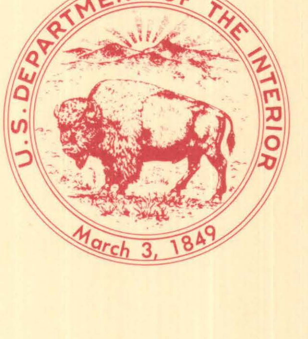
The Microtine Rodents of the Cheetah Room Fauna, Hamilton Cave, West Virginia, and the Spontaneous Origin of *Synaptomys*

U.S. GEOLOGICAL SURVEY BULLETIN 1853



AVAILABILITY OF BOOKS AND MAPS OF THE U.S. GEOLOGICAL SURVEY

Instructions on ordering publications of the U.S. Geological Survey, along with prices of the last offerings, are given in the current-year issues of the monthly catalog "New Publications of the U.S. Geological Survey." Prices of available U.S. Geological Survey publications released prior to the current year are listed in the most recent annual "Price and Availability List." Publications that are listed in various U.S. Geological Survey catalogs (**see back inside cover**) but not listed in the most recent annual "Price and Availability List" are no longer available.

Prices of reports released to the open files are given in the listing "U.S. Geological Survey Open-File Reports," updated monthly, which is for sale in microfiche from the U.S. Geological Survey, Books and Open-File Reports Section, Federal Center, Box 25425, Denver, CO 80225. Reports released through the NTIS may be obtained by writing to the National Technical Information Service, U.S. Department of Commerce, Springfield, VA 22161; please include NTIS report number with inquiry.

Order U.S. Geological Survey publications **by mail** or **over the counter** from the offices given below.

BY MAIL

Books

Professional Papers, Bulletins, Water-Supply Papers, Techniques of Water-Resources Investigations, Circulars, publications of general interest (such as leaflets, pamphlets, booklets), single copies of Earthquakes & Volcanoes, Preliminary Determination of Epicenters, and some miscellaneous reports, including some of the foregoing series that have gone out of print at the Superintendent of Documents, are obtainable by mail from

U.S. Geological Survey, Books and Open-File Reports
Federal Center, Box 25425
Denver, CO 80225

Subscriptions to periodicals (Earthquakes & Volcanoes and Preliminary Determination of Epicenters) can be obtained ONLY from the

Superintendent of Documents
Government Printing Office
Washington, D.C. 20402

(Check or money order must be payable to Superintendent of Documents.)

Maps

For maps, address mail orders to

U.S. Geological Survey, Map Distribution
Federal Center, Box 25286
Denver, CO 80225

Residents of Alaska may order maps from

Alaska Distribution Section, U.S. Geological Survey,
New Federal Building - Box 12
101 Twelfth Ave., Fairbanks, AK 99701

OVER THE COUNTER

Books

Books of the U.S. Geological Survey are available over the counter at the following Geological Survey Public Inquiries Offices, all of which are authorized agents of the Superintendent of Documents:

- **WASHINGTON, D.C.**--Main Interior Bldg., 2600 corridor, 18th and C Sts., NW.
- **DENVER, Colorado**--Federal Bldg., Rm. 169, 1961 Stout St.
- **LOS ANGELES, California**--Federal Bldg., Rm. 7638, 300 N. Los Angeles St.
- **MENLO PARK, California**--Bldg. 3 (Stop 533), Rm. 3128, 345 Middlefield Rd.
- **RESTON, Virginia**--503 National Center, Rm. 1C402, 12201 Sunrise Valley Dr.
- **SALT LAKE CITY, Utah**--Federal Bldg., Rm. 8105, 125 South State St.
- **SAN FRANCISCO, California**--Customhouse, Rm. 504, 555 Battery St.
- **SPOKANE, Washington**--U.S. Courthouse, Rm. 678, West 920 Riverside Ave..
- **ANCHORAGE, Alaska**--Rm. 101, 4230 University Dr.
- **ANCHORAGE, Alaska**--Federal Bldg, Rm. E-146, 701 C St.

Maps

Maps may be purchased over the counter at the U.S. Geological Survey offices where books are sold (all addresses in above list) and at the following Geological Survey offices:

- **ROLLA, Missouri**--1400 Independence Rd.
- **DENVER, Colorado**--Map Distribution, Bldg. 810, Federal Center
- **FAIRBANKS, Alaska**--New Federal Bldg., 101 Twelfth Ave.

The Microtine Rodents of the Cheetah Room Fauna, Hamilton Cave, West Virginia, and the Spontaneous Origin of *Synaptomys*

By CHARLES A. REPENNING and FREDERICK GRADY

Remarkably primitive rodents indicate the need for
revisions in evolutionary concepts of bog lemmings and
heather voles

U.S. GEOLOGICAL SURVEY BULLETIN 1853

DEPARTMENT OF THE INTERIOR
DONALD PAUL HODEL, Secretary

U.S. GEOLOGICAL SURVEY
Dallas L. Peck, Director

March 3, 1849

UNITED STATES GOVERNMENT PRINTING OFFICE, WASHINGTON: 1988

For sale by the
Books and Open-File Reports Section
U.S. Geological Survey
Federal Center, Box 25425
Denver, CO 80225

Library of Congress Cataloging in Publication Data

Repenning, Charles Albert, 1922–
The microtine rodents of the Cheetah Room Fauna, Hamilton Cave, West Virginia, and the spontaneous origin of Synaptomys.
(U.S. Geological Survey bulletin ; 1853)
Bibliography: p.
1. Cricetidae, Fossil—West Virginia—Hamilton Cave. 2. Paleontology—West Virginia—Hamilton Cave. I. Grady, Frederick. II. Title. III. Series.
QE75.B9 no. 1853 [QE882.R6] 557.3 s [569'.323] 88-600217

CONTENTS

FIGURES

The Microtine Rodents of the Cheetah Room Fauna, Hamilton Cave, West Virginia, and the Spontaneous Origin of *Synaptomys*

By Charles A. Repenning *and* Frederick Grady[1]

Abstract

The Cheetah Room fauna of Hamilton Cave, West Virginia, is a full complement of vertebrates including microtine rodents. The microtines are represented by a new species of the subgenus *Mimomys* (*Cromeromys*) that was formerly known only from Eurasia, a new species of *Phenacomys* similar to *P. albipes, Allophaiomys pliocaenicus, Lasiopodomys deceitensis* that was formerly known only from the arctic region, *Microtus paroperarius, Pitymys hibbardi, Ondatra annectens*, a bog lemming intermediate between the genera *Mictomys* and *Synaptomys*, and *Atopomys salvelinus*. The transitional morphologic variations, between ancestor and descendants, of *Phenacomys*, the bog lemming, and *Pitymys hibbardi*, as well as the presence of *Microtus paroperarius*, are the principal reasons for an age assignment of between 740,000 and 850,000 years.

The history of the bog lemmings begins 4 million years ago in southeastern Europe with *Plioctomys mimomiformis*, of unknown ancestry. This species dispersed eastward across Asia to Beringia, where its youngest record is 2.4 million years old; during this first 1.6 million years of the history there was no detected morphologic change in the dentition. However, between 3 and 2.6 million years ago these bog lemmings also dispersed southward from Beringia to the United States on both sides of the Rocky Mountains, during which dispersal they evolved east of the cordillera into a new species, *Plioctomys rinkeri*, and to the west into a new genus and species, *Mictomys vetus*.

By 2.0 million years ago *Mictomys* spread eastward around the southern end of the Rocky Mountains and *Plioctomys* became extinct. More than 1 million years later *Synaptomys* abruptly evolved out of a southeastern population of *Mictomys* in one of the more remarkable morphologic transitions known in vertebrate paleontology, as recorded in the Cheetah Room fauna.

INTRODUCTION

Fossil rodents were discovered in the Cheetah Room of Hamilton Cave, John Guilday Cave Preserve, Pendleton County, West Virginia, in 1981 by Miles Drake and Carole Sneed of the Potomac Speleological Club. The name of the room derives from the later discovery of the skeleton of a cheetah-like felid. A large variety of fossil mammals and other vertebrates is known from the Cheetah Room fauna and comes from the top 75 cm of cave earth; most of the fauna is still under study. Seventy-five centimeters could represent an appreciable period of time, but no changes in the fauna were noted during excavation.

The microtine fauna contains a new species of the genus *Mimomys* nearly identical to the European *Mimomys tornensis* Janossy and van der Meulen (1975), a new species of the genus *Phenacomys* that is related to *P. albipes, Allophaiomys pliocaenicus, Lasiopodomys deceitensis, Microtus paroperarius, Pitymys hibbardi, Ondatra annectens*, a bog lemming intermediate between *Synaptomys* and *Mictomys*, and *Atopomys salvelinus*. The last species is under study by Alisa Winkler and Frederick Grady and is not discussed here.

Mimomys and *Lasiopodomys* are not known from faunas of central or western conterminous United States that are of the same approximate age; *Pitymys hibbardi* and *Atopomys salvelinus* represent two lineages that seem to have a fossil and, in the case of *Pitymys*, living distribution only in the eastern and central United States; and the suggested origin of the southern bog lemming is in the southeastern United States. These regional distributions suggest a provinciality that may be related to differing environments. Conversely, it would seem that *Allophaiomys* and *Microtus paroperarius*, known from the Rocky Mountains to the Atlantic, and *Phenacomys*, known from the Pacific to the Atlantic coasts, had broader environmental tolerances. The suggestion of a provincial environmental difference may bear on the

---

Publication approved by the Director, U.S. Geological Survey, April 12, 1988.

[1] National Museum of Natural History, Mail Stop 121, Smithsonian Institution, Washington, D.C. 20560.

spontaneous origin of *Synaptomys*, but no other external cause is yet recognized.

Age of the Fauna

Based upon the gradation between the bog lemmings *Mictomys* and *Synaptomys*, to be described, the Cheetah Room fauna is believed to be older than the Fyllan Cave fauna of Texas, which contains two specimens of *Synaptomys cooperi* (TMM 40682-629, a first lower molar, and TMM 40682-295, a second lower molar) and which is in reversely magnetized deposits (Alisa Winkler, written commun., 1987). The Cheetah Room fauna is thus considered to be older than the Brunhes Normal Polarity Chron, beginning 740,000 years ago.

Although *Microtus* and *Lasiopodomys* are known from Canada and Alaska as much as 2.1 million years ago (Repenning and others, 1987), there is no record of them east of the Rocky Mountains in the conterminous United States until the beginning of the Nebraskan glaciations (as used by Repenning, 1984) 850,000 years ago. The oldest prior record of *Microtus paroperarius* in the lower-latitude United States is from the 820,000-year-old part of the Hansen Bluff faunal sequence of Colorado (Rogers and others, 1985). Although the sample of this species from the Cheetah Room fauna is very small, it more resembles that from Hansen Bluff than it does younger records. The Cheetah Room fauna is thus considered to be somewhat younger than 850,000 years but possibly no younger than 820,000 years. *Lasiopodomys* from the Cheetah Room fauna is the first record of this genus from the conterminous United States, but its older records from Canada and Alaska suggest some antiquity.

Individual variation in the dental morphology of the species *Pitymys hibbardi* from the Cheetah Room fauna overlaps that of both ancestral *Allophaiomys pliocaenicus* and the descendant species of *Pitymys*, and also suggests some antiquity, although the suggestion is vague in terms of radiometric years. Similarly, the stage of evolution of the new species of *Phenacomys*, to be described, is intermediate between 1.7-million-year-old ancestors and 13,000-year-old and living descendants, although this condition is certainly more vague in terms of age.

Terminology

Although recently criticized for a lack of standardization (Martin, 1987), the terminology herein used for parts of the teeth is as standard as we consider possible. It is that used and explained by Repenning (1983) and is based upon those terms that seem most frequently used in several languages of the Northern Hemisphere. There are, of course, conflicts in terminology: for example, reports in the Russian languages frequently refer to the "anteroconid complex" as the "paraconid section." When it appears that a non-English-language term has been applied more consistently and with better understanding than an English language term, such a term may be used: for example, due to the work of Wighart von Koenigswald, "Schmelzmuster" has a particular meaning, regarding the patterns of enamel rod orientation and their distribution throughout the enamel layer forming the surfaces of the cheek teeth, that would be lost by translation into the English.

The evolution of dental terminology may be reviewed in Hinton (1926, p. 102–124), who was more concerned with homologies than with a standard terminology; Hibbard (1950, fig. 16), who was concerned with standardization; Repenning (1968, fig. 10), who was concerned with the origin of the features of the anteroconid complex (called "anterior cingulum"); van der Meulen (1973, p. 29–33, 52–59, and fig. 10), who was concerned with standardization by use of alphanumeric symbols; and Repenning (1983, p. 474), who was concerned with standardization of terms in the anteroconid complex.

Martin's (1987) whimsical discussion of the standardization of terminology simply stated that he prefers the alphanumeric symbols. These symbols have proven cumbersome to some, requiring frequent reference to the explanation for translation, as perhaps is illustrated by the repetition of the explanation of van der Meulen's symbols appearing in most of his publications, as well as in most publications by other authors who use these symbols, as Martin (1987). We do not prefer them.

Abbreviations

Lower molars are indicated by a lower case "m" and upper molars by an upper case "M."

For brevity, the abbreviation "m.y." is used in parenthetical statements to indicate "million years."

Specimens are identified by the catalog numbers of the institution in which they are housed, preceded by one of the following abbreviations:

F:AMNH: Frick collection: the American Museum of Natural History, New York.
HNHMB: Hungarian Natural History Museum, Budapest.
ISM: Illinois State Museum, Springfield.
IVPP:AS: Institute of Vertebrate Paleontology and Paleoanthropology: Academia Sinica, Beijing.
KU: University of Kansas, Museum of Natural History, Lawrence.
TMM: Texas Memorial Museum, Austin.
UA: University of Alaska, Fairbanks.

UC: University of Colorado Museum, Boulder.

UCMP: University of California Museum of Paleontology, Berkeley.

UF/FGS: Florida State Museum, University of Florida, Gainesville; specimen formerly in the collection of the Florida Geological Survey.

USGS: uncataloged specimens in the reference collection of the U.S. Geological Survey, Denver.

USNM: National Museum of Natural History, Washington.

ZZSD:PAN:C: Institute of Systematic and Experimental Zoology: Polish Academy of Science: Cracow.

Acknowledgments

The National Speleological Society, owner of Hamilton Cave, has supported and encouraged the studies of fossil vertebrates. Excavations of Hamilton Cave were financed in part by the National Geographic Society through a grant to Blaire Van Valkenburgh, Bjorn Kurten, and Frederick Grady. In addition to Miles Drake and Carole Sneed, many other volunteers helped haul out sacks of fossil-bearing cave earth from Hamilton Cave, in particular Tom Kaye, Bob Hoke, Dave West, Donald Keller, and Cindy Keller. Anthony D. Barnosky, Thomas M. Bown, Robert S. Hoffmann, and Alisa J. Winkler read versions of the manuscript and provided many helpful suggestions. Jordi Agusti, Charles S. Churcher, Oldrich Fejfar, Lawrence J. Flynn, Russell W. Graham, John E. Guilday, R. Dale Guthrie, Claude W. Hibbard, Robert S. Hoffmann, James G. Honey, J. Howard Hutchison, Murray L. Johnson, Kazimierz Kowalski, Robert A. Martin, Pierre Mein, Robert Purdy, Robert L. Rausch, Karel L. Rogers, Richard H. Tedford, S. David Webb, Melissa C. Winans, and Alisa J. Winkler provided specimens used in the study of the Cheetah Room microtines.

SYSTEMATICS

The classification here used follows that briefly discussed by Repenning (1987). The microtine (or arvicolid, as usually discussed) rodents are considered polyphyletic and consist of five separate cricetid subfamilies that independently evolved microtine-type cheek teeth out of low-crowned cricetid rodent teeth. The ancestries of three of these five subfamilies have been traced through the fossil record to different cricetid rodents with low-crowned cheek teeth; the two subfamilies with unknown ancestry are both lemmings, but otherwise they have no similarity in the fossil record and are grouped in separate subfamilies.

These five subfamilies are subdivided into tribes by more or less conventional criteria. The word "microtine" is used as a descriptive term referring to the type of tooth common to all of these five cricetid subfamilies: a tooth with tall, triangularly prismatic cusps.

Because this classification is relatively new, a diagnosis of the dental characters is provided for each discussed microtine taxon. These give only the diagnostic dental characters and are not concerned with diagnosis by other characters, although the authors believe that these other characters are conformable with the classification. Within the diagnoses, brackets are used for explanatory notes and are not to be considered part of the diagnosis.

Several very useful diagnostic characters are lost with the development of rootless cheek teeth in the microtine rodents, such as: (1) relative dentine tract development, (2) relative vertical height of the individual reentrants on the buccal surface of m1, and (3) relative degree of wear required to obliterate islets and other enamel irregularities that are evident only in the early stages of wear. With the loss of these characters found only on rooted teeth, the lineage of a specimen is less easily determined and individual variability becomes more troublesome. As will become evident, the average condition of the population thus becomes more important in the identification of microtine species with rootless cheek teeth.

Among microtines with rootless cheek teeth, it is commonplace to find some individuals of any population whose dental morphology overlaps that of closely related species. For this reason, small samples of fossil species often can be only questionably identified. Also for this reason, not only typical, but also extreme dental morphologies are illustrated herein.

Family CRICETIDAE
Subfamily ARVICOLINAE, Bonaparte, 1837 (following Kretzoi, 1969)

Dental diagnosis.—Cricetid rodents with hypsodont, triangularly prismatic cusps on their cheek teeth [microtines]; m1 with posterior loop and three basic alternating triangles, differing from the Ondatrinae and the Dicrostonychinae; anteroconid complex with single rounded to globular cap, differing from the Prometheomyinae; M3 with alternating triangles differentiated, not lophate, differing from the Lemminae.

Included tribes.—Arvicolini, Clethrionomyini, Lagurini, Microtini, and Pitymyini.

Tribe ARVICOLINI, Kretzoi, 1955

Dental diagnosis.—Arvicoline rodents with rooted cheek teeth, for the most part, differing from the Microtini, Pitymyini, and Lagurini; no additional triangles in the anteroconid complex of m1, differing from the Clethrionomyini; M3 with no more than two completely formed alternating triangles, differing from all tribes except some Lagurini.

Included genera.—Allophaiomys, ?Aratomys, Arvicola, Borsodia, Hibbardomys, Kislangia, Mimomys, Phaiomys, Phenacomys, Promimomys, and *Villanyia.*

Discussion.—The teeth of *Arvicola* are rootless, those of *Phenacomys* have additional triangles, and those of *Allophaiomys* (and *Phaiomys*) are rootless, but *Allophaiomys* appears ancestral to both the Tribe Microtini and the Tribe Pitymyini. Rather than establish separate tribes for each of these three genera because they deviate from the above diagnosis, they are placed in the ancestral Tribe Arvicolini by default.

Genus MIMOMYS, Forsyth Major, 1902

Dental diagnosis.—Arvicolinine rodents with rooted cheek teeth, differing from *Arvicola, Allophaiomys,* and *Phaiomys*; m1 with cap of anteroconid complex skewed lingually, differing from *Villanyia* and *Borsodia,* with primary wings and *Mimomys* Kante of anteroconid complex [marked x on fig. 1*A*] prominent, differing from *Promimomys* and, for the most part, *Phenacomys,* and with islet derived from a buccal reentrant preserved in most lineages and more persistent in early stages of evolution, differing from *Phenacomys, Kislangia, Borsodia,* and *Villanyia*; M3 with one buccal triangle and basined posterior loop (becoming an islet with wear) or two alternating triangles and hooked, but not elongate, posterior loop formed by lingual breaching of basined posterior loop so that an islet does not form, differing from *Villanyia* and *Borsodia,* which have an elongate posterior loop.

Included subgenera.—Cromeromys, Cseria, and *Mimomys* in Eurasia; *Cosomys, Cromeromys, Ogmodontomys,* and *Ophiomys* in North America. Other subgenera have been named in Eurasia (as *Katamys* and *Tjanshanomys*) but have been applied to only one species in most cases; they may merit subgeneric distinction.

Discussion.—Von Koenigswald and Martin (1984a) recently have suggested that *Mimomys* never was present in North America. This opinion was based upon differences they described in the Schmelzmuster, the pattern of the enamel rods and its distribution within the enamel on the sides of the cheek teeth cusps. All other morphologic features and the history of dispersal of *Mimomys* throughout the Northern Hemisphere contradict this opinion (Hinton, 1932; Wilson, 1934; Wood and others, 1941; Stirton, 1951; Repenning and Fejfar, 1977; Repenning, 1978; Repenning, 1980). In addition, the Schmelzmuster patterns examined by these authors were from some of the most endemically divergent species known from North America. The evidence of von Koenigswald and Martin (1984a) is here considered inadequate.

Subgenus CROMEROMYS, Zazhigin, 1980

Dental diagnosis.—A subgenus of *Mimomys* with no enamel islet in anteroconid complex of m1 or posterior loop of M3, differing from subgenera *Mimomys* and *Cseria* and older species of subgenera *Cosomys* and *Ophiomys; Mimomys* Kante present in many individuals, tending to be anteriorly placed relative to other subgenera; dentine tracts very well developed on the anterobuccal side of the anteroconid cap and exceptionally elongate and parallel sided on both buccal and lingual salient angles of the posterior loop of m1 except in the oldest known form (*Cromeromys* ex gr. *intermedius* of Zazhigin), differing from older species of other subgenera; m3 with completely confluent central triangles, more so than with other subgenera; M3 short with transversely wide posterior loop not extended posteriorly [fig. 1*B*], not having the basined posterior loop of early forms of other subgenera but characteristic of later forms of the genus and differing from *Borsodia*; cement present in all known forms, tending to be very heavy in most, differing from the subgenera *Mimomys* and *Cseria* in its early development and from *Borsodia* and *Hibbardomys* and the subgenera *Cosomys, Ophiomys, Ogmodontomys* in its presence; m1 is 2.5 to 3.1 mm in length, averaging smaller than in the subgenera *Mimomys, Cosomys,* and *Ogmodontomys.*

Included species.—Mimomys tornensis Janossy and van der Meulen, *M.* ex gr. *intermedius* of Zazhigin, *M. irtyshensis* Zazhigin, *M. intermedius* of Zazhigin; *M. newtoni* of Zazhigin, *M. gansunicus* Zheng, *M. virginianus* n. sp., and possibly *M. monohani* Martin [referred to the new genus *Loupomys* by von Koenigswald and Martin (1984a) on the basis of simplified Schmelzmuster, which has not been examined in the species of *Cromeromys*].

Discussion.—Zazhigin (1980) erected the genus *Cromeromys,* basing it on *Cromeromys irtyshensis* with the conception that *Mimomys savini* (= *intermedius*) and *Mimomys newtoni* should be included in it. However, at least some individuals of both *M. savini* and *M. newtoni* have an enamel islet with little wear. Repenning (in Repenning and others, 1987) agreed with the reality of *Cromeromys* because the characters of the genus (as defined) appeared very early in the history of the Arvicolini and carried well into the Pleistocene, apparently reflecting a discrete lineage. He also noted that some of the characters of *Cromeromys* were also characteristic of the genus *Mimomys* in North America (early loss of the islets and retention of the *Mimomys* Kante, but not the presence of cement).

Repenning (in Repenning and others, 1987) failed to note, however, the inconsistency in retaining the similarly distinct North American forms within *Mimomys* as subgenera, while recognizing *Cromeromys* as a full genus. For this reason, a more balanced classification is used here and *Cromeromys* is considered a subgenus of *Mimomys*.

Although Zazhigin's inclusion within *Cromeromys* of *Mimomys savini* and *Mimomys newtoni* (from the Cromerian of Europe, the source of his name) does not seem appropriate, at least one species of *Cromeromys* is present in Europe. This has been named *Mimomys tornensis* by Janossy and van der Meulen (1975). In the original description this species was described as being from the later Villanyian Osztramos-3 fauna of Hungary (the type locality) and from the early Biharian Kamyk fauna of Poland, where it occurs with *Allophaiomys pliocaenicus*. Therefore the temporal range of *Cromeromys* in central Europe is possibly 1 million years long, between 1.5 and 2.5 million years ago.

The subgenus has a longer time range in Asia; Zazhigin (1980) reported *Cromeromys* from the Beteke fauna of Kazakhstan (about 3.5 m.y. old) and from Tiraspolian faunas in the region of the Ob River valley (possibly as young as 850,000 years). A good evolutionary sequence of species is present during this time span, and this sequence is biostratigraphically useful. In China, *Mimomys gansunicus* Zheng belongs in this subgenus and Zheng and Li (1986) reported it from Nihewanian faunas (about 1.5 m.y. old).

Prior to its discovery in Hamilton Cave, West Virginia, the sugenus *Cromeromys* was unknown in North America (with the possible exception of *Mimomys monohani*). The Cheetah Room faunal record appears to be slightly younger than other known records of *Cromeromys*.

MIMOMYS (CROMEROMYS) VIRGINIANUS, new species

(Figure 1*A*–*E*)

Holotype.—USNM 264308, a right first lower molar, little worn (fig. 1*A*).

Type locality.—Cheetah Room, Hamilton Cave, Pendleton County, West Virginia; 0–50 cm of floor deposits.

Dental diagnosis.—A species of *Mimomys* (*Cromeromys*) similar to *M.* (*Cromeromys*) *tornensis* Janossy and van der Meulen and to *M.* (*Cromeromys*) *irtyshensis* Zazhigin except smaller; from *M.* (*C.*) *tornensis* it further differs in having less inflation of the cap of the anteroconid complex and in being less hypsodont. The first lower molar is about 2.5 mm long, smaller than other species, and all teeth have two roots, although the double-rooted ancestry is evident in the fused anterior roots of the upper second and third molars.

Etymology.—Latin: masculine: "of Virginia." The species is named for its occurrence in the original State of Virginia and in reference to its eastern occurrence in the United States.

Description and comparison.—Only eight teeth of this species have been found: three m1, two M3, two M2, and one M1; one M3 is questionably assigned (fig. 1*C*). Based upon this sample, individuals of the species are small; the recovered first lower molars measure 2.5, 2.5, and 2.4 mm in length of the occlusal surface, the type specimen being the smaller one. According to Janossy and van der Meulen (1975), *Mimomys* (*Cromeromys*) *tornensis* varies between 2.8 and 3.1 mm in this dimension. Zazhigin (1980) stated that *Mimomys* (*Cromeromys*) *irtyshensis* measures 2.95 mm in the same dimension. Zheng and Li (1986) indicated that the m1 of *Mimomys* (*Cromeromys*) *gansunicus* is 2.92 mm long; a referred specimen (F:AMNH 116248) from Nan Zhuang Gou, Yushe Basin, Shanxi Province, measures 3.1 mm, and three uncataloged mandibles in IVPP:AS recently collected in the Yushe Basin at field locality number YS-5 measure 3.1, 3.1, and 2.6 mm in this dimension.

The M3 of all forms (not known in *M. gansunicus*) is very similar except that of *M.* (*C.*) *virginianus* has a prominent dentine tract on the lingual salient angle of its anterior loop, rather than on the buccal one as in *M. tornensis*. The dentine tract in *M. virginianus* appears to be in the same position as in the M3 of *Cromeromys irtyshensis* figured by Zazhigin (1980, fig. 23-5). The M3 is similar to that of *Phenacomys* except for the dentine tract and the presence of cement (fig. 1*B*).

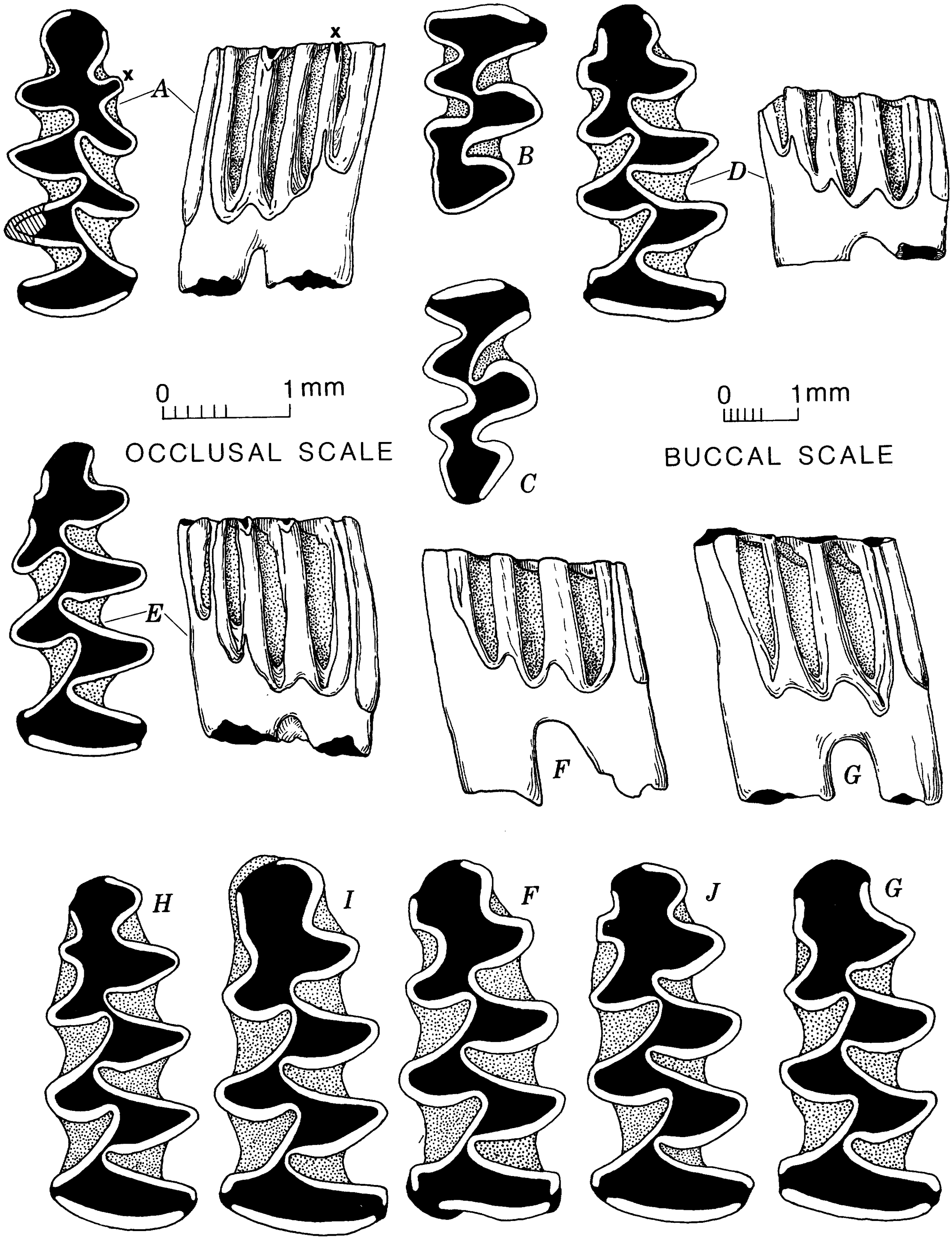
The second M3 from the Cheetah Room fauna is questionably assigned as it has dentine tracts on both buccal and lingual salient angles of the anterior loop as well as one on the posterior face of the rather narrow and posteriorly extended posterior loop; this tooth has cement only in one reentrant, a situation believed abnormal.

Discussion.—Although the subgenus *Cromeromys* is reported from both eastern and western Asia in deposits that may be only about 10,000 years older, the occurrence of *Mimomys* (*Cromeromys*) *virginianus* in a fauna so young and from the eastern United States is surprising. With the possible exception of *Mimomys monohani*, it is the only record of this subgenus in North America, although *Phenacomys* appears to be a derivative of this subgenus (Repenning and others, 1987).

Genus PHENACOMYS, Merriam, 1889

(Heather voles)

Dental diagnosis.—Arvicolinine rodents differing from all other genera of the tribe by having a first lower molar with additional triangles in a notably variable



anteroconid complex, lingual alternating triangles and reentrants asymmetrically elongated; differing also from subgenus *Mimomys* (*Mimomys*) in that the *Mimomys* Kante is largely lost in the anteroconid of all but the most primitive species and enamel islets are never present; differs from subgenus *Mimomys* (*Cromeromys*) in lack of cementum; last upper molar as in *M.* (*Cromeromys*) except for the lack of cement. Progressively greater hypsodonty, elongation of dentine tracts, and complexity of anteroconid complex define subgenera.

Included subgenera.—As discussed herein, the genus *Phenacomys* has three lineages in the living fauna, which are here grouped into the subgenera *Phenacomys, Arborimus*, and *Paraphenacomys*; the last is a new name (fig. 2).

Discussion.—Johnson (1973) has suggested that the differences between the living *Phenacomys intermedius* and *Phenacomys longicaudus* merit generic distinction and placed the latter in the genus *Arborimus*, Taylor. The dental distinction between *Phenacomys intermedius* and *Arborimus longicaudus* lies in the deeper fourth buccal reentrant (most anterior) on the occlusal surface of the first lower molar of *Phenacomys*. In *Arborimus* the posterior three buccal reentrants of m1 are usually of less uniform length below the occlusal surface than in *Phenacomys intermedius*, and the fourth (most anterior) is conspicuously less elongate; when only half worn the fourth buccal reentrant can be entirely lacking in *Arborimus*, whereas it is present in *Phenacomys* until the tooth crown is nearly worn away (fig. 3).

In the fossil record as far back as 2 million years ago, these two variations are found as individual differences within single populations; polarization of the characters that separate *Phenacomys* from *Arborimus* took place less than 400,000 years ago (fig. 2). (See Repenning and others, 1987, under *Phenacomys deeringensis*; and Repenning, in press.)

The teeth of the living species *albipes* resemble those of *Phenacomys intermedius*; and its tail length, in proportion to body length, is intermediate between *Phenacomys intermedius* and *Arborimus longicaudus*, as is its behavior. *Phenacomys albipes* is unique in the living fauna in that it has a shorter dentine tract on the buccal salient angle of the posterior loop of the first lower molar than either of the other two genera and their species. Although the species *albipes* has also been assigned to *Arborimus* (Maser and others, 1981), this shorter dentine tract indicates that assignment of the species and lineage to either *Phenacomys* or *Arborimus* is inappropriate.

In the fossil record longer dentine tracts on the buccal angle of the posterior loop of the first lower molar are evident 2.1 million years ago, in *Phenacomys deeringensis*. These longer dentine tracts break the enamel continuity on the occlusal surface before the tract on the buccal face of the anteroconid complex does, whereas in the living species *Phenacomys albipes* the tract on the posterior loop breaks the enamel pattern after the tract on the buccal face of the anteroconid complex (fig. 3).

The past 2.4 million years have seen a gradual lengthening of the dentine tract of the posterior loop in the fossil record of the lineage leading to *P. albipes*, as opposed to an abrupt lengthening between *P. gryci* (2.4 m.y. ago) and *P. deeringensis* (2.1 m.y. ago) in the lineage leading to *P. intermedius* and *Arborimus longicaudus* (fig. 2).

This indication of two lineages leading to the living species currently recognized as belonging to the genus *Phenacomys*, lineages that began more than 2 million years ago, is supported by the fauna from Locality 47 in the Old Crow Basin, Yukon Territory, Canada, which has two forms of *Phenacomys*: a representative of *Phenacomys deeringensis*, with a long tract, and *Phenacomys gryci*, with a very short tract. The fauna from this locality is under study by R.E. Morlan and appears to be about 1.7 million years old. These differences are shown in figure 3.

Because of this history of diversification, it seems most appropriate to consider *Arborimus*, Taylor as a subgenus of *Phenacomys*, Merriam, rather than as a full genus, and to erect a third subgenus to include *Phenacomys albipes*.

Subgenus PHENACOMYS, Merriam, 1889

(Figure 3*F*, 3*G*)

Dental diagnosis.—A subgenus of *Phenacomys* with buccal dentine tract on the posterior loop of the first lower molar longer than that on the buccal face of the anteroconid complex, differing from Subgenus *Paraphenacomys*, new name; and, in forms younger than about 400,000 years, fourth buccal reentrant of the same tooth deep in occlusal view and nearly as long in buccal view as the posterior three, differing from Subgenus *Arborimus*.

Included species.—*Phenacomys deeringensis* (2.1 to 1.7 m.y. old) and *P. intermedius* (living). There are at least three unnamed species older than the approximately 400,000-year-old polarization of characters that led to *Arborimus*.

Discussion.—As mentioned, polarization of characters that now separate the subgenera *Phenacomys* and

Figure 1 (facing page). Dentition of *Mimomys* (*Cromeromys*) spp. *Mimomys* (*Cromeromys*) *virginianus* from the Cheetah Room fauna, Hamilton Cave, West Virginia. *A*, Holotype, right first lower molar in occlusal and buccal views, USNM 264308. x, *Mimomys* Kante. *B*, Right last upper molar in occlusal view, USNM 264309. *C*, Right last upper molar in occlusal view, questionably assigned, USNM 264310. *D*, Left first lower molar in occlusal and buccal views, USNM 264311. *E*, Left first lower molar in occlusal and buccal views, USNM 264312. *Mimomys* (*Cromeromys*) *tornensis* from the Osztramos-3 fauna, Hungary. *F*, Left first lower molar in buccal and occlusal views, HNHMB topotype. *H–J*, Left first lower molars in occlusal views, HNHMB topotypes. Drawings of these specimens were provided by Oldrich Fejfar. *Mimomys* (*Cromeromys*) *tornensis* from Kamyk fauna, Poland. *G*, Left first lower molar in buccal and occlusal views, USGS specimen.

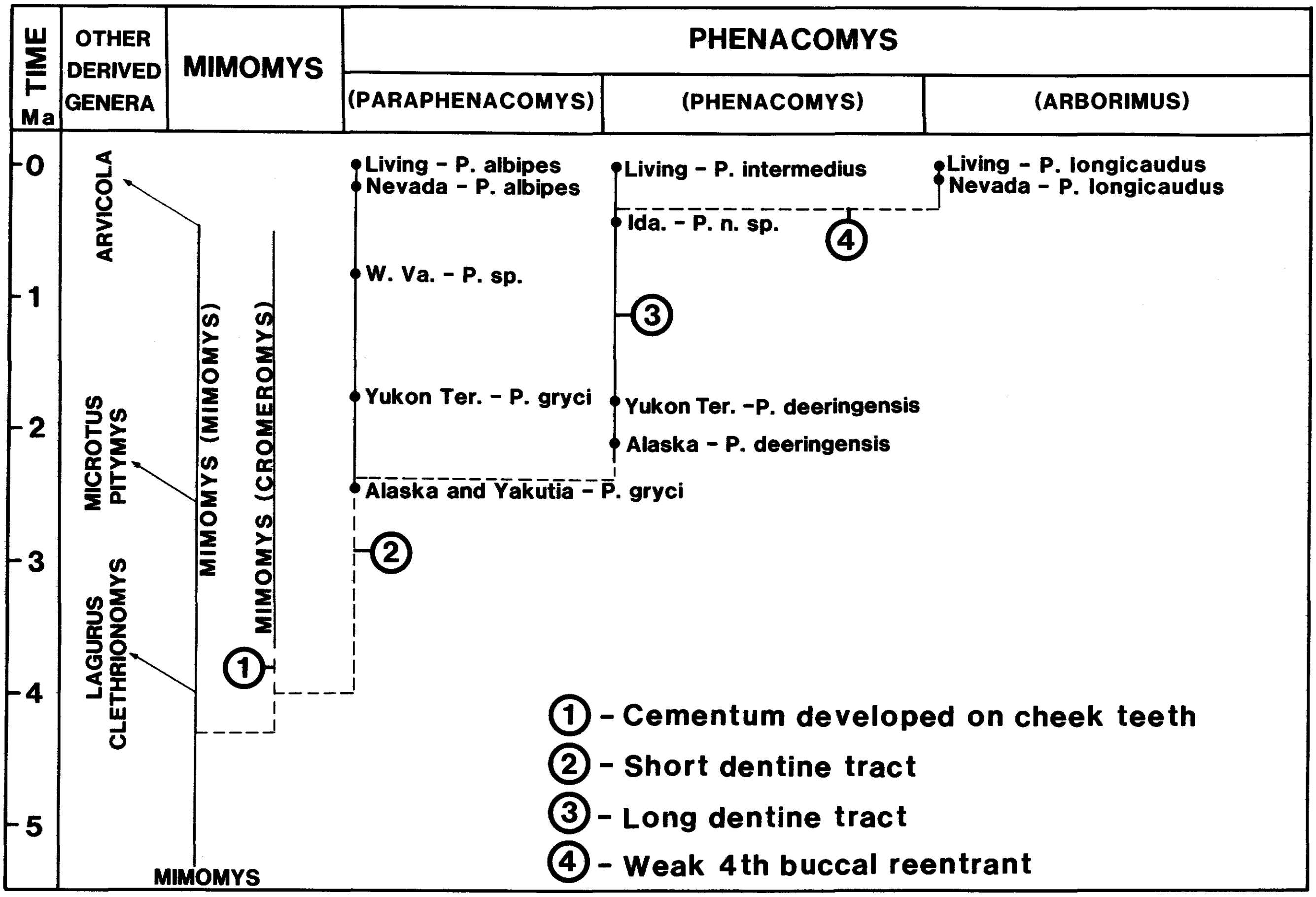


Figure 2. Inferred phylogeny of the *Phenacomys* lineage.

Arborimus can be traced back less than 400,000 years ago (younger than the Booth Canyon fauna of eastern Idaho, unpublished, Idaho State Museum locality; see Repenning, in press). Those older fossil forms, as old as the 2.1 million-year-old *Phenacomys deeringensis*, that have these characters as individual morphologic variants are also included in this subgenus. The subgenus is known only in North America from 2.1 million years ago to the present.

Subgenus ARBORIMUS, Taylor, 1915

(Figure 3*H*)

Dental diagnosis.—A subgenus of *Phenacomys* with buccal dentine tract on the posterior loop of the first lower molar longer than that on the buccal face of the anteroconid complex, differing from the Subgenus *Paraphenacomys*, new name; and fourth buccal reentrant of the same tooth shallow in occlusal view and much shorter in buccal view than the second buccal reentrant, differing from Subgenus *Phenacomys.*

Included species.—*Phenacomys longicaudus* and *Phenacomys* n. sp. (Johnson and George, in press). No fossil species have been recognized or named.

Discussion.—The subgenus is known only from the western conterminous United States. At present only one possible fossil record of *Phenacomys* (*Arborimus*) *longicaudus* is known: AMNH 301:6678 from the 6,000 year-old Gatecliff Shelter, Nye County, Nevada (Grayson, 1983; Repenning, in press).

Subgenus PARAPHENACOMYS, new name

(Figure 3*A-E*)

Dental diagnosis.—A subgenus of *Phenacomys* with relatively low crowned cheek teeth and buccal dentine tract on the posterior loop of the first lower molar shorter than that on the buccal face of the anteroconid complex, differing from other subgenera.

Etymology.—Greek: masculine: "near *Phenacomys.*" The subgenus is named for its close relationship with the subgenus *Phenacomys.*

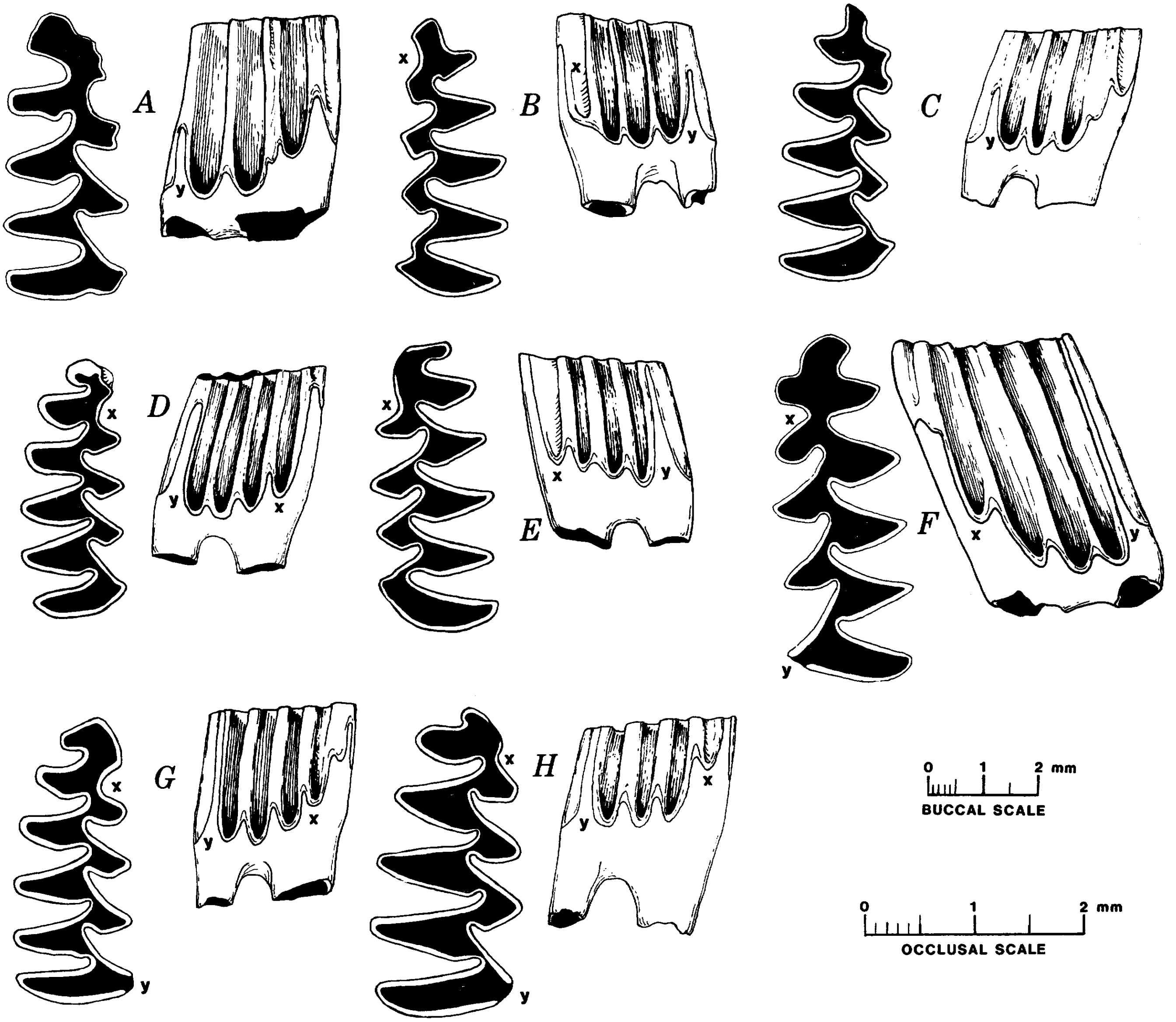


Figure 3. First lower molars of *Phenacomys*. x, fourth buccal reentrant; y, Dentine tract in buccal salient angle of posterior loop. *A, Phenacomys* (*Paraphenacomys*) *gryci* from the Fish Creek fauna, North Slope, Alaska, USNM 264317, age 2.4 m.y. *B, P.* (*Paraphenacomys*) *brachyodus* from the Cheetah Room fauna, West Virginia, Holotype, USNM 264319, age about 800,000 years. *C, P.* (*Paraphenacomys*) *brachyodus* from the Cheetah Room fauna, West Virginia, USNM 264318. *D, P.* (*Paraphenacomys*) *albipes* from the Smith Creek Canyon Fauna, Nevada, Univ. Arizona uncataloged specimen, age about 13,000 years. *E, P.* (*Paraphenacomys*) *albipes* from Benton County, Oregon, Burke Museum 34501, modern. *F, P.* (*Phenacomys*) *deeringensis* from Cape Deceit fauna, Seward Peninsula, Alaska, Univ. Alaska 636, age 2.1 m.y. *G, P.* (*Phenacomys*) *intermedius* from Glacier National Park, Montana, USGS 6824, modern. *H, P.* (*Arborimus*) *longicaudus* from Tillamook County, Oregon, Burke Museum 34492, modern.

Type species.—Phenacomys albipes Merriam, 1901.

Included species.—Phenacomys albipes, P. brachyodus n. sp., and *P. gryci.*

Discussion.—The subgenus is known in North America from 2.4 million years ago to the present and presumably is also known in Beringian Asia 2.4 million years ago (Repenning and others, 1987).

In the living fauna *Phenacomys* (*Paraphenacomys*) *albipes* is restricted to the coastal forests of Oregon and northernmost California; today it is a rare species. It is known from one fossil record, uncataloged first lower molar in the University of Arizona from the ±13,000-year-old Smith Creek Cave fauna, White Pine County, Nevada (Mead and others, 1982; Repenning, in press).

PHENACOMYS (PARAPHENACOMYS) BRACHYODUS, new species

(Figure 3*B*, 3*C*)

Holotype.—USNM 264319, a left first lower molar, little worn (fig. 3*B*).

Type locality.—Cheetah Room, Hamilton Cave, Pendleton County, West Virginia. 0–50 cm of floor deposits.

Dental diagnosis.—A species of the subgenus *Paraphenacomys* differing from *P.* (*Paraphenacomys*) *gryci* in having a more elongate buccal dentine tract on the posterior loop of m1 and better developed additional wings on the anteroconid complex of the first lower molar; differing from *P.* (*Paraphenacomys*) *albipes* in having a shorter buccal dentine tract on the posterior loop. First lower molar is about 2.5 mm long, shorter than most other species of the genus but within the range of variation of some.

Etymology.—Greek: masculine: "short tooth." In reference to the low crowned cheek teeth and short buccal dentine tract on the posterior loop of the first lower molar.

Description and comparison.—Six cheek teeth, including two m1, of *Phenacomys brachyodus* are in the microtine sample from the Cheetah Room fauna. The two first lower molars are small (occlusal lengths are 2.45 and 2.50 mm) and, when compared with modern specimens of equal root development, the two fossil m1s appear lower crowned; this apparent lower crown is paralleled by remarkably short dentine tracts on the buccal salient angle of the posterior loop of the first lower molar (fig. 3*B*, 3*C*).

No species of the subgenera *Phenacomys* or *Arborimus* has a dentine tract on the buccal salient angle of the posterior loop of the first lower molar that is as short as that on the two first lower molars from the Cheetah Room fauna. In addition, the few known specimens of the subgenus *Paraphenacomys* that are younger than the Cheetah Room fauna, including the living *P. albipes*, do not have as short a dentine tract, suggesting progressive evolution of the feature. Only the oldest known species, *Phenacomys* (*Paraphenacomys*) *gryci*, has a shorter tract on the posterior loop than do the specimens from the Cheetah Room fauna.

The late Pliocene species *Phenacomys* (*Phenacomys*) *deeringensis* (Guthrie and Matthews, 1971) has much more elongate dentine tracts on this angle of this tooth; they break the enamel pattern of the occlusal surface before wear intersects the dentine tract on the buccal face of the anteroconid complex (fig. 3*F*).

Development of the dentine tracts is a universally recognized taxonomic criterion in the microtine rodents, and in *Phenacomys* differences in this development clearly indicate the existence of two lineages that derive from ancestral *Phenacomys gryci*. Subgenus *Paraphenacomys* is characterized by relatively slow development of the dentine tract on the buccal side of the posterior loop of the first lower molar; Subgenera *Phenacomys* and *Arborimus* are characterized by early and rapid development of this tract to the condition in which it is more elongate than the tract on the buccal face of the anteroconid complex of the first lower molar. The presence of two forms of *Phenacomys* (R.E. Morlan, writen commun., 1986) from the presumed 1.7 million-year-old Locality 47, Old Crow Basin of Yukon Territory, one form being *P. deeringensis* with elongate tract and the other *P. gryci* with very short tract, supports the concept of two contemporaneous lineages.

The *Paraphenacomys* lineage includes all forms derived from the ancestral *Phenacomys gryci* in which the dentine tract on the buccal face of the anteroconid complex interrupts the enamel pattern of the occlusal surface before the buccal tract of the posterior loop does so. Not many examples are known, although many fossil records have not been examined for this character. Those known are shown in figure 3; they include *Phenacomys gryci* from northern Alaska and Yukon Territory (2.4–1.7 m.y. old), *Phenacomys brachyodus* from the Cheetah Room fauna (ca. 0.8 m.y. old), *P. albipes* from the Smith Creek Cave fauna, Nevada (Repenning, in press; ca. 0.013 m.y. old), and living *P. albipes* from coastal Oregon and northern California.

The presence of *Phenacomys* (*Paraphenacomys*) *brachyodus* in the Cheetah Room fauna indicates a former distribution to the Atlantic coast, possibly only in Canada during interglacial periods, that would seem comparable to the modern distribution of *Phenacomys* (*Phenacomys*) *intermedius*. The environmental factors that caused its present restriction to the wet Pacific hemlock and coastal Douglas fir forests of western Oregon are unknown but fascinating. It should be noted that the 13,000-year-old record from Smith Creek Cave in easternmost Nevada is associated with dry subalpine Douglas fir forests (Mead and others, 1982) and that the present limited range may reflect some change in habit as well as environment (Repenning, in press).

Genus ALLOPHAIOMYS, Kormos, 1932

Dental diagnosis.—Arvicolinine rodents differing from all other genera except *Arvicola* in having rootless cheek teeth; as in *Arvicola* anteroconid complex of m1 consists of a simple trefoil with prominent primary wings and a more or less globular cap frequently skewed lingually; prominent dentine tracts on the anterobuccal face of the cap of the anteroconid complex and on both buccal and lingual salient angles of the posterior loop; M3 simple, lacking a fully developed third alternating triangle, posterior loop usually extended to the rear, and dentine tracts on both buccal and lingual salient angles of the anterior loop and on the posterior surface of the posterior loop; teeth well cemented; mean length of m1 less than 3.0 mm, differing from *Arvicola*.

Discussion.—*Allophaiomys* and *Arvicola* are very similar because both are basically *Mimomys* without roots on their cheek teeth. Even their Schmelzmuster is essentially the same and is comparable to that of *Mimomys* (von Koenigswald, 1980). In *Allophaiomys* the lingual and buccal reentrants anterior to the primary wings of the anteroconid complex tend to be more nearly of equal size than in *Arvicola*, the posterior loop of the last upper molar usually is more elongate posteriorly, the buccal reentrants and the second alternating triangle of m3 tend to be more weakly formed, and the cement in the reentrants of the teeth usually is more heavily deposited than in *Arvicola*; but the two genera are difficult to separate. The most consistent difference is the mean length of the first lower molar of *Arvicola*, which is greater than 3.0 mm. The two genera are almost temporally exclusive of each other; *Allophaiomys* is known from perhaps 2.5 million years ago in Asia until about 450,000 years ago in Europe and North America (excepting its living relic, *Phaiomys*, of the Himalayas and the Tibetan Plateau). In contrast, populations referred to *Arvicola* appear to evolve out of *Mimomys savini*, by the loss of roots on the cheek teeth, no earlier than about 500,000 years ago.

Except for large size, there is absolutely no morphologic similarity between the teeth of *Arvicola* and *Microtus richardsoni* of North America, which is sometimes considered closely related to *Arvicola* (Hall, 1981). *Microtus richardsoni* may be a late Pleistocene North American derivative of *Microtus xanthognathus*, based upon the similarity of their teeth, and certainly is not phylogenetically close to *Arvicola* of Eurasia, which has very different teeth.

It has been almost universally recognized that both *Pitymys* and *Microtus* evolved from *Allophaiomys* (Kretzoi, 1969; Chaline, 1974; van der Meulen, 1978, fig. 15; Repenning, 1983; and possibly Martin, 1987). This has led to a problem in classification.

It has been assumed, without discussion, that *Allophaiomys* cannot be grouped with *Mimomys* because it has no roots on its teeth. However, if *Pitymys* and *Microtus* are grouped separately, there is an equal problem deciding into which group *Allophaiomys* should be placed. No one has suggested that a separate tribe be erected for this single genus (or generic pair). Solutions have been either to place *Allophaiomys* (and *Phaiomys*) in the *Pitymys* group, or to put all forms concerned under the single genus *Microtus*. The first is incorrect as it does not allow for the derivation of *Microtus* from *Allophaiomys*; and the second seems to only lower the dilemma in rank until it is not prominent. The second also requires that an author either use the trinomial name throughout the discussion, or slip back into speaking of the subgenera of *Microtus* (*Allophaiomys*, *Pitymys*, *Microtus*, etc.) as though they were genera (van der Meulen, 1978, for example); this confuses the reader, and perhaps sometimes the writer as well.

As here classified, *Allophaiomys* is considered a genus of the Tribe Arvicolini that has no roots on its cheek teeth and *Pitymys* and *Microtus* are thus allowed to be classified as the separate lineages that they are.

ALLOPHAIOMYS PLIOCAENICUS Kormos, 1933

Dental diagnosis.—A species of *Allophaiomys* with average width of the commissure between primary wings and cap of anteroconid complex of m1 slightly narrower, and average length of anteroconid complex (relative to the posterior part of the tooth) slightly longer than in the only other defined species, *Allophaiomys deucalion* Kretzoi [see van der Meulen, 1974, for discussion].

Discussion.—Thirty first lower molars of *Allophaiomys pliocaenicus* are in the collection from the Cheetah Room fauna. These were compared with 10 from the Kentuck fauna of Kansas, 13 from the Wathena fauna of Kansas, 9 from the Java fauna of South Dakota, a single large individual from the Aries fauna of Kansas, 1 from the Hanover Quarry fauna of Pennsylvania, 2 from the Wellsch Valley fauna of Saskatchewan, and 4 from Kamyk, Poland.

Particular attention was paid to the criteria of van der Meulen (1978) in his definition of *Allophaiomys guildayi* from Cumberland Cave, Maryland (defined as *Microtus* (*Pedomys*) *guildayi*). It was obvious that individual variation in the species represented in the Cheetah Room fauna overlapped the typical morphology of *Allophaiomys guildayi*, but the majority of individuals did not conform to it. The teeth from the Cheetah Room fauna averaged 10 percent smaller than the four Polish specimens compared, but the size range of all population samples compared was great.

It was a matter of prudent nomenclature in 1975 when R.A. Martin pointed out that specimens from the United States were very similar to the form called *Allophaiomys pliocaenicus* in Europe and referred them to "*Allophaiomys* sp. cf. *A. pliocaenicus* Kormos." In the 13 years that have since passed, many additional localities and specimens have been found and no one has been able to satisfactorily demonstrate a difference. This seems reason enough to assign the North American fossils to the Eurasian species until it can be established that they differ from it.

Tribe MICROTINI, Simpson, 1945

Dental diagnosis.—Arvicoline rodents with rootless cheek teeth; differing from the Pitymyini in having anteroconid complex on m1 with at least the buccal primary wing of *Allophaiomys* developed into an additional triangle (alternating triangle 4) by being pinched off through elongation of the third lingual reentrant that meets the enamel wall of the third buccal reentrant [fig. 4]; M3 primitively "simple," like that found in living North American species of *Pitymys* and fossil species of *Allophaiomys* [figs. 4*D*, 4*G*], having only two buccal and two lingual cement-filled reentrants; M3 of derived morphotypes "complex" with three cement-filled reentrants on buccal and lingual sides (in North America, all included in *Microtus*) [fig. 4*J*]; most anterior buccal reentrant of M3 not reduced and about opposite most anterior lingual reentrant, differing from the Lagurini.

Included genera.—Lasiopodomys, *Microtus*, and *Proedromys*.

Discussion.—These three genera are considered as subgenera of *Microtus* by neo-mammalogists and are separated here because they can be separately diagnosed from their dentition. Although not all are represented in the Cheetah Room fauna, they are here diagnosed, discussed, and illustrated in figure 4, in explanation of the nomenclature used.

There are many additional subgenera within *Microtus* that are not here separated because the history of their development is not known, but it is expected that they will be separately diagnosed according to this history when it is known. Even in the strict sense here used, the genus *Microtus* is very large.

Genus PROEDROMYS, Thomas, 1911

(Bedford's vole, figure 4*A*)

Dental diagnosis.—Microtinine rodents with anteroconid complex of m1 having one additional triangle and no trace of a secondary lingual wing on its cap [marked x on fig. 4], differing from all other genera of the tribe except those fossils that are included in *Lasiopodomys*; M3 reduced, differing from other genera of the tribe, and all other microtines [fig. 4*A*].

Discussion.—This genus is known only from China, both living and fossil, but retains a very primitive m1 that differs from that of *Allophaiomys* only in the closing of the buccal primary wing of the anteroconid complex (fig. 4*A*). It is unique in its loss of the posterior parts of M3 when compared with that tooth of *Allophaiomys* (compare fig. 4*A* with 4*G*), but it is remarkable in the similarity of its m1 to that of fossil species here included in the genus *Lasiopodomys*, including the species from the Cheetah Room fauna. Zheng and Li (in press) reported *Proedromys* cf. *bedfordi* from the Gongwangling fauna, Shaanxi, between 740,000 and 1 million years old, and they reported the living species in more recent faunas. The genus is monospecific.

Genus LASIOPODOMYS, Lataste, 1887

(Transbaikalian vole)

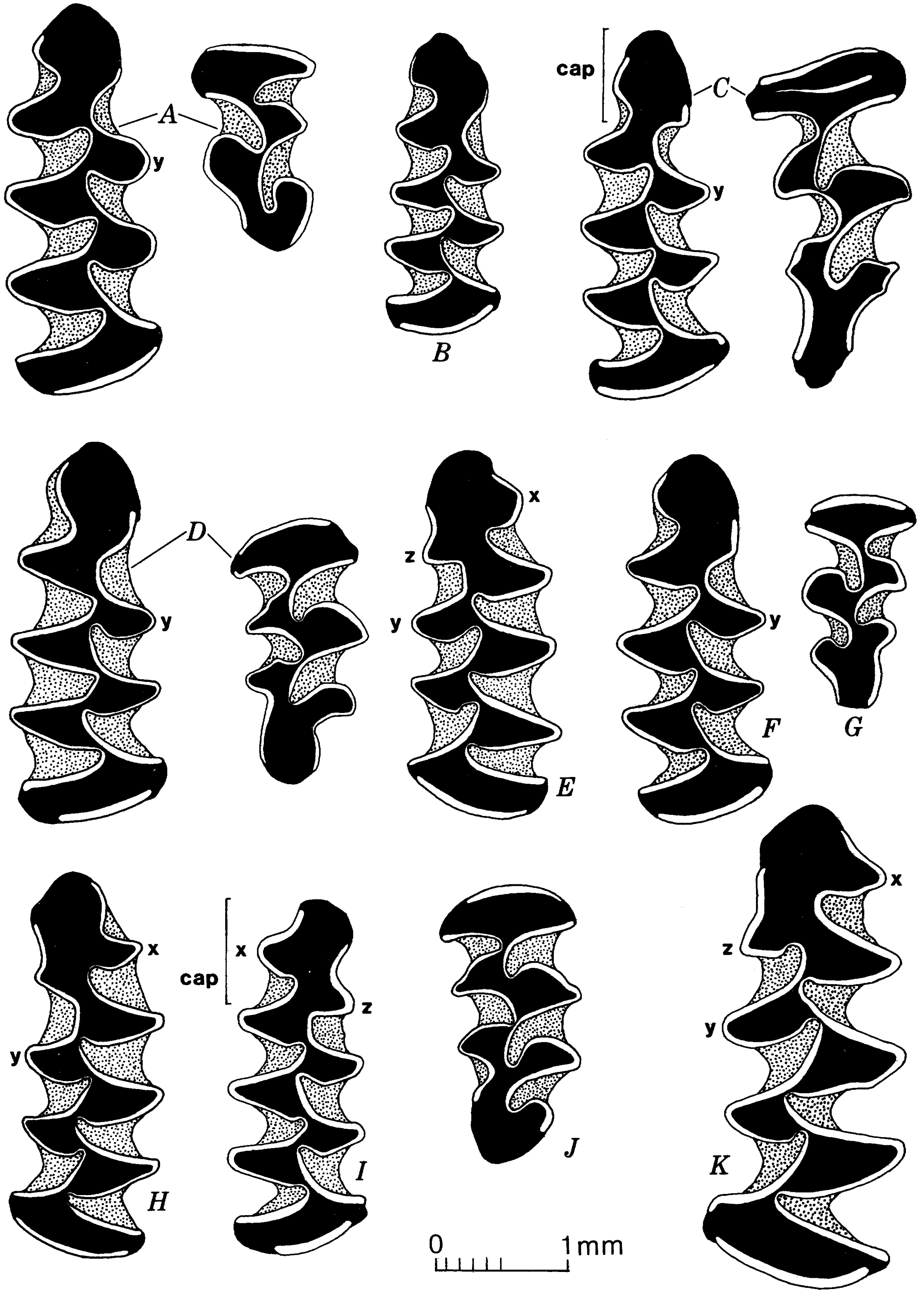
Dental diagnosis.—Microtinine rodents with anteroconid complex of m1 having one or two additional triangles, and differing from *Microtus* in having no trace of a secondary lingual wing in older forms or only a very weak secondary lingual wing in some late Pleistocene and living individuals; M3 neither reduced nor complicated, remaining as in *Allophaiomys*, and differing from *Proedromys* in its lack of reduction and from *Microtus* in its lack of later complication [fig. 4*B*–4*D*, 4*F*, and 4*G*].

Included species.—Lasiopodomys brandti, L. brandtoides, L. deceitensis, and *L. praebrandti.*

Discussion.—Repenning (1980 and later) has suggested that one North American fossil species with a simple M3, like that in *Allophaiomys*, and with no secondary wings on the anteroconid cap of m1, as in *Allophaiomys* and *Proedromys*, might better be assigned to this genus, rather than to *Microtus*. Although another fossil locality has been found in North America containing this species (Locality 47, Old Crow Basin, Yukon Territory, Canada), little has been discovered that supports the suggestion.

The difficulty in defending the generic assignment lies in the lack (except for the Chinese fossil *Lasiopodomys brandtoides*) of a record of forms intermediate

Figure 4 (facing page). First lower molars of Tribe Microtini. Features of the anteroconid complex: x, secondary lingual wing; y, first additional triangle; z, second additional triangle (or secondary buccal wing); cap, cap of anteroconid complex. *A*, *Proedromys* sp. cf. *P. bedfordi* from Gongwangling locality, Shaanxi, China, IVPP:AS specimens: right first lower and left last upper molars; this is a reduced M3, compare with *G*. Drawings of these specimens were provided by Zheng Shaohua and Li Chuankuei. *B*, *Lasiopodomys praebrandti* from Kudun locality, Transbaikalia, ZZSD:PAN:C MF1551-76: right first lower molar. *C*, *Lasiopodomys deceitensis* from Cape Deceit fauna, Alaska: right first lower molar, UA 418, and right last upper molar, little worn, UA 244, a "simple" morphotype comparable to that in *D*. *D*, *F*, and *G*, *Lasiopodomys deceitensis* from Cheetah Room fauna, West Virginia. *D*, Associated right first lower and right last upper molar, USNM 264316; a "simple" morphotype, but if cement were present in the posterolingual reentrant it would be "intermediate"; *F*, Right first lower molar, USNM 264319; *G*, Left last upper molar, USNM 264318, also a "simple" morphotype. *E*, *Microtus paroperarius* from the Cheetah Room fauna: left first lower molar, USNM 264317; note weak lingual and buccal secondary wings, comparable to *K*. *H*, *I*, *J*, *M. paroperarius* from the Sunbrite Ash Pit, Kansas, USGS specimens. *H*, Left first lower molar with strong lingual secondary wing; *I*, Right first lower molar with moderate lingual and buccal secondary wings; *J*, Right last upper molar; this is a "complex" morphotype. *K*, *M. paroperarius* from Locality CT2 of the Hansen Bluff faunal sequence, Colorado, UC specimen of a large-sized population; this tooth is from associated upper and lower dentitions and the individual had a "simple" M3 similar to *D*.


A
y
B
cap
C
y
D
y
x
z
y
E
y
F
G
x
cap
x
z
y
H
I
J
x
z
y
K
0
1mm

between these presumed early forms of *Lasiopodomys* and the living form, *Lasiopodomys brandti*, which has somewhat more complicated first lower molars. The living species, from western Transbaikalia, usually has the second additional triangle fully closed as well as a very weak secondary lingual wing in some individuals; it is known in the fossil record of Siberia and China for the last million years.

Erbaeva (1976) named *Lasiopodomys praebrandti* (fig. 4*B*) from the Kudun fauna south of Lake Baikal (about 2 million years old) and attempted to trace the history of the genus to the living species; her record had a gap between the latest Pliocene and the beginning of late Pleistocene, a gap comparable in time with that known in North America. In Transbaikalia this time gap covers the transition between the earlier *L. praebrandti*, with "almost" one additional triangle in the anteroconid complex (fig. 4*B*) to that of the living form, having two clear cut and fully closed additional triangles. In North America no specimen is known with a fully closed second additional triangle, although the first is fully closed in *Lasiopodomys deceitensis*. *Microtus oregoni* has a well-developed secondary lingual wing and therefore qualifies as a species of *Microtus*, although it has a "simple" M3.

In addition, Erbaeva (oral commun., 1982) has subsequently decided that her species probably belongs in *Allophaiomys* because the constriction in the enamel pattern never quite closes off the first additional triangle of the anteroconid complex. However, in her sample the prevalence of a distinct narrowing of the commissure between this incomplete triangle and the cap of the anteroconid complex at least suggests that it is a species of *Allophaiomys* that was evolving toward the Microtini.

The use of this genus is primarily defended by the persistent "simple" last upper molar and the lack of a well-developed secondary lingual wing on the anteroconid cap of the first lower molar (marked x on fig. 4).

LASIOPODOMYS DECEITENSIS (Guthrie and Matthews, 1971)

(Figure 4*C*, 4*D*, 4*F*, and 4*G*)

Dental diagnosis.—A species of *Lasiopodomys* with the first additional triangle of anteroconid complex of m1 completely closed, differing from *Lasiopodomys praebrandti*; commissure between the cap of complex and second additional triangle broadly confluent, differing from *Lasiopodomys brandti*; no well-developed secondary lingual wing of the anteroconid complex cap, differing from *Microtus*. Length of m1 about 2.8 mm, larger than *L. praebrandti*.

Discussion.—The resemblance of the m1 in this species to that of *Proedromys* is remarkable (fig. 4*A*, 4*C*, 4*D*, and 4*F*), but the distinctly reduced M3 of the Chinese genus is not found with the North American forms. Eighty rootless third upper molars were in the collection from the Cheetah Room fauna. They were sorted by degrees of complication: "simple" with two lingual and two buccal cement-filled reentrants (fig. 4*D* and 4*G*); "intermediate" with three lingual and two buccal cement-filled reentrants (fig. 4*D* if the posterior lingual reentrant contained cement); and "complex" with three buccal and three lingual cement-filled reentrants (fig. 4*J*). Sixty-nine last upper molars were "simple" and could belong to *Pitymys, Allophaiomys*, or *Lasiopodomys* in the fauna. Seven were "intermediate" and could belong to *Pitymys, Allophaiomys, Lasiopodomys*, or *Microtus*. Four were "complex" and, in North America, could only belong to *Microtus*. In Eurasia they could also belong to *Pitymys* or *Neodon*.

In the Cheetah Room fauna there are 31 first lower molars assigned to *Lasiopodomys deceitensis*, 52 that are assigned to *Pitymys hibbardi*, 30 assigned to *Allophaiomys pliocaenicus*, and only 8 that are believed to be assignable to *Microtus paroperarius*. From these proportions it would seem that about 20 of the last upper molars belong to *Lasiopodomys deceitensis*; they could be either "simple" or "intermediate" in form. There is only one associated dentition in the microtines of the Cheetah Room fauna and it is of *Lasiopodomys deceitensis* (fig. 4*D*). It almost has an "intermediate" last upper molar, but this does not differ from those of the type population from Alaska (fig. 4*C*).

Lasiopodomys deceitensis was described (as *Microtus deceitensis*) from the Cape Deceit fauna of the Seward Peninsula, Alaska (Guthrie and Matthews, 1971). This fauna is about 2.1 million years old by a variety of lines of correlation (Repenning and others, 1987). The species is also known from the unpublished Locality 47 of the Old Crow Basin, Yukon Territory, Canada, which is under study by R.E. Morlan and which is believed to have been deposited during the Olduvai event (Repenning and others, 1987). The presence of the species in the much younger Cheetah Room fauna may require reevaluation of the age interpretation of Locality 47; the normal polarity determination of the sediments could represent the Jaramillo event, rather than the Olduvai event, as has been inferred. If so, there are three other unusually late records of microtine rodents in the fauna.

As mentioned, assignment of this species to the genus *Lasiopodomys* is based upon the assumption that the retention of a primitive M3 and the lack or virtual lack of a secondary lingual wing on the anteroconid cap of m1 define a single lineage. This assumption remains untested because there is a genuine (and unusual) "missing link" in the fossil record.

Genus MICROTUS, Schrank, 1798

(Meadow mice)

Dental diagnosis.—Microtinine rodents differing from *Proedromys* and *Lasiopodomys* in having an anteroconid complex of m1 with a secondary lingual wing [marked x on fig. 4] developed on the cap, secondary buccal wing variably present; M3 may be "simple" in early fossil forms, but is universally "complex" in younger fossil and living forms. Two or more additional triangles formed from the primary wings (a total of five or more alternating triangles) on m1 of many forms, differing from *Proedromys* and early *Lasiopodomys*; the second additional (fifth alternating) triangle is the lingual primary wing of the anteroconid in *Allophaiomys* and *Proedromys* but is not completely, or is variably, closed off from the cap of the anteroconid complex cap in several forms. The "simple" M3 of *Microtus oregoni* is an exception, as noted by Repenning (1983), and the Central American *Herpetomys* and *Orithriomys* are not understood.

Included species.—Microtus paroperarius and many more advanced species.

Discussion.—Much remains unknown about the phylogenetic patterns of the various species of fossil and living *Microtus*. R.A. Martin (1987, p. 273) stated: "a classification should at its best be a hypothesis regarding the relationships of monophyletic groups." In agreement with this, there seems to be little point in altering the existing classification until firm evidence clarifies it. However, it is recognized that the genus potentially contains several subgenera that could be elevated to generic status once their diversification is understood.

The oldest known species in the United States east of the Rocky Mountains is *Microtus paroperarius* Hibbard. This species and at least two others are known from the much older Locality 47 in the Old Crow Basin, Yukon Territory, and are under study by R.E. Morlan. This species is also known from the much older Wellsch Valley fauna, Saskatchewan, and is under study by C.S. Churcher. A fairly large variety of species between 1 and 2 million years old has been recognized in northern Eurasia.

MICROTUS PAROPERARIUS Hibbard, 1944

(Figure 4*E* and 4*H*–4*K*)

Dental diagnosis.—A species of *Microtus* morphologically close to the living *Microtus oeconomus* [=*M. operarius* Nelson of Hibbard, 1944] in structure of m1 but differing in that cap of anteroconid complex is less inflated and reentrant anterior to secondary lingual wing less developed. Differing from many other species in that second additional triangle is prominent but still broadly confluent with cap; lingual secondary wing [marked x on fig. 4] usually less prominent than in *M. oeconomus* because of weak reentrant anterior to it; M3 "simple" [as fig. 4*D* and 4*G*] in forms older than about 850,000 years and "complex" [fig. 4*J*] in those younger than about 610,000 years. Size variable and length of M1 ranges from 3.6 mm [Loc. CT2, Hansen Bluff fauna, Colorado, fig. 4*K*] to 2.15 mm [Alfred Shoemaker loc., Nebraska, mentioned by Paulson, 1961; see also van der Meulen, 1978, table 3].

Discussion.—The oldest prior records in the United States of *Microtus paroperarius* are from Hansen Bluff, Colorado, and are about 820,000 years (Rogers and others, 1985). At Locality CT2 in the base of the Hansen Bluff faunal succession, the only associated upper and lower dentition of *Microtus paroperarius* known to us has a "simple" third upper molar (like fig. 4*D*; it is from the specimen whose m1 is shown in fig. 4*K*). However, of 20 last upper molars from four closely spaced localities in the lower part of the Hansen Bluff succession (Localities CT1, CT2, CT3, and PP2), only 8 (40 percent) were of this "simple" morphotype, and these could belong to either *Pitymys* or *Microtus* in the fauna; the remaining 60 percent were of the "complex" morphotype (similar to fig. 4*J*) and had to belong to *Microtus*. Thus, more than 60 percent of the individuals of *Microtus paroperarius* from the 820,000-year-old level in the Hansen Bluff faunal sequence had a "complex" last upper molar.

All last upper molars from the type Cudahy population and the referred Sunbrite Ash Pit locality, Kansas, appear to have the "complex" M3, although one cannot be certain because the associated *Pitymys meadensis* introduced "simple" M3s into the fossil sample; these are about 610,000 years old.

At Locality 47 in the Old Crow Basin of Yukon Territory (under study by R.E. Morlan) and in the Wellsch Valley fauna of Saskatchewan (under study by C.S. Churcher), first lower molars assignable to *Microtus paroperarius* are found with "simple" last upper molars. However, "complex" M3s occur in Locality 47 and at least two other species of *Microtus* are present; the disposition of the last upper molars to species from Locality 47 is still uncertain. These two faunas seem to have been deposited during the Olduvai Normal Polarity Subchron (1.89–1.67 m.y. old).

Microtus paroperarius appears to represent a monophyletic lineage that shows progressive evolution in the morphology of M3 over a known time period extending from about 1.8 million years ago until about 400,000 years ago. Its extinction in the United States appears to have occurred shortly following the invasion of *Microtus pennsylvanicus*.

Identification of *Microtus paroperarius* in the Cheetah Room fauna is tenuous. The eight first lower molars assigned to this species are difficult to separate from *Lasiopodomys deceitensis*; figure 4*E* shows the first lower molar that is most obviously assignable to *M. paroperarius* because its development of a secondary lingual wing on the anteroconid complex (marked x on the figure) is strongest.

Only the presence of four "complex" M3s (discussed under *Lasiopodomys deceitensis*) certainly indicates that some specimens present must represent *Microtus*, as here restricted. It is on the strength of these four last upper molars that the eight m1s with weak secondary lingual wings have been removed from the sample of m1s assigned to *Lasiopodomys*. Without the "complex" last upper molars, these first lower molars assigned to *Microtus paroperarius* would have been included in *Lasiopodomys deceitensis* and would have been considered as advanced individuals (the "missing link") trending toward the living *L. brandti*, and as supporting the generic assignment.

It would appear that the Cheetah Room fauna lived sometime between 850,000 years ago, when *Microtus paroperarius* entered the United States (Repenning, 1984), and considerably before 610,000 years ago, when the species had evolved a "complex" last upper molar in essentially all of its population and a much more pronounced lingual secondary wing on the anteroconid cap of its first lower molar. The development of secondary wings in the Cheetah Room fauna more closely resembles the condition found in the 820,000-year-old sample from Hansen Bluff (fig. 4*K*) than those from the 610,000-year-old type sample from the Cudahy fauna (fig. 4*H* and 4*I*), suggesting a more similar age, and the rarity of "complex" M3s in the fauna from West Virginia suggests an even older age.

Tribe PITYMYINI, Repenning, 1983

Dental diagnosis.—Arvicoline rodents with rootless cheek teeth and an anteroconid complex on m1 with one or more *pairs* of additional triangles—the first *pair* (triangles 4 and 5) approximately opposing, differing from the Microtini; development of further additional triangles also occurs as opposing pairs; M3 "simple" with only two cement-filled reentrants on both buccal and lingual sides in North America, differing from advanced *Microtus*, but may be "complex" in Eurasia. Basic pattern of the configuration of cap varies with species.

Included genera.—Neodon, Pitymys, and *Tyrrhenicola*, questionably also *Herpetomys* and *Orithriomys*.

Discussion.—There are two known specimens, both of *Pitymys quasiater*, that contradict the extremely simple M3 in North American *Pitymys*; KU-19876 (Repenning, 1983) and KU-24465 (Martin, 1987), both from Veracruz, Mexico. The M3s on these specimens are "complex," but the vast majority of individuals of this species have an M3 that conforms to the diagnosis. It would appear that the species group including *P. quasiater* (Repenning, 1983), derived from immigrants from Eurasia, is evolving a "complex" M3 as did those in Eurasia at an earlier date.

In North America the tribe Pitymyini includes the genus *Pitymys*. In the Old World the tribe includes *Neodon, Pitymys,* and *Tyrrhenicola*. Possibly also to be included in North America are the Central American forms *Orithriomys umbrosus*, which has a very primitive m1 and a "simple" M3 like those of *Allophaiomys* (it may represent a southern holdover comparable to *Phaiomys* in Asia), and *Herpetomys guataemalensis*, which has an advanced, *Pitymys*-like m1 but a "complex" M3 (like a few individuals of *Pitymys quasiater* from central Mexico).

Genus PITYMYS, McMurtrie, 1831

(Pine voles)

Dental diagnosis.—Pitymyinine rodents with "simple" M3. Two individuals of *Pitymys quasiater* that are exceptions have been noted above.

Included species.—Pitymys aratai, P. cumberlandensis, P. hibbardi, P. mcknowni, P. meadensis, P. nemoralis, P. ochrogaster, P. pinetorum, and *P. quasiater*, in North America. Corbet (1978) listed 15 species in Eurasia, several of which have been included under the genera *Neodon* and *Phaiomys* by others. Martin (1987) has questioned the reality of *P. mcknowni* and *P. hibbardi* with reason (also see Repenning, 1983).

Discussion.—As diagnosed, *Pitymys* would include North American *Pedomys* but not all species included under either *Pitymys* or *Neodon* in the Old World. Two lineages of *Pitymys* exist in North America: the *pinetorum* species group and the *quasiater* species group. The *pinetorum* species group, to which the name *Pitymys* belongs, is native to North America and probably not known in the Old World, whereas the *quasiater* species group is derived from the Old World forms that immigrated to the United States with *Microtus paroperarius* about 850,000 years ago (Repenning, 1983).

By virtue of belonging to the same monophyletic group, *Pedomys* belongs in the *pinetorum* species group. The *quasiater* group is immigrant to North America probably a few tens of thousand years before the Cheetah Room fauna lived, and it is not represented in this fauna; it is present in the possibly younger Hansen Bluff faunal sequence in the Rocky Mountains and in the younger Cudahy fauna of the Great Plains. To it belong the species of the Old World assigned to *Pitymys* and to *Neodon*.

To rectify this double-lineage *Pitymys* in North America, it would be simplest to put the *quasiater* species group in a different genus. The genus *Neodon* is logical, but such an action would have three consequences:

1. Considerable work necessary to learn the history of Old World Pitymyinines well enough to be certain that the *pinetorum* species group never dispersed there, and, hence, that the species group, or the genus *Pitymys*, is

not present in the Old World. Several living species in Eurasia appear to conform to the characters of the *pinetorum* species group, including the *Pitymys savii* group of Miller (1912) as well as *Neodon carruthersi* and *N. irene.*

2. The politics involved in convincing Old World researchers that there is no *Pitymys* in their faunas.

3. The politics involved in convincing North American researchers that several of their species of *Pitymys* belong in the genus *Neodon.*

The two species groups differ in the complication of the anteroconid complex, as well as in origin. The *pinetorum* species group usually has obviously wide confluence between the dentine fields of the opposing first pair of additional triangles (triangles 4 and 5) and that of the more anterior part of the anteroconid complex. The part of the anteroconid complex anterior to the paired additional triangles also is less complicated. Although it usually has secondary wings, they are weakly formed in most individuals (about 96 percent) because of shallow reentrants marking their anterior limits; they seldom approach the condition of being secondary additional triangles. This lineage evolved in North America from North American *Allophaiomys* as indicated by van der Meulen (1978) and by the Cheetah Room fauna. It contains the generic type species, *Pitymys pinetorum.*

The *quasiater* species group usually has complete, or nearly complete, closure between the dentine fields of the first pair of opposing additional triangles and the more anterior part of the anteroconid complex. The anterior part of the anteroconid complex is more prominent in the *quasiater* species group and has a more complicated structure, to the point of frequently developing a second pair of opposing additional triangles (triangles 6 and 7). This lineage appears to have immigrated to the United States about 850,000 years ago as *Pitymys meadensis* (Repenning, 1983).

PITYMYS HIBBARDI Holman, 1959

(Figure 5)

Dental diagnosis.—A species of *Pitymys* in the *pinetorum* species group with no or only very weak development of secondary wings on the cap of the anteroconid complex, differing from the *quasiater* species group, and a small, plain, crescentic cap, differing from other species of the *pinetorum* species group. The buccal additional triangle (triangle 4) may slope posteriorly and have a rounded salient angle as in many individuals of *P. pinetorum* or may be sharply triangular and project from the midline of the tooth at an angle closer to normal as in *Pitymys ochrogaster.* First lower molar varies in length from 2.4 mm to 3.0 mm in the Cheetah Room fauna, and the type specimen is 3.2 mm in this dimension (fig. 5).

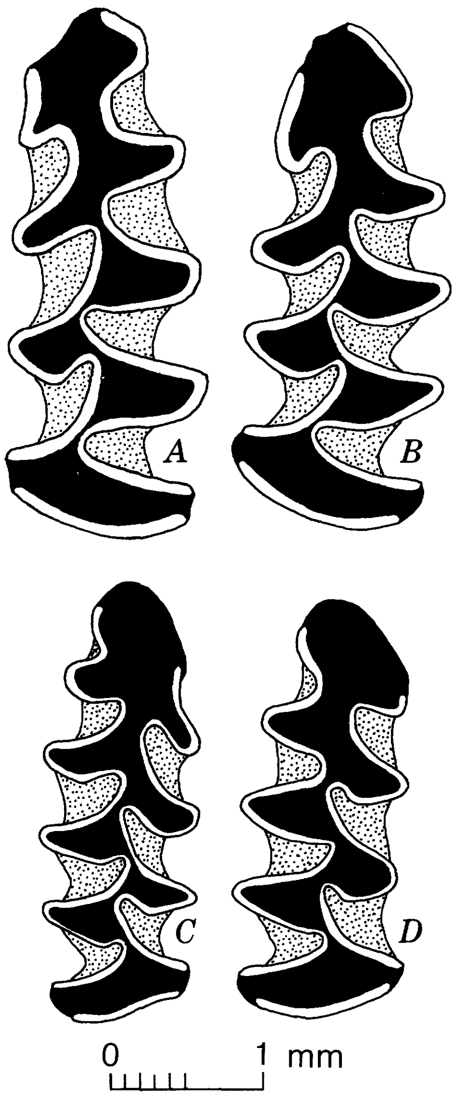


Figure 5. First lower molars of *Pitymys hibbardi. A* and *B*, left; *C* and *D*, right. *A*, Holotype from the Williston fauna of Florida, UF/FGS V5929. *B*, Typical form from the Cheetah Room fauna, USNM 264313. *C*, Individual overlapping the morphology of *Pitymys pinetorum* from the Cheetah Room fauna, USNM 264314. *D*, Individual overlapping the morphology of *Allophaiomys pliocaenicus* from the Cheetah Room fauna, USNM 254315.

Discussion.—*Pitymys hibbardi* was named from the Rancholabrean Williston fauna of Florida (Holman, 1959) and seems remarkably primitive for so geologically young a species (fig. 5*A*). Virtually nothing is known of its geochronologic range, however, the Cheetah Room fauna being its second or third fossil record. Martin (1987) suggested that the species is *Pitymys pinetorum*, which it could be on the basis of the type material (a single specimen), as individuals of *P. pinetorum* overlap the morphology of *P. hibbardi.* (See van der Meulen, 1978, fig. 13-C.) However, only 3 of the 52 first lower molars from the Cheetah Room fauna overlap the typical morphology of *Pitymys pinetorum*. (See van der Meulen, 1978, fig. 13-A,B,D, and F-K; also see fig. 5*C* of the present report.) It is here considered a valid species.

Martin (1987) stated that a decision will be made regarding the reality of *Pitymys hibbardi* upon the completion of work in progress. Should this work show the population from the type locality of *P. hibbardi* to be indistinguishable from *P. pinetorum*, a new species will have to be erected for the Cheetah Room specimens.

The morphology of the anteroconid complex of the first lower molar of *Pitymys hibbardi* from the Cheetah Room fauna has a range of individual variation that overlaps both *Allophaiomys pliocaenicus* and typical *Pitymys ochrogaster* and *Pitymys pinetorum*. In the sample are three m1s that overlap the form typical of *Pitymys pinetorum* (fig. 5*C*) and perhaps a dozen m1s that could not certainly be assigned to either *Pitymys* or *Allophaiomys*. (These last have been counted with *Allophaiomys*, and fig. 5*D* shows an m1 that was counted as *Pitymys* but is close to *Allophaiomys*.) Thus the sample from the Cheetah Room fauna supports the interpretation of van der Meulen (1978) that the North American lineage of *Pitymys* derives from the North American population of *Allophaiomys*, an interpretation that was based on study of a considerably younger fauna. From the variation in the buccal additional triangle of *Pitymys hibbardi* from the Cheetah Room fauna, both *Pitymys pinetorum* and *P. ochrogaster* could be derived from it.

Subfamily ONDATRINAE, new form

Dental diagnosis.—Cricetid rodents with hypsodont, triangularly prismatic cusps on their cheek teeth; m1 with posterior loop and *five* basic alternating triangles, differing from all other microtine subfamilies except possibly the Dicrostonychinae; triangle 4 may be weak in early forms, obscured by a shallow third buccal reentrant that leaves an islet in early wear, but triangle 5 always present; anteroconid complex based upon a single, semicircular anteroconid cap with lingual reentrant and wing evolving before buccal one, differing from the Arvicolini; M3 with two to three alternating triangles; teeth rooted except in *Neofiber*, and first upper molar retains primitive lingual third root; large size.

Included tribes.—Ondatrini and Pliomyini.

Discussion.—The Ondatrinae trace their ancestry back to the little-known genus *Ischymomys* described by Gromov and Polyakov (1977) under the authorship of V.S. Zazhigin. This genus is from the Ermak Series (late Hemphillian equivalent) along the Ishim River near Petropavlovsk, northernmost Kazakhstan, but very little is known of it. Although very low crowned, its cheek teeth are characterized by five alternating triangles on m1 and its M3 had an anterior loop, two alternating triangles, and a posterior loop that was basined; some M3s show a breaching of the posterior basin.

By Late Ruscinian time in Europe (Blancan II equivalent in North America), early ondatrines appeared in Europe (*Pliomys* and *Dolomys*) with five alternating triangles on the first lower molar. These contrast strongly with the coeval primitive arvicolines that had only three. Not until it was realized that the ondatrines began their history of hypsodonty with five alternating triangles could this seeming inconsistency be properly evaluated.

Tribe ONDATRINI, Kretzoi, 1955

Dental diagnosis.—Ondatrine rodents of large size with anterobuccal reentrant of M3 unreduced, differing from the Tribe Pliomyini; size increases with evolution; one genus is rootless.

Included genera.—*Dolomys, Ischymomys, Neofiber, Ondatra*, and *Pliopotamys*.

Discussion.—These are the muskrats, and they have a history that began in Asia more than 5 million years ago, in Europe about 4.3 million years ago, and in North America 3.7 million years ago. Although never a diverse group, the Ondatrini were and are widespread and conspicuous members of many faunas.

Genus ONDATRA, Link, 1795

(Muskrats)

Dental diagnosis.—Ondatrinine rodents of large size, differing from other genera; with rooted cheek teeth, differing from *Neofiber*; differing from *Pliopotamys* in presence of well-developed fifth lingual reentrant in the anteroconid complex of at least little-worn first lower molars; cement usually present to some degree and cellular; the dentine tract on the lingual salient angle of the posterior loop of the first lower molar progressively elongated, but essentially absent on the oldest species, *Ondatra idahoensis*; length of m1 averages more than 4.5 mm.

Included species.—*Ondatra annectens, O. idahoensis, O. nebraskensis*, and *O. zibethicus*.

Discussion.—Nelson and Semken (1970) have established a progressive increase in size from *Pliopotamys* to the living species of *Ondatra*, as well as considerable overlap. Regrettably, it appears that any single specimen of *Ondatra* is virtually unidentifiable to species because of individual variability in length of the first lower molar. Furthermore, generic assignment can be questionable in the region of transition between *Pliopotamys* and *Ondatra; Pliopotamys meadensis* is a good example of a species that has individuals that fall into the two different genera; some have a fifth lingual reentrant that is well formed, and many have an m1 that is longer than 4.5 mm, and the lingual dentine tract on the posterior loop of m1, while low, is higher than in *Ondatra idahoensis.*

ONDATRA ANNECTENS (Brown), 1908

Dental diagnosis.—A species of *Ondatra* with four buccal reentrants on the first lower molar, differing from *O. idahoensis*; differing from other species in that the fourth buccal and the fifth lingual reentrants are not as deep as the more posterior reentrants and are lost with wear, and dentine tract on the buccal salient angle of the posterior loop of m1 does not reach the occlusal surface until roots are fully formed; length of m1 4.9 to 6.1 mm.

Discussion.—This species covers a variety of very similar forms that span the time between the beginning of Irvingtonian I faunas (Olduvai event, about 1.8 m.y. ago; Java fauna, South Dakota; El Casco fauna, California) to the end of Irvingtonian II faunas (about 450,000 years ago; Cumberland Cave fauna, Maryland; Cudahy fauna, Kansas). During this period of 1.35 million years the first lower molar of this species varies in length with no apparent relationship to time (Martin and Tedesco, 1976).

Eight first lower molars have been recovered from the Cheetah Room locality, of which three are complete enough to measure their anteroposterior length. These measure 4.9, 4.9, and 5.0 mm; they are smaller than has been reported from the Cudahy fauna of Kansas. In addition, it appears that the dentine tract on the lingual salient angle of the posterior loop of this tooth would interrupt the enamel pattern of the occlusal surface at a later stage of wear than on the Cudahy specimens seen. One is tempted to suggest that they represent a slightly older stage of evolution, but the results of the studies of others, such as Martin and Tedesco (1976) and Nelson and Semken (1970), caution against this. The first upper molar has three distinct roots, and the lingual root is not fused to the anterior one as it is in living *Ondatra.*

Subfamily LEMMINAE, Gray, 1825

Dental diagnosis.—Cricetid rodents with rootless cheek teeth formed by hypsodont, triangularly prismatic cusps; m1 with a posterior loop, three basic alternating triangles, and an anteroconid complex that is a simple trefoil consisting of two wings and a roughly rectangular cap with no enamel on its anterior face, differing from the Prometheomyinae, Ondatrinae and the Dicrostonychinae; M3 with three hypsodont lophs, one formed by the anterior loop, another by the anterior alternating triangle, and the third by the posterior alternating triangle in confluence with the anterior part of the breached posterior loop, the posterior part forming a hooked loop lacking enamel on its posterior face, differing from all other subfamilies; reentrants with cement and lower incisor medial to the cheek teeth, differing from at least early forms of all other subfamilies except the Dicrostonychinae.

Included tribes.—Lemmini and Synaptomyini.

Discussion.—The oldest lemmine is a full-fledged lemmine with rooted and cemented cheek teeth differing little in pattern from the living *Lemmus.* It is from Bashkir A.S.S.R. and is correlative to the western European Late Ruscinian faunas, about 4 million years old. The subfamily is marked by little change in the dentition and its ancestry is not known.

Tribe SYNAPTOMYINI, von Koenigswald and Martin, 1984b

Dental diagnosis.—Lemmine rodents with anterolingual reentrant of M3 reduced or not elongate; central buccal reentrant extends more than halfway across the tooth, differing from the Lemmini.

Included genera.—Mictomys, Plioctomys, and *Synaptomys,* to be discussed.

Discussion.—The genus *Synaptomys* was established in 1858 by Baird to include the North American bog lemmings, the northern *Synaptomys borealis* (Richardson) and the southern *Synaptomys cooperi* Baird. Howell (1927) revised the genus and established as subgenera the names *Mictomys,* True for the northern form, and *Synaptomys,* Baird for the southern.

Gromov and Polyakov (1977) included *Synaptomys,* with *Lemmus* and *Myopus,* in the Tribe Lemmini and von Koenigswald and Martin (1984b) elevated this grouping to the Subfamily Lemminae, and restored the northern *Mictomys* to full generic status with three subgenera: *Metaxyomys, Kentuckomys,* and *Mictomys.*

Von Koenigswald and Martin also retained two subgenera in the southern *Synaptomys*: *Plioctomys* and *Synaptomys.* They placed both genera, *Mictomys* and *Synaptomys,* in the Tribe Synaptomyini.

Thus far, the Tribe Synaptomyini would seem to include two genera: *Synaptomys* and *Mictomys. Synaptomys* would include two subgenera: *Plioctomys* and *Synaptomys*; *Mictomys* would include three subgenera: *Metaxyomys, Kentuckomys,* and *Mictomys.* For the following reasons, we feel that at least three genera should be recognized—*Plioctomys, Mictomys,* and *Synaptomys*—and that *Mictomys* should include only two subgenera, *Kentuckomys* and *Mictomys.*

The case for Plioctomys.—Suchov (1976) defined *Plioctomys* as a subgenus of *Synaptomys,* thereby making *Synaptomys* the oldest known living microtine genus. Von Koenigswald and Martin (1984b) noted that *Plioctomys* had a distinctive Schmelzmuster that was shared by *Synaptomys rinkeri* Hibbard from the latest Blancan faunas of the Great Plains of the United States. Schmelzmuster is a distinctive character of value in taxonomy; thus these authors moved Hibbard's species to the subgenus *Plioctomys*, following the taxonomy of Suchov. Significantly, in spite of the different Schmelzmuster of subgenus *Plioctomys*, when compared to that of the subgenus *Synaptomys*, these authors did not question the assignment of subgenus *Plioctomys* to the genus *Synaptomys*.

In 1956 C.W. Hibbard introduced the name *Synaptomys* (*Synaptomys*) *rinkeri* [=*Plioctomys rinkeri* (Hibbard) in our terminology, modifying von Koenigswald and Martin] for a fossil lemming that he described from the late Pliocene Dixon fauna of Meade County, Kansas. In so doing he stated (1956, p. 169), "I find no characters in *Synaptomys* (*S.*) *rinkeri* that would keep it from being the ancestral stock of the Recent *S. cooperi* or from being ancestral to other later Pleistocene forms of the subgenus *Synaptomys*, exclusive of the *S. vetus* group." The "*S. vetus* group" was then considered by some to be closely related to the living subgenus *Mictomys* (Wilson, 1934), although Hibbard (1956, p. 169) believed that it represented a "side branch that split off from the *Synaptomys* stock during the Pliocene," implying a position intermediate between the lineages of the subgenera *Mictomys* and *Synaptomys* as he was using these names.

Hibbard's assumption of a rectilinear relationship between the 2.6- to 2.0-million-year-old *Plioctomys rinkeri* and living *Synaptomys cooperi* is most recently repeated in the retention of *Plioctomys* as a subgenus of *Synaptomys* by von Koenigswald and Martin (1984b) and is most recently illustrated by Repenning and others (1987) (this report, fig. 6).

With the exception of placing "*Synaptomys* (*S.*) *rinkeri*" in the subgenus *Plioctomys*, the evolutionary concepts expressed in 1956 by Hibbard have remained unchanged; and this is strange as the species and its subgenus *Plioctomys* [as used by von Koenigswald and Martin (1984b)] seem to have become extinct 2 million years ago, whereas *Synaptomys* (*Synaptomys*) *cooperi* does not appear in the fossil record until perhaps 1.2 million years later, sometime before 740,000 years ago in the Fyllan Cave fauna of Texas (Alisa Winkler, written commun., 1987).

These intervening 1.2 million years are marked by an absence of both *Plioctomys* and *Synaptomys*; this is a gap in the fossil record as long as the combined temporal spans of both *Plioctomys rinkeri* and *Synaptomys cooperi*. Moreover, this gap is marked by an abundance of *Mictomys* in a dozen or so faunas across the Great Plains, in the area where *Plioctomys* is last seen and where *Synaptomys* is first seen, as well as in those faunas containing *Mictomys* west of the Rocky Mountains where *Plioctomys* and *Synaptomys* would not be expected. Although a 1.2-million-year gap in the fossil record between *Plioctomys* and *Synaptomys*, a gap during which *Mictomys* is well known, might be enough to arouse some doubt in the relationship, none has been suggested in publication.

The lemmings from the Cheetah Room fauna of Hamilton Cave, West Virginia, indicate that the relationship between *Plioctomys* and *Synaptomys* is far less direct than supposed. They show that the similarity between the two is not real but is secondarily derived; *Synaptomys* did not evolve directly from *Plioctomys* in the conventional sense supposed by Hibbard. The similarity between *Synaptomys* and *Plioctomys* consists of the symmetrical arrangement of the alternating triangles along the tooth axis of the lower teeth, rather than a buccal position characteristic of *Mictomys*, and a deep anterior buccal reentrant on the m1 of *Synaptomys* presumably retained from *Plioctomys*. But the deep anterior buccal reentrant is not the same on the two, as the alternating triangles insert at the middle of the posterior face of the anteroconid complex in *Plioctomys* and at the buccal corner of this face in *Synaptomys*, and the deep posterior buccal reentrant clearly derives from a deepening of this reentrant as it is found in *Mictomys* (fig. 6).

As will be discussed, the sample from the Cheetah Room fauna indicates that a reversal of both characters resulted in the development of *Synaptomys* out of *Mictomys*. For this reason we see no direct relationship between *Plioctomys rinkeri* and *Synaptomys cooperi* and elevate *Plioctomys* to full generic status, ancestral to, but not included in, the genus *Synaptomys*.

Thus the Tribe Synaptomyini includes three genera: *Plioctomys, Mictomys*, and *Synaptomys*. *Mictomys* alone contains subgenera: *Mictomys, Kentuckomys*, and *Metaxyomys*. *Kentuckomys* seems to be a valid subgenus based upon its relatively long lower incisor and distinctive Schmelzmuster (von Koenigswald and Martin, 1984b).

The case against Metaxyomys.—The lack of reduction of the anterior buccal reentrant of the first lower molar in *Synaptomys vetus* from the Grand View fauna of Idaho (fig. 6), and other faunas, has led to the introduction of a separate subgeneric name, *Synaptomys* (*Metaxyomys*) *vetus*, with the concept, first expressed by Hibbard (1956), of an evolutionary intermediate position between the lineages of the living *Mictomys* and *Synaptomys*, not questioning the direct derivation of *Synaptomys* from *Plioctomys* (Zakrzewski, 1972; von Koenigswald and Martin, 1984b). The posterior buccal reentrant of m1 is reduced in *Synaptomys vetus*, as it is in *Mictomys*, but the anterior one is not, presumably as in *Synaptomys*.

As indicated by von Koenigswald and Martin (1984b), two diagnostic characters mark the lower first molar of *Mictomys*: (1) confluence of triangles 1 and

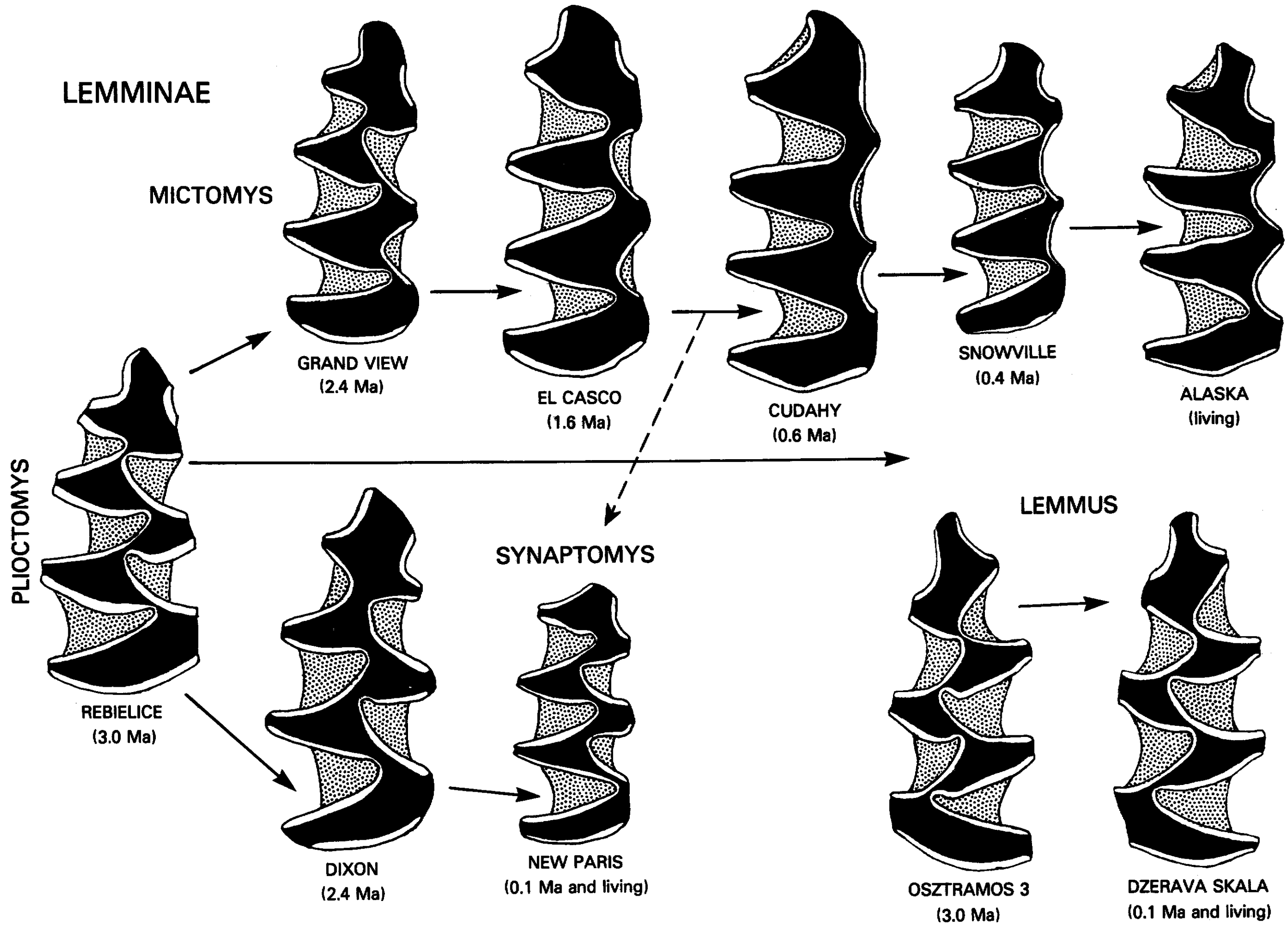


Figure 6. Right lower first molars of the Tribe Synaptomyini and left lower first molars of the Tribe Lemmini. Reproduced with slight modification from Repenning and others, 1987. This diagram shows the conventional concept of evolution of the Synaptomyini prior to discovery of the Cheetah Room fauna of Hamilton Cave; *Synaptomys cooperi* (from New Paris fauna, Pennsylvania) is considered as being derived from *Plioctomys rinkeri* (specimen from Dixon fauna, Kansas). Dashed arrow shows derivation indicated by the Cheetah Room fauna. Other specimens shown are *Plioctomys mimomiformis* from Rebielice-Krolewskie fauna, Poland; *Mictomys vetus* from Grand View fauna, Idaho; an early form of *Mictomys kansasensis* from El Casco fauna, California; *Mictomys meltoni* from Cudahy fauna, Kansas; *Mictomys* n. sp. from Snowville fauna, Utah; and *Mictomys borealis* from Alaska. The two left lower molars of *Lemmus* are from Osztramos-3 fauna, Hungary, and Dzerava-Skala fauna, Czechoslovakia.

2 with consequent shallowing of the posterior buccal reentrant, and (2) buccal shifting of the tooth axis with consequent shallowing of both buccal reentrants. As shown in figure 6, confluence develops first and is evident in *Synaptomys vetus*. Buccal shifting of the tooth axis had not yet begun in this species and became evident only in *Mictomys kansasensis*, of which an early form from the El Casco fauna of California is shown in figure 6.

Lack of buccal shifting of the tooth axis in both *Synaptomys vetus* and the species of *Plioctomys* is also shown by the central position of the commissure between the alternating triangles and the posterior face of the anteroconid complex; as pointed out above, this differs from the condition in *Synaptomys*. Thus the structure of the first lower molar of *Synaptomys vetus* does not indicate a lineage separate from those represented by living *Mictomys* and *Synaptomys*, but indicates that the species is transitional from *Plioctomys* to *Mictomys* and has developed one of the two apomorphic characters that define *Mictomys*. The other character, shifting of the tooth axis, has not yet developed; and in this character *S. vetus* retains the plesiomorphic condition of *Plioctomys*. The species *Synaptomys vetus* is, instead, the first of the *Mictomys* lineage and the subgenus *Metaxyomys* is here suppressed, as it is based upon a demonstrably false concept of the phylogenetic pattern in the monophyletic lineage of *Mictomys*.

Genus MICTOMYS, True, 1894

(Northern bog lemmings)

Dental diagnosis.—A synaptomyinine rodent with alternating triangles 1 and 2 completely confluent on the lower molars, differing from *Synaptomys* and *Plioctomys.*

Included species.—Mictomys anzaensis, M. borealis, M. kansasensis, M. landesi, M. meltoni, and *M. vetus,* as well as at least one unnamed species.

Discussion.—The genera *Synaptomys* and *Mictomys* now live only in North America, although the ancestral form, *Plioctomys mimomiformis,* is first known from deposits in Bashkir A.S.S.R. that are about 4 million years old and is last known in Siberian (Sher and others, 1979) and Alaskan (Repenning and others, 1987) Beringia from deposits about 2.4 million years old.

As established through the similarity of their Schmelzmuster by von Koenigswald and Martin (1984b), *Plioctomys* also spread southward to the conterminous United States by 2.6 million years ago. This immigration into the United States was as the derived species *P. rinkeri* (Hibbard), which dispersed down the eastern side of the Rocky Mountains, and as the derived genus, *Mictomys vetus* (Wilson), which dispersed down the Pacific Coast.

Mictomys vetus and *Plioctomys rinkeri* appeared in the United States at the same time; *Mictomys* is first known about 3 meters below the Gauss/Matuyama polarity boundary in Idaho and Arizona; *Plioctomys rinkeri* is first known about 3 meters below the same polarity boundary in northern Texas (G.E. Schultz, oral commun., 1985).

Genus SYNAPTOMYS, Baird, 1858

(Southern bog lemmings)

Dental diagnosis.—A synaptomyinine rodent with alternating triangles 1 and 2 not confluent on the lower molars, differing from *Mictomys*; alternating triangles of the first lower molar connected to the buccal corner of the anteroconid complex, differing from *Plioctomys.*

Included species.—Synaptomys cooperi, including the large race that has been called *Synaptomys australis.*

Discussion.—The bog lemmings of the Cheetah Room fauna in Hamilton Cave present a problem and at the same time suggest an ancestry for *Synaptomys cooperi* other than the direct derivation from *Plioctomys rinkeri* as envisioned by C.W. Hibbard in 1956. This problem centers on the transitional morphology of the lower molars from the Cheetah Room fauna.

The distinction between the teeth of the two living bog lemming genera *Mictomys* and *Synaptomys* lies almost entirely in characters of the lower cheek teeth (fig. 7). In *Mictomys* the posterior buccal reentrants of all lower cheek teeth are weakly developed, resulting from complete confluence between the posterior two alternating triangles (triangles 1 and 2). In the more modern of the species of *Mictomys,* the anterior buccal reentrant is similarly reduced and a buccal location of the commissure between the anteroconid complex and the anterior alternating triangle (triangle 3) results.

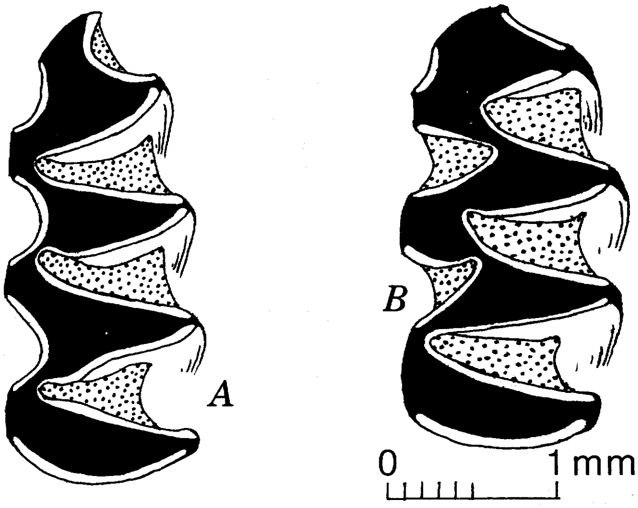


Figure 7. Left lower first molars of living bog lemmings, occlusal views. *A, Mictomys borealis dalli,* Seward Peninsula, Alaska. R.L. Rausch No. 26132. *B, Synaptomys cooperi,* Springfield, Illinois. ISM No.688275. Note depth of the two primary buccal (left side) reentrants and the effect on the configuration of the alternating triangles.

In *Synaptomys* the buccal reentrants are more like those of other microtine rodents, and the central alternating triangle (triangle 2) is completely separated (or nearly so) from the posterior one (triangle 1) by a narrowing, or even closure, of the dentinal areas of the triangles within the enamel margins. In addition, the connection between the anteroconid complex and the most anterior alternating triangle (triangle 3) tends to be more centrally located, although not in the same way that it is centrally located in *Plioctomys* or even in the earliest species of *Mictomys, Mictomys vetus* from the late Pliocene.

In *Synaptomys* the commissure between the anteroconid complex and the anterior alternating triangle originates on the third triangle at the center of the tooth, but it inserts on the buccal side of the anteroconid complex. In *Plioctomys* (fig. 6, Rebielice) and *Mictomys vetus* (fig. 6, Grand View; fig. 8*A*), the insertion of the commissure is in the center of the posterior side of the anteroconid complex because the anterior buccal reentrant is not reduced and the anterior lingual reentrant not correspondingly elongated, which would require that the insertion of the commissure be on the buccal side of the anteroconid complex.

As discussed, the lack of reduction of the anterior buccal reentrant in *Mictomys vetus,* which led to the

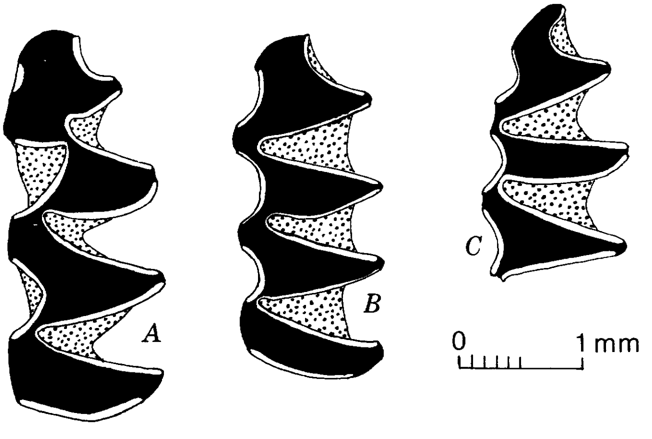


Figure 8. Left lower first molars of *Mictomys*. *A*, *Mictomys vetus* from the Grand View fauna, Idaho; age about 2.4 million years, USGS specimen. Posterior (lower) buccal reentrant is reduced, but anterior one is still as deep as in ancestral genus *Plioctomys*. *B*, Unnamed species of *Mictomys* from the Snowville fauna, Utah; age about 500,000 years, UCMP 124887. Similar to living species except that base of the incisor is farther back, buccal reentrants are somewhat deeper, lingual triangles are thicker in anteroposterior dimension, and enamel wall on posterior side of triangles is thin. This species greatly resembles *Mictomys* (*Kentuckomys*) *kansasensis*. *C*, Fragment of tooth from the Cheetah Room fauna that has the features of *Mictomys*, USNM 184100, a right first lower molar with drawing reversed.

introduction of the separate subgeneric name, *Mictomys* (*Metaxyomys*) *vetus*, is not intermediate, but is a primitive state in the rectilinear evolution of *Mictomys* (fig. 6). The similarity of the anteroconid commissure of *Synaptomys cooperi* to that of *Mictomys vetus* is not real, but secondarily derived.

Figure 8*A* shows a left lower molar of *Mictomys vetus* from the Grand View fauna of Idaho with unreduced and incompletely reduced buccal reentrants. Figure 8*B* shows the corresponding tooth of an unnamed species of *Mictomys* from Snowville, Utah, believed to be about 500,000 years old. This unnamed species has much greater reduction of the buccal reentrants, but the lingual triangles are broader anteroposteriorly and the enamel is noticeably thicker on the anterior faces of the triangles than in the living species; the species greatly resembles *Mictomys* (*Kentuckomys*) *kansasensis*, but its Schmelzmuster is not known; the position of the base of the lower incisor varies from being opposite the middle of m3 to being opposite the anterior face of this molar. The same species, called "*Synaptomys* (*Mictomys*) sp." by Gidley and Gazin (1938), is known from Cumberland Cave, Maryland, and van der Meulen (1978, p. 132) has noted how it differs from named species.

Seventy-two bog lemming teeth have been recovered in the Cheetah Room locality of Hamilton Cave, of which 22 are first lower molars; figure 8*C* shows the only first lower molar (incomplete) that conforms to the characters of *Mictomys*. This single tooth most resembles the living species *M. borealis*, rather than contemporary *M. kansasensis* or *M. meltoni*; but the sample size is too small to suggest significance. The rest of the bog lemming lower molars from the Cheetah Room fauna are intermediate between *Mictomys* and *Synaptomys* (5 of 21 first lower molars or 24 percent) or conform to the characters of *Synaptomys cooperi* (16 of 21 first lower molars or 76 percent). A sample of the first lower molars is shown in figure 9.

As shown in figure 8*C* and figure 9, the recovered sample of bog lemming teeth from the Cheetah Room fauna indicates that the population was morphologically

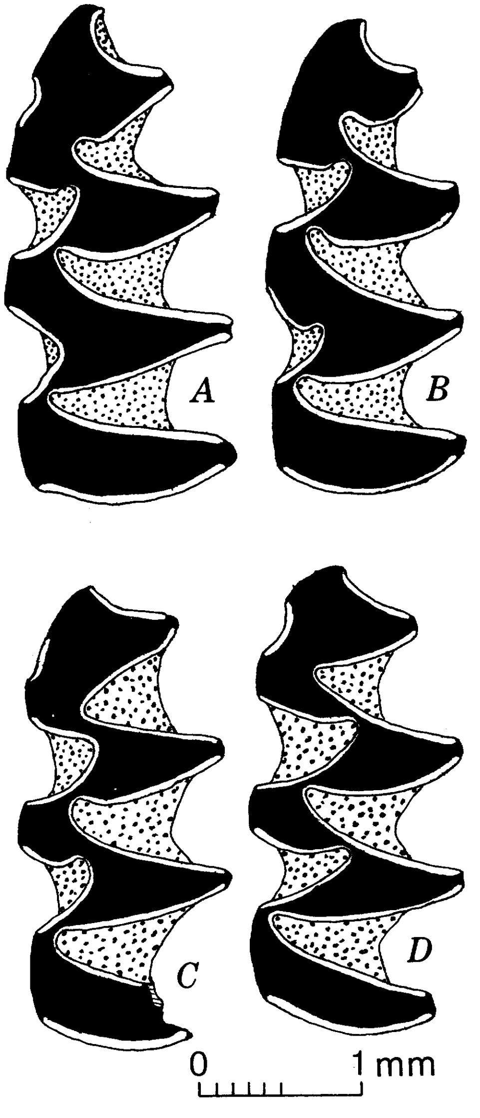


Figure 9. Left lower first molars of bog lemmings from the Cheetah Room fauna of Hamilton Cave, West Virginia. Specimens show a gradation of features from almost those of *Mictomys* on upper left to those of *Synaptomys* on lower right. *A*, USNM 184091; *B*, USNM 23888; *C*, USNM 264306; *D*, USNM 264307.

intermediate between *Mictomys* and *Synaptomys*. The development of the genus *Mictomys* is recorded by about 1,760,000 years of fossil history before the existence of the Cheetah Room fauna and before any record of *Synaptomys cooperi*. That part of the population represented by this fauna that conforms to the characters of *Synaptomys* would seem to be the oldest record of any bog lemming that could be called *Synaptomys cooperi*.

Although some of this variable population resembles the ancestral genus *Plioctomys* in the development of the alternating triangles, none of it has the anteroconid complex attached to the alternating triangles in the central manner found in *Plioctomys*. Instead, the variation in the Cheetah Room faunal sample shows that the pattern of the tooth enamel on the first lower molar of *Synaptomys cooperi* may derive from a secondary deepening of the buccal reentrants of *Mictomys*. Thus, as has been discussed, *Plioctomys* is here given full generic status and suppressed as a subgenus of *Synaptomys*, which appears to be a derivative of *Mictomys*.

Von Koenigswald and Martin (1984b) presented a cladogram showing the relationships of the Subfamily Lemminae in which five characters were used to diagnose the included taxa. These were:

1. *Structure of the last upper molar*, used to separate the Tribes Synaptomyini and Lemmini; in the present report this character is given in the tribal diagnoses.

2. *Asymmetry of the reentrants and triangles on the lower teeth*, used to separate *Plioctomys, Synaptomys*, and *Mictomys*; they are discussed at length herein with an analysis of their cause and parallel development. This character is discussed in the diagnoses. The significance of this character in the bog lemmings of the Cheetah Room fauna appears to be little, as the sample of the population is clearly shifting from one extreme to the other (figs. 8*C* and 9).

3. *Confluence of the first and second alternating triangles on the lower teeth*, used to separate *Mictomys* from *Synaptomys* and *Plioctomys*. This has been discussed at length herein, is the basis of diagnosis of the two genera, and varies individually in the sample from the Cheetah Room fauna (fig. 9).

4. *Position of the base of the lower incisor*, described in terms relative to the last two lower molars. This is an awkward character in that relatively complete specimens are needed for evaluation and individual variation is great. Von Koenigswald and Martin (1984b) listed three conditions for the base of the lower incisor: (a) behind the last molar, (b) between the second and third molar, and (c) at the second molar. Shorter incisors were considered more derived.

Six modern specimens of *Synaptomys cooperi* from Pennsylvania, Illinois, Missouri, and Kansas were examined for this character; and the posterior limit of the incisor capsule varied from 0.8 mm behind the posterior face of the last molar to opposite the middle lingual salient angle of this tooth. One fossil specimen of this species from New Paris, Pennsylvania, had the base of the incisor at the anterior face of the m3, whereas the specimen described by Gidley and Gazin (1938) from Cumberland Cave, Maryland, had it at the posterior face of m3. One mandibular ramus from the Cheetah Room fauna (a *Synaptomys cooperi* morphotype) was complete enough to interpret; it had the base of the incisor at least as far back as the middle of the last molar. Thus the position of the base of the incisor in *Synaptomys cooperi* appears to be primitive and to vary between conditions (a) and (b).

Two specimens of *Mictomys borealis* from Alaska had the base of the incisor at the posterior salient angle of the second molar, condition (c) (advanced). The unnamed species of *Mictomys* believed to be about 500,000 years old (fig. 8*B* from the Snowville fauna, Utah) had the base of the incisor at the middle of the last molar, condition (a); however, this species from Cumberland Cave, Maryland (Gidley and Gazin, 1938) had the base of the incisor at the anterior face of the last molar, condition (b). Although living *Mictomys borealis* may be advanced in this character, fairly modern fossil species of the genus appear to be more primitive.

On the other hand, the oldest species of the genus, *Mictomys vetus* from the approximately 2.4-million-year-old Grand View fauna of Idaho (fig. 8*A*), has the base of the incisor in front of the anterior face of the last molar, condition (b) (moderately advanced, more so than many of its descendants).

Although of a limited sample, these observations are in agreement with those indicated by von Koenigswald and Martin (1984b), except that they did not indicate the individual variability in the position of the base of the incisor. The observations of the position of the base of the lower incisor may be summed up as follows: the most primitive condition is found in *Synaptomys cooperi* (living and fossil), in the late Pleistocene unnamed species of *Mictomys*, and in the subgenus *Mictomys* (*Kentuckomys*); the most advanced condition is found in the living *Mictomys borealis*; and the oldest species assigned to *Mictomys, Mictomys vetus*, has a condition intermediate between most advanced and most primitive (the condition in *Plioctomys* is unknown, although attainable). We find this character quite variable and difficult to interpret.

5. *Schmelzmuster*. We have not examined the enamel structure and rely upon the statements of von Koenigswald and Martin (1984b). These show that *Mictomys borealis, Mictomys meltoni*, and *Synaptomys cooperi* have the same Schmelzmuster, whereas *Mictomys vetus* and the two species of *Plioctomys* share a more primitive enamel type. This suggests to us that the

Schmelzmuster favors an interpretation that *Synaptomys cooperi* is more closely related to *Mictomys meltoni* and *M. borealis* than to *Plioctomys rinkeri.*

The conclusions of von Koenigswald and Martin (1984b) are not challenged here and are matters of agreement in almost all cases. We depart from their opinions only in regard to the inclusion of *Plioctomys*, as a subgenus, in the genus *Synaptomys*; and this seems to be supported by the characters that they use, as well as by the Cheetah Room fauna. *Synaptomys* differs from *Plioctomys* in its Schmelzmuster, the position of the base of its incisor, the origin of the lack of confluence of triangles 1 and 2 on the lower teeth, and the origin of the symmetry of the triangles and reentrants on the lower teeth. They share a similar last upper molar, which separates both of them from the Tribe Lemmini.

We are unable to assign the bog lemming population from the Cheetah Room fauna to a genus or a species, although 76 percent of the sample seen does not differ from *Synaptomys cooperi.*

BOG LEMMING HISTORY

The history of the bog lemmings (fig. 10) begins in eastern Europe about 4 million years ago. The earliest known form is fully hypsodont with no roots on the cheek teeth, and its teeth are fully cemented, apomorphic characters totally unknown in any other microtine rodents of that early age except for the North American genus *Pliolemmus*, Subfamily Prometheomyinae, whose teeth are rootless but have no cement. The ancestor of the bog lemmings is unknown.

It appears that the brown lemmings (*Lemmus* and *Myopus*) were derived from the same unknown ancestor, or possibly from the earliest bog lemming, and therefore the taxonomic structure of von Koenigswald and Martin (1984b) is here used with the recognition that it differs only in rank from that of Gromov and Polyakov (1977).

The earliest known genus of bog lemming, *Plioctomys*, is of a very generalized nature, and it is as appropriate an ancestor of *Lemmus* as it is of *Mictomys*

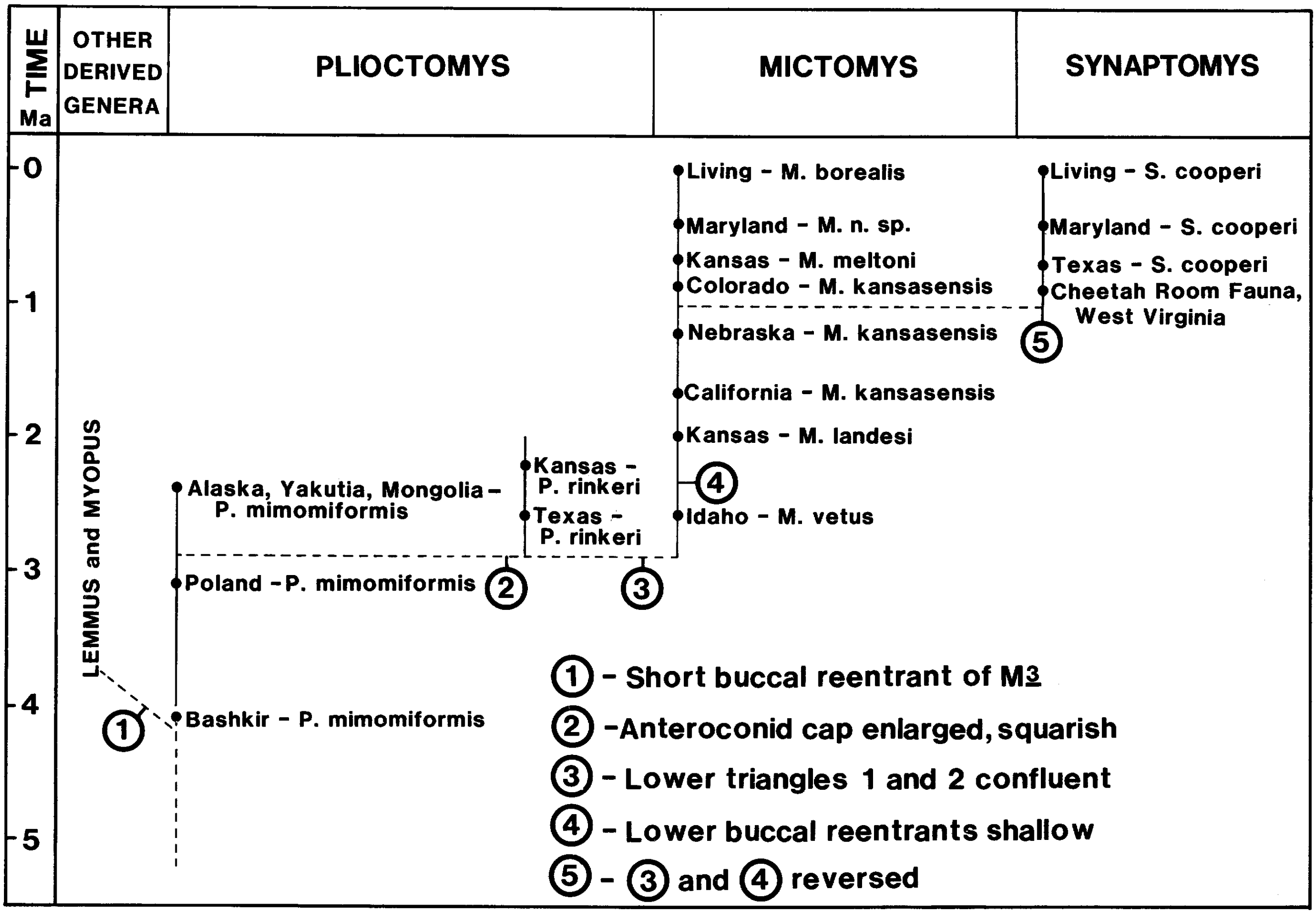


Figure 10. Inferred phylogeny of the Synaptomyini.

(Kowalski, 1977). Nevertheless, *Plioctomys* is not greatly different from living genera of the Lemminae. This minimal tendency for change is characteristic of the subfamily and is even more evident in the Tribe Lemmini, including living *Lemmus* and *Myopus*, which are indistinguishable by dental characters from their earliest known fossil relatives, all of which have been placed in the more specialized genus *Lemmus* (fig. 6).

Plioctomys, first known from southern Russia, is also known from Poland, Hungary, Mongolia, Yakutiya, Alaska, and the Great Plains of the United States. From its earliest record until about 2.4 million years ago, the latest records in Yakutiya and Alaska, no change is recognized in the morphology of its teeth (Repenning and others, 1987). However, probably after 3 million years ago, part of the population of *Plioctomys* dispersed southward in North America, following two routes, one on either side of the Rocky Mountains. They arrived in the conterminous United States at the same time on both sides of the cordillera; their first fossil records are about 2.6 million years old and about 5 meters below the Matuyama/Gauss polarity boundary in Idaho, Arizona, and Texas.

The southward-dispersing *Plioctomys* populations evolved en route, and the immigrants moving down the east side of the Rocky Mountains to the Great Plains did so as a new species, *Plioctomys rinkeri* (the Texas record), while those entering the United States west of the Rocky Mountains did so as a new genus and species, *Mictomys vetus* (the Idaho and Arizona records).

Mictomys was successful, and its history up to and including the living fauna is well recorded. By 2.0 million years ago it had dispersed east of the Rocky Mountains. At this time *Plioctomys rinkeri* seems to have become extinct, as there are no younger records; the youngest record of the ancestral species is 2.4 million years old in Yakutiya and Alaska and *P. rinkeri* was the last representative of the genus *Plioctomys* (fig. 10).

As indicated by the bog lemmings from the Cheetah Room fauna of Hamilton Cave, West Virginia, between 850,000 and 740,000 years ago, possibly before 820,000 years ago, a population of *Mictomys* in southeastern United States evolved into the living genus *Synaptomys*. To judge from the variation in the Cheetah Room fauna, this major transition in tooth morphology took place spontaneously, with no obvious environmental or other external pressure, and in a very short time. In view of the age of the fauna, it seems possible that the change simply reflects genetic drift in isolation from populations of *Mictomys* to the west of the first Nebraskan ice sheet of the North American ice ages, Hamilton Cave lying perhaps 160 km east of the eastern edge of the continental ice sheet. It seems to be an obvious case of reversal of at least one evolutionary trend in changing morphology.

Far from being the most ancient of living microtine genera, as it appeared to be when Suchov (1976) described *Synaptomys* (*Plioctomys*) *mimomiformis* from the Simbugino fauna of Bashkir A.S.S.R., *Synaptomys* now appears to be nearly the most recent of living microtine genera; only Old World *Arvicola* is known to have appeared more recently, although North American subgenus *Phenacomys* (*Arborimus*) may also be younger.

SUMMARY AND CONCLUSIONS

The microtine rodents of the Cheetah Room fauna of Hamilton Cave, Pendleton County, West Virginia, provide surprising information about a number of microtine lineages.

1. The deposits of the Cheetah Room are remarkably old, probably the oldest cave deposits known in the eastern United States. They appear to date between about 850,000 years ago, when *Microtus paroperarius* first entered the United States with the first advance of the Nebraskan glaciation [correlated with the first peak of Oxygen Stage 22, Richmond and Fullerton (1986)], and the 740,000-year-old beginning of the Brunhes Chron. The absence of representatives of the immigrant *Pitymys quasiater* species group and the primitive condition of *Microtus paroperarius* suggest that the fauna may be older than the 820,000-year-old faunas from Hansen Bluff, Colorado.
2. The Cheetah Room fauna may contain the only North American record of the subgenus *Mimomys* (*Cromeromys*), a subgenus widespread in Eurasia, where it ranges in age from possibly 3.5 million to possibly 850,000 years. The probable temporal correlation of the fauna with the first of the Nebraskan ice sheets suggests that older North American records may have been in Canada.
3. The morphology of the new subgenus and species of *Phenacomys, P.* (*Paraphenacomys*) *brachyodus*, indicates that this genus is represented by at least three lineages in the living fauna that are given subgeneric designation herein.
4. The primitive microtinine species *Lasiopodomys deceitensis* is well represented in the Cheetah Room fauna. This constitutes the first non-arctic record of this species and thus hints at a relationship with the first ice sheets. Assignment of this species to the genus is tentative, as the fossil record is not complete enough to link these early forms with the name-bearing living species.
5. Although rare in the Cheetah Room fauna, the presence of the primitive species *Microtus paroperarius* seems indicated by the presence of "complex" last upper molars. The first lower molars in the fauna presumed to belong to this species are difficult to separate from *Lasiopodomys deceitensis* and more closely match specimens of *Microtus paroperarius* from the 820,000-year-old

parts of the Hansen Bluff faunal sequence of Colorado than they do the 610,000-year-old type sample from the Cudahy fauna of Kansas, suggesting a comparable age.

6. An excellent sample of a vole assigned to *Pitymys hibbardi* shows a complete transition between ancestral *Allophaiomys pliocaenicus* and descendants *Pitymys pinetorum* and *Pitymys ochrogaster*, supporting the interpretations of van der Meulen, published 10 years ago. *Allophaiomys pliocaenicus* itself is well represented in the fauna, suggesting that its range extended from the Rocky Mountains to the East Coast before the ice ages.

7. One of the more remarkable morphologic transitions known in vertebrate paleontology is recorded in the bog lemmings of the Cheetah Room fauna. In this transition the living genus *Synaptomys* is seen to spontaneously derive from a population of the living genus *Mictomys* in the southeastern United States, a derivation not previously considered possible. Almost every conceivable variation of individual morphology is represented in the sample. Demonstrable origin of *Synaptomys* from a source other than the primitive lemming *Plioctomys rinkeri* requires that *Plioctomys* be recognized as a full genus rather than as a subgenus of the genus *Synaptomys*.

REFERENCES CITED

Baird, S.F., 1858, Mammals—Explorations and surveys for a railroad route....: Washington, D.C., xlvii+757 p.

Chaline, J., 1974, Esquisse de l'évolution morphologique, biometrique et chromosomique du genre *Microtus* (Arvicolidae, Rodentia) dans le Pleistocene de l'hemisphere nord: Société Géologique de France, Bulletin 16, p. 440–450.

Corbet, G.B., 1978, The mammals of the Palaearctic Region—A taxonomic review: British Museum (Natural History), 314 p.

Erbaeva, M.A., 1976, The origin, evolution, and intraspecific variability of Brandt's vole from the Anthropogene of western Transbaikalia, *in* Gromov, I.M., ed., Rodent evolution and history of their Recent fauna: Academy of Sciences U.S.S.R., Zoological Institute, Proceedings, v. 66, p. 102–116. [In Russian.]

Gidley, J.W., and Gazin, C.L., 1938, The Pleistocene vertebrate fauna from Cumberland Cave, Maryland: United States National Museum Bulletin 171, 99 p.

Grayson, D.K., 1983, The paleontology of Gatecliff shelter, Chapter 6 *in* Thomas, D.H., ed., The archaeology of Monitor Valley, 2, Gatecliff shelter: American Museum of Natural History Anthropological Papers, Part 1, p. 99–126.

Gromov, I.M., and Polyakov, I.Yu., 1977, Polevki [voles] (Microtinae), Mammals, Part III, *in* Fauna of the U.S.S.R.: Academy of Sciences U.S.S.R., Zoological Institute, New Series No. 116, No. 8, 504 p. [In Russian.]

Guthrie, R.D., and Matthews, J.V., Jr., 1971, The Cape Deceit fauna—Early Pleistocene mammalian assemblage from the Alaskan arctic: Quaternary Research, v. 1, p. 474–510.

Hall, E.R., 1981, The mammals of North America: New York, John Wiley, 1181+90 p.

Hibbard, C.W., 1944, Stratigraphy and vertebrate paleontology of Pleistocene deposits of southwestern Kansas: Geological Society of America Bulletin, v. 55, p. 707–754.

______1950, Mammals of the Rexroad formation from Fox Canyon, Kansas: University of Michigan, Museum of Paleontology Contributions VIII, p. 113–192.

______1956, Vertebrate fossils from the Meade Formation of southwestern Kansas: Michigan Academy of Sciences, Arts, and Letters Papers XLI, p. 145–203.

Hinton, M.A.C., 1926, Monograph of the voles and lemmings (Microtinae), living and extinct: British Museum (Natural History), 488 p.

______1932, Note on "*Cosomys*" Wilson from the Pliocene of California: Journal of Mammalogy, v. 13, p. 280–281.

Holman, J.A., 1959, Birds and mammals from the Pleistocene of Williston, Florida: Florida State Museum, Biological Sciences Bulletin 5, 24 p.

Howell, A.B., 1927, Revision of the American lemming mice (Genus SYNAPTOMYS): U.S. Dept. of Agriculture, Bureau of Biological Survey, North American Fauna 50, 38 p.

Janossy, Denes, and van der Meulen, A.J., 1975, On *Mimomys* (Rodentia) from Osztramos-3 north Hungary: Nederlandse Akademie van Wetenschappen (Koninklijke)-Amsterdam, Proceedings, Series B, v. 78, p. 381–391.

Johnson, M.L., 1973, Characters of the heather vole, *Phenacomys*, and the red tree vole, *Arborimus*: Journal of Mammalogy, v. 54, p. 239–244.

Johnson, M.L., and George, S.B., in press, Speciation within the *Arborimus longicaudus*-complex, with a description of a new species: Natural History Museum, Los Angeles County; Contributions to Science.

von Koenigswald, Wighart, 1980, Schmelzstructur und Morphologie in den Molaren der Arvicolidae (Rodentia): Abhandlung der senckenbergischen naturforschenden Gesellschaft 539, p. 1–129.

von Koenigswald, Wighart, and Martin, L.D., 1984a, The status of the genus *Mimomys* (Arvicolidae, Rodentia, Mamm.) in North America: Neues Jahrbuch fur Geologie und Palaeontologie, Abhandlungen 168, p. 108–124.

______1984b, Revision of the fossil and Recent Lemminae (Rodentia: Mammalia): Carnegie Museum of Natural History Special Publication 9, p. 122–137.

Kowalski, Kazimierz, 1977, Fossil lemmings (*Mammalia, Rodentia*) from the Pliocene and early Pleistocene of Poland: Acta Zoologica Cracoviensia, v. 22, p. 297–317.

Kretzoi, Miklos, 1969, Skizze einer Arvicoliden-Phylogenie—Stand 1969: Vertebrata Hungarica, v. XI, p. 155–188.

Martin, R.A., 1975, *Allophaiomys* Kormos from the Pleistocene of North America, *in* Smith, G.R., and Friedland, N.E., eds., Studies on Cenozoic paleontology and stratigraphy in honor of Claude W. Hibbard: University of Michigan Museum of Paleontology, p. 97–110.

______1987, Notes on the classification and evolution of some North American fossil *Microtus* (Mammalia; Rodentia): Journal of Vertebrate Paleontology, v. 7, p. 270–283.

Martin, R.A., and Tedesco, Richard, 1976, *Ondatra annectens* (Mammalia:Rodentia) from the Pleistocene Java Local Fauna of South Dakota: Journal of Paleontology, v. 50, p. 846–850.

Maser, Chris, Mate, B.R., Franklin, J.F., and Dyrness, C.T., 1981, Natural history of Oregon coastal mammals: Pacific Northwest Forest and Range Experiment Station, U.S. Forest Service, General Technical Report PNW-133, 496 p.

Mead, J.I., Thompson, R.S., and Van Devender, T.R., 1982, Late Wisconsinian and Holocene fauna from Smith Creek Canyon, Snake Range, Nevada: San Diego Society of Natural History Transactions, v. 20, p. 1-26.

van der Meulen, A.J., 1973, Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy), with special reference to the phylogeny of Microtus (Arvicolidae, Rodentia): "Quaternaria" XVII, 144 p.

______1974, On *Microtus* (*Allophaiomys*) *deucalion* (Kretzoi, 1969), (Arvicolidae, Rodentia), from the upper Villanyian (lower Pleistocene) of Villany-5, S. Hungary: Nederlandse Akademie van Wetenschappen (Koninklijke)-Amsterdam, Proceedings, Series B, v. 77, p. 259-266.

______1978, *Microtus* and *Pitymys* (Arvicolidae) from Cumberland Cave, Maryland, with a comparison of some New and Old World species: Carnegie Museum Annals, v. 47, p. 101-145.

Miller, G.S., 1912, Catalogue of the mammals of western Europe: British Museum (Natural History), 1019 p.

Nelson, R.S., and Semken, H.A., 1970, Paleoecological and stratigraphic significance of the muskrat in Pleistocene deposits: Geological Society of America Bulletin, v. 81, p. 3733-3738.

Paulson, G.R., 1961, The mammals of the Cudahy fauna: Michigan Academy of Science, Arts, and Letters Papers XLVI, p. 127-153.

Repenning, C.A., 1968, Mandibular musculature and the origin of the Subfamily *Arvicolinae* (*Rodentia*): Acta Zoologica Cracoviensia, v. XIII, p. 29-72.

______1978, Faunal exchanges between Siberia and North America: American Quaternary Association, Abstracts, fifth biennial meeting, Edmonton, p. 40-55.

______1980, Faunal exchanges between Siberia and North America: Canadian Journal of Anthropology, v. 1, p. 37-44.

______1983, *Pitymys meadensis* Hibbard from the Valley of Mexico and the classification of North American species of *Pitymys* (Rodentia:Cricetidae): Journal of Vertebrate Paleontology, v. 2, p. 471-482.

______1984, Quaternary rodent biochronology and its correlation with climatic and magnetic stratigraphies, *in* Mahaney, W.C., ed., Correlation of Quaternary chronologies: Norwich, GeoBooks, p. 105-118.

______1987, Biochronology of the microtine rodents of the United States, Chapter 8 *in* Woodburne, M.O., ed., Cenozoic mammals of North America—Geochronology and biochronology: Berkeley, University of California Press, p. 236-268.

______in press, The fossil record of *Arborimus* and *Phenacomys*, Chapter 2 *in* Johnson, M.L., and Maser, Chris, eds., Tree voles of the Old Growth Forest: American Society of Mammalogists Special Publication.

Repenning, C.A., Brouwers, E.M., Carter, L.D., Marincovich, Louie, Jr., and Ager, T.A., 1987, The Beringian ancestry of *Phenacomys* (Rodentia: Cricetidae) and the beginning of the modern Arctic Ocean Borderland biota: U.S. Geological Survey Bulletin 1687, 31 p.

Repenning, C.A., and Fejfar, Oldrich, 1977, Holarctic correlation of microtid rodents, *in* Sibrava, Vladimir, ed., Project 73-1-24 "Quaternary glaciations in the Northern Hemisphere," Report No. 4, Session in Stuttgart: IUGS-UNESCO ICP, Prague, p. 234-250.

Richmond, G.M., and Fullerton, D.S., 1986, Summation of Quaternary glaciations in the United States of America: Quaternary Science Reviews, v. 5, p. 183-200.

Rogers, K.L., Repenning, C.A., Forester, R.M., Larson, E.E., Hall, S.A., Smith, G.S., Anderson, Elaine, and Brown, T.J., 1985, Middle Pleistocene (Late Irvingtonian) climatic changes in south-central Colorado: National Geographic Research, v. 1, p. 535-563.

Sher, A.V., Kaplina, T.N., Kouznetsov, Yu.V., Virina, E.I., and Zazhigin, V.S., 1979, Late Cenozoic of the Kolyma Lowland: XIV Pacific Science Congress, Tour Guide XI, Academy of Sciences U.S.S.R., Moscow, 115 p.

Stirton, R.A., 1951, Principles in correlation and their application to late Cenozoic Holarctic continental mammalian faunas: International Geological Congress, Report of the 18th Session, Great Britain, 1948. pt. II, p. 74-84.

Suchov, V.P., 1976, Remains of lemmings in the Bashkirian Pliocene deposits: Academy of Sciences U.S.S.R., Proceedings of the Zoological Institute, v. 66, p. 117-121. [In Russian.]

Wilson, R.W., 1934, A rodent fauna from later Cenozoic beds of southwestern Idaho: Carnegie Institution of Washington Contributions to Paleontology 440, p. 119-135.

Wood, H.E., 2nd, Chaney, R.W., Clark, John, Colbert, E.H., Jepsen, G.L., Reeside, J.B., Jr., and Stock, Chester, 1941, Nomenclature and correlation of the North American continental Tertiary: Geological Society of America Bulletin, v. 52, p. 1-48.

Zakrzewski, R.J., 1972, Fossil microtines from the late Cenozoic deposits in the Anza-Borrego Desert, California, with a description of a new subgenus of *Synaptomys*: Natural History Museum, Los Angeles County, Contributions in Science 221, 12 p.

Zazhigin, V.S., 1980, Late Pliocene and Anthropogene rodents of the south of western Siberia: Academy of Sciences U.S.S.R., Transactions 339, 156 p. [In Russian.]

Zheng, Shaohua, and Li, Chuankui, 1986, A review of Chinese *Mimomys*: Vertebrata PalAsiatica, v. XXIV, p. 81-109.

______in press, Comments on fossil arvicolids of China, *in* Fejfar, Oldrich, and Heinrich, Wolf-Dieter, eds., International Meeting, evolution, phylogeny, and biostratigraphy of arvicolids (Rodentia, Mammalia): Geological Survey of Czechoslovakia, Praha.

INDEX

[Major page references in italic]

★ U.S. GPO: 1989 673-047/86028

SELECTED SERIES OF U.S. GEOLOGICAL SURVEY PUBLICATIONS

Periodicals

Earthquakes & Volcanoes (issued bimonthly).
Preliminary Determination of Epicenters (issued monthly).

Technical Books and Reports

Professional Papers are mainly comprehensive scientific reports of wide and lasting interest and importance to professional scientists and engineers. Included are reports on the results of resource studies and of topographic, hydrologic, and geologic investigations. They also include collections of related papers addressing different aspects of a single scientific topic.

Bulletins contain significant data and interpretations that are of lasting scientific interest but are generally more limited in scope or geographic coverage than Professional Papers. They include the results of resource studies and of geologic and topographic investigations; as well as collections of short papers related to a specific topic.

Water-Supply Papers are comprehensive reports that present significant interpretive results of hydrologic investigations of wide interest to professional geologists, hydrologists, and engineers. The series covers investigations in all phases of hydrology, including hydrogeology, availability of water, quality of water, and use of water.

Circulars present administrative information or important scientific information of wide popular interest in a format designed for distribution at no cost to the public. Information is usually of short-term interest.

Water-Resources Investigations Reports are papers of an interpretive nature made available to the public outside the formal USGS publications series. Copies are reproduced on request unlike formal USGS publications, and they are also available for public inspection at depositories indicated in USGS catalogs.

Open-File Reports include unpublished manuscript reports, maps, and other material that are made available for public consultation at depositories. They are a nonpermanent form of publication that may be cited in other publications as sources of information.

Maps

Geologic Quadrangle Maps are multicolor geologic maps on topographic bases in 7 1/2- or 15-minute quadrangle formats (scales mainly 1:24,000 or 1:62,500) showing bedrock, surficial, or engineering geology. Maps generally include brief texts; some maps include structure and columnar sections only.

Geophysical Investigations Maps are on topographic or planimetric bases at various scales; they show results of surveys using geophysical techniques, such as gravity, magnetic, seismic, or radioactivity, which reflect subsurface structures that are of economic or geologic significance. Many maps include correlations with the geology.

Miscellaneous Investigations Series Maps are on planimetric or topographic bases of regular and irregular areas at various scales; they present a wide variety of format and subject matter. The series also includes 7 1/2-minute quadrangle photogeologic maps on planimetric bases which show geology as interpreted from aerial photographs. Series also includes maps of Mars and the Moon.

Coal Investigations Maps are geologic maps on topographic or planimetric bases at various scales showing bedrock or surficial geology, stratigraphy, and structural relations in certain coal-resource areas.

Oil and Gas Investigations Charts show stratigraphic information for certain oil and gas fields and other areas having petroleum potential.

Miscellaneous Field Studies Maps are multicolor or black-and-white maps on topographic or planimetric bases on quadrangle or irregular areas at various scales. Pre-1971 maps show bedrock geology in relation to specific mining or mineral-deposit problems; post-1971 maps are primarily black-and-white maps on various subjects such as environmental studies or wilderness mineral investigations.

Hydrologic Investigations Atlases are multicolored or black-and-white maps on topographic or planimetric bases presenting a wide range of geohydrologic data of both regular and irregular areas; principal scale is 1:24,000 and regional studies are at 1:250,000 scale or smaller.

Catalogs

Permanent catalogs, as well as some others, giving comprehensive listings of U.S. Geological Survey publications are available under the conditions indicated below from the U.S. Geological Survey, Books and Open-File Reports Section, Federal Center, Box 25425, Denver, CO 80225. (See latest Price and Availability List.)

"Publications of the Geological Survey, 1879- 1961" may be purchased by mail and over the counter in paperback book form and as a set of microfiche.

"Publications of the Geological Survey, 1962- 1970" may be purchased by mail and over the counter in paperback book form and as a set of microfiche.

"Publications of the U.S. Geological Survey, 1971- 1981" may be purchased by mail and over the counter in paperback book form (two volumes, publications listing and index) and as a set of microfiche.

Supplements for 1982, 1983, 1984, 1985, 1986, and for subsequent years since the last permanent catalog may be purchased by mail and over the counter in paperback book form.

State catalogs, "List of U.S. Geological Survey Geologic and Water-Supply Reports and Maps For (State)," may be purchased by mail and over the counter in paperback booklet form only

"Price and Availability List of U.S. Geological Survey Publications," issued annually, is available free of charge in paperback booklet form only.

Selected copies of a monthly catalog "New Publications of the U.S. Geological Survey" available free of charge by mail or may be obtained over the counter in paperback booklet form only. Those wishing a free subscription to the monthly catalog "New Publications of the U.S. Geological Survey" should write to the U.S. Geological Survey, 582 National Center, Reston, VA 22092.

Note.--Prices of Government publications listed in older catalogs, announcements, and publications may be incorrect. Therefore, the prices charged may differ from the prices in catalogs, announcements, and publications.