correct combination would then be *Leidymys alicae* (Black), which can be distinguished from *L. nematodon* and *L. blacki* by its smaller size. *Leidymys blacki* (Macdonald) is about the same size as *L. nematodon. Leidymys nematodon* can be separated from the above species by the less compressed nature of its cusps.

LEIDYMYS PARVUS (Sinclair), 1905

Peromyscus parvus Sinclair, 1905.
Leidymys parvus (Sinclair) Clark and others, 1964.

Type.—UCMP 84, partial maxilla with M^{1-2} and left ramus with M_1.

Type locality.—"Turtle Cove," probably Grant County, Oregon.

Horizon.—"Upper *Diceratherium* level," John Day beds, Oregon, lower Miocene.

Emended diagnosis.—Smaller than *L. nematodon.*

LEIDYMYS LOCKINGTONIANUS (Cope), 1881
Figures 15, 16

Eumys lockingtonianus Cope, 1881a.
Paciculus lockingtonianus (Cope) Cope, 1881b.
Leidymys lockingtonianus (Cope) Wood, 1936.

Type.—AMNH 7028, skull.

Type locality.—"The Cove," John Day River, Grant County, Oregon.

Horizon.—Middle John Day beds, early Miocene.

Emended diagnosis.—Largest species of *Leidymys;* upper molars broad; infraorbital foramina very large; incisive foramina more anterior than in *L. nematodon;* upper incisors with two faint ridges on labial sides.

Description.—Very large cricetid, skull short and broad, cranium rounded, dorsal surface convex with apex above M^3; nasals sloping to point lower than top of occipital crest; sagittal crests double and lyrate with broadest point above posterior root of zygomatic arch; rostrum short and broad, ventral surface nearly flat; external nares broken but apparently large and heart shaped; nasals broad and terminating posteriorly in nearly straight suture anterior to orbits; frontals long and terminating posteriorly above posterior roots of zygomatic arches; jugal extending anteriorly to anterior root of zygomatic arch; incisive foramina broad and elongate, posterior border of foramina anterior to M^1; palatal surface flat with only shallow grooves along medial sides of molars; palatine-maxillary suture "V"-shaped with anterior most margin medial to M^2; posterior palatine notch slightly posterior to M^3, short rounded posterior spine present; auditory bulla large with large circular external auditory meatus. Upper molars heavily worn on holotype and of little use except anterocone large and buccal.
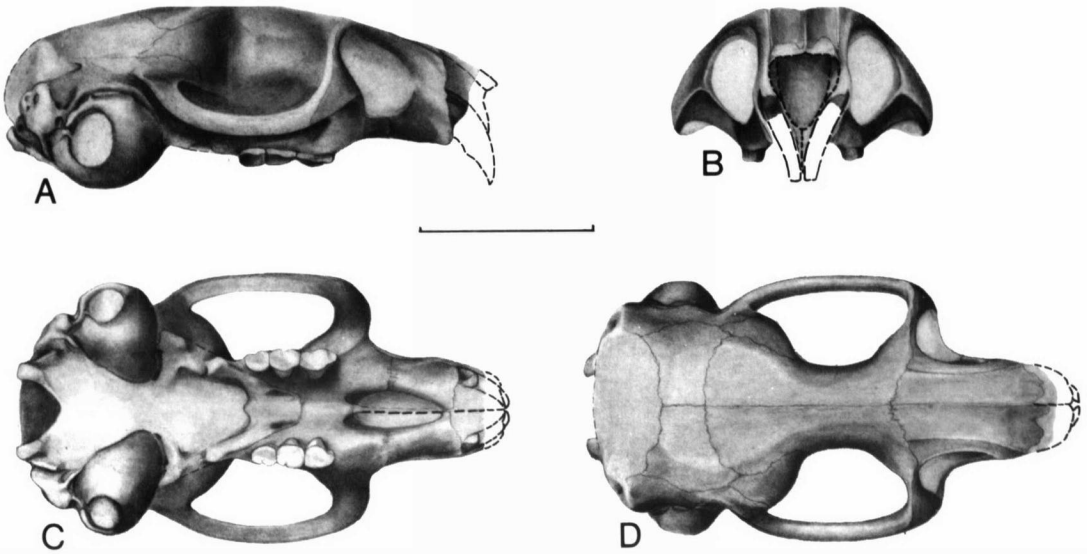
Fig. 15. *Leidymys lockingtonianus*, reconstruction of skull, AMNH 7028 (holotype). A, lateral view; B, anterior view; C, ventral view; D, dorsal view. Scale = 1.5 cm.

Ramus heavy; masseteric lines meeting in "V" with ventral line heavy and extending below anterior edge of M_1 just anterior to and below this shelf. M_2 terraced with small mesolophid connecting to posterior arm of protoconid closing off basin; M_1 and M_3 not preserved.

Discussion.—*Leidymys lockingtonianus* is the largest known Oligocene or Miocene North American cricetid. It resembles *L. nematodon* in having a double saggital crest, large buccal anterocone, terraced molars, and in the ridging of its lower incisors. It has an enormously enlarged (hystricomorphous) infraorbital foramina. Wood (1936) also noted the foramina but ascribed their size to damage on the specimen. The specimen is damaged in this area but careful examination of it and comparison to other early cricetids confirms the large size of these foramina. Unfortunately, no other species of *Leidymys* has this area preserved.

Tribe GERINGINI, new

Type genus.—*Geringia.*
Geographic distribution.—California, Oregon, Montana, Wyoming, South Dakota, and Nebraska.
Diagnosis.—Cricetid rodents having M^1 with five lophs and anterior margin nearly straight; molars hypsodont and showing planar wear; body of ramus inflected labially where masseteric lines meet.

GERINGIA, new genus

Type Species.—*Geringia mcgregori* (Macdonald), 1970.
Geographic distribution.—South Dakota and Nebraska.
Geologic range.—Upper Oligocene (Whitneyan) to lower Miocene (Geringian).
Diagnosis.—Cricetid rodents near size of *Peromyscus*; M^1 anterocone obsolete causing nearly straight anterior margin (*Eumys, Eoeumys, Leidymys,* and *Scottimus* have definite M^1 anterocone); upper molars nearly square, with M^{1-2} usually five crested and wearing rapidly to three-crested eomyidlike configuration; M^3 relatively small; M_1 with anterior basin, and posterior "V" formed by mesolophid and hypolophid; teeth all relatively high crowned; broad lower incisor with one ventral ridge; hind limbs not elongated as in *Paciculus.*
Discussion.—This genus is closely related *Paciculus,* but *Paciculus* has a slightly more

distinct anterocone and is highly modified for saltatorial locomotion. With wear, the upper teeth of *Geringia* develop a three-crested pattern reminiscent of the Oligocene eomyid *Paradjidaumo* whereas the M_1 develops a pattern of lakes similar to that found on *Zapus* (Alker, 1969). *Geringia* is the most common cricetid in the Gering fauna and is the only one that occurs at all the microfauna localities. It is also known from the Sharps fauna, but does not occur outside the central Great Plains. The discovery of an articulated skull and mandible puts our knowledge of this genus on a particularly firm basis and permits the association of upper and lower dentitions with certainty.

GERINGIA MCGREGORI (Macdonald), 1970
Figures 17-19, 21-23

Paciculus mcgregori Macdonald, 1970.

Type.—LACM 9271, partial cranium.
Type locality.—LACM 1959.
Horizon.—Sharps Formation, Arkaree Group; Miocene.
Emended diagnosis.—Largest species of

Fig. 16. A. *Geringia gloveri*, stereophotograph of right ramus with M_{1-2}, LACM 15434 (holotype). B. *Paciculus insolitus*, stereophotograph of right ramus with M_1, AMNH 7024. C. *Leidymys lockingtonianus*, stereophotograph of right ramus with M_2, AMNH 7023. All occlusal views; scale = 3 mm.
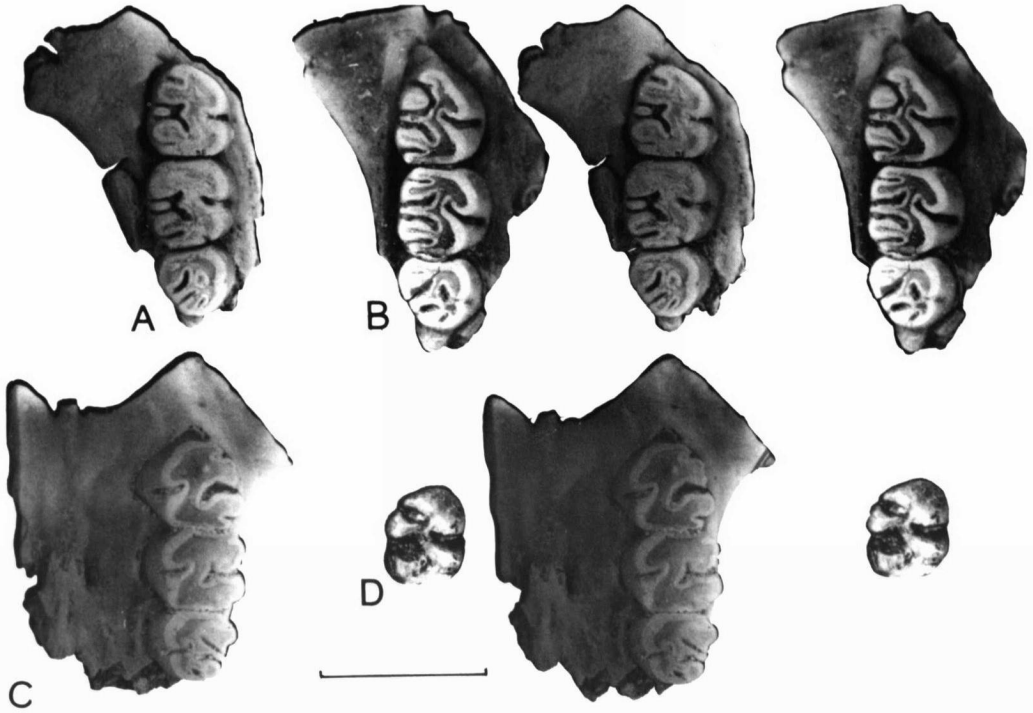
Fig. 17. Stereophotographs of *Geringia mcgregori*. A. Right maxilla, occlusal view, UNSM 66163. B. Right maxilla, occlusal view, UNSM 11552. C. Left maxilla, occlusal view, UNSM 11537. D. Right M^1, UNSM 11525. Scale = 3 mm.

genus.

Description.—Skull elongate; double saggital ridges as in *Leidymys;* braincase low and flattened dorsally; infraorbital constriction fairly broad; rostrum longer and broader than in *Eumys* and cranium much longer and narrower; bulla very large and heart shaped with apex pointing anteriorly towards midline of ramus; external auditory meatus large and roughly oval in outline; zygomatic arches not preserved but anterior roots not so broad as in *Eumys;* palate broad and upper cheek tooth rows converging posteriorly (they diverge posteriorly in some *Eumys*); pterygoids low and thin and not quite extending posteriorly to auditory bulla; palatine short and terminating anteriorly across from lingual root of M^2; palatine bearing short posterior spine; posterior palatine notch across from middle of M^3 and bearing short posterior spine; incisive foramina large and elongate, posterior margin of incisive foramina well anterior to M^1; palatine foramina across from M^2 and set in deep grooves extending posteriorly until they turn laterally behind M^3; palate shallow; anterior border of palatine across from center of M^2; two small depressions (muscle attachments) in front of M^1; anterior root of zygomatic arch just anterior to M^1; palatines terminating posteriorly in cup-shaped depressions at apex of "V"s formed by pterygoids and ridges running from palatines to bulla (this is area of origin of internal pterygoid muscle and suggests high development); "V"-shaped depressions for origins of *longus capitis* and *rectus capitis anticus* muscles deep and separated by a ridge; large foramen just dorsal to posterior edge of pterygoid (probably basisphenoid canal, for the foramen ovale is just lateral to it and the anterior lacerate foramen just behind; however, the highly fractured condition of the bone makes detailed discussion of cranial foramina impossible); small stylomastoid foramen present between bulla and thin paraoccipital process; bulla with large socket internally for paraflocculus, facial canal large and internal auditory meatus small.

M^1 with three roots, anterocone not distinct and included in thick anteroloph with protocone, teardrop-shaped paracone may or may not attach to anteroloph with protocone, teardrop-shaped with thin connection to hypocone, hypocone incorporated into posteroloph. Lingual reentrant angles of M^{1-2} narrow and directed anteriorly. M^2 shorter than M^1 and almost square in outline, otherwise similar to M^1. M^3 much smaller than M^2, almost circular in outline, structure basically similar to that of M^2 except reentrant angle closing lingually to isolate a lake, mesoloph and metacone directed posteriorly.

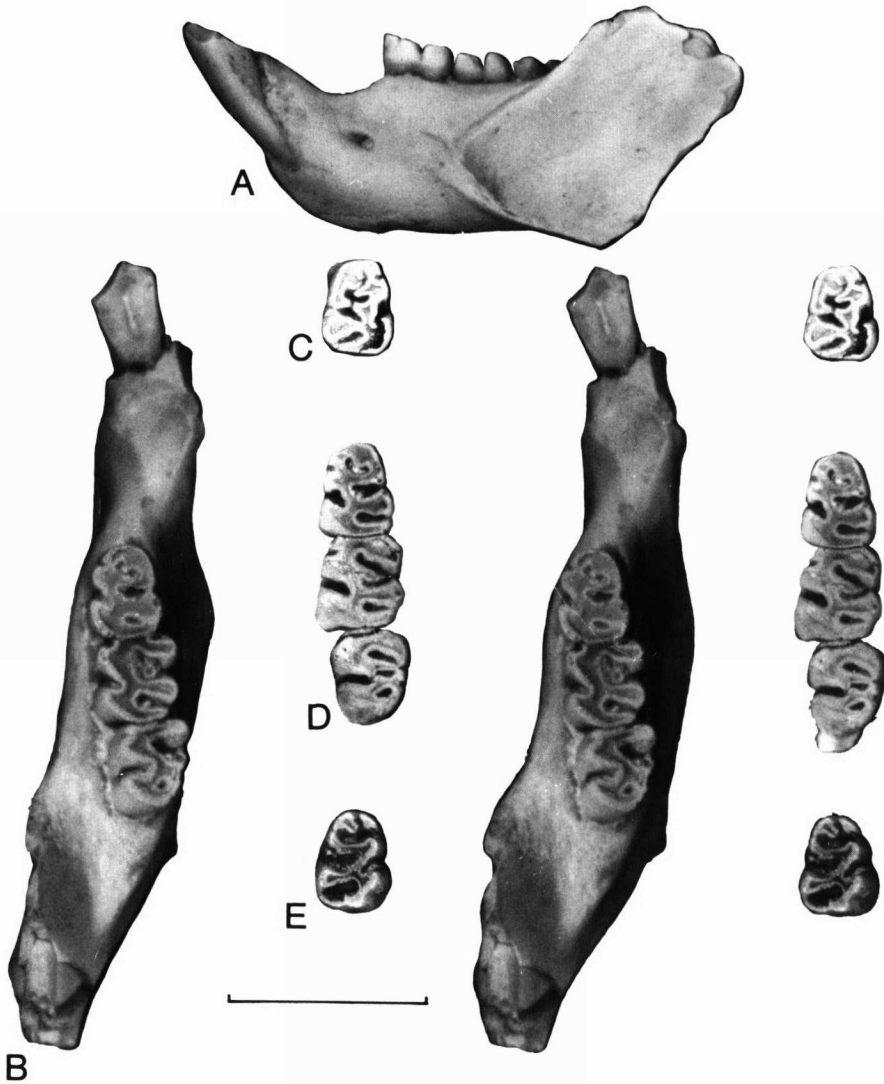Ramus short and heavy with short thick diastema; large mental foramen situated

Fig. 18. *Geringia mcgregori.* A. Left ramus with M_{1-3}, labial view, UNSM 66162, scale = 5 mm. B. Stereophotograph of left ramus with M_{1-3}, occlusal view, UNSM 66162, scale = 3.5 mm. C. Stereophotograph of right M_1, UNSM 11521, scale = 3.5 mm. D. Stereophotograph of left M_{1-3}, occlusal view, UNSM 11725, scale = 3.5 mm. E. Stereophotograph of right M_1, occlusal view, UNSM 11738, scale = 3.5 mm.

about halfway up and anterior to M_1; ventral and dorsal masseteric lines meeting in broad "V" under anterior edge of M_2; ventral masseteric line ventrally situated and distinctly set apart from ventral border of ramus; masseteric fossa forming fairly deep linear depression along lower border of dorsal masseteric crest; depression between ascending ramus and M_3 very shallow; ramus with long distinct angle. Incisors broad, robust and almost flat, with single median ridge; incisor enamel thin, almost absent on lingual side and extending only very slightly onto labial side.

Lower molars high crowned and exhibiting planation. M_1 with metaconid joined to small anteroconid and both cusps incorporated into curving loph, joining protoconid to enclose somewhat circular valley opening labially (it will close with wear); small mesostylid may be attached to loph lingually; protoconid leading into ectolophid extending diagonally to join hypolophid just labial to its midpoint; short anteriorly directed mesolophid joining posterolophid; posterolophid curving around posterior border of tooth, in some joining entoconid to form basin, but usually leaving valley open, forming "V" with hypolophid. M_2 with small remnant of distinct anterior cingulum on some teeth; metaconid and entoconid higher on some specimens; metaconid extending into metalophid running across anterior edge of tooth; protoconid joining metalophid and ectolophid; mesolophid arising from ectolophid at its juncture with protoconid; mesolophid variably joining metaconid and closing off basin; lingual reentrant square; labial reentrant inclined posteriorly; ectolophid joining hypolophid as in M_1; posterolophid as in M_1. M_3 with posterior end narrower than anterior, otherwise similar to M_2.

Humerus shorter and much more massive than in *Onychomys* and shaft not so straight; greater tuberosity and head of humerus similar to those in *Onychomys* but lesser tuberosity relatively smaller; general shape and massiveness of humerus somewhat like that of kangaroo rats (*Dipodomys*) but slightly more elongate and with large deltoid crest as in *Onychomys*; lateral epicondylar ridge prominent and starting at level of deltoid crest, leading into distinct lateral epicondyle; entepicondylar foramen more laterally placed (above trochlea) than in *Onychomys* (above medial epicondyle); medial epicondyle about as in *Onychomys*, and separated from medial epicondyle by ridge; femur shorter and more robust than in *Onychomys*; head of femur relatively small and neck narrow; greater trochanter at same level as head (in *Onychomys* it extends further proximally); lesser trochanter small while lateral crest large extending distally past the midpoint of femur; ulna and humerus about same length and femur only slightly longer; ulna robust with olecranon process slightly twisted medially; brachial ridge not as sharp as in *Onychomys* and joining low medial ridge; lateral concavity long and deep, and olecranon process thinner on its lateral edge than in *Onychomys*.

Discussion.—Geringia, the most abundant rodent in the Gering Formation, shows con-
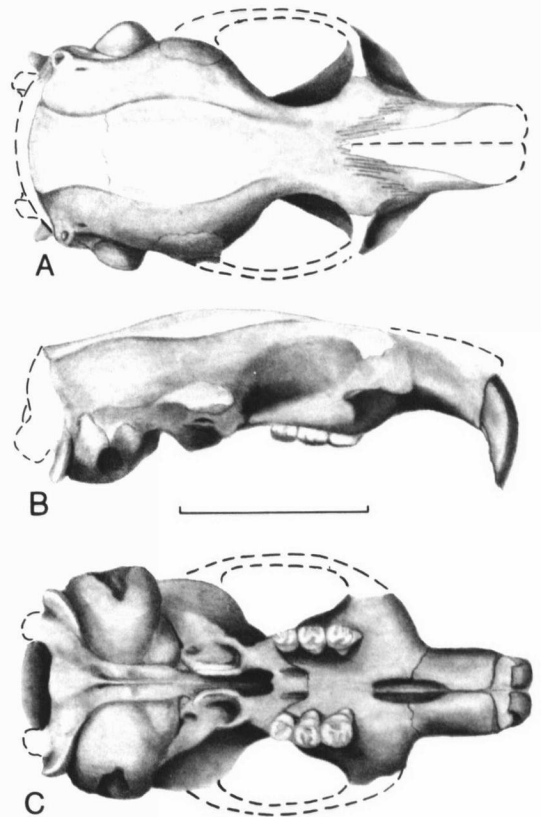

Fig. 19. *Geringia mcgregori*, reconstruction of the skull, UNSM 11553; A, dorsal view; B, lateral view; C, ventral view; scale = 10 mm.

siderable variability in size and teeth. The mesolophs or mesolophids may be well developed, nearly absent, or broken up into small cuspules (mesostyle, etc.). This development may vary from one molar to another on a single jaw or from one side to the other on a palate or a mandible. Size is also variable, and it might be questioned whether *G. gloveri* is really separate from *G. mcgregori. Geringia* is a smaller cricetid than *Paciculus* with more specialized incisors and a less specialized skeleton (see Fig. 23). They appear to have had about the same size relationship to each other as *Peromyscus* presently has to *Onychomys*.

GERINGIA GLOVERI (Macdonald), 1970

Eumys gloveri Macdonald, 1970.

Type—LACM 15434, right ramus with M_{1-2}.

Type locality.—LACM 2018.

Horizon.—Monroe Creek Formation, Arkaree Group; Miocene.

Emended diagnosis.—Smaller than *Geringia mcgregori.*

PACICULUS Cope, 1879

Type species.—*Paciculus insolitus* Cope, 1879.

Geographic distribution.—South Dakota, Nebraska, Colorado, Wyoming, California, Montana, and Oregon.

Stratigraphic distribution.—Lower Miocene (Arikareean).

Emended diagnosis.—"M^{1-2} with five compressed transverse crests, all of subequal width and length; paracone and metacone little if any more prominent than central cusp; all five crests subparallel; protocone uniting with lingual margin of anterocone" (Wood, 1936). Anterocone of M^1 also tending to be reduced, lingual reentrants only slightly inclined; posterior extension on incisive foramina anterior to M^1; molars hypsodont; M_1 with anterior basin, posterior "V" mesolophids well developed; lower incisor with one lingual and three labial ridges; incisor small and compressed; ramus thickened labially near midline; masseteric lines meeting in "V" on ramus and forming anterior labial

shelf; hind limbs elongated.

Discussion.—The ridging on the enamel of the lower incisor and the crown pattern of the lower molars suggest that *Leidymys* may have given rise to *Paciculus. Leidymys* has terraced molars whereas *Paciculus* shows planar wear on the molars. The increase in crown height of the molars may go with the development of saltatorial locomotion in this genus. It is the most widespread Arikareean cricetid. Wilson (1949b, p. 55, fig. 2) described from the Kew Quarry fauna a cricetid jaw with M_2 that has ridged incisors and a strong masseteric crest. These features suggest that it may represent *Paciculus* and that at least that part of the Sespe Fauna is Arikareean.

PACICULUS INSOLITUS Cope, 1879
Figures 16, 20

Type.—AMNH 7022, partial palate with M^{1-2}.

Type locality.—"The Cove," John Day River, probably Grant County, Oregon.

Horizon.—John Day beds, lower Miocene (Arikareean).

Emended diagnosis.—Size large; anterocone fairly prominent on M^1; long mesolophid in M_1.

Description.—Palate broad and shallow with incisive foramina. M^1 with buccal anterocone present but confluent with anteroposteriorly compressed protocone to form diagonally oriented anterior loph; paracone connected by paraloph to center of mure; mesoloph confluent with anterior arm of hypocone to form transverse loph; metacone connected by mesoloph to form transverse loph; other cingula not developed; internal reentrant slightly inclined anteriorly. M^2 nearly square in outline; anterior cingulum forming straight anterior loph and confluent with hypocone; internal reentrant more inclined. M^3 about half size of M^2 and triangular. Ramus with long narrow diastema; dorsal and ventral masseteric lines meeting anteriorly as "V" with ramus expanded labially at ventral masseteric line to form shelf that terminates anteriorly under anterior portion of M_1; mental foramen just anterior to M_1 and at same level as ventral
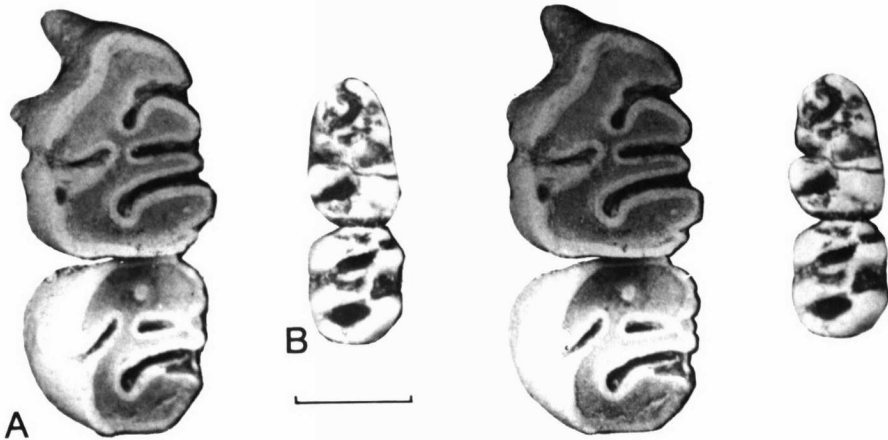
Fig. 20. Stereophotographs of *Paciculus*. A. *P. insolitus,* left M$^{1-2}$, AMNH 7022 (holotype), scale = 2 mm. B. *P. nebraskensis,* left M$_{1-2}$, UNSM 66166 (holotype), scale = 4 mm.

masseteric line; symphysial flange well developed. Lower incisor not compressed, with ventral border flat; lingual border nearly straight, labial border slightly rounded; enamel not extending to lingual border and only short distance on labial; ventral surface of incisor with two labial ridges, one nearly central, and one lingual. M$_1$ high crowned with planar wear; anteroconid attached labially to protoconid and lingually to metaconid thus enclosing lake; mesolophid long; mure diagonal to long axis of tooth and joining large entoconid; hypoconid connecting with posterior cingulum, posterior cingulum extending lingually to join entoconid.

Discussion.—Wood (1936, p. 4-5) in his discussion of *Paciculus insolitus* did not mention the lower dentition, and Clark, Dawson, and Wood (1964, p. 44) stated that the association is unknown but might be represented by *Cotimus*. Alker (1969, p. 172) also stated that the correct association of upper and lower teeth had not been demonstrated for *Paciculus*. However, in his description, he did correctly assign lower teeth (the holotype of *P. nebraskensis*) to *Paciculus*. After all of this discussion, it is surprising to find that Cope (1884, pl. 64, figs. 31-32) correctly associated and illustrated the M$^{1-2}$ and M$_{1-3}$ of *P. insolitus*. The specimens are at about the same stage of wear and might even represent the same individual as the type. This lower dentition is presently lost, but M.C. McKenna

graciously sent me another partial ramus from Cope's collection that also seems to represent *P. insolitus* (Fig. 16B).

PACICULUS MONTANUS Black, 1961

Paciculus montanus Black, 1961a.

Type.—YPM 14927, right maxilla with M$^{1-2}$.

Type locality.—Secs. 3 and 8, T. 10 N., R. 5 E., Meagher County, Montana.

Horizon.—Lower Miocene (Arikareean).

Emended diagnosis.—Small *Paciculus;* molars with relatively well-developed buccal anterocone; terraced dentition with much inclined lingual reentrants.

Description.—Palate shallow. M^1 with distinct buccal anterocone connected lingually to protocone; paracone connecting narrowly to mure; mesoloph long; posterior arm of metacone attaching to posterior cingulum, confluent lingually with protocone and connected to hypocone by metaloph. M^2 similar to M^1. M^3 in YPM 14026 a small triangular tooth with three transverse lophs and no hypocone.

Discussion.—In the presence of large buccal anterocones, highly inclined internal reentrants, long narrow molars, and somewhat terraced wear pattern this species is much like *Leidymys;* however, it can be separated from *Leidymys* and associated with *Paciculus* by

the lingual attachment of the anterocone to the protocone.

PACICULUS WOODI (MacDonald), 1963

Figure 13

Eumys woodi Macdonald, 1963.

Holotype.—SDSM 54330, partial left ramus with M_{1-2}.

Type locality.—SDSM V54s, N½, sec. 30, T. 40 N., R. 43 W., South Dakota.

Horizon.—Lower part of Sharps Formation, upper Oligocene (Whitneyan).

Emended diagnosis.—Mesolophid well developed; molars higher crowned than in *Leidymys;* lower crowned and with less planar wear than in *P. insolitus* or *P. nebrascensis.*

Discussion.—The presence of the

Leidymys-like ridging pattern indicates that *"Eumys" woodi* belongs to either *Paciculus* or *Leidymys.* The long mesolophid on M_1 also separates it from *Geringia.* It is remarkably similar to *Leidymys blacki* (Fig. 13); however, it can be separated from *Leidymys* by its higher-crowned teeth with planar wear. It is the most primitive species of *Paciculus* and might be ancestral to *Paciculus nebraskensis.*

PACICULUS NEBRASKENSIS Alker, 1969

Figures 20-23

Type.—UNSM 66166, left and right M_1 and right M_2 associated with partial skeleton.

Type locality.—UNSM Mo-108.

Horizon.—Lower Miocene, Gering Formation, 0-10 feet above Brule-Gering contact (Alker, 1969, p. 174).
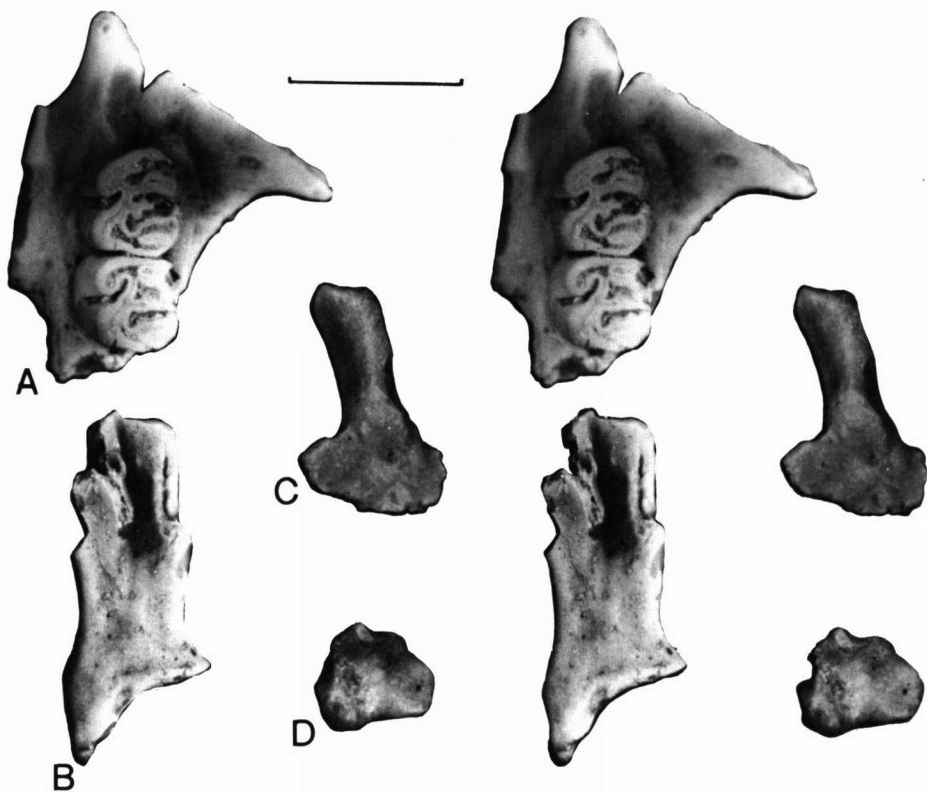
Emended diagnosis.—Dentition slightly

Fig. 21. A. *Paciculus nebraskensis,* left maxillary with M^{1-2}, occlusal view, UNSM 11527. B. *P. nebraskensis,* stereophotograph of maximal end of left scapula, lateral view, UNSM 66166 (holotype). C. *Geringia mcgregori,* stereophotograph of calcaneum, UNSM 11532. D. *G. mcgregori,* stereophotograph of distal end of tibia, UNSM 11532. Scale = 3 mm.

smaller and with shorter mesolophids than *Paciculus insolitus.*

Description.—Cricetid about size of *Onychomys;* palate broad; posterior border of incisive foramina slightly anterior to anterior border of M^1. M^1 with anterocone indistinct and incorporated with anteroloph connecting protocone and paracone; ante-
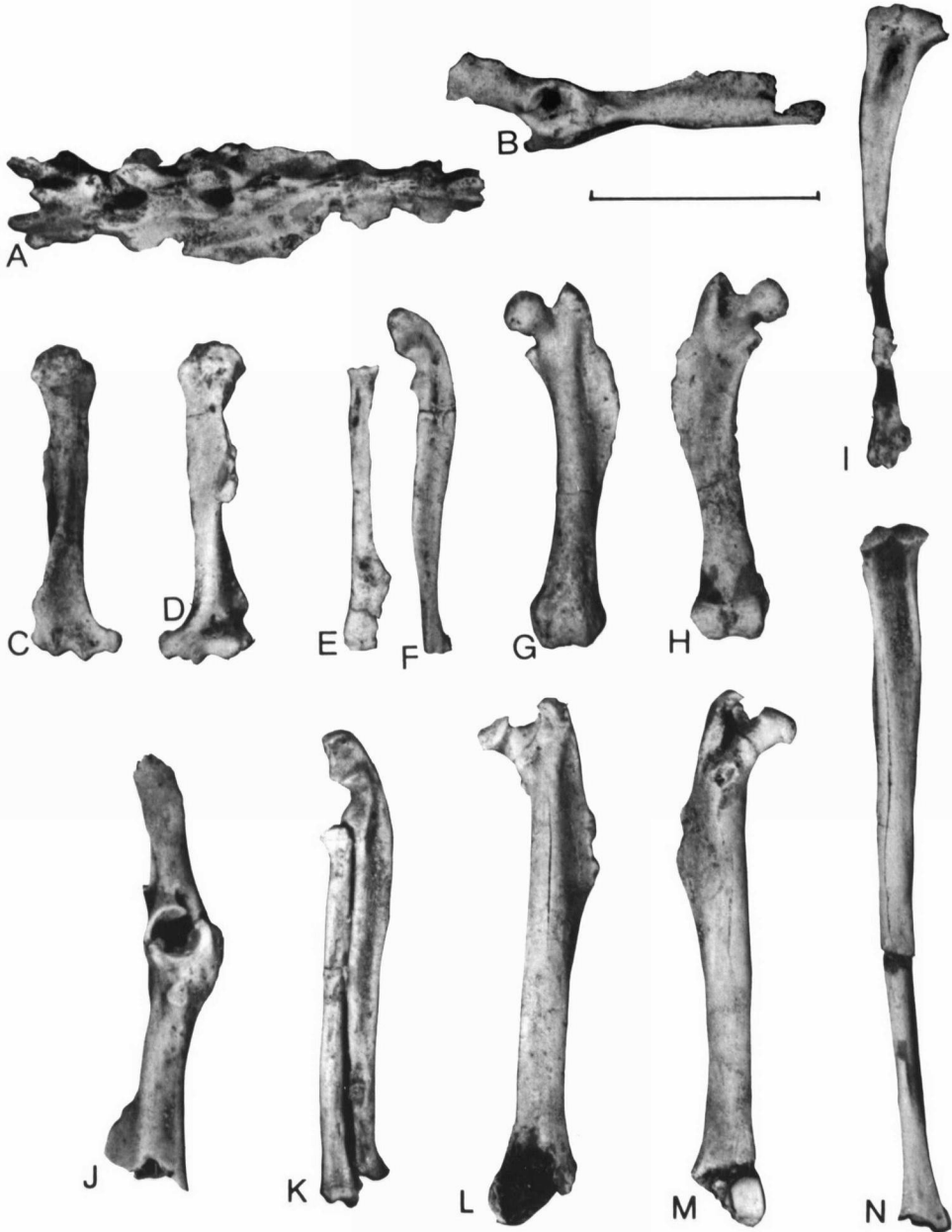

Fig. 22. A-I, skeletal elements of *Geringia mcgregori*, UNSM 11532. A, sacrum with fused lumbar and caudals; B, right pelvis; C, right humerus, anterior view; D, right humerus, posterior view; E, left radius, lateral view; F, left ulna, lateral view; G, left femur, anterior view; H, left femur, posterior view; I, left tibia, posterior view. J-N, skeletal elements of *Paciculus nebraskensis*, UNSM 66166 (holotype). J, left pelvis; K, left radius and ulna, lateral view; L, left femur, anterior view; M, left femur, posterior view; N, left tibia, posterior view. Scale = 1cm.
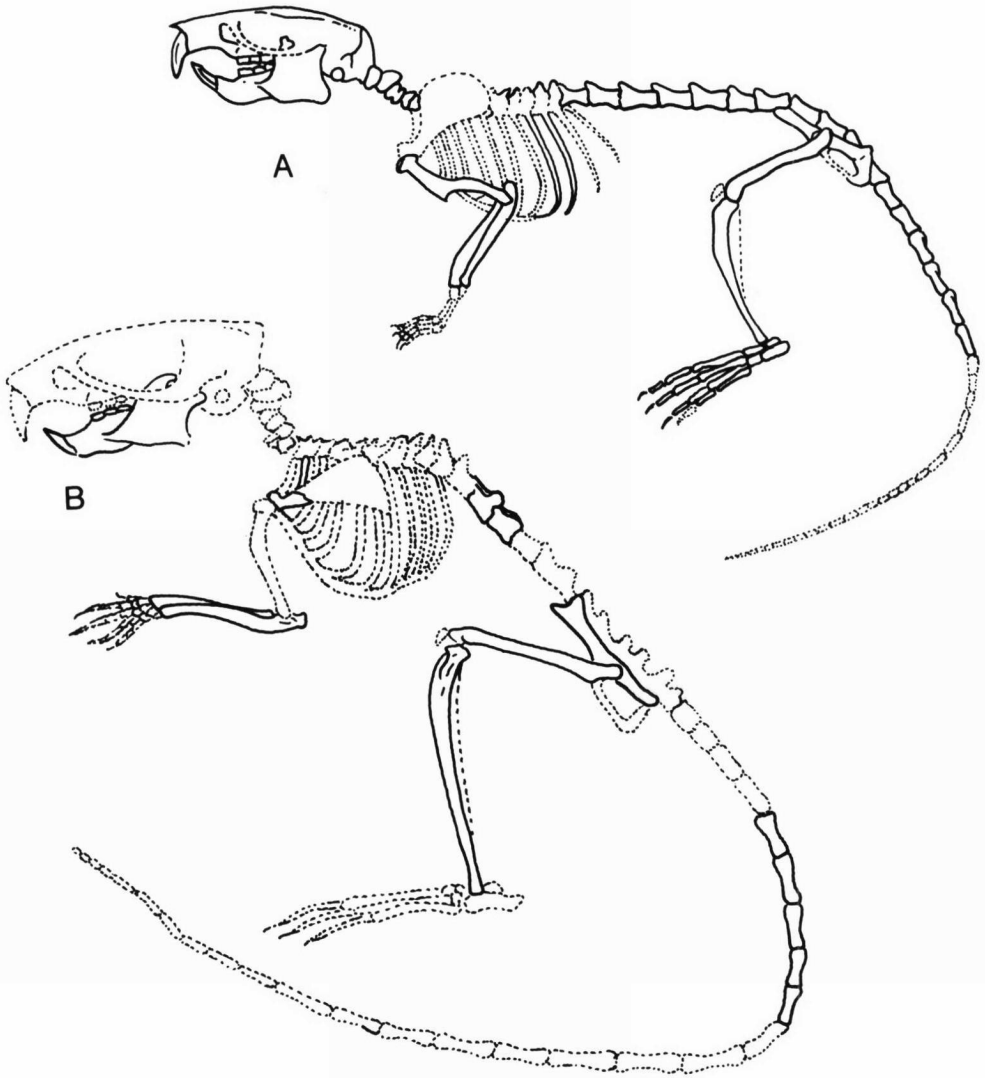
Fig. 23. Reconstructions of cricetid skeletons; missing portions represented by dashed line. A. *Geringia mcgregori*, UNSM 11532. B. *Paciculus nebraskensis*, UNSM 66166 (holotype); position and reconstruction based on illustration of the saltatorial heteromyid *Cupidinimus* published by Wood (1935). Both natural size.

roloph may bear small, buccally directed crest; protocone and paracone also connected by crest; mesoloph long, reaching to buccal border in some specimens; hypocone and metacone connected by metaloph; posterior cingulum prominent; metacone and paracone highly compressed. Lower incisor slender with one lingual and three labial ridges on ventral enamel. Anterior part of ramus apparently slender with long diastema (in part due to immaturity); anterior-ventral portion of mandi-ble inclined posteriorly, ending in slight flange; coronoid process fairly long and recurved posteriorly as in *Onychomys*. Molars very high crowned. On M_1 metaconid and entoconid high and distinct on unworn teeth; anterolophid coming off anteriorly from metaconid, swinging posteriorly and giving off short spur, spur uniting with protoconid; protoconid sending off thin loph medially uniting with small, sharp-pointed mesostylid; mesostylid fused at base with

metaconid (closing off anterior part of tooth to form deep lake), giving off short mesolophid inclined ventrally and directed anteriorly and joining base of mesostylid; hypolophid running from hypoconid to ectolophid slightly anterior of juncture of ectolophid and entoconid; entoconid joined by posterolophid to hypoconid (closing off another deep lake). M_2 with metaconid and entoconid also high and distinct, protoconid and hypoconid low and incorporated with lophs; mure connected to posterolophid, posterolophid joining base of entoconid, forming small narrow basin (with wear, lower molars would be completely lophate and cingula of these teeth are completely incorporated in these high thin lophs).

Femur very elongate; lateral crest extending further distally than in *Onychomys*; tibia more elongate and more gently curved than in *Peromyscus* or *Onychomys*; crest of tibia much more distal than in *Onychomys*; distal end of tibia wide mediolaterally and short anteroposteriorly; lateral malleolus not extending distally as in *Onychomys* and confluent with articular surface (distal end of tibia similar to that in *Dipodomys*); gluteal notch on pelvis well defined; femoral process and illial ridge well developed; distinct notch on dorsal border of ischium posterior to acetabulum; medial surface across from acetabulum deeply excavated; scapula with narrow elongate neck; glenoid fossa narrow and constricted in middle; coracoid process poorly developed; ulna about same length and curved much as in *Onychomys*; olecranon process broader proximally than in that species; distinct lateral cavity present; radius with more nearly circular distal articulation and more robust than in *Onychomys*; caudal vertebrae large and elongate with enough preserved to indicate long tail.

Discussion.—The teeth of the holotype of *P. nebraskensis* are very similar to isolated lower teeth from the Monroe Creek fauna of Wyoming shown to me by Craig Black. Black has associated an M^1 having a prominent and distinct anterocone with these teeth. The horizon cited from Alker (1969) is based on identification of the associated matrix by T.M. Stout. The holotype is a specimen collected by Sidney R. Sweet, a private collector, and does not have precise stratigraphic data accompanying it. However, upper teeth that seem referable to *P. nebraskensis* do occur in the lower Gering of UNSM Mo-104, and when the matrix and preservation of the specimen are considered, Stout's interpretation of the horizon must be nearly correct. The holotype is from a very young individual in which the molars are completely formed but not erupted and the epiphyses are not fully fused. *P. nebraskensis* is a rodent about the size of *Onychomys* with extremely long slender legs. The hind limbs appear to have been longer than the forelimbs and it seems reasonable to assume that the rodent was saltatorial (Fig. 21). The material that Alker (1969) referred to *P.* cf. *P. insolitus* belongs to *Geringia mcgregori*. As he based his diagnosis of *P. nebraskensis* on comparisons with his *P.* cf. *P. insolitus*, it is not suitable for separating *P. nebraskensis* from *P. insolitus*. However, *P. nebraskensis* may be separated from the latter species by its slightly smaller size and the lesser development of the mesolophid in *P. nebraskensis* (contrary to Alker, 1969, who characterized *P. nebraskensis* by its larger size and long mesolophid on M_1).

CONCLUSIONS

Origin and early radiation.—The cricetids are small rodents whose early members probably shared the following derived characters: large infraorbital foramina unconstricted ventrally; double sagittal crest; large incisive foramina; tooth formula $I \frac{1}{1} C \frac{0}{0} P \frac{0}{0} M \frac{3}{3}$; uniserial incisor enamel, and a large buccal anterocone on M^1.

The earliest rodent that has been considered a cricetid is *Simimys* (Wilson, 1935a,b) from the late Eocene Pearson Ranch local fauna of Ventura County, California. It shares with known early cricetids an enlarged infraorbital foramen and the loss of the premolars (Lindsay, 1977; Vianey-Liaud,

1974). It seems likely that *Simimys* is not a cricetid. Its M^1 is more lophate than that of the earliest known cricetid, *Nonomys* (Emry & Dawson, 1972, p. 9), and lacks the distinct buccal anterocone characteristic of the early cricetid stock. Lillegraven and Wilson (1975) also concluded that *Simimys* is not a cricetid. They point out that it has a derived character (foramen for the infraorbital nerve) shared with dipodoid rodents but not with any known cricetid.

The derivation of the cricetids from the eomyid *Namatomys* (Lindsay, 1968) is also extremely unlikely. *Namatomys* is not at all similar to any of the Oligocene cricetids and is too late in time to be seriously considered an ancestral stock. It seems likely that the cricetids along with many other rodent families may be derived from the late Eocene sciuravids. The sciuravids are, in fact, the only Eocene rodents to show the various specializations in the jaw musculature and the dentition that we must expect in the basal stock of the Cricetidae. This fact, coupled with the tendency for reduction in $P\frac{4}{4}$ and the rather close similarity between the crown pattern of M_{1-3} in *Pauromys* and the earliest and most primitive cricetid *Nonomys* (Fig. 1), leads me to support a sciuravid origin for the cricetids. The sciuravids may also be ancestral to the dipodoids and a sister group relationship between the dipodoids and cricetids seems likely.

Eoeumys is a member of the basal stock of the Oligocene and Miocene cricetid radiation in North America and may occur in the Chadronian of Wyoming, on the basis of a skull presently being studied by John Wahlert. It is very close to certain Eurasian cricetids, notably *Eucricetodon* and *Pseudocricetodon*, and it seems likely that there was an exchange of cricetids between North America and Eurasia in the Chadronian (lower Oligocene). As the place of origin of the cricetids is unknown, the direction of this exchange is not clear; however, it seems likely that it took place soon after the probable time of origin of the Cricetidae (late Eocene).

Eoeumys .is abundant in the lowermost part of the Orella Formation (Orella A of Schultz & Stout, 1955) in Nebraska. These beds have produced only fragmentary evidence of *Eumys* (Alker, 1967). It seems likely that *Eumys* diverged from an *Eoeumys*-like ancestor in the Chadronian and developed into at least two lineages (*Eumys elegans* and *Wilsoneumys planidens*). *Eoeumys* became rare through Oligocene time in Nebraska, and may have graded into two separate lineages (*Leidymys* and *Scottimus*) in the Whitneyan, but *Eumys* became increasingly abundant. At the same time there is evidence that the climate became progressively drier (Schultz & Falkenbach, 1968). One possible interpretation of these events is that *Eumys* became a steppe form while *Eoeumys* required a more mesic habitat. That portion of the *Eoeumys* population that remained in the grasslands evolved into another steppe form, *Scottimus* (Wood, 1937; Galbreath, 1953; Black, 1961c). At the same time other species of *Eoeumys* were probably differentiating in more mesic habitats to form the basal stock for the North American Miocene cricetid radiation, including *Geringia*, *Paciculus*, and *Leidymys*. This interesting radiation is obscured by the almost complete absence of small mammal faunas from mesic sediments of the correct age. During the latest Oligocene in Nebraska, only the three steppe cricetids, *Eumys brachyodus*, *Wilsoneumys planidens*, and *Scottimus lophatus*, appear to have been present. All three of these forms became extinct near the Oligocene-Miocene boundary with only *Eumys* being certainly present in the Geringian. However, even *Eumys* is known only from one Geringian locality, and this locality is near the base of the Gering Formation. This extinction may be related to a return of mesic conditions and the subsequent expansion of the genera *Leidymys*, *Geringia*, and *Paciculus*.

The dentitions of *Eoeumys exiguus* and *E. vetus* have been discussed in detail (Wood, 1937, p. 254-255; Galbreath, 1953, p. 71-72; Alker, 1968; Dawson & Black, 1970). They do have pinnately ridged incisors (but not as illustrated by Alker), well-developed buccal cingula (and in some examples lingual cingula) on the molars, posterior cingular confluent with the metaconid and entoconid in some examples and strong transverse lophs. Dawson and Black (1970) suggested that many of these features may not be characteristic of *Eoeumys exiguus*. If so, these features would serve fur-

ther to separate that species from *E. vetus*. It seems likely that they were correct in their conclusion that *Paracricetodon* has not been found in North America. The relatively large size and elongate shape of the M^3 in *Paracricetodon* contrasts strongly with the smaller, rounder M^3 of *Eoeumys*. Although *Eoeumys* probably did give rise to *Scottimus* as well as *Paciculus, Leidymys,* and *Geringia,* Black's (1961a, p. 3) placement of *Eoeumys exiguus* in *Scottimus* is probably not the best arrangement. It is easily separated from that genus by the shape of M^1, which has a more distinctly buccal anterocone, and by the ridging on the lower incisors. It stands closer to *Leidymys* in many features, but differs from that genus in the presence of pinnately ridged lower incisors.

Geringia and *Paciculus* show an increase in hypsodonty over that in the lower dentitions of *Eoeumys*. Almost all of the features found in these genera also occur in *Eoeumys,* including the anterior basin and posterior "V" on M_1 and the high angular protoconid on that tooth. The high buccal crests found on *Geringia* and *Paciculus* are the cingula much increased in height. *Geringia* and *Paciculus* represent cricetids with planar grinding surfaces. Perhaps associated with this is the development of small, square eomyidlike molars. The typical Oligocene eomyids *Adjidaumo* and *Paradjidaumo* have not been found in the Gering or Sharps formations where *Geringia* is abundant, and (unless *Zetamys* is an eomyid) no eomyids are presently known from the Gering. During the late Oligocene there was apparently a tendency in all the lineages of North American cricetids for the cheekteeth to become shorter and more square with a general tendency for the late Oligocene and early Miocene cricetids to develop less shear and more grinding on the molars. This is especially evident on the M^1 in *Eumys brachyodus, Scottimus lophatus,* and *Paciculus* and reached its extreme condition in *Geringia.*

Eoeumys exiguus has a double sagittal crest and smooth upper incisors as do *Leidymys* and *Geringia*. The infraorbital foramina are large, and the M^1 has a large buccal anterocone. The lower jaw of *Eoeumys exiguus* is elongate, and not robust like the

ramus of *Eumys,* the diastema is long and slender and the dorsal margin may be depressed as far below the cheek teeth as in *Eumys*. The mental foramen is situated on the diastema slightly above the midline of the ramus (just above the incisor) and considerably in front of the M_1. The anteroventral margin of the ramus bears a slight dependent flange. The dorsal and ventral masseteric lines meet low on the ramus at a sharp angle under the posterior margin of M_1. They extend a short distance anteriorly as a ridge. There is a very shallow depression between M_3 and the ascending ramus. The lower incisor is pinnately ridged. Most of these features probably also occur in the common ancestor of the Eurasian and North American cricetids.

Phylogeny and taxonomy.—Mein and Freudenthal (1971) based their classification (at the subfamily level) largely on the position of the incisive foramina. The Paracricetodontinae, Cricetodontinae, Cricetinae, Anomalomyinae, and Plataeanthomyinae have short incisive foramina that terminate anterior to M^1. In the Eucricetodontinae and Melissiondontinae the incisive foramina terminate posterior to M^1. They did not consider taxa that occur outside of the Tertiary of Europe, and in attempting to apply Mein and Freudenthal's criteria to North American cricetids, I was confronted in the Eumyinae with variation in the size and position of the incisive foramina (Fig. 24A-G) that encompassed all the variation thought to characterize their subfamilies. My inclusion of *Geringia* and *Paciculus* in Eucricetodontinae also changes the diagnosis of that subfamily, as they have their incisive foramina anterior to M^1 (Fig. 24L,M). They are both closely related to *Leidymys* based on a number of characters, and *Leidymys* does have the foramina across from M^1. Although the incisive foramina is of some use, especially in characterizing genera, I would not give it the weight given it in Mein and Freudenthal's classification. The earliest cricetids that I have examined have long incisive foramina across from M^1, but this must be a derived condition as sciuravids have short incisive foramina much anterior to M^1, and I interpret short incisive foramina in cricetids as reversals rather than as primitive. This is clearly the case in the Geringini and in

Coloradoeumys.

Mein and Freudenthal pointed out that the entepicondylar foramen is absent from the humeri of the Cricetodontinae (except for
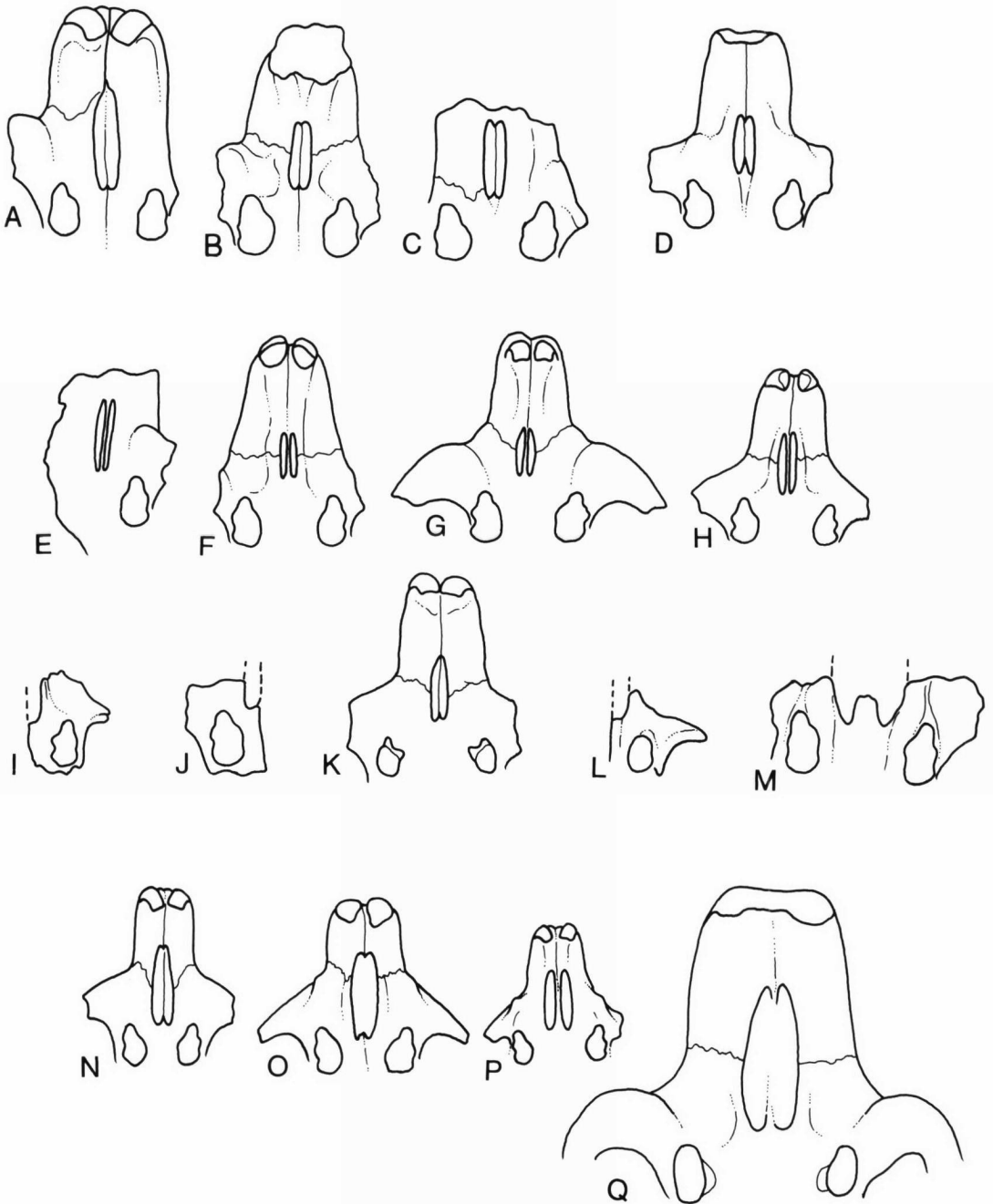

Fig. 24. Incisive foramina of early cricetids. A-F, *Eumys;* G, *Coloradoeumys;* H, I, *Eoeumys vetus;* J, *Scottimus lophatus;* K, *Geringia mcgregori;* L, *Paciculus nebraskensis;* M, *Leidymys nematodon;* N, *Eucricetodon incertum;* O, *Megacricetodon* aff. *gregarium;* P, *Ruscinomys lavocati;* Q, *Leidymys lockingtonianus.* N-P after Hartenberger, 1967, pl. 1, 3, 4; not drawn to scale.
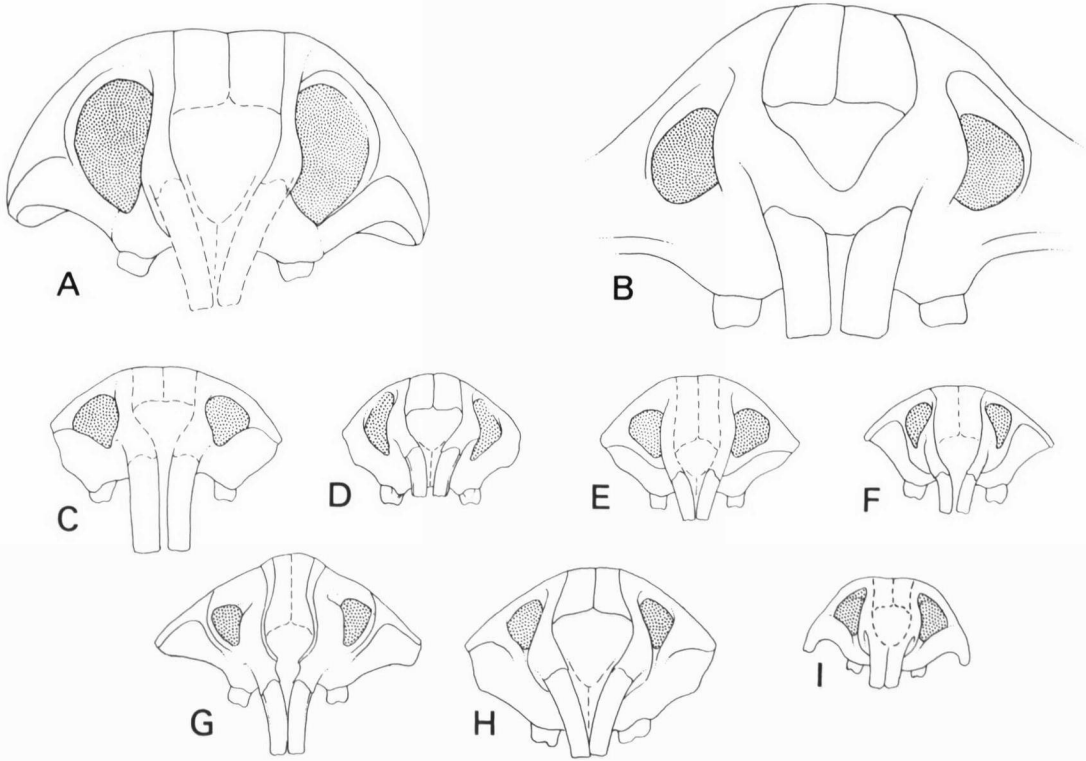
Fig. 25. Infraorbital foramina of early cricetids. a, *Leidymys lockingtonianus;* B, *Cricetops dormiter;* C, *Geringia mcgregori;* D, *Eoeumys vetus;* E, *Eucricetodon incertum;* F, *Megacricetodon* aff. *gregarium;* G, *Coloradoeumys galbreathi;* H, *Eumys elegans;* I, *Ruscinomys lavocati.* E, F, I after Hartenberger, 1967, pl. 1-3; not drawn to scale.

Fahlbuschia) but present in the Cricetinae. The Paracricetodontinae and Anomalomyinae also lack entepicondylar foramina on the humeri but they are present in the Hesperomyinae. Skeletal material is unknown for most of the North American cricetids, but in *Geringia* there is no entepicondylar foramen on the humerus. Entepicondylar foramina on the humeri occur in paramyids and must be considered a primitive feature for the Cricetidae.

The infraorbital foramen (Fig. 25) is another feature of considerable use in classifying fossil cricetids. Modern cricetids are "myomorphs," having the deep masseter muscle passing high through the infraorbital foramen and inserting dorsally on the maxilla, and the infraorbital canal is constricted ventrally. In known sciuravids the infraorbital foramen is small and a muscle probably does not pass through it. In *Eoeumys* the infraorbital foramen is large and not much constricted ventrally. I interpret this as the basic form from which the other patterns are derived. The "myomorph" pattern results from progressive constriction of the ventral margins of the infraorbital foramen and has developed independently in at least the eumyines and the cricetines. The other tendency is for the foramen to enlarge until it is essentially hystricomorphous as in *Leidymys* (Fig. 25A).

At the generic level, I have found the configurations of the lower incisors and the features on their enamel to be the most useful characters. The eumyines all have smooth incisor enamel, and the genera *Coloradoeumys* and *Eumys* have lower incisors with a characteristic heart-shaped cross section, with the enamel extending labially, halfway up the side of the incisor. *Wilsoneumys* has a lower incisor with a triangular cross section and a flat anterior surface. Except for *Scottimus,* which may have smooth enamel, all eucrice-

todontines in North America have lower incisors with a triangular cross-section and ridged enamel (Fig. 26). The ridging on the enamel can be segregated into three basic types (Fig. 26A-C): the *Eoeumys* type with many small pinnate ridges (found only in *Eoeumys*); the *Leidymys* type with three large evenly spaced ridges (the inner one is almost centrally located) and one or two small closely spaced lingual ridges (found in *Leidymys* and *Paciculus*); and the *Geringia* type with large flat incisors bearing a single medial ridge (found in *Geringia*). The upper incisors may or may not be ridged. Primitively the incisors were probably smooth as they are in paramyids and sciuravids. The earliest ridge pattern is the *Eoeumys* pattern and I believe that the *Leidymys* pattern can be derived from it by the loss of most of the ridges and the emphasizing of five longitudinally oriented ridges, and the *Geringia* pattern can be obtained by the further loss of all ridges in the *Leidymys* pattern except the central one.

At the generic level in the Oligocene and Miocene cricetids of North American, the M^1 seems to be the most diagnostic tooth, especially in the shape and position of the anterocone. In *Eoeumys* it is a large, conical, buccal cusp almost one-third the length of the tooth. In *Eumys* the M^1 is less elongate and the relative size of the anterocone decreases with time. In *Leidymys* the M^1 is also more square and the relative size of the anterocone reduced. In *Paciculus* the anterocone is reduced and in *Geringia* it is completely assimilated into the anteroloph. Also in *Paciculus* the protocone attaches lingually to the anterocone whereas in *Leidymys* it attaches to the center of the anterocone through an anterior mure. In *Eoeumys* there was probably no connection primitively between the anterocone and the protocone, and these connections arose as the teeth became more hypsodont and lophate. In *Scottimus* and *Wilsoneumys* the buccal arrangement of the anterocone is modified so that the large triangular anterocone is centered on the tooth.

The anterocone on M^1 never seems to bifurcate as it often does in the Cricetodontinae. The molars themselves may either show planar wear (*Paciculus, Geringia, Wilsoneumys*) or may be terraced (see Hershkovitz, 1962, p. 86-88, for a thorough discussion of these terms). The cusps on the molars tend to lie across from each other rather than being strongly alternating.

The masseteric lines on the rami are of some taxonomic value. In *Leidymys, Paciculus,* and *Geringia* the ventral line is very strongly developed and continues anteriorly as a shelf under M_1. Primitively, the dorsal and ventral masseteric lines meet in a "V," but in *Eumys brachyodus, Wilsoneumys,* and *Scottimus* they meet in a broad curve.
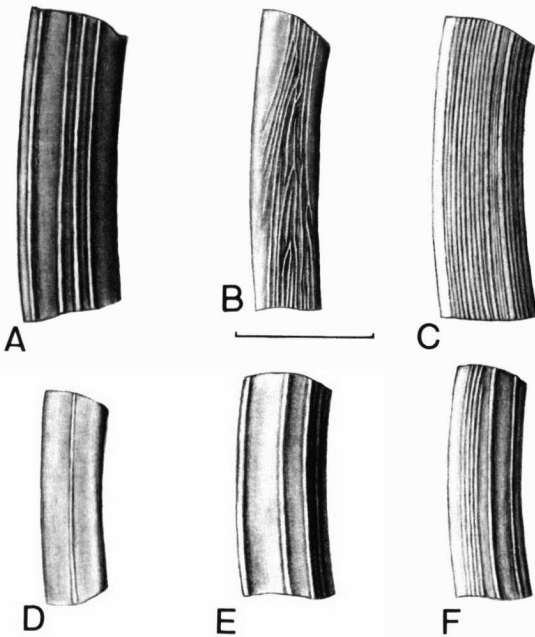

Fig. 26. Ventral views of left lower incisors. A, *Leidymys blacki;* B, *Eoeumys vetus;* C, *Yatkolamys edwardsi;* D, *Geringia mcgregori;* E, *Paciculus insolitus;* F, *Eucricetodon collatum.* Scale = 3 mm.

REFERENCES

Alker, Julius, 1966, A review of *Eumys elegans* Leidy, 1856 (Muridae: Mammalia): Proc. Nebr. Acad. Sci., v. 75, p. 12.

———, 1967, Review of the North American fossil cricetine rodents: unpubl. Ph. D. diss., Univ. Nebraska, Lincoln, 303 p.

_____, 1968, The occurrence of *Paracricetodon* Schaub (Cricetidae) in North America. J. Mammal., v. 49, p. 529-530.

_____, 1969, *Paciculus* (Cricetinae, incertae sedis) teeth from the Miocene of Nebraska: J. Paleontol., v. 43, p. 171-174.

Berggren, W. A., 1972, A Cenozoic time-scale—Some implications for regional geology and paleobiogeography: Lethaea, v. 5, p. 195-215.

Black, C.C., 1961a, Rodents and lagomorphs from the Miocene Fort Logan and Deep River formations of Montana: Postilla, no. 48, 20 p.

_____, 1961b, Fossil mammals from Montana, Pt. 1, Additions to the late Miocene Flint Creek local fauna. Ann. Carnegie Mus., v. 36, p. 69-76.

_____, 1961c, New rodents from the early Miocene deposits of Sixty-Six Mountain, Wyoming: Breviora, no. 146, 7 p.

_____, 1963, Miocene rodents from the Thomas Farm local fauna, Florida: Bull. Mus. Comp. Zool. Harv. Univ., v. 128, p. 483-501.

Clark, J.B., Dawson, M.R., and Wood, A.E., 1964, Fossil mammals from the lower Pliocene of Fish Lake Valley, Nevada: Bull. Mus. Comp. Zool. Harv. Univ., v. 131, p. 27-63.

Cope, E.D., 1879, Second contribution to a knowledge of the Miocene fauna of Oregon: Proc. Am. Philos. Soc., v. 18, p. 370-376.

_____, 1881a, On the Nimravidae and Canidae of the Miocene Period: U.S. Geol. Geogr. Surv. Territ., v. 6, p. 165-181.

_____, 1881b, Review of the Rodentia of the Miocene Period of North America: U.S. Geol. Geogr. Surv. Territ., v. 6, p. 361-386.

_____, 1881c, The Rodentia of the American Miocene: Am. Nat., v. 15, p. 586-587.

_____, 1884, The Vertebrata of the Tertiary formations of the West: Rept. U.S. Geol. Surv. Territ., v. 3, p. 1-1009.

Dawson, M.R., 1968, Middle Eocene rodents (Mammalia) from northeastern Utah: Ann. Carnegie Mus., v. 39, p. 327-370.

_____, and Black, C.C., 1970, The North American cricetid rodent "*Eumys*" *exiguus*, once more: J. Paleontol., v. 44, p. 524-526.

Emry, R.J., and Dawson, M.R., 1972, A unique cricetid (Rodentia, Mammalia) from the early Oligocene of Natrona County, Wyoming: Am. Mus. Novit., no. 2508, 14 p.

_____, and _____, 1973, *Nonomys*, new name for the cricetid (Rodentia, Mammalia) genus *Nanomys* Emry and Dawson: J. Paleontol., v. 47, p. 1003.

Evernden, J.F., Savage, D.E., Curtis, G.H., and James, G.T., 1964, Potassium-argon dates and the Cenozoic mammalian chronology of North America: Am. J. Sci., v. 262, p. 145-198.

Galbreath, E.C., 1953, A contribution to the Tertiary geology and paleontology of northeastern Colorado: Univ. Kans. Paleontol. Contrib., Artic. 13 (Vertebrata 4), 120 p.

Hartenberger, J.L., 1967, Contributions à l'étude de l'anatomie cranienne des rongeurs, 1, Principaux types de Cricétodontines: Paleovertebrata, v. 1, p. 47-64.

Hershkovitz, P., 1962, Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group: Fieldiana, Zool., v. 46, p. 1-524.

Leidy, Joseph, 1856, Notices of remains of extinct Mammalia discovered by Dr. F.V. Hayden in Nebraska Territory: Proc. Acad. Nat. Sci. Philadelphia, v. 8, p. 88-90.

_____, 1869, The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America: J. Acad. Nat. Sci. Philadelphia, v. 7, p. 1-472.

Lindsay, E.H., 1968, Rodents from the Hartman Ranch local fauna, California: Paleobios, no. 6, 22 p.

_____, 1972, Small mammal fossils from the Barstow Formation, California: Univ. Calif. Publ. Geol. Sci., no. 93, 104 p.

_____, 1977, *Simimys* and the origin of the Cricetidae (Rodentia: Muroidea): Geobios, v. 10, p. 597-623.

_____, 1978, *Eucricetidon asiaticus* (Matthew and Granger), an Oligocene rodent (Cricetidae) from Mongolia: J. Paleontol., v. 52, p. 590-595.

Lillegraven, J.A., and Wilson, R.W., 1975, Analysis of *Simimys simplex*, an Eocene rodent (?Zapodidae): J. Paleontol., v. 49, p. 856-874.

MacDonald, J.R., 1963, The Miocene faunas from the Wounded Knee area of western South Dakota: Bull. Am. Mus. Nat. Hist., v. 125, p. 139-238.

_____, 1970, Review of the Miocene Wounded Knee faunas of southwestern South Dakota: Bull. Los Angeles. Cty. Mus. Nat. Hist. Sci., v. 8, p. 1-82.

McKenna, M.C., 1965, Stratigraphic nomenclature of the Miocene Hemingford Group, Nebraska: Am. Mus. Novit., no. 2228, 21 p.

Martin, J.E., 1976, Small mammals from the Miocene Batesland Formation of South Dakota: Contrib. Geol., Univ. Wyo., v. 14, p. 69-98.

Martin, L.D., 1972, The mammalian fauna of the lower Miocene Gering Formation and the early evolution of the North American Cricetidae: unpubl. Ph.D. diss., Univ. Kansas, Lawrence, 219 p.

_____, 1974, New rodents from the lower Miocene Gering Formation of western Nebraska: Occas. Pap. Mus. Nat. Hist. Univ. Kans., no. 32, 12 p.

_____, 1975, Biostratigraphic relationships of the early Miocene Gering fauna: Proc. Nebr. Acad. Sci., v. 85, p. 41.

_____, and Corner, R.G., 1980, A new genus of cricetid rodent from the Hemingfordian (Miocene) of Nebraska: Univ. Kans. Paleontol. Contrib., Pap. 103, 6 p.

Matthew, W.D., 1889, Is the White River Tertiary an aeolian formation?: Am. Nat., v. 33, p. 404-408.

_____, and Granger, Walter, 1923, Nine new rodents from the Oligocene of Mongolia: Am. Mus. Novit., no. 102, p. 1-10.

Mein, Pierre, and Freudenthal, Matthew, 1971, Une nouvelle classification des Cricetidae (Mammalia, Rodentia) du Tertiaire de l'Europe: Scr. Geol., no. 2, 37 p.

Obradovich, J.D., Izett, G.A., and Naeser, C.W., 1973, Radiometric ages of volcanic ash and pumice beds in the Gering sandstone (earliest Miocene) of the Arikaree Group, southwestern Nebraska: Abstr. Pro-

grams, G.S.A. 26th Ann. Meeting, Rocky Mountain Sec., v. 5, p. 499-500.

Osborn, H.F., 1910, The age of mammals in Europe, Asia, and North America: MacMillan Co., (New York), 635 p.

Rensberger, J.M., 1975, *Haplomys* and its bearing on the origin of the aplodontoid rodents: J. Mammal., v. 56, p. 1-14.

Repenning, C.A., 1968, Mandibular musculature and the origin of the subfamily Arvicolinae (Rodentia): Acta Zool. Cracov., v. 13, p. 29-72.

Russell, L.S., 1972, Tertiary mammals of Saskatchewan, Part II, The Oligocene fauna, non-ungulate orders: R. Ont. Mus., Life Sci. Contrib. 84, p. 1-63.

Schultz, C.B., and Falkenbach, C.H., 1968, The phylogeny of the oreodonts, Part I, Merycoidodontinae, Eporeodontinae, and Leptaucheniinae, three subfamilies of oreodonts, with an appendix to the revision of the Merycoidodontidae, Part II, Summary and conclusions concerning the Merycoidodontidae: Bull. Am. Mus. Nat. Hist., v. 139, p. 1-498.

Schultz, C.B., and Stout, T.M., 1955, Classification of Oligocene sediments in Nebraska: Bull. Univ. Nebr. State Mus., v. 4, p. 17-52.

Setoguchi, T., 1978, Paleontology and geology of the Badwater Creek area, central Wyoming, Part 16, The Cedar Ridge local fauna: Bull. Carnegie Mus. Nat. Hist., no. 9, 61 p.

Simpson, G.G., 1945, The principles of classification and a classification of mammals: Bull. Am. Mus. Nat. Hist., v. 85, p. 1-350.

Sinclair, W.J., 1905, New or imperfectly known rodents and ungulates from the John Day series: Univ. Calif. Publ., Dep. Geol., Bull., v. 4, p. 125-143.

Stehlin, H.G., and Schaub, Samuel, 1951, Die Trigonodontie der simplicidentaten Nager: Schweiz. Naturf. Ges. Schweiz. Palaeontol. Abh., v. 67, p. 1-385.

Stock, Chester, 1935, New genus of rodent from the Sespe Eocene: Geol. Soc. Am. Bull., v. 46, p. 61-68.

Tedford, R.H., 1970, Principles and practices of mammalian geochronology in North America: Proc. North Am. Paleontol. Conv., F, p. 666-703.

Thaler, L., 1966, Les rongeurs fossiles du Bas-Languedoc dans leur rapports avec l'histoire des faunes et la stratigraphie d'Europe: Mem. Mus. Nat. Hist. Nat. Paris Ser. C, v. 17, p. 1-295.

Vianey-Liaud, M., 1974, L'anatomie cranienne des genères *Eucricetodon* et *Pseudocricetodon* (Cricetidae, Rodentia, Mammalia); essai de systématique des Cricétidés oligocènes d'Europe occidentale: Geol.

Mediterr., v. 1, p. 111-132.

White, T.H., 1954, Preliminary analysis of the fossil vertebrates of the Canyon Ferry Reservoir area: Proc. U.S. Nat. Mus., v. 103, p. 305-438.

Wilson, J.A., 1975, Geochronology, stratigraphy, and typology: Fieldiana, Geol., v. 33, p. 193-204.

————, Twiss, P.C., DeFord, R.K., and Clabaugh, S.E., 1968, Stratigraphic succession, potassium-argon dates, and vertebrate faunas, Vieja Group, Rim Rock County, Trans-Pecos Texas: Am. J. Sci., v. 266, p. 590-604.

Wilson, R.W., 1935a, Cricetine-like rodents from the Sespe Eocene of California: Proc. Nat. Acad. Sci. USA, v. 21, p. 26-32.

————, 1935b, *Simimys,* a new name to replace *Eumysops* Wilson, preoccupied: a correction: Proc. Nat. Acad. Sci. USA, v. 21, p. 179-180.

————, 1949a, On some White River fossil rodents: Carnegie Inst. Washington Publ., v. 584, p. 27-50.

————, 1949b, Rodents and lagomorphs of the Upper Sespe: Carnegie Inst. Washington Publ., v. 584, p. 51-65.

————, 1960, Early Miocene rodents and insectivores from northeastern Colorado: Univ. Kans. Paleontol. Contrib., Artic. 24 (Vertebrata 7), 92 p.

Wood, A.E., 1935, Two new genera of cricetid rodents from the Miocene of western United States: Am. Mus. Novit., no. 789, 3 p.

————, 1936, The cricetid rodents described by Leidy and Cope from the Tertiary of North America: Am. Mus. Novit., no. 822, 8 p.

————, 1937, The mammalian fauna of the White River Oligocene, Part II, Rodentia: in W.B. Scott, G.L. Jepsen, and A.E. Wood, The mammalian fauna of the White River Oligocene. Trans. Am. Philos. Soc., n. s., v. 28, p. 155-269.

————, 1969, Rodents and lagomorphs from the "Chadronia" Pocket," early Oligocene of Nebraska: Am. Mus. Novit., no. 2366, 18 p.

————, 1974, Early Tertiary vertebrate faunas, Vieja Group, Trans-Pecos Texas, Rodentia: Bull. Tex. Mem. Mus. No. 21, 111 p.

————, and Wilson, R.W., 1936, A suggested nomenclature for the cusps of the cheek teeth of rodents. J. Paleontol., v. 10, p. 388-391.

Wood, H.E., 2nd, Chaney, R.W., Colbert, E.H., Jepsen, G.L., Reeside, J.B., Jr., and Stock, C., 1941, Nomenclature and correlation of the North American continental Tertiary: Geol. Soc. Am. Bull., v. 52, p. 1-48.