Allophaiomys and the Age of the Olyor Suite, Krestovka Sections, Yakutia

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Allophaiomys and the Age of the Olyor Suite, Krestovka Sections, Yakutia

By CHARLES A. REPENNING

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MARCH 3, 1849

Microtine history indicates mosaic evolution and complex
dispersal patterns around the Northern Hemisphere;
by reflecting this history and evaluating stage of population
evolution, microtine biochronology can discriminate time
periods as brief as 5,000 years

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ALLOPHAIOMYS AND THE AGE OF THE OLYOR SUITE, KRESTOVKA SECTIONS, YAKUTIA

By CHARLES A. REPENNING

ABSTRACT

Upper Pliocene and lower Pleistocene sediments along the Krestovka River, near its junction with the Kolyma River in eastern Yakut A.S.S.R., northeastern Siberia, provide two records of environmental deterioration in the Arctic Ocean Borderland. Both records precede major continental glaciation elsewhere in the Northern Hemisphere. The Olyor Suite of the Krestovka Sections contains the younger of these two records, but its age has been debated. Clarification of its age is of importance to early Pleistocene terrestrial history in the Arctic Ocean Borderland and in adjacent temperate regions of the Northern Hemisphere.

During the late Pliocene and Pleistocene the most time-discriminate fossil mammals are those microtine rodents that derive from the genus *Allophaiomys* of the microtine tribe Arvicolini. Most of these derived taxa belong to the tribes Microtini and Pitymyini. The history of usage of the genus *Allophaiomys* indicates that the definition of the genus has not been uniform and that some current definitions are too broad, overlapping the definition of derived taxa. The use of varied nomenclatures has resulted both in differences of opinion regarding the age of the Olyor Suite of the Krestovka Sections and in confusion of other correlations throughout the Northern Hemisphere.

Primarily through examples from North American fossil faunas, the history of *Allophaiomys* and its derived genera is outlined, and taxa are defined uniformly. The adoption of these uniform definitions is recommended; other definitions of these genera cannot be applied without altering generic concepts that are based upon the type populations, and without uniform definitions biochronologic correlation of events in the evolutionary history of the subfamily Arvicolinae is impossible.

At present, the most accurate Northern Hemisphere terrestrial correlations for approximately the last 2 million years rely almost exclusively on this history of *Allophaiomys* and its derivatives, and these correlations cannot be realized without uniformity of nomenclature. Review of the global record of these microtine rodents indicates that those found in the older part of the Olyor Suite of the Krestovka Sections cannot be as old as the Olduvai Normal-polarity Subchron (not as old as 1.67 Ma) but that they are older than the Jaramillo Normal-polarity Subchron (older than 0.97 Ma). An age possibly as great as 1.5 million years is suggested for the onset of deposition of the Olyor Suite in the Krestovka Sections of Yakutia.

The provincial history of the evolution of these lineages in at least eastern Asia must become much better known before this age approximation can be refined. Worldwide, the determination of this history is made difficult by the essential lack of external time control between the Olduvai and Jaramillo Normal-polarity Subchrons of the Matuyama Reversed-polarity Chron. This is a period of reversed geopolarity approximately as long as the Brunhes Normal-polarity Chron, containing few documented polarity events that might serve as temporal subdivisions.

Greater integrative understanding of the provincial history of the microtines in the United States indicates that a potential exists for inferring age assignments that differ as little as 5,000 years. Establishing this age precision requires thorough evaluation of the stage of evolution of fossil populations, which in turn requires sufficiently large samples possessing some external age control, to provide temporal calibration of the evolutionary history. Between lineages deriving from *Allophaiomys* the rates of evolution can vary greatly, and the accuracy of biostratigraphic correlation varies directly with the rate of evolution. The rate of evolution in nominally identical lineages may also vary between faunal provinces; therefore accurate correlation, again, requires an understanding of provincial history.

In addition to radiometric age determination, external age control is recognized throughout the Northern Hemisphere in sufficiently well documented (1) paleomagnetic determinations, (2) climate change trends, (3) mammalian dispersal events, and (4) known history of other mammalian types including other associated microtine rodents. When used herein, the sufficient documentation of these external age controls is explained, defended, and integrated.

The estimation of the age of the Olyor Suite in the Krestovka Sections of Yakutia requires that the time-calibrated history of evolution and of dispersal throughout the Northern Hemisphere be understood for those microtines that have been found as fossils within that depositional unit. This requires that they be correctly identified. From 1977 to the present many publications have listed the genus *Allophaiomys* as being present in the Olyor faunas, imparting a rather specific age suggestion that has been interpreted

to be more than 2.1 million years for the oldest fauna. But this genus is not present in the Olyor Suite, and what was called *Allophaiomys* has a different age significance that, at this location, cannot be older than an estimated 1.4 million years. Paleomagnetic polarity of the section, in concert with the age implication of the microtine rodents, indicates that the Olyor cannot be as old as 1.67 million years.

INTRODUCTION

In 1966 fossiliferous upper Pliocene and Pleistocene continental deposits were discovered by A.V. Sher in the lower part of the drainage basin of the Kolyma River of northeasternmost Yakut A.S.S.R. (fig. 1), the Kolyma Lowlands. The region is located at approximately lat 69° N., long 160° E., and has been continuously studied since 1966 by scientists from the Academy of Sciences of the Union of Soviet Socialist Republics, Moscow State University, and other Soviet institutions (Sher and others, 1979). The Kolyma River is in the western part of Beringia, a vast area covering the Arctic Ocean Borderland in northeastern Siberia and northwestern North America that has never been covered by continental glaciation. From the Kolyma River, Beringia extends eastward to the headwaters of the Yukon River in northern Yukon Territory, Canada.

The Krestovka Sections (locality 31, fig. 1), located along the Krestovka River near its junction with the Kolyma River, contain two records of climatic deterioration. These periods of climatic deterioration are recorded in continental deposits, the deposition of which ended with the development of major continental glaciation elsewhere in the Northern Hemisphere. The termination of continental deposition with the development of major continental glaciation appears in several records of the Arctic Ocean Borderland, as well as in lower latitudes, and seems to be related to eustatic lowering of sea level (resulting in a lowering of terrestrial base levels on adjacent lands).

The older stratigraphic units of the Krestovka Sections have been described as the Begunov Suite of probable early Pliocene age and the Kutuyakh Beds of late Pliocene age (Sher and others, 1979). (The terms "suite" and "beds" are approximately equivalent to "formation" in North American literature according to Giterman and others, 1982.) The Begunov Suite is still not certainly dated but is now thought more likely to be of late middle Pliocene age, and to have been deposited during the Gauss Normal-polarity Chron on the basis of its normal polarity and the similarity of its flora to that from Ocean Point, Alaska (Nelson and Carter, 1985, 1991; Repenning and Brouwers, 1992). The Kutuyakh Beds are of late middle and early late Pliocene age, as originally interpreted; they were deposited during the last of the Gauss Chron and into the beginning of the Matuyama Reversed-polarity Chron (Sher and others, 1979).

The Begunov Suite and the Kutuyakh Beds, between less than 3 and about 2.4 million years old (Sher and others, 1979; Repenning and Brouwers, 1992), record both a reduction in the variety of arboreal vegetation and a decrease in its total abundance. This record ends with sparse forest-tundra and the oldest known permafrost in the lower latitudes of the Arctic Ocean Borderland (Sher and others, 1979). In the Krestovka Sections, permafrost first appears in the younger part of the Kutuyakh Beds, at the time when the beginning of continental glaciation is conspicuously indicated elsewhere in the Northern Hemisphere. The age of this part of the Krestovka Sections has not been debated.

In contrast to the less severe conditions beginning the earlier climatic record, the climatic record in the overlying Olyor Suite of the Krestovka Sections begins with sparse forest tundra and deteriorates to full tundra, more severe than the taiga that exists in the Krestovka area today. During the coldest period recorded by the fossil flora in the Olyor Suite, the reversed paleomagnetic polarity recorded in the older part of the Olyor changes to normal. The age of the Olyor Suite of the Krestovka Sections and the identity of the normally polarized event constitute the second subject of discussion in this report.

An erosional unconformity separates the Kutuyakh deposits from the overlying Olyor Suite in the Krestovka Sections. Different opinions about the age of the Olyor Suite have been published, with consequent variation in the opinions about the time encompassed by this unconformity. Sher and others (1979), strengthened by Sher (1986), suggested that deposition of the Olyor Suite, as recorded in the Krestovka Sections, began during the last part of the Matuyama Chron and continued into the Brunhes Chron. Similarly, Virina and others (1984) indicated that deposition of the Olyor Suite in its type section (some 150 km[1] (93 mi) north of the Krestovka Sections) began before the Jaramillo Normal-polarity Subchron and continued into the Brunhes. No non-biochronologic data (external to the mammalian history) exist for estimating the age of the oldest (pre-Jaramillo) part of the type Olyor, and the base of the type Olyor is not exposed.

Repenning (1984) indicated that the history of microtine rodents, in combination with the history of climatic changes recorded by Sher and others (1979), suggested that deposition of the Olyor Suite must have begun more than 2 million years ago. This interpretation, based upon published faunal lists, is now known to be wrong for two reasons. First, it has recently been recognized that the application of taxonomic names (particularly *Allophaiomys*) in the identification of microtines from the Olyor Suite differs greatly between the present author and others who have examined this fauna. Second, new information about the global history

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[1] Note that in this report the primary system of measurement units—the unit cited first—is that of the country from which the data were gathered and published. North American data were given first in inches, feet, and miles; European and northeastern Asian data were given first in metric. Conversion to the other system is given in parentheses.

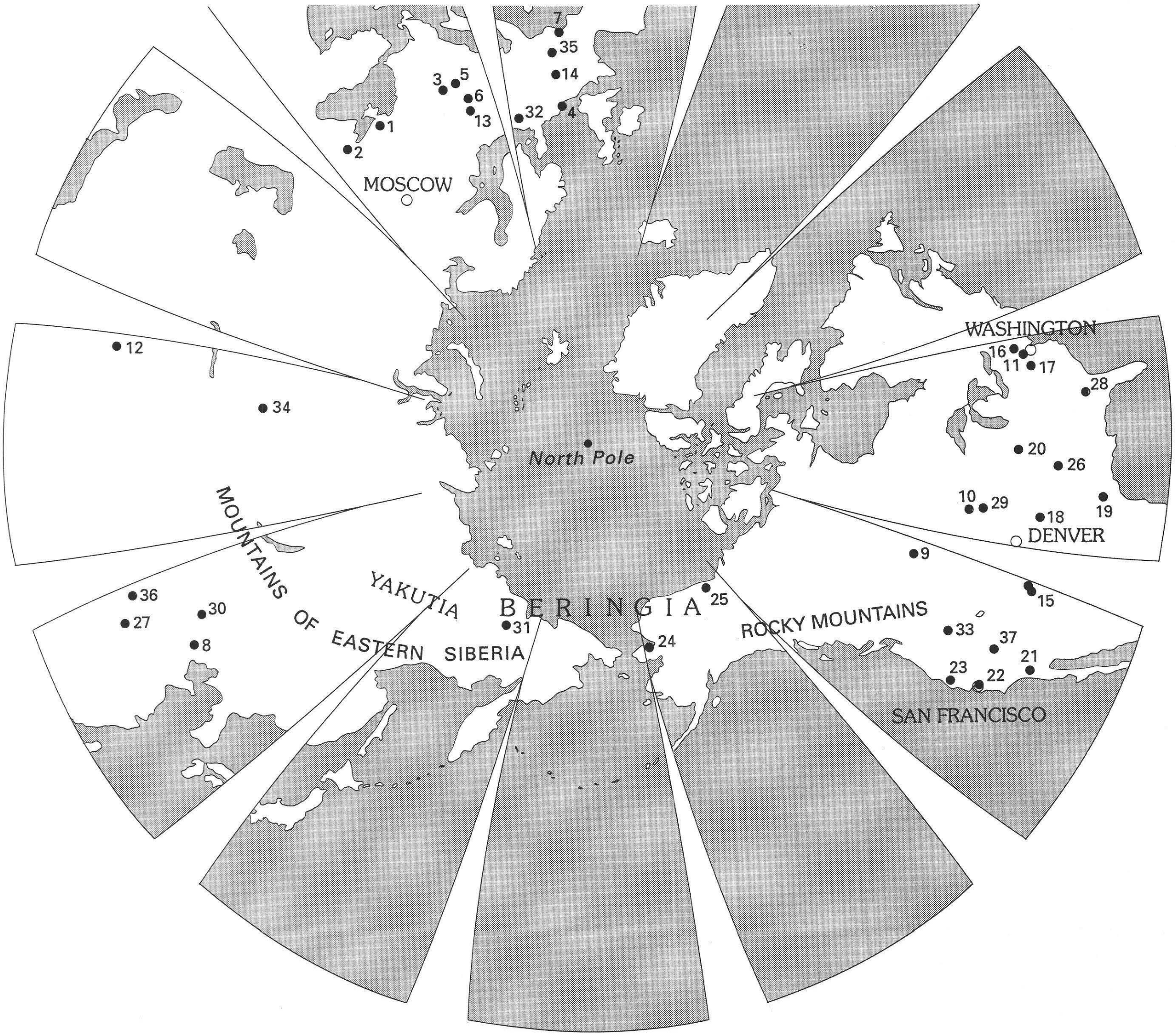

Figure 1. Index map of Northern Hemisphere north of Tropic of Cancer showing localities mentioned. **1,** Karay-Dubina, Ukraine. **2,** Shamin, Russia. **3,** Betfia–2 (Puspokfurdo), Romania. **4,** Zuurland Borehole, Holland. **5,** Villany–5, Hungary. **6,** Holstejn, Czechoslovakia. **7,** Mas Rambault and Balaruc, France. **8,** Huangkan and Choukoutien (CKT)–18, P.R.C. (People's Republic of China). **9,** Wellsch Valley, Saskatchewan. **10,** Java, South Dakota. **11,** Cumberland Cave, Maryland. **12,** Ladak, Kashmir. **13,** Kamyk, Poland. **14,** Valerots, France. **15,** Hansen Bluff, Colorado, and SAM Cave, New Mexico. **16,** Hanover Quarry Fissure, Pennsylvania. **17,** Cheetah Room, West Virginia. **18,** Cudahy, Nash, and Aries, Kansas. **19,** Fyllan Cave, Texas. **20,** County Line, Illinois. **21,** Anza-Borrego Desert, California. **22,** Irvington, California. **23,** Cape Mendocino, California. **24,** Cape Deceit, Alaska. **25,** Localities CRH–47, CRH–64, and CRH–11, Yukon Territory. **26,** Conard Fissure, Arkansas. **27,** Gongwangling, P.R.C. **28,** Georgia, U.S.A. **29,** Ft. Pierre, South Dakota. **30,** Northeast Mongolia, P.R.C. **31,** Krestovka Sections, Kolyma Lowlands, Yakutia. **32,** Germany. **33,** Froman's Ferry, Idaho. **34,** Razdolie, Western Siberia. **35,** Leman Basin, Switzerland. **36,** Minchow, Kansu, P.R.C. **37,** Magruder Mtn., Nevada (near Deep Springs, California).

of these rodents, some not previously published, indicates that the age of the Olyor must be closer to the age of the latest Matuyama and early Brunhes Chrons, as was originally claimed by Sher and others (1979). Consequently, it is unlikely that the oldest faunas in the Olyor Suite of the Krestovka Sections are much older than 1.5 million years. The unconformity below the Olyor Suite thus must be about 1 million years long, lasting from about 2.4 to about 1.5 million years ago. The time of the first significant continental glaciation of the Northern Hemisphere, peaking about 2.1 million years ago, does not seem to be recorded in the deposits of the Krestovka Sections.

Incorporation and interpretation of these revised data indicate that the oldest deposits in the Olyor Suite in the Krestovka Sections are, possibly, about the same age as those of the type Olyor 150 km to the north, and that deposition was interrupted, in the Krestovka Sections, by a second unconformity in the normally polarized part of the Olyor Suite. This unconformity represents at least the 150,000 years of reversed polarity between the Jaramillo and the Brunhes and includes the time of the beginning of deposition of the Nebraskan tills in the United States. However, the possibility that the oldest normal polarity represents the Jaramillo event is not supported by known microtine and climatic history. Explanation of the age significance of the microtine faunas related to this oldest normal polarity is the first and major subject of discussion in this report. The second and shorter subject of discussion is the application of this biochronologic information to the faunas of the Krestovka Olyor Suite, and the consideration of polarity patterns and climatic trends involved, to determine the age of the oldest part of the formation.

ACKNOWLEDGMENTS

This is a summary of the global record of the genus *Allophaiomys* and of its derivative genera, as well as an application of this record to the interpretation of the age of the Olyor Suite of the Krestovka Sections in Yakutia. In its compilation, advice and specimens have been provided by many individuals. I would particularly like to acknowledge, with thanks, the help of Oldrich Fejfar (Prague, Czechoslovakia), Kazimerz Kowalski (Krakow, Poland), Wighart von Koenigswald (Bonn, Germany), Vladimir S. Zazhigin and Alexy Tesakov (Moscow, Russia), Shaohua Zheng (Beijing, People's Republic of China), Anthony Barnosky (Berkeley, California), Karel Rogers (Alamosa, Colorado), Russell Graham (Springfield, Illinois), Lawrence Flynn (Cambridge, Massachusetts), and Robert Martin (Rome, Georgia). All have provided thoughtful discussion about the methods of evaluating variability as well as specimens in illustration.

Thanks are also extended to the professionals in charge of the collections from which specimens for the study were borrowed. These include the following institutions (with their acronyms): Geological Institute, Academy of Sciences of the Union of Soviet Socialist Republics, Moscow (GIN); Hungarian Natural History Museum, Budapest (HNHMB); National Museum of Natural History [United States], Washington (USNM); Carnegie Museum of Natural History, Pittsburgh (CM); Illinois State Museum, Springfield (ISM); National Museums of Canada, Ottawa (NMC); Natural History Museum of Los Angeles County, California (LACM); University of California Museum of Paleontology, Berkeley (UCMP); University of California Museum of Vertebrate Zoology, Berkeley (UCMVZ); and the University of Alaska, Fairbanks (UA). Specimens not credited to the above acronyms are in my collection in the Denver, Colorado, offices of the U.S. Geological Survey.

Andrei V. Sher of the Paleontologic Institute, Academy of Sciences of the U.S.S.R., Moscow, was the key to the understanding of the age of the Olyor Suite of the Krestovka Sections in the Kolyma Lowlands of Yakutia, western Beringia. He made this discussion of the age of the Olyor Suite possible by inviting me to visit Moscow and review the fossil microtines from there; without this opportunity I would never have guessed their true identity.

Vladimir S. Zazhigin of the Geological Institute of the Academy of Sciences of the U.S.S.R., who studied the specimens from Yakutia, kindly showed and discussed his entire collection from Yakutia and from other Asian localities for nearly 2 weeks and otherwise offered me his hospitality. His student, Alexy Tesakov, greatly facilitated this examination and review, thanks to his ability to speak English and to his knowledge of microtine rodents.

R. Farley Fleming, USGS, spent many hours discussing with me the philosophy of various evolutionary theories and of classification, with the detachment that only a paleobotanist could have. Although I do not believe that he would agree, I have concluded that the present report is not concerned with evolutionary theories, but only with the facts of evolution as found in the fossil record. To those who disagree, I can only apologize for failing to find significance in theory.

Anthony D. Barnosky, Thomas M. Bown, William A. Bryant, Oldrich Fejfar, Patricia A. Holroyd, Andrei V. Sher, Alexy Tesakov, and Alisa J. Winkler were kind enough to review the manuscript—a major effort because of its complications. Kazimerz Kowalski also made helpful comments. Lorna Carter, editor for the U.S. Geological Survey, again has earned my gratitude for identifying wording that could be more understandably phrased.

I think that none of these friends would appreciate my suggesting that they agreed with me.

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EXPLANATION OF THE PROBLEM

Different opinions previously put forth (fig. 2) regarding the age of the Olyor Suite of the Krestovka Sections resulted from unrecognized differences in the operational definition used by specialists when dealing with Kormos' (1932) genus *Allophaiomys*. These differences have a bearing on the definitions of the genera *Microtus* and *Lasiopodomys*, genera of the tribe Microtini that derive from *Allophaiomys* as shown by Chaline (1966). What some would refer to these genera, others would call *Allophaiomys*.

In Chaline's usage, all three genera, *Allophaiomys*, *Lasiopodomys*, and *Microtus* (as well as the tribes Microtini, Pitymyini, and part of the Arvicolini recognized here) are included in the single genus *Microtus*. V.S. Zazhigin and A.V. Sher, the principal Russian authorities on the Krestovka Sections and their microtine rodents, have considered

Allophaiomys as a genus separate from *Microtus* since at least 1976. The present author has considered both *Allophaiomys* and *Lasiopodomys* as genera distinct from *Microtus* since approximately the same time. Fundamentally, these differences in the definitions of these taxa have resulted in the differing interpretations of the age of the Olyor Suite. Secondarily, different interpretations of the evolutionary history of the taxa further dictated different age assignments. In the present report, the three genera are considered separate, representing two different tribes.

The problem relates to the concept of a type specimen. All students of microtine rodents recognize that all individuals in a type population of a microtine species do not exactly match the type specimen; even Kormos (1932) realized this, for he illustrated more than one individual (to show variation), even though he selected a type specimen for *Allophaiomys pliocaenicus*. Anyone using his specific name *A. pliocaenicus* is forced to guess how much individual variability can be acceptable—unless that person has the opportunity to examine the type population in Budapest. In fact, this type collection no longer completely exists, because representative specimens have been removed from it and donated to other collections throughout Europe. However, enough remain in the type sample to give a good idea of the range of variability.

It is in deciding upon the acceptable range of variability that definitions begin to vary. The only recourse is to return to the type population sample and determine the "typical" variability.

In association with V.S. Zazhigin, Sher and others (1979) and Sher (1986) had reported *Allophaiomys* in the older deposits of the Krestovka Olyor Suite as high as the earliest record of *Microtus*. Above this horizon only *Microtus* is reported from the formation. Just above the horizon of the first *Microtus*, the paleomagnetic polarity changes from reversed to normal. These authors placed great temporal significance on this change in the microtine fauna and its position immediately below the polarity change. They cited evidence from Markova (1982) that *Microtus* replaced *Allophaiomys* in the Ukrainian Karay-Dubina fauna that is older than reversed deposits underlying the Brunhes Normal-polarity Chron. The Karay-Dubina fauna was assumed to be younger than the Jaramillo event, but this event was not recorded in the sediments. Markova's presumed replacement of *Allophaiomys* by *Microtus* in a fauna presumably between the Jaramillo and the Brunhes was the strongest reason for Zazhigin and Sher to assign the same age to what they presumed to be the same replacement of genera in the Olyor, and the first normal polarity immediately upsection from it was, accordingly, assigned to the Brunhes Chron.

Zazhigin did not question Markova's identifications; had he done so he would have seen that what she called *Microtus* was what he called *Allophaiomys* (fig. 16). Using Markova's definitions of the genera, the Olyor fauna had primitive *Microtus* replaced by more advanced *Microtus* just below the beds with normal polarity, and there was no *Allophaiomys* at all in the Krestovka Olyor, nor was there any *Microtus* as advanced as that from the Olyor in the Karay-Dubina fauna.

If the Olyor fauna under discussion had been found north of the Black Sea (that is, in Markova's area of study), it would have been called "noticeably younger" than the Karay-Dubina fauna. But the Olyor fauna lived 125° farther east and 22° farther north than did the Karay-Dubina fauna; the living microtine faunas of the two areas are not at all the same today, and there is no reason to think that they were the same in the past. That a difference is reasonable and logical—and present—was not at all evident from the published faunal list of Sher and others (1979).

The microtine rodents from the Olyor Suite of the Krestovka Sections have not been described or illustrated prior to the present report (figs. 15, 16). The specimens illustrated by Markova as *Allophaiomys* (only three first lower molars) from Karay-Dubina, north of the Black Sea, appear to show a form similar to that named by Kormos from relatively nearby Romania. What Markova compared with a living species of *Microtus* ("Microtus ex gr. *oeconomus*," fig. 7, Nos. 23–32 of Markova, 1982; compare with figs. 11, 16, and 17 of the present report) is a form of *Lasiopodomys* now (but not in 1984) seen to be no more advanced than the specimens from the oldest faunas of the Olyor Suite, which had been listed as *Allophaiomys* (Sher and others, 1979).

Incorrectly, the present author assumed (Repenning, 1984) that a typical form, comparable to what Markova (fig. 7, Nos. 12–14 of Markova, 1982) had called *Allophaiomys*, was what Zazhigin had listed as *Allophaiomys* in the compilation of the published Olyor faunal list. Further, he assumed that what had been called *Microtus* was an early form of *Lasiopodomys* similar to what Markova had referred to as *Microtus* ex gr. *oeconomus*. These assumptions seemed to be corroborated by other statements about the primitive nature of *Microtus* from the Olyor (Sher and others, 1979) and reference to its similarity to *Microtus ratticepoides* (Sher, 1986), a species referred to *Lasiopodomys* by the present author. But neither assumption was correct.

It now is obvious that what was called *Allophaiomys* from the Olyor Suite by Zazhigin is identical to what Markova called *Microtus* from the Karay-Dubina fauna (this report, fig. 16). Also, what was called *Microtus* from the Olyor Suite by Zazhigin is what the author would also call *Microtus* and is more advanced than any form known from the Karay-Dubina fauna. Thus the replacement of *Allophaiomys* by *Microtus*, cited as evidence for the age of the Olyor Suite on the basis of the presumed age of the Karay-Dubina fauna, was a replacement of and by forms that differed in the definitions of Zazhigin and Markova.

Typical *Allophaiomys*, like that called such by Markova, has been recognized in European deposits that date from the beginning of the Olduvai Normal-polarity Subchron (Zuurland Borehole; van Kolfschoten, 1988, 1990) and from deposits older than the Olduvai event in China (Zheng and Li, 1990). The genus is reported later in the present report from near the base of the Olduvai in the United States (p. 31; fig. 7*E*). Records as old or older have been inferred elsewhere by faunal composition and geomagnetic polarity control external to the biochronology; these suggestively support an early age. Such records include the type locality, Puspokfurdo, Romania (faunal control); Villany-5, Hungary (faunal control); Kudun, western Transbaikalia (faunal control); Huangkan and CKT–18, China (People's Republic of China) (faunal and paleomagnetic control); and Java, South Dakota (faunal control) (fig. 1). Most of these published older records are reviewed in the present report.

Species usually assigned to *Microtus* (most approximately the age of the Jaramillo event but a few nearly as old as the Olduvai event) and presumed to be older than the age reported by Markova (1982) include: *Microtus "arvalides," M. "gregaloides," M. "ratticepoides," M. deceitensis, M. californicus*, primitive *M. paroperarius*, and ?*M. oeconomus*. Some, but not all, of these are referred to the genus *Lasiopodomys* in the present report.

In addition, the age of the Karay-Dubina fauna of the Ukraine, described by Markova (1990), is not nearly as certain as suggested in most correlations; the fauna lies well below the oldest paleomagnetic control and well below the base of the Brunhes Chron (Velichko and others, 1983; Markova, 1982, 1990). In the present report it is considered older than the Jaramillo Subchron on faunal grounds. No paleomagnetic control of the section exists to indicate that the fauna is younger than, older than, or equal in age to the Jaramillo event.

Allophaiomys was a temperate to subtropical rodent, and *Microtus* has arctic to temperate tolerances. Throughout the Northern Hemisphere evidence is abundant that the faunal replacement of *Allophaiomys* by *Microtus* was time transgressive: both genera moved southward with climatic deterioration throughout the hemisphere. The reverse was also true: *Allophaiomys* moved northward during periods of warming temperatures. (See Repenning, 1990; and Repenning and Brouwers, 1992.) In the most southerly regions (North Africa, Israel, Kashmir, southern China, and most of the United States), *Microtus* of Asian origin first appeared during the Brunhes Normal-polarity Chron, nearly 1 million years after its oldest record in areas farther north. These conditions influenced Repenning's (1984) interpretation of the age of the Olyor Suite, and led to his earlier, erroneous age interpretation.

The oldest records of *Microtus* (usage of both Zazhigin and the present author, and as herein defined) are about 1.4 million years old. However, this great age seems inconsistent with other records, and there is reason to be concerned about the independent origin of the genus at different times in different regions, as is discussed under the major heading "Provinciality" beginning on page 74. Before the recognition of reasons for inferring multiple origins of the genus *Microtus*, in the strict sense here used, Repenning (1984) reasoned that if primitive *Microtus* evolved in the Arctic Ocean Borderland (a possibility now considered uncertain), then the oldest primitive *Microtus* could be as old as or older than the Olduvai Normal-polarity Subchron in the Arctic. The climatic trends reported from the Olyor Suite seemed to indicate that the Olyor had to be somewhat older than 2.0 million years. This conclusion now appears wrong and overly simplified.

In an effort to resolve the differences of opinion regarding the age of the Olyor Suite of the Krestovka Sections, A.V. Sher invited the author to visit Moscow and to review the microtine fauna from this formation in 1990. Once examination of the oldest microtine fauna of the Krestovka Olyor Suite began in V.S. Zazhigin's office, it was obvious that the author's interpretation of the age of the fauna was in error. Great differences also became evident in the use of taxonomic nomenclature between Zazhigin, who had identified the Olyor microtine fauna, and the present author, who interpreted the age of the fauna from Zazhigin's faunal list.

Nothing in the Olyor fauna belongs to the genus *Allophaiomys* as defined by Kormos (1932), as illustrated by Markova (1982), or as here defined. Instead, the author assigns to *Lasiopodomys* (primitive *Microtus* of many authors including Markova, 1982) all of the microtines in the fauna that Zazhigin assigned to *Allophaiomys*. Although Zazhigin was recognizing *Allophaiomys* as a genus distinct from *Microtus*, his morphologic concept of *Allophaiomys* was similar to that of Chaline (1972) in that it included morphotypes totally unknown in the type population. The present author includes these in *Lasiopodomys;* Markova (1982, 1990) included them in *Microtus*, which has been a common procedure.

When the present author (Repenning, 1984) inferred the age of the Olyor Suite from the faunal lists given by Sher and others (1979), he was mistaken about the nature of the fauna. When Sher and others (1979) and Sher (1986) inferred the age of the Olyor Suite from faunal lists given in Markova (1982) for the Karay-Dubina fauna, they were mistaken about the nature of that fauna. What was listed as *Allophaiomys* from the Olyor fauna has no similarity to what was listed as *Allophaiomys* in the Karay-Dubina fauna; instead it is identical to what was listed as *Microtus* in the Karay-Dubina fauna (fig. 16). Without uniform taxonomic definitions it is impossible to correlate from faunal lists.

As *Allophaiomys* is recognized in the present report, by Markova in 1982, and by Kormos in 1932, no record of the genus exists either in the Olyor Suite of the Krestovka Sections or in the rest of Beringia. The time of its dispersal to North America, just before the beginning of the Olduvai event, is not recorded in Beringian fossil records. That *Allophaiomys* passed through Beringia enroute to North America is obvious from the fossil record in the United States, but its date of passage must be inferred from the age of its earliest North American record.

As well as lacking a record of *Allophaiomys*, Beringian fossil faunas also lack a record of tribe Pitymyini. The tribe Pitymyini (Repenning, 1983) is the other major group derived from *Allophaiomys*, in addition to tribe Microtini including *Microtus* and *Lasiopodomys*. Like *Allophaiomys* (but unlike the Microtini), the Pitymyini are temperate-climate rodents and are not found in the Arctic region. However, the pitymyinine genus *Terricola* (replacing the North American name *Pitymys* in Eurasian faunas, following Chaline and others, 1988), also dispersed to North America but has no record in Beringia. The Pitymyini will also be discussed in this report, but in less detail than those lineages present in the Olyor Suite.

The present author takes the lack of any fossil record of *Allophaiomys* or *Terricola* in Beringia as a suggestion of the lack of any Beringian records of the times of their dispersals, which were about 1,900,000 and 850,000 years ago, at the beginning of the Olduvai event and between the time of the Jaramillo event and that of the Brunhes Chron. For 1 million years after the beginning of the Olduvai event, *Allophaiomys* was common in the United States east of the Rocky Mountains. After 850,000 years ago *Terricola* is known from many faunas in the United States west of the Mississippi River and from Mexico (Repenning, 1983).

The time of the dispersal of *Allophaiomys* through Beringia immediately followed the first major continental glaciation of North America, and the dispersal of *Terricola* immediately preceded the second. As has been stated, Beringia was not glaciated, but continental ice elsewhere in the Northern Hemisphere, and the resulting lowered sea level, seem to have been unfavorable conditions for preserving deposition in Beringia. The same phenomenon has been observed in lower latitudes such as the East Coast of the United States, where deposits during glacial periods are rare (T.A. Ager, written commun., 1992).

V.S. Zazhigin, A.V. Sher, and the author have agreed (1990) that differences in the definitions of the genus *Allophaiomys* and of those genera derived from *Allophaiomys* are a major handicap to global correlations of terrestrial deposits of late Pliocene and early Pleistocene age. This handicap is nowhere more obvious than in interpreting the biostratigraphy of Eurasian and North American Beringia, where differing taxonomic definitions resulted in a difference of about 1 million years in age interpretation within a biostratigraphy potentially capable of 5,000-year age discrimination (fig. 2).

Allophaiomys was once present throughout the Northern Hemisphere, from the Arctic Ocean (briefly) to the Mediterranean and Black Seas and to the Gulf of Mexico. Its definition, distribution patterns, and history are of significance over a much greater area than the Arctic Ocean Borderland. The same distribution and significance were later assumed by the complex genera *Microtus*, *Pitymys*, and *Terricola*. Review and definition of the microtine genus *Allophaiomys*, and its derivatives *Lasiopodomys*, *Microtus*, *Pitymys*, and *Terricola*, are thus important to intercontinental correlation throughout the Northern Hemisphere. *Allophaiomys* is not present in the faunas of the Olyor Suite, and this puts an entirely different constraint on the interpretation of the age. What is present, that was called *Allophaiomys*, adds a different constraint to the interpretation.

By analysis of North American microtine history, a biochronology for the eastern two-thirds of the United States from 2 million years ago until today is here produced. Although still imperfectly known over some periods of time, this biochronology is reasonably discriminate to the unprecedented precision of between 5,000 and 10,000 years during other periods. This precision is made possible only by observing a uniform taxonomy, by estimating stage of evolution through consideration of the population structure in fossil samples, and by inferring dispersal patterns.

The known microtine biochronology, in combination with a cold peak in the climatic record of the Arctic Ocean and its borderland, indicates that the oldest normal polarity in the Olyor Suite of the Krestovka Sections must represent the Cobb Mountain Normal-polarity Subchron, as is also discussed (fig. 14). If present in the Krestovka Sections, the Jaramillo Subzone of the Matuyama Zone must be unconformably overlain by the Brunhes Zone, either in the youngest part of the Olyor Suite or in overlying stratigraphic units. The microtine faunal samples known from these units are too small in specimen numbers to be definitive (A.V. Sher, oral commun. 1990).

The Cobb Mountain event was defined by Mankinen and others (1978) from a record in central California, U.S.A., and is one of the best dated of the short polarity reversals of the Brunhes and late Matuyama Chrons; it is 1.10 million years old. Although of short duration (possibly only 10,000 years) the event has been widely recognized (Mankinen and Grommé, 1982). The present report is the first to recognize the Cobb Mountain event by means of microtine biochronology, in association with a climatic extreme in Yakutia and, by rate of sedimentation and the same climatic correlation, in CESAR core 14 on the east end of the Alpha Cordillera, Arctic Ocean.

What has emerged from this investigation of the differences of opinion about the age of the Olyor Suite in Yakutia is an understanding of the evolution of many microtine rodents, and of their distribution patterns throughout the Northern Hemisphere. This understanding is so complex that serious questions arise about the current concepts and applications of biochronology, evolution, and classification. The complexity seems overpowering, but is not more complex than late Pliocene and early Pleistocene climate change in the Northern Hemisphere, to which it is closely tied. Understanding is a prerequisite for compiling the terrestrial record of this climate change (for example, Repenning and Brouwers, 1992).

CONVENTIONS

In this discussion the cricetid rodents with alternating, hypsodont, triangularly prismatic cusps on their cheek teeth are called "microtine rodents." The term as here used is vernacular and has reference neither to systematic nomenclature

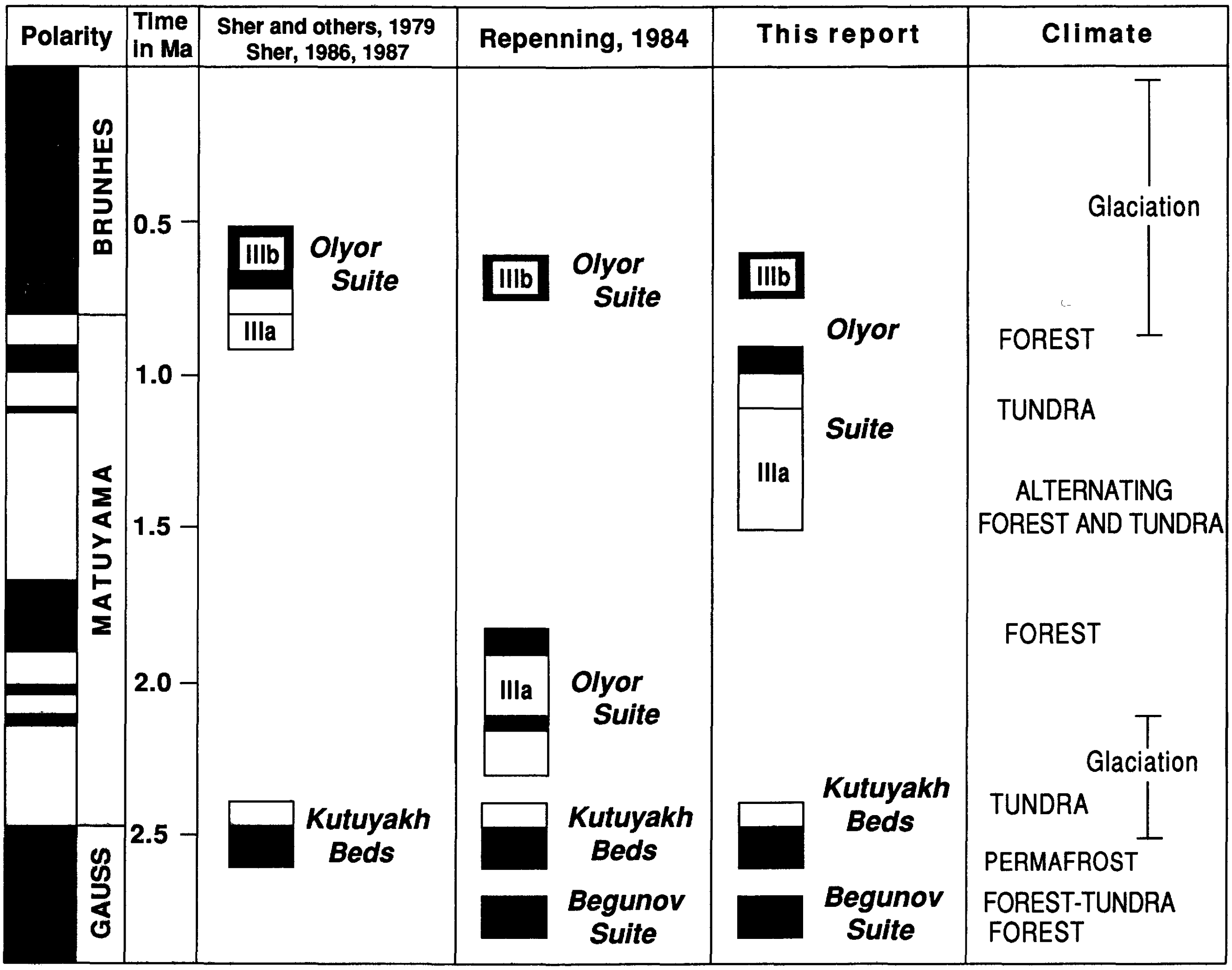


Figure 2. Different age assignments of formations in the Krestovka Sections, and associated geopolarity and climate evidence.

nor to taxonomic rank. It is synonymous with "arvicolid" and "arvicoline" as widely used, especially in Europe, although these two terms are also still used with reference to formal nomenclature: to the herein-abandoned family Arvicolidae and to the subfamily Arvicolinae. There remains, in the classification here followed (Repenning and others, 1990), a tribe Microtini, vernacular reference to which is spelled "microtinine" and a tribe Arvicolini, informally called "arvicolinine."

VERNACULAR NOMENCLATURE

In 1896 G.S. Miller abandoned the genus *Arvicola* and, somewhat improperly by modern rules, also Gray's (1821) family Arvicolidae that was based upon this genus. Miller substituted Cope's (1891) term Microtidae. It was a frail and somewhat questionable procedure that he made even more questionable in 1912 by reinstating the genus *Arvicola*, but neglecting to return to Gray's familial term, which he had rejected 16 years before.

Nevertheless, from 1896 until 1962 the group of hypsodont cricetid rodents herein called "microtines" were included in the family Microtidae of Cope and the members of this family were universally referred to as the "microtine rodents" in vernacular usage and in reference to the family Microtidae. But in 1962 M. Kretzoi reminded the world that the family name Arvicolidae of Gray (1821) had priority (it did not, according to Section VI, Art. 23b, of the International Code of Zoological Nomenclature under which rule it was a *nomen oblitum*), and Kretzoi's observation was noted by Repenning (1968). After that time the group was referred to as the family Arvicolidae, vernacular "arvicolid," until it was generally recognized that the family had multiple origins out of other members of the family Cricetidae with low-crowned cheek teeth. The family Arvicolidae was thus seen as an evolutionary grade of cricetid specialization, rather than an evolutionary lineage, and did not merit familial recognition. Thus the recognition of either family Arvicolidae or family Microtidae became a subject of conceptual discussion, rather than of nomenclatorial ordinance.

Most workers now recognize several subfamilies of "microtines" in the family Cricetidae, the subfamily Arvicolinae being restricted to the clade containing the genus *Arvicola,* and a separate family, Arvicolidae or Microtidae, is not recognized. The classification here followed (Repenning and others, 1990) recognizes five microtine cricetid subfamilies: Lemminae, Prometheomyinae, Arvicolinae, Ondatrinae, and Dicrostonychinae. The subfamily Arvicolinae contains several tribes, one of which is the tribe Microtini, members of which this report addresses.

Although no longer considered as representing a unique family, these hypsodont cricetid rodents, comprising several cricetid subfamilies, still need a vernacular term by which to refer to them; and the present author uses the term "microtine," as have many (but not most) in the United States. The vernacular term "microtine" was universally used prior to Kretzoi's synonymy of 1962, and the author's preference, followed in this report, probably reflects his great antiquity. European workers, on the other hand, are more impressed by the synonymy of Kretzoi in formal classification and, although the familial status of the group, and Kretzoi's synonymy, have no bearing on the vernacular name (as the familial Arvicolidae is not used), they use "arvicoline" or the familial termination "arvicolid" as a vernacular term. This is acceptable; there are no rules governing the use of vernacular terms.

"Microtine," "arvicoline," and "arvicolid" are all informal terms for the same thing; they refer to the hypsodont cricetid rodents formerly included in the family Arvicolidae, or the family Microtidae between 1896 and 1962. The preference now is largely a matter of where one is born, and the author of this report prefers "microtine" out of habit prior to 1965, when he became aware of Kretzoi's synonymy. "Arvicoline" and "arvicolid" are just as appropriate, although the family is no longer recognized, but many microtines do not belong to the subfamily Arvicolini. All microtines are cricetid rodents, not arvicolid rodents; some microtines are arvicoline rodents.

The present report develops a history of the genus *Allophaiomys* (tribe Arvicolini of the subfamily Arvicolinae) and those genera that evolved from it (forming several other tribes of the same subfamily); all are microtine rodents and also all are arvicoline cricetid rodents, but not all microtines are arvicoline rodents, such as lemmings and muskrats.

TIME SCALES

History cannot be developed without some temporal control for the occurrence of events. There is an increasing awareness that the only truly synchronous global time markers currently available in the study of Earth history are the global magnetic polarity reversals. Even these have an element of imprecision, in that these reversals are not instantaneous but occur over a short period of time and even incorporate periods of no polarity. However, in comparison with all other methods of estimating historical synchroneity on a global scale, geomagnetic polarity reversals may be considered as instantaneous time markers. A second criterion for synchroneity is global climate change, although this is more difficult to recognize and correlate.

The weakness of using polarity reversals is the inability to tell one reversal from another; at a polarity boundary the Earth's polarity changes from normal to reversed, or the other way, and so appears identical, paleomagnetically, to half of the other polarity boundaries that have ever taken place. At present, the only way to identify a particular polarity reversal is to have some rather close measure of its geologic age, a measure accurate enough to eliminate ambiguity, or to have a complete record from the present so that one can count back in time to identify the polarity reversal of concern, such as is done in oceanic cores. The last procedure assumes that the record examined does not contain any previously unidentified polarity reversals or any missing reversals because of depositional hiatus; associated biochronologic controls usually can help identify such irregularities.

Because of the global synchroneity of geomagnetic polarity reversals, greater efforts are being made to incorporate these reversals in the designated type stratigraphic sections that contain the benchmarks for the definitions of geologic time units. Present tradition seeks to avoid ambiguity by requiring that these benchmarks be placed at physical, visible changes in lithology. These changes usually do not quite coincide with invisible polarity reversals, thus introducing ambiguity into the correlation between the strongest evidence of synchroneity and the definition of a presumably synchronous geologic time boundary.

Possibly we are approaching a time when tradition will be abandoned in favor of accuracy and rationality. Possibly it will be seen that units of time should be defined on the evidence of time. Since the concept of time-transgressive rock units became accepted, the world has recognized that mappable, visible rock units do not coincide with invisible time units. There is no such thing as a "time-rock unit"; either the time represented in the concept is not a temporal unit or the rock represented is not a lithologic unit.

But custom still demands that we define time units on the basis of what can be seen in rock units at a type section. The demand is a holdover from earlier periods when geologic time could only be guessed, and stratigraphic succession was the only evidence of greater or lesser age. But, as the demand persists, an explanation of geologic time terms mentioned must be made. Note that as much as possible, these terms are avoided in this report, and age is indicated in radiometric years.

The early-middle Pleistocene boundary is here placed at the beginning of the Brunhes Normal-polarity Chron (about 0.79 Ma; Izett and Obradovich, 1991). This is an approximation until international agreement is reached—a type section for the stratigraphic authentication of this time boundary has not been selected.

The Pliocene-Pleistocene boundary is placed just after the end of the Olduvai Normal-polarity Subchron of the Matuyama Reversed-polarity Chron (about 1.67 Ma)—the type section has been selected at Vrica, Italy (Aguirre and Pasini, 1985).

Arbitrarily, the Gauss-Matuyama polarity boundary (2.48 Ma) is approximately used as the boundary between middle and late Pliocene. However, a global microtine dispersal event took place shortly before this polarity reversal (2.6 Ma in Repenning, 1987, and revised to 2.56 Ma in the present report on the basis of the first increase in activity of the Scandinavian Ice Sheet; Jansen and others, 1988). The middle-late Pliocene boundary is usually considered to be at this dispersal event in discussing microtine ages. This usage is one of convenience in the lack of a formal definition; it is not a statement that a biologic event is any more reliable as a time horizon than is a sedimentation event.

Microtine age terminology used herein for the Pliocene and Pleistocene in the United States is that of Repenning (1987), with the exception that Irvingtonian III replaces Rancholabrean I, and Rancholabrean II is herein referred to as undivided Rancholabrean. Microtine age terminology for Eurasia follows that used by Repenning, Fejfar, and Heinrich (1990), with revisions where now recognized.

DENTAL MORPHOLOGY

The terminology of the parts of microtine teeth (fig. 10) follows that of Repenning (1983); dimensions follow the scheme of van der Meulen (1973 and later publications) with one significant addition here called Dimension A–A′. Specifically defined morphologic terms of the first lower molar (M/1) are capitalized to call attention to their specified meaning; these include numbered Triangles, Anteroconid Complex (protoconid complex in the [former] U.S.S.R.), Primary Wings, Secondary Wings, Cap, and Dimensions A–A′, B–B′, and C–C′. Dimension D–D′ of van der Meulen (1978), the width of the Cap when no Secondary Wings are present, is mentioned but not used. In 1973 van der Meulen used dimension "d–d′" (in his fig. 22) in the sense that Dimension A–A′ is used herein, which is not quite the same as his 1978 use of D–D′.

In nearly all publications, the assignment of last upper molars (M\3) to species, which have been identified on the basis of the morphology of the first lower molar (M/1), is not done on a statistical basis, and the taxonomic assignments reflect entirely the preconceptions of the author. Nevertheless, in some circumstances it is not possible to identify a microtine species without consideration of the nature of its last upper molar.

Herein, when the faunal sample size merits it, assignment of the last upper molars to the species recognized by their first lower molars is made on the basis of the proportions of first lower molars in the sample. If a determined percentage of first lower molars in the sample belong to one species, it is assumed that the same approximate percentage of the sample applies to the last upper molars. This assignment is, of course, made within the context of the known last upper molar morphologies that have been associated with a particular first lower molar morphology in the history of the lineage. Direct associations are rare; there are very few fossil specimens in which the first lower and last upper molars of an individual microtine rodent are physically associated, and the association is usually made from a faunal sample of isolated teeth.

In describing the microtine rodents of the Cumberland Cave fauna, Maryland, van der Meulen (1978) distinguished three types of last upper molars: A, B, and C. He included in his Morphotype C the complex morphotype (with a posterior hook; this report, fig. 10) that is associated with typical *Microtus paroperarius* and many living species. His figure illustrating the types of M\3 (van der Meulen, 1978, fig. 6) did not show great development of Morphotype C and it is more typically illustrated in his figure 11H and I. Other M\3 morphotypes could be defined, but the rarity of associated first lower and last upper molars in fossil faunas seems to obscure the value of such precision. In the present report van der Meulen's M\3 Morphotypes A and B are referred to as "simple" and his Morphotype C is called "complex."

Van der Meulen's (1978) M\3 Morphotype B is one in which the two central triangles are very confluent (this report, figs. 3*L* and 13*K*), and he reported Morphotype B in his species *Pitymys cumberlandensis*, a North American lineage. Here, Morphotype B is included in the "simple" pattern. Individual examples of Morphotype B are present in many populations of *Allophaiomys*, as well as in other genera.

Chaline (1974) considered this M\3 pattern (van der Meulen's Morphotype B) to be characteristic of *Allophaiomys laguroides* from Betfia–2, a species that he had earlier (Chaline, 1972) considered synonymous with *A. pliocaenicus*. In 1974 he stated that this form of M\3 led directly from *Microtus* (*Allophaiomys*) *pliocaenicus laguroides* (his nomenclature) to his subgenus *Microtus* (*Meridiopitymys*).

In contrast, Ognev (Vol. VI, 1948) thought that what Chaline (1972) later called subgenus *Meridiopitymys* should be placed in *Microtus* (*Micrurus*) of Forsyth-Major (1877), if separated from North American *Pitymys*. But in his Volume VII (1950) Ognev recognized no morphologic reason for such separation of Eurasian forms from North American *Pitymys* and did not use *Micrurus*, but continued the usage of *Pitymys* for Eurasian forms.

In the present report Old World "*Pitymys*" is removed from that North American genus and placed in *Terricola*, as was done by Chaline and others (1988). *Micrurus*

Forsyth-Major is recognized as the junior homonym of *Micrurus* Wagler (1824), a coral snake; and *Meridiopitymys* Chaline (1974) is considered a junior synonym of *Terricola* because van der Meulen's last upper molar Morphotype B does not seem to be restricted to a single lineage.

Although van der Meulen (1978) has stated that his M\3 morphotypes also differ in their enamel-thickness differentiation, it has not been obvious in the present study that the morphotypes can be correlated with enamel-thickness patterns except in a most general way.

"Simple" M\3s are associated with all populations of *Allophaiomys*, and usually have "intermediate" enamel-thickness differentiation (no difference in enamel wall thickness); primitive populations have a high percentage of "*Mimomys*" enamel-thickness differentiation (enamel is thicker on the posterior walls of the prisms of the lower teeth). "Complex" M\3s appear to be associated with *Allophaiomys* only in those populations where individual variation in the M/1 morphology strongly overlaps the characters of some derived genera, and these overlapping variants sometimes have "*Microtus*" enamel-thickness differentiation (anterior walls of the alternating triangles on the lower teeth have thicker enamel). Although somewhat variable in the living genera *Pitymys* and *Pedomys*, all other living genera derived from *Allophaiomys* have "*Microtus*" differentiation apparently with only one exception: *Microtus xanthognathus* from the Canadian taiga, which varies from an "intermediate" to very weak "*Microtus*" enamel-thickness differentiation. Martin (1987) noted that "*Microtus*" enamel-thickness differentiation is also not present in the Central American species *Microtus oaxacensis*, *Herpetomys guatemalensis*, and *Orithriomys umbrosus*. These last three species have not been reviewed from a satisfactorily large sample in this study, and are not discussed.

The most primitive populations of *Allophaiomys* have some individuals with "*Mimomys*" enamel-thickness differentiation, but this is also occasionally found in later populations and in *Lasiopodomys* (fig. 16A). *Lasiopodomys*, *Pitymys*, *Pedomys*, and some species of living *Microtus* and *Terricola* (using genera as defined in the appropriate sections that follow) retain a "simple" M\3, but the living forms usually have "*Microtus*" enamel differentiation. Enamel-thickness differentiation follows a broad trend from the "*Mimomys*" type to the "*Microtus*" type, which is also seen in the evolution of *Arvicola* (von Koenigswald, 1973), but it appears to proceed in a rather inexact way and cannot be correlated with other characters.

Efforts have been made to reproduce enamel thickness faithfully in the illustrations of this report. The enamel-thickness pattern is uniform in all cheek teeth of the individual, but the pattern is reversed between the upper and lower teeth.

The posterior loop and the three basic triangles (fig. 10) are features on the first lower molars of all microtine rodents (except the Ondatrinae and Dicrostonychinae, which have more basic triangles), and are not discussed. The posterior loop of the first lower molar extends lingually in all microtine rodents; thus the first basic triangle (most posterior; T.1) is on the lingual side (fig. 10). Except for *Proedromys*, the posterior salient angle of the last upper molar extends lingually in all microtine rodents.

Salient angles are the lateral points of triangles, wings, and hooks, on both sides of the tooth; they are not specifically defined here but are conventionally numbered from the rear of the lower tooth forward in buccal and in lingual sequences, including the buccal and lingual angles of the posterior loop. The abbreviations LSA and BSA (lingual and buccal salient angles) are often used in describing microtine teeth, but are not used herein.

Reentrants (sometimes called synclines) are the valleys between the triangles, on either side of the tooth, in which the enamel walls of the triangles turn toward the midline; in the microtines here discussed they are filled with cementum (stippled on the illustrations). Reentrants are usually numbered in the same manner as are salient angles, in buccal and lingual series (fig. 10). The abbreviations LRA and BRA (lingual and buccal reentrant angles) are often used in describing microtine teeth (and are illustrated in fig. 10), but are seldom used in the descriptions of the present text.

In contrast to the numbering of the salient angles and the reentrant angles, triangles are numbered anteriorly in one sequence and exclude the posterior loop. The sequence disregards which side of the tooth is represented, but, as the triangles alternate, the even numbers are buccal. Thus "lingual salient angle 2" would be on Triangle 1, or "lingual salient angle 4" would be on Triangle 5 (or the lingual Primary Wing if it has not formed a triangle; fig. 10). The abbreviation "T" is often used for triangles in describing microtine teeth, but is used only occasionally herein.

In all figures anterior is shown upward. Scale is shown on each figure. In all figures, as many specimens as feasible have been shown to illustrate variability. The ownership of specimens illustrated is indicated by the acronyms given in the "Acknowledgments" section (p. 4). Specimens not credited to these acronyms are in the author's collection in the U.S. Geological Survey, Denver, Colorado.

"Typical" is used here in a double context, referring to either the type specimen or the type population. Where used to describe an **individual** it refers to the morphology of the **type specimen**. Where used to describe a **sample of a population** it refers to the range of morphologic variations included in the **type population**; this range includes some concept of the proportions of various morphotypes within the type population. The definition of a type species with great variability should, therefore, include the "typical" morphology (and the type specimen should be within this group), the approximate percentage of this variant in the total sample of the population, and some indication of the morphologic extremes of the type sample. The concepts of both the morphology of the type specimen and the limiting range of variation recognized in the type population are included in the word "typical," but the application of these descriptions varies depending upon whether an individual or the entire known sample is being discussed.

Both morphology and variability are needed to judge stage of evolution and identity of the taxon represented by a population sample. Populations that contain some individuals with a morphotype similar to the most common ("typical") morphology of the type population may have a different range of variation than the type population; such are not considered "typical" populations, although they may contain "typical" individuals. Individual variants within any population may be called "typical" morphotypes if they are similar to the type specimen, but, if the population variability differs to any significant extent from that of the type population, the name given to the type population should not be used. As might be expected, few fossil populations are "typical" (with the morphologic range varying as does the type population), but most populations contain some individuals that are morphologically "typical" individuals. The word "typical" is placed in quotation marks where it is thought that its meaning, as defined here, might be misunderstood.

VARIABILITY AND EVOLUTION

G.G. Simpson (1945, p. 14) said: "The thing that is actually classified is an inference, a purely subjective concept, which approximates a real, but unobservable, morphologic unit, which in turn approximates an equally real but even less observable genetic unit." This purely subjective concept is seldom discussed but is in the mind of anyone required to identify a specimen; it is the identifier's opinion of the amount of variability that can be tolerated within the named taxon to which the specimen might belong. The type specimen of the named taxon is presumed, often incorrectly, to show the midpoint of whatever variability can be tolerated. The concept of the range of tolerable variability is often formed by comparison with a similar living taxon whose range of variability has been established by sampling. But the purely subjective nature of this concept of tolerable variation is what permits the separation of the "splitters" from the "lumpers."

Now, nearly half a century after Simpson's statement, greater efforts and improved techniques provide a much more detailed view of the "unobservable" morphologic unit, particularly for micromammals. This improved view, resulting from the study of population samples, eliminates the need to make inferences based upon similar living taxa. In samples of significant size the range of individual variability of the population is directly observable. While the type specimen remains the name bearer, the morphologic variability of the species is defined by the type population, by direct observation of a statistically useful sample of the morphologic unit. This range of variation is genetically controlled and taxonomically significant, and it should be included in diagnosis.

Frequently, fossil species are found to have greater morphologic variability than living populations of a similar taxon. Although this condition raises doubt about the single-taxon nature of the population and encourages enthusiasts to invent more names than there are taxa, this difference in the range of variability reflects evolution; it may reflect evolution through the time of fossil accumulation by "time averaging," which will vary with collecting techniques as well as depositional rates. To the extent that the sample represents a single population, variability is taxonomically significant, a significance that is hidden by the application of several names to variants of a single population, of a single taxon.

Since C.R. Darwin first made the discussion popular, the process of evolution has been almost constantly debated. But to understand evolution there is no need to psychoanalyze the statements of everyone who has voiced an opinion; the process is logical, and only logic is needed to understand it. The elementary point of logic is that the history of evolution is reconstructed by consideration of known facts and by suggesting hypotheses that seem to describe and explain these facts, not by creating a hypothesis and then manipulating facts to fit.

To his detriment, the present author is not versed in the many hypotheses expressed in the literature. To his surprise, he finds that not all of those engaged in the study of the **facts** of evolution, and their significance in classification, have thought out the **logic** of the fossil record of evolution. Should the reader wish more details of the thoughts of others regarding the process of evolution (and resulting classifications) than are discussed herein, the author recommends the more explicit publication of P.D. Gingerich (1979) called, "The stratophenetic approach to phylogeny reconstruction in vertebrate paleontology."

The author has one objection to Gingerich's paper, and that is to his term, "stratophenetic," for a completely logical and conventional approach to the interpretation of the fossil evidence of evolution. The term denotes stratigraphic superposition as evidence of chronologic sequence, which is the least questionable of several methods that Gingerich has used to establish chronologic sequence, as he noted (1979, p. 54). However, the term would better be "chronophenetic," because time sequencing of morphologic change is what Gingerich achieved by determination of stratigraphic superposition, and he also established and defended this time sequencing by other means, in addition to superposition.

Without temporal sequencing of data, the discovery of evolutionary history (or any history) is a matter of chance; and the historical interpretation relies entirely on the preconceptions of the interpreter. Additional means are now available to establish time sequence, means that were not functionally usable in the late 1970's, when Gingerich composed his explanation of the evolutionary interpretation of the fossil record. And others are available in the Pliocene and Pleistocene (of concern to the present report) that are not yet available in the early Tertiary of the Bighorn Basin of Wyoming, the source of Gingerich's illustrations.

The fossil record of the microtine rodents is notable in its minimal control by stratigraphic superposition, although when available such evidence is considered irrefutable. Temporal sequencing is established more often by (1) paleomagnetic stratigraphy, (2) stratigraphically sequenced (with the fossils of concern) radiometrically dated rocks or chemically identifiable tephra that have been so dated in other regions, (3) correlation with other known microtine biochronologies, (4) known (and dated) dispersal data, (5) climatic events recognizable as those that have been dated elsewhere, (6) occasionally by association with other fossil types having significant biochronologic constraints, and (7) occasionally by dated tectonic events. These all, in addition to stratigraphic superposition, provide "chronophenetic" information. But all require careful evaluation of the evidence, an evaluation usually and obviously unnecessary with the evidence of stratigraphic superposition.

The testimony of the present report, of Gingerich (1979), of Bown and Rose (1987), and of other authors is that populations evolve through progressive changes in the range of their individual variability. This testimony has been stated earlier by others in other situations (Walliser, 1964; Murphy, Matti, and Walliser, 1981; and Woodburn, 1987). Shaw (1969) observed the phenomenon in the fossil record of conodonts and suggested that it caused such confusion that the use of binomial nomenclature should be abandoned in paleontology and replaced by character-complex codes. However, not all possible solutions to the problem were considered, nor were all implications.

As pointed out by Fejfar and Horacek (1983), typical *Allophaiomys pliocaenicus* has a few individuals in its population that overlap the morphology of *Terricola.* (Except for *Phaiomys* morphotypes, the characters of no other derived genus are involved in the individual variability of the type population.) In younger, more advanced populations (sometimes a different named species), there is an increase in the percentage of individual variation in the direction of *Terricola,* and a minor but significant proportion of individuals have this morphology. With continued development of this change in variation, more than half the population later attains a *Terricola* morphology; it is at this point that the population must be assigned to *Terricola*—no longer can it be called *Allophaiomys.* Finally, the population of *Terricola* polarizes or stabilizes its morphologic variability so that few or no individuals remain with an *Allophaiomys* morphology, and then it can be called "typical" *Terricola.* The present report contains many examples.

Such evolution through shifting individual variability in morphotype modes obviously occurs, with time, within a population. At least within the microtine rodents, it does not occur in all populations around the world at the same time nor with the same vector. Multiple origins of the microtine tribes and genera here recognized are documented in the following discussion. (See fig. 14.) As much as possible, species are used to represent groups of a single origin, but much work remains to be done to confirm this in many examples. (Note, again, that in illustrations of this report, as many specimens as reasonable have been figured to illustrate population variability.)

Species are not fixed, sharply diagnosable morphologic units, as we have tried to think of them since January 1, 1758 (the arbitrary date of Linnaeus' tenth edition of Systema Naturae); they are stages in the continuum of evolutionary change, having broadly definable morphologies that characterize that stage, but are sharply definable only by their specific range of variability within a population.

The definition of a species varies with the temporal constraints of a population. Species are much more easily defined in the instant of neozoology than in the time-depth of paleozoology, but one wonders how much change might be noticed if the details available today were available over the 235 years since 1758. Until a "paleontologic" view of "present" is available, there seems little hope that scientific emotion will be inclined to view species as other than the static forms envisioned by Linnaeus.

Allophaiomys was the common ancestor of many taxa, as suggested by Kormos (1932), maintained by Kretzoi (1959), and demonstrated by Chaline (1966). Particularly in their earlier forms, all of these descendants show considerable variability in tooth pattern that overlaps the dental pattern of typical *Allophaiomys;* none show the typical range of morphologic variation, however. Today all lineages of greatest antiquity (most removed in time from *Allophaiomys*) include no individuals with a typical *Allophaiomys* morphotype. The most recently derived lineage, North American *Pedomys,* still contains some individuals with a typical *Allophaiomys* morphotype (R.A. Martin, written commun., 1989).

The entire process is gradational, and during most of the historical record of every lineage each population has some individuals that have the morphotype of its ancestral or of its descendant taxon, rather than of the modal morphology of the population, to which the population must be assigned.

The range of morphologic variability in samples of living populations often, but not always, appears to be less than that observed in past populations. However, this is in part an illusion, as no lineage has stopped evolving just because it is now part of the living fauna. The modern situation is mostly an artifact of the circumstance that no descendant taxon of the future has yet been named; thus no defined future character states exist to be overlapped by existing genetic variance.

Taxonomy is the practice of attaching names to stages within a continuum, but the practice tends to obscure that continuum by making it seem discontinuous. Our concepts of evolution are influenced by the taxonomy of others.

The genetic-morphologic variability under discussion is that of defined taxa. Morphologic variability that does not overlap established taxon diagnoses is assumed to be random and of no evolutionary significance. Should the expanding record show that such a character has significance, then a new taxon needs diagnosis and naming, and the diagnosis should be based upon the character state that the record indicates is significant. "Before" and "after" character states must be recognized before the path of evolution can be documented.

Only by outguessing evolution could a taxon of the future be named; to do so would be as pointless as tabulating random character states of unknown significance in the hope of discovering the path of evolution in the past. When a person first considers a specimen of a new taxon, that person's first statement is, "It looks kinda like so-and-so. But it doesn't have this and it has that." The first thought is of overlapping character states. The second is in diagnosis (Simpson, 1945, p. 22). From the moment of first consideration, classification is not based on random characters but on those of established significance, and their relative degree of significance is considered in detail. Only by outguessing evolution can the pattern of evolution be determined without consideration of the temporally sequenced fossil record.

An interesting situation, not yet statistically defended, appears to be indicated in the living *Pitymys pinetorum* and may well be paralleled in other living species. Its apparent immediate ancestor, *Pitymys cumberlandensis*, seems clearly to have had less individual variability in its single diagnostic character (enamel-thickness differentiation) than does the living species. The ancestral species had primarily an intermediate enamel-thickness differentiation and remained stable in this character state for at least 135,000 years. Yet the living species (*P. pinetorum*) appears to vary uncertainly but apparently quite widely between intermediate and "*Microtus*" enamel-thickness differentiation, possibly differing greatly in degree of variability between local populations, as will be discussed. The living species has increased its phenotypic variability in this character and may, in the future, polarize again into a stable character state with "*Microtus*" enamel-thickness differentiation, an evolutionary direction shown by all closely related lineages.

The change in the range of individual variability within populations can be judged, or measured statistically, and compared with similar populations through time to evaluate relative stages of evolution. Such evaluations that are conformable to known age controls provide useful biochronologic information, as well as great detail of the record of evolution.

Evaluation of phenotypic variance within populations exposes problems in the identification of taxa and demonstrates that such identification is dependent on population characteristics. In well-represented fossil samples of *Allophaiomys* (perhaps 25 or more first lower molars) containing morphotypes of one of its descendant genera, a complete gradation in dental patterns is often found between the morphotypes of the two diagnosed species. In such faunas, determining whether one or two species are present requires an abundance-of-morphotypes criterion: if the distribution is bimodal, two species are represented and some individuals between the modes cannot be certainly named. Bimodality, of course, is significant only if intergradation of morphotypes is continuous between the modes, thus identifying a single population. If not continuous, two populations and two taxa are present.

Chaline (1966, 1972) was possibly the first to fully rationalize the taxonomic implication of this morphologic variability in the tooth patterns of the *Allophaiomys-Microtus* and *Allophaiomys-Pitymys* lineages; he was the first to thoroughly document it. This documentation was made by the description of fossil microtine faunas in France with intergrading morphotypes of these lineages.

At first Chaline did not fully comprehend the significance of the great population variability and introduced a variety of new names. These can be seen, from his abundant illustrations, to represent individual morphotype variants within single populations. Thus in many cases single species with great morphologic variability were represented. The specific identity of the populations, to which he applied several names, can only be determined by a statistical evaluation of the entire sample and is not attempted herein, although in many cases Chaline provided enough illustrations of these variable, apparently single-species populations to suggest their identity.

In a very real sense Chaline provided the evidence of evolution and then hid it behind the artificial definitions of his classification. In most of his examples, diagnosis of his taxa was impossible because only a single, intergrading population was represented. The study is a classic example of the difference between evolutionary gradation and systematic, diagnostic classification. One could diagnose most individuals of a single population as morphologically distinguishable species if one did not consider the probable structure of the (presumably) interbreeding population.

Although the morphologic transition between fossil forms documented by Chaline clearly showed the anagenetic relationship between *Allophaiomys* and its descendants, it also created the impression of gene mixing—that the fossil and living genera (*Allophaiomys*, *Terricola*, and *Microtus*) all belonged in a single genus (for which Chaline selected *Microtus*). But morphologic intergradation does not indicate gene mixing, only genetic similarity; *Allophaiomys* has been extinct for 825,000 years, but some living derivatives still have individual variation that overlaps its dental morphology. In this discussion, morphologic intergradation is considered to indicate only temporal proximity to either linear (anagenetic) morphologic change or divergence toward a different taxonomic diagnosis. The condition could result from brief separation of subpopulations as well as from drift throughout the entire population; it is difficult to separate the causes, but in many cases it seems to occur with climatic change and the resulting morphologic change is coupled with change in environmental tolerance. Several examples are discussed herein.

The morphologic intergradation that Chaline documented also seemed to show that all evolution out of *Allophaiomys* took place in France. However, the intergrading individual variability was the product of global conditions. Actually, France was on the fringe of some major evolutionary events and did not experience many of the major episodes in the evolution of lineages out of *Allophaiomys* that are known elsewhere. For example, in the nomenclature employed in the present report *Lasiopodomys* evolved from *Allophaiomys* and into *Microtus*; Markova (1982, 1990) described these forms from the Karay-Dubina and Shamin faunas north of Black Sea, van der Meulen (1973) described some from Italy, but in the French records of Chaline *Lasiopodomys* is missing, although the relationship between *Allophaiomys* and *Microtus* is evident in his faunas. Also in France, at least at the time of Chaline (1972), there appears to have been no fossil sample of *Allophaiomys* that had the minimal individual variability of the type population at Betfia–2, Romania. The individual variation in all of his samples is greater than that of the type population. Chaline recorded no microtine fauna that is comparable to that found in the older part of the Olyor Suite of Krestovka Sections, although these can be found elsewhere.

Even with complete knowledge of population variability, species distinctions are vague during the speciation process, as is the definition of a fossil species as an isolated breeding unit. The *Allophaiomys-Microtus* and *Allophaiomys-Pitymys* lineages, identified only by their tooth morphology, apparently have been undergoing constant speciation for nearly 2 million years and in different places. During this time at least 10 genera (many more have been named), with very many species, have evolved from the single species *Allophaiomys pliocaenicus*. The evidence is abundant and worldwide.

Kretzoi (1958) has indicated that more than 1,100 microtine species have been named, and the majority of them are the descendants of *Allophaiomys pliocaenicus*. The gradation of dental morphology between taxa has caused many to consider all as belonging to a single genus, the genus *Microtus* (following Chaline, 1966).

Since Chaline's first defense of an all-inclusive genus *Microtus* in 1966, increasingly intensive study of fossil microtine rodents, in large part stimulated by Chaline's studies, has resulted in the discovery of many fossil faunas throughout the world that show aspects of the evolution of *Allophaiomys*. In 1966, for example, no one was aware that *Allophaiomys* had been an abundant part of the North American fauna for more than a million years. Chaline's interpretations and documentation were farsighted and enlightening a quarter of a century ago, but today interpretations must be made from the much larger record currently known, and from the sharply definable genera that eventually evolved. The microtine rodents of the *Allophaiomys-Microtus* lineage from the Olyor Suite of the Krestovka Sections constitute one of these faunas that cannot be judged by 1966 standards.

Since 1966, this overlapping morphologic variability has been considered as evidence of *in situ* evolution of *Allophaiomys* into more derived forms in many faunas. The origin of *Microtus* and (or) *Pitymys* (*sensu lato*) has thus been claimed from France to China, and in the United States because of such morphologic overlap. Most frequently both *Allophaiomys* and a derived genus have been reported from a single fauna. However, all such records are suspect until evidence is presented indicating that a single, morphologically intergrading population is not present. What has been lacking in previous interpretations is any consideration of population structure.

In many cases where two taxa have been listed, consideration of the population structure indicates that only one taxon is present. In a few cases, the defining morphologic characters of the two taxa plot out bimodally and do not intergrade, and the original listing of two taxa is justifiable.

It is emphasized that for taxonomic purposes the evaluation of overlapping variability applies to only those characters of taxonomic significance in diagnosis. Until it is established that the character to be evaluated is significant in the recognition of the stage of evolution within the lineage, evaluating its variation within the population has little value. Many variations in dental characters of microtine rodents occur throughout the group and have no taxonomic significance—for example, the strange irregularities on the triangles of *Terricola meadensis* from the Hansen Bluff fauna (fig. 13*G*). The occurrence of similar irregularities in individuals of other taxa should never be, and hardly ever has been, considered significant; they have never been found to conform to a pattern.

Examples of population variability are discussed in the following consideration of the history of *Allophaiomys* and its living and extinct descendants. The evaluation of these morphologic modes is a statistical procedure and cannot be made with small samples, although in some cases a supposition can be made on the basis of the likelihood of features of the sample to be found in typical populations. In these cases, however, the resulting taxonomic assignment is qualified.

The populations for which taxonomic assignment is most difficult are those in which the single morphologic mode falls approximately on the sharply defined boundary of a systematic diagnosis, such as the single population of *Microtus paroperarius* and *Lasiopodomys deceitensis* in the Cumberland Cave fauna of Maryland, discussed later in this report (p. 53). This large sample had been assigned to *Microtus paroperarius* by van der Meulen (1978), although nearly half the individuals have a first lower molar morphotype that is included in the definition of *Lasiopodomys deceitensis*.

No *Lasiopodomys* morphotypes are present in the "typical" or type population of *Microtus paroperarius* from the Cudahy fauna of Kansas. However, because of van der Meulen's assignment of the Cumberland Cave population, including a high percentage of *Lasiopodomys* morphotypes, to *M. paroperarius*, samples of *Lasiopodomys* from other localities have been assigned to *Microtus paroperarius* (Guilday and others, 1984; Miller and others, 1987). In the Cumberland Cave case, no matter how large a sample and no matter how certain the statistical evidence of the mode being slightly on one side or the other of the defined boundary, to call the entire population by either name is a misrepresentation.

Several devices, such as informal numbered stages of morphologic differences between named taxa or a slash between taxonomic names (instead of the dash used herein), have been used to indicate the intermediate morphologic position of particular populations between two named forms (Krishtalka and Stuckey, 1985; Bown and Rose, 1987; Repenning, 1987).

The common opinion of all who have considered this problem is that the addition of new names for intermediate forms in such anagenetic evolutionary gradation would unnecessarily enlarge the nomenclature. Unfortunately, too many have not considered the problem and have simply introduced new names or expanded the definition of existing names to include atypical morphotypes. Thus the "typical" characterizations become obsolete, and confusion in nomenclature is begun. Only the morphological variations of the type population can be considered as "typical."

Repenning (1987) used hyphenated names to indicate morphologically intermediate populations and this device is followed herein; such treatment would list "*Microtus paroperarius-Lasiopodomys deceitensis*" in the Cumberland Cave fauna. The identification of this population as *Microtus paroperarius* by van der Meulen (1978) has caused misidentifications in other publications because it has been assumed that his identification indicated that the individual variation in this population from Cumberland Cave was typical of the species.

Although awkward and not considered by the rules of nomenclature, use of a hyphenated double-name device calls attention to the fact that a population is not typical but has a variation that includes significant percentages of the morphotypes of two defined taxa. Furthermore, it suggests that the so-designated population is part of an anagenetically evolving lineage and that it is not a "typical" population of either name used. It should prevent the assumption that this great a variation is permissible under one name, under either applicable name. To give the intermediate population a new name is to compound the problem, and to list two species where only one population has existed is to hide the phylogenetic relationships.

Herein, proportions of differing morphotypes representing between 40 and 60 percent of the population sample are described as hyphenated double-names; if proportions are unequal, the most abundant morphotype is named first. Populations with more than 60 percent of one morphotype are assigned to that genus and species, and the remaining 39 percent or less are considered as individuals overlapping the morphology of another taxon.

Such intermediate faunas are not common. Most populations fall clearly on one or the other side of the boundaries of taxonomic definitions. In this report the hyphenated, double-name device is used only once, for this population from Cumberland Cave. In the case of the *Allophaiomys* and *Lemmiscus* population from SAM Cave, New Mexico, morphotypes of *Lemmiscus* constitute only 21 percent of the population and the entire population is assigned to *Allophaiomys,* with the notation that its variability overlaps the morphology of *Lemmiscus*.

The Cumberland Cave population of *Microtus paroperarius-Lasiopodomys deceitensis* certainly is not typical of either taxon; the type population of *Microtus paroperarius* from the Cudahy fauna of Kansas differs greatly from the population in Cumberland Cave and it is not clear why van der Meulen used this name. Similarly, the type population of *Lasiopodomys deceitensis* contains no *Microtus* morphotypes. Although 41 percent of the population has a *Lasiopodomys* morphology and 15 percent has a morphology typical of *Lasiopodomys deceitensis*, and although van der Meulen had specimens of *Lasiopodomys deceitensis* from the type population, Cape Deceit, Alaska, in his study collection, he appears to have failed to note the similarity.

The SAM Cave, BOT–4 locality, population of *Allophaiomys* n.sp. certainly is not typical of *Allophaiomys pliocaenicus*, and a new species name is considered appropriate. But because only 21 percent of its individuals overlap the morphology of *Lemmiscus* the hyphenated name *Allophaiomys-Lemmiscus* does not seem appropriate. It would seem appropriate to mention in the diagnosis of *Allophaiomys* n.sp. that 21 percent of the type population has a *Lemmiscus* dental morphotype, and that up to 40 percent of overlap with the *Lemmiscus* morphotype could be tolerated under the name *Allophaiomys* n.sp. The population is not large enough to be confident of the exact percentage. What seems most inappropriate is to give a new name to each population that differs by a minor percentage in its overlapping morphotypes. That many names are neither needed, nor helpful, nor defendable. Contradictory morphotype proportions are discussed in the pages to follow with regards to the differences between the Hanover Quarry Fissure and Cumberland Cave faunas.

The *Microtus paroperarius-Lasiopodomys deceitensis* population from the Cumberland Cave fauna has only one morphologic mode that is essentially intermediate between the two defined taxa; the population represents linear, anagenetic evolution from one artificial systematic definition into another. If a bimodal distribution of diagnostic character states is **not** found in an intergrading population, the population represents only **one** natural species, despite morphologic overlap of defined characters of two systematic species in the population. This is the crux of the incompatibility built into the Linnaean binomial classification: the attempt to subdivide the gradation of evolution into sharply defined systematic units.

Bimodal distribution of diagnostic character states in a morphologically intergrading population has an entirely different significance. It indicates diversification. It does not indicate that the population has diversified nor does it indicate that it is about to diversify; it indicates that the population lived near the time of diversification, either before or after. Later faunas will show increasing polarity toward their separate complex of diagnostic character states. Populations with a bimodal distribution of diagnostic character states are considered as representing two taxa, even though it is not possible to know if they have evolved genetic isolation.

Great individual variability is, of course, also present in faunas lacking *Allophaiomys* or *Allophaiomys* morphotypes. However, as Chaline (1966) noted, this overlap of morphologic characters decreases with time as populations, species, and genera polarize in their phenotypic characters. Polarization in populations as a result of decreasing morphologic variability is a recognizable evolutionary trend and identifies genetic change. Degree and range of population variability are, thus, of taxonomic significance. An estimate of morphologic variability within the type population, thus, should be an essential part of any diagnosis. This report relies upon this variability as a tool to distinguish the evolutionary stage of any fossil population.

Several fossil microtine species are essentially *nomina vana*, in Simpson's (1945) sense, because they are based upon a single specimen for which no population characteristics are available. This inadequacy may be provisionally corrected by reference of the species to a different population in which adequate population characteristics are evident, but such proxy characterization is always subject to correction by the later discovery of the character variation in the type population. Examples of this procedure in *Pedomys llanensis* and *Pitymys hibbardi* are discussed later. For both species, population characteristics have been provided by reference of the species to other faunas, but these characterizations are subject to nullification if a satisfactory type population should ever be discovered.

VARIATION AND BIOCHRONOLOGY

Recognition of the proportions of the morphologic variations of one microtine lineage in several faunas allows the several populations to be broken down into progressive evolutionary units of the lineage. These may be checked and verified against the population characteristics of other elements of the fauna, but, with most microtines, such similar populations are too closely spaced in time to be verified by any other means of approximating time.

For example, in populations described as having both *Allophaiomys* and *Terricola* morphotypes (a very common association in Eurasia), the following are recognizable: (1) a "typical" *Allophaiomys* population (the type population, Betfia–2 fauna; fig. 14); (2) an advanced *Allophaiomys* population with a significant minority of individuals overlapping the *Terricola* morphology (Mt. Peglia–1 fauna); (3) an *Allophaiomys-Terricola* population with a morphologic mode near the sharply defined boundary of systematic diagnosis (possibly Razdolie fauna); (4) a primitive *Terricola* population in which a significant minority of individuals still overlaps the *Allophaiomys* morphology (possibly Karay-Dubina); and (5) a "typical" *Terricola* population in which essentially all individuals have a *Terricola* morphology (living). With large samples, these can be further subdivided in terms of "more advanced" or "less advanced," but such estimates require stronger statistical evidence to be credible.

Population analysis thus can provide a biostratigraphy in which one of five definable stages may exist in a fauna that usually would be described as containing both *Allophaiomys* and *Terricola*, a condition not true of any of the five stages given in the example above, because all have intergrading morphotypes and must be considered a single population, hence only one taxon. Each of the five stages is composed of a single natural species, and they differ only in their range of morphologic variation between systematic species.

Such evaluation of the proportions of morphotypes within a sample of a population that is intergrading between two defined morphologies provides much more biochronologic discrimination than does referring the population to one or two artificial taxonomic categories. In the discussion of faunas that follows, the use of such population stages results in a temporal discrimination that appears to be sensitive to a period of about 5,000 years. However, such faunal variation can only be recognized in a sample large enough to suggest an approximate proportion of morphotypes. If only one specimen of *Allophaiomys* and one specimen of *Terricola* are in the sample, whether they represented an advanced *Allophaiomys* population, a primitive *Terricola* population, or two populations—one of *Allophaiomys* and one of *Terricola*—would be indeterminate.

Morphologic gradation between two defined morphologies must be demonstrable in the sample to indicate individual variability in one population during linear evolution. Bimodal distribution of morphotype frequencies must be present to indicate diversification of taxa. Many faunal lists show, for example, both *Allophaiomys* and *Pitymys*, suggesting budding or accomplished diversification. However, study of morphotype frequency within such a sample usually shows a great majority of one morphotype and only a few specimens of the other, indicating the presence of only one taxon with great individual variability. The difference is biochronologically significant.

In the present discussion, therefore, it is important to note that the presence of a few individuals with an *Allophaiomys* dental pattern, grading within the fossil (or living) population into the dominant morphology of a taxon recently derived from *Allophaiomys*, is **not** considered an association of both descendant and ancestor. The reverse is also true: populations of *Allophaiomys* with a few individuals that overlap the characters of more derived forms **do not** constitute associations of both ancestral and descendant taxa. This is in contrast to nearly all published faunal lists, which customarily list both morphotypes as taxa of the fauna. This custom imparts an erroneous biologic and chronologic implication of two discrete taxa.

Both of the preceding examples show the extent of variability and indicate either a probable past or future "hyphenated boundary" population in a linear sequence of evolution like that discussed from Cumberland Cave; or they may indicate a future bimodal distribution of characters and diversification into two lineages from one. But only one taxon is in the population used as an example. Hence, only one should be **listed** for the fauna.

To list two taxa on the basis of two morphotypes in an intergrading population implies an entirely different stage and condition in evolution. Minor percentages of morphologic variants that overlap the defined morphology of another taxon may be acknowledged by the words "primitive" or "advanced," separated from the name by a comma, or they may be discussed in the text.

Thus, the Cheetah Room fauna of West Virginia contains one intergrading population with 75 percent of its individuals having a *Lasiopodomys deceitensis* morphology and 25 percent having a *Microtus paroperarius* morphology; the population should be listed as "*Lasiopodomys deceitensis*, advanced." In the same fauna occurs one intergrading population with 63 percent *Pitymys* and 37 percent *Allophaiomys* morphotypes, distributed in a distinctly bimodal pattern—the majority of *Allophaiomys* morphotypes look "typical" and the majority of *Pitymys* morphotypes look "typical"; relatively few individuals appear intermediate. This population should be listed as "*Allophaiomys* sp. and *Pitymys hibbardi.*" In the Cumberland Cave fauna of Maryland an intergrading population with 41 percent *Lasiopodomys deceitensis* morphotypes and 59 percent *Microtus paroperarius* morphotypes is present, but one mode in morphotypes is present, and it falls close to the boundary of the two generic definitions; this population should be listed as "*Microtus paroperarius-Lasiopodomys deceitensis.*"

Note again that the recognition of one or more taxa cannot be made with a small sample because of the lack of statistical significance. Although not discussed in this report, the fauna from Fyllan Cave, Texas (locality 19, fig. 1) presents an example (A.J. Winkler, written commun., 1990). Four first lower molars of *Allophaiomys* morphotype are in the sample and, morphologically, these could represent typical *Allophaiomys pliocaenicus*. They are associated with the North American bog lemming *Synaptomys* and are in reversely magnetized deposits; an age younger than the Cheetah Room fauna (≈ 840,000 yr B.P.) and older than the Brunhes Chron (≈790,000 yr B.P.) is indicated. This bracketed range suggests that the fauna would be uniquely young for a fauna containing typical *Allophaiomys pliocaenicus*, although typical **morphotypes** of *Allophaiomys pliocaenicus* are known in younger populations of *Pedomys llanensis* (Pfaff, 1990). The sample could represent *Allophaiomys guildayi*, but it is too small to evaluate the nature of the population and demonstrate the variability that characterizes this later species.

The four specimens from Fyllan Cave should be identified only as *Allophaiomys* sp. even though the small sample is morphologically conformable with *Allophaiomys pliocaenicus*. An identification as *Allophaiomys guildayi*? could be justified on the basis of present knowledge of the history of this lineage and of the age of the Fyllan Cave fauna. The fauna appears to be too old to justify an identification as ?*Pedomys llanensis* and too young to justify an identification as *Allophaiomys pliocaenicus*?.

Possibly the only reason that variability appears conspicuous in the descendants of *Allophaiomys* is that its fossil record is very well documented. The author knows of no other mammalian group where consideration of recognizable evolutionary grades can lead to debating differences in age that may be as little as 5,000 years apart, as will be considered in some of the following faunal discussions.

It is difficult to conceive of a situation in the evolution of any mammal that does not involve considerable individual variability during speciation. However, the overall rate of evolution of a group must be reflected in the range of variability of a population. Depending upon what genera are recognized, the descendants of *Allophaiomys* averaged four or five genera (including all divergent lineages) evolving in about 1 million years (fig. 14) and a much greater number of species. Mammalian groups evolving at the rate of one new genus in 1 million years might be expected to show much less individual variability in individual populations; thus, the degree of population variability would seem to say something about the evolutionary rate of a lineage.

MULTIPLE ORIGINS

The degree of gradational variability observed in many fossil microtine faunas here considered displays the evolution of descendant genera out of ancestral *Allophaiomys*. These faunas occur throughout the Northern Hemisphere. Multiple origins, separated both geographically and temporally, are indicated. The lineages derived from North American populations of *Allophaiomys* are *Lemmiscus*, *Pitymys*, and *Pedomys*. One endemic lineage of *Microtus* evolved in North America out of immigrant *Lasiopodomys*, itself derived from *Allophaiomys* in Asia. *Terricola, Lasiopodomys, Phaiomys, Proedromys, Hexianomys,* and most lineages of *Microtus* evolved out of Eurasian populations of *Allophaiomys* (or *Lasiopodomys* in the case of *Microtus* and possibly *Proedromys* and *Hexianomys*). *Proedromys* and *Hexianomys* are endemics of the Oriental faunal region. *Pitymys* and *Pedomys* are endemics of the eastern United States faunal region, and *Lemmiscus* is endemic both to the eastern and western regions of the United States.

In North American localities only one derived lineage is seen to develop at one time and out of one population of *Allophaiomys*. The author has seen no multiple generic origins from single populations of *Allophaiomys* in Eurasian faunas, but these populations have not been so closely examined. These records suggest that when a population begins to change by shifting its range of variability, it follows one pattern only. Only evolution toward a single set of character states, characterizing only one derived lineage, occurs in any single population. *Allophaiomys* may evolve into *Lemmiscus* in a population of the highlands of New Mexico, and another population, perhaps at a different time, may evolve into *Pedomys* near sea level along the Atlantic Coast; but no population evolves in two directions to become two derived genera at the same time and out of the same population, and perhaps not in the same environmental situation. Different populations, usually at different times and often in different areas, evolve toward different derived lineages.

As an example (fig. 14), in the Cheetah Room fauna of West Virginia, *Lasiopodomys*, derived earlier from *Allophaiomys* in Asia and an immigrant first to Beringia and then to the United States, is seen to have been experiencing a change in individual variation towards *Microtus*. This was a change that passed the midpoint of individual variation toward *Microtus* later, in the Cumberland Cave fauna of Maryland. Also in the Cheetah Room fauna *Allophaiomys*, also an immigrant from Asia but a million years earlier than *Lasiopodomys*, is seen to have evolved a bimodally split population containing two lineages, one a continuation of *Allophaiomys* and the other the first *Pitymys*. *Allophaiomys* finally became extinct in North America after the Cumberland Cave fauna lived by evolving a major *Pedomys* morphotype variation at about the same time that *Lasiopodomys* morphotypes had disappeared from *Microtus* populations (in the Trout Cave No. 2 fauna of West Virginia).

Later populations of *Pedomys* had increasingly minor percentages of *Allophaiomys* morphotypes in association with increasingly typical populations of *Microtus paroperarius*, which contain no *Lasiopodomys* morphotypes. Acording to Martin (1987) some individuals of living *Pedomys ochrogaster* still have an *Allophaiomys* dental morphotype. *Pedomys* and endemic *Microtus* rapidly dispersed westward to the east side of the Rocky Mountains but never left the eastern United States faunal province, in contrast to territorial reclusion of *Pitymys*.

There is no microtine fossil fauna in the world known to the author in which one genus, as *Allophaiomys*, was simultaneously evolving into two others, as *Lasiopodomys* and *Terricola*. From published information, the Razdolie fauna of Western Siberia (Zazhigin, 1980) seems to be the most likely to show this, but the author's examination of this fauna was too brief to be certain; from Zazhigin's (1980) published description and illustrations the *Lasiopodomys* appears to be established in the Razdolie fauna and the generic intergradation appears to be between *Allophaiomys* and *Terricola*. This represents a reverse historical sequence to that shown from the two faunas of Monte Peglia, Italy (van der Meulen, 1973), in which *Allophaiomys* first evolved into *Terricola* and then, in a later fauna, into *Lasiopodomys*. These examples from Monte Peglia are, however, clearly at different times and presumably from different populations of *Allophaiomys*; van der Meulen recognized them as different species of *Allophaiomys*.

The lineages derived from *Allophaiomys* reveal few records of bimodal morphologic trends and none of multiple diversification at the scale of individual populations. But there are many examples of two lineages in the same fauna that have been derived from *Allophaiomys*, each showing different degrees and direction of population evolution away from *Allophaiomys*. In such cases population structure indicates that one is more removed from *Allophaiomys* than the other (different times of derivation) and presumably all can be explained by the reintroduction of *Allophaiomys* from an adjacent province.

Nearly all the examples considered here indicate anagenetic evolution from *Allophaiomys* into a derived taxon. Only one population from North America is known that shows bimodal distribution of morphotypes. This is the population of *Allophaiomys* and *Pitymys* in the Cheetah Room fauna, indicating a divergence of the genus *Pitymys* from *Allophaiomys* and the continuation of both *Allophaiomys* and *Pitymys* together. The populations of *Allophaiomys* and *Lemmiscus* n.sp. from several localities in SAM Cave, New Mexico, may indicate divergence of the two genera or linear evolution from *Allophaiomys* toward *Lemmiscus*, but the examination is not complete. The BOT–4 sample from SAM Cave contains only 13 first lower molars with a *Lemmiscus* morphotype, statistically a rather weak sample for drawing conclusions about population structure. A younger fauna is needed to show possible divergent bimodality, and the BOT–4 fauna appears to be the youngest in SAM Cave. The nearby and later faunas of Hansen Bluff, unfortunately, contain neither genus and do not help decide whether the trend in SAM Cave was *Allophaiomys* **into** *Lemmiscus* or *Lemmiscus* **branching from** *Allophaiomys* and the continuation of both.

There are many records of two populations within one fauna, each evolving from *Allophaiomys* into a different derived lineage; but in all cases considered the faunal sample indicates separate populations, one much farther along in evolutionary transition than the other.

In the Cumberland Cave fauna of Maryland, perhaps as little as 10,000 years younger than the Cheetah Room fauna, the remaining and last-recognized population of *Allophaiomys* in North America was evolving directly into the genus *Pedomys*, very similar to *Pitymys*. This took place in faunal association with a separate population of *Pitymys* having no individual morphologic overlap with *Allophaiomys* (as was the case in the Cheetah Room fauna). Only about 16 percent of the *Allophaiomys* population has a typical *Pedomys* morphotype; hence the *Pitymys* population of Cumberland Cave was more polarized in morphologic variation. It seems clear that the population of *Allophaiomys* in the Cumberland Cave fauna was evolving directly into a *Pedomys* morphotype and that the *Pitymys* population was morphologically stable (polarized).

Diversification does not appear to result in the extinction of the ancestral taxon, but proceeds by morphologic divergence of part of one population toward a second defined morphotype, presumably because of some environmental constraint. The author believes that anagenesis within a single lineage is by far the most common pattern and that only it results in the extinction of the ancestral taxon. But such extinction occurs only in a provincial sense and the taxon may survive in other provinces.

Thus it seems possible for an ancestor to become extinct through linear evolution in one faunal province and to become reintroduced from an adjacent province, although no such records are recognized (but some are suspected) in this report. The occurrence of *Allophaiomys* with descendant genera throughout the Northern Hemisphere indicates the persistence of an ancestral taxon, at times possibly through diverging morphotypes but probably more often from interprovincial faunal exchange subsequent to provincial extinction.

Diversification of lineages also is more of a geographic-provincial event than a worldwide phenomenon, as usually conceived. This has been pointed out at least since 1969 (Shaw), but the worldwide use of "first" appearances and "last" appearances in biochronology persists. The frequent occurrence of ancestral *Allophaiomys* with *Lasiopodomys* and *Terricola*, and of ancestral *Lasiopodomys* with *Microtus*, may indicate interprovincial exchange rather than diversification within one province. However, as discussed, where the origination of a taxon can be established by population characteristics, it appears to consist of the development of a new taxon from an ancestral stock, and never the termination of an ancestral stock by splitting into two descendant lineages. At least from the present record of population structure, *Allophaiomys* appears to have become extinct only through unimodal, anagenetic evolution into derived genera, including *Pedomys* in North America and presumably *Phaiomys* in Asia.

The tribes Microtini and Pitymyini evolved more than once out of *Allophaiomys*, as presumed by Chaline (1966). The tribe Pitymyini has at least three separate origins out of *Allophaiomys*: *Pitymys* and *Pedomys* in North America and *Terricola* at least once in Eurasia. The tribe Microtini has at least an equal number of geographically and temporally separate origins: once in North America and at least twice in Eurasia, possibly more. These multiple origins raise questions of procedure and concept in systematic nomenclature. This report accepts multiple origins in its concept of classification until the history of a lineage is sufficiently well documented that its subdivision, by different origins, can be defended and morphologically identified.

Multiple origins also raise questions of biochronologic significance. These multiple origins have occurred at different times and cannot have the same age significance everywhere. Such separate origins at different times will continue to raise questions until the mosaic of evolution into the living fauna is much better known.

Only a small and early part of microtine history is revealed in the present discussion, but this small part is surprisingly complex (fig. 14). In the eastern region of the United States, the presence of *Microtus paroperarius* indicates an origination out of *Lasiopodomys* very close to 830,000 years ago and about 400,000 years before the immigration of *Microtus* from Asia, but, as yet, the origin of no other species of the genus, as here defined, can be so closely dated. One lineage of *Microtus*, however, appears to have evolved in Asia possibly 1.5 million years ago, as it is present in the western province of the United States perhaps 1.4 million years ago. Other lineages of *Microtus* may have evolved before 1.0 million years ago, to judge from the European fossil record; but their actual time of evolution has not yet been identified.

The generalized temporal (not phylogenetic) sequence of genera that have evolved out of *Allophaiomys* appears to be: *Terricola*, *Lasiopodomys*, *Proedromys*, *Pitymys*, *Pedomys*, and *Phaiomys*. *Microtus* evolved out of *Lasiopodomys*, and did so at least three times. The history of *Phaiomys* is not known, and it could well be living *Allophaiomys* in which polarization of characters has changed it to a condition noticeably different from that of fossil *Allophaiomys*. Some records seem to result from a sequence different than that given above; *Lasiopodomys* seems more removed from *Allophaiomys* than does *Terricola* in Western Siberia. This may reflect the nature of the lineages, however, as the Pitymyini seem to retain *Allophaiomys* morphotypes for a longer time than do the *Lasiopodomys* lineages.

These histories are discussed in the pages that follow and there the changes in population structure that led to them are arranged into biochronologies. The constructed biochronologies are applicable only intraprovincially, although dispersal history interlocks the provincial biochronologies at specific times. Most of the evidence presented is in the United States east of the Rocky Mountains, and there this biochronology is the most detailed.

CLASSIFICATION

All taxa discussed in some detail are placed in one of three tribes of the subfamily Arvicolinae: the Arvicolini, Microtini, or the Pitymyini. The classification basically follows that of Kretzoi (1969) except that he did not use a tribe Pitymyini, which was used and explained by Repenning (1983); it has been outlined for all microtine (arvicolid) rodents in Repenning, Fejfar, and Heinrich (1990). The classification used here differs only in that the genus *Lemmiscus* is removed from the tribe Lagurini and placed in the tribe Microtini, as will be discussed. The definition used for the subfamily Arvicolinae is that used by Repenning and Grady (1988) and it was there diagnosed as "Cricetid rodents with hypsodont, triangularly prismatic cusps on their cheek teeth (microtine cricetids); m1 with posterior loop and three basic alternating triangles, differing from the Ondatrinae and Dicrostonychinae; Anteroconid Complex with single rounded to globular Cap, differing from the Prometheomyinae [and no or variable number of secondary triangles or wings]; M3 with alternating triangles differentiated, not lophate, differing from the Lemminae" [and lower incisor passing beneath the cheek teeth within the mandibular corpus, differing from the Dicrostonychinae and the Lemminae] (bracketed phrases added here).

The subfamily Arvicolinae includes five tribes: Arvicolini, Microtini, Pitymyini, Clethrionomyini, and Lagurini. The Arvicolini are ancestral. The Pitymyini and the Microtini derive from the arvicoline genus *Allophaiomys*. The Clethrionomyini retain rooted cheek teeth (for the most part). The Lagurini derive from the lineage of the arvicoline genus *Mimomys*. Only the first three tribes listed at the beginning of this paragraph are discussed in the present report. This is the first publication to include the North American genus *Lemmiscus* in the tribe Microtini, rather than the tribe Lagurini; otherwise the generic content of these tribes is as listed in Repenning, Fejfar, and Heinrich (1990).

The present report outlines the history and defines the taxonomic units of *Allophaiomys* of the tribe Arvicolini, the derived tribes Microtini, and (in less detail) Pitymyini, to illustrate and emphasize that the interpretation of the age of the Olyor Suite, as represented in the Krestovka Sections in the Kolyma Lowlands of Yakutia, cannot be made without a uniform nomenclature and without knowledge of the differing provincial histories of its taxa.

This age interpretation cannot be made simply by comparison of the microtine faunal lists from the Olyor Suite with those of some province elsewhere in the world without knowledge of the history of evolution and dispersal in all areas that might represent the source of the faunal elements. At present this information in the provinces of Asia and Beringia is sparse, although recent and current work in both areas is improving it rapidly (Zazhigin, 1980; Zheng and Li, 1990; Morlan, in progress). To make an age interpretation of the Olyor Suite, the application of taxonomic nomenclature must be uniform, the evidence of stage of evolution must be understood, dispersal patterns must be recognized, and provincial differences in the timing of evolution and of dispersal must be considered.

The present report integrates the records from North America with those of Eurasia to provide the known background that is needed for the evaluation of the age of the Krestovka Olyor. Nevertheless, this global synthesis of history is incomplete at present and the size of the population samples from the Olyor Suite in the Krestovka Sections is minimal for the interpretation. The small sample and poorly understood history of adjacent Asia preclude the hope that such interpretation will have the precise biochronologic control that can be inferred for many localities in the eastern three-quarters of the United States. As is discussed herein, evidence for the history of *Allophaiomys* and its derivatives is weaker to the west of the Rocky Mountains in the United States than it is in the eastern three-quarters of the country.

To synthesize this history, an entirely different classification than that currently conventional is used. It should be pointed out, however, that the classification here used differs little from that used before Chaline (1966) and Ognev (1948, 1950). Both Ognev and Chaline explained their classification as being based upon that of Miller (1896), but an examination of Miller's 1896 classification shows almost no similarity to those of Ognev and Chaline. The main similarity of all three is that the genus *Microtus* includes many taxa that others have subsequently considered as separate genera. In the systematics of Miller, Ognev, and Chaline these taxa are held together by the common condition of rootless cheek teeth.

Neither Ognev nor Chaline noted that Miller abandoned this classification in 1912, when he published his monumental treatise on the mammals of western Europe, or that the classification of Miller (1912) had been used throughout the world, with refinements by others (for example, Hinton, 1923, 1926), until the time of Ognev's and Chaline's publications. Other than mentioning Miller (1896), neither Ognev nor Chaline defended their classifications. However, the monumental size of Ognev's works and the revolutionary concepts of Chaline's works have had great impact, and their classification has been widely adopted, but not defended, since about 1970.

The presently conventional all-inclusive genus *Microtus* comprises all forms from *Allophaiomys pliocaenicus* of the tribe Arvicolini (as defined by Kretzoi, 1954) to *Microtus arvalis* of the tribe Microtini (Simpson, 1945), as well as all forms in the other major *Allophaiomys*-derived lineage, the tribe Pitymyini (Repenning, 1983). To place all these in one genus hides their entire evolutionary history under a blanket of generic anonymity and excessive specific profusion. All taxa shown in figure 14 would have been included in the genus *Microtus* in the taxonomy of Chaline and Ognev.

Equally defeating for historic-systematic clarification, the current proliferation of subgeneric, specific, and subspecific names, based upon individual variations within single populations, produces only hopeless confusion. There is little need to name a form intermediate in position between currently named taxa of one lineage, unless it serves to help identify some previously unrecognized ramification or evolutionary stage of this lineage. The purpose of taxonomy is to identify definable stages in a known history for ease in communication, not to produce names.

Although the reasons usually are not specified, the genera *Allophaiomys*, *Lasiopodomys*, *Microtus*, *Terricola*, *Pedomys*, *Phaiomys*, *Pitymys*, and *Proedromys* and many other less well understood names are all included, as subgenera, in the genus *Microtus* by many modern microtine students, presumably following Chaline (1972) or Ognev (1950). This defeats the purpose of classification, as each of these above named genera (and probably many of those not named) has a separate history, represents a separate lineage (or lineages) directly or indirectly derived from ancestral *Allophaiomys*, and contains a number of species, fossil and living, that must be discussed in an understood phylogenetic context. Chaline (1966) demonstrated that his usage of genus *Microtus* was polyphyletic.

The presently conventional, all-inclusive definition of *Microtus* includes more living species than the 20 or so other living microtine genera combined. As used by Chaline, and followed by many other microtine students, the size of the genus *Microtus*, and its admitted polyphyletic composition, demand division into several generic lineages.

Those genera just listed, as well as *Lemmiscus*, are here recognized as full genera, as most of them were by Hinton (1926). Other genus-group (subgenera of Chaline and Ognev) forms unnamed above, and here retained as subgenera of *Microtus* or *Terricola*, may also be recognized as distinct lineages when their history is further revealed. The history of each genus here recognized is known in varying detail, and begins between 700,000 and 2 million years ago. All but *Allophaiomys* still live, and *Allophaiomys* is extinct only in the sense that its individual variability has polarized, in the living *Phaiomys*, into a uniform pattern with remarkably little morphologic variability. As mentioned previously, such polarization indicates genetic change just as strongly as any other morphologic change, and should be equally recognized in classification.

The ancestral genus *Allophaiomys* appears to be less than possibly 200,000 years older than the first derived genus, presumably *Lasiopodomys* from the Kudun fauna of Transbaikalia (Erbaeva, 1976; age interpretation from Repenning and others, 1990), in the Oriental faunal region; the oldest records of *Allophaiomys* that are dated by paleomagnetic events appear, at present, to be from pre-Olduvai faunas of China (Zheng and Li, 1990) and they appear to be about 2 million years old. Other records in Asia, undated by external evidence, may be older. By the beginning of the Olduvai event, *Allophaiomys* had dispersed to the United States and to Holland.

Of those genera listed previously, Chaline's 1972 discussion of the classification of *Microtus* considered (as subgenera) only the genera *Microtus*, *Allophaiomys*, and *Terricola* (his *Pitymys*; subsequent work by Chaline and associates (1988) has emphasized, but not explained, the appropriateness of *Terricola* in Eurasia). Chaline also considered the subgenera *Stenocranius*, *Iberomys*, and *Suranomys*, which are here retained as subgenera of *Microtus* because their history is still unknown.

Chaline's discussion of his classification was written as though he intended that it followed the tradition of Miller (1896). However, a comparison of Chaline's all-inclusive *Microtus* with Miller's all-inclusive *Microtus* reveals almost no similarity, as has been mentioned. Miller's (1896) *Microtus* included 12 subgenera, all but 2 of which (*Microtus* and *Chilotus*) have subsequently been considered as separate genera by most authorities, including Chaline. Thus, it would be incorrect to state that the systematic nomenclature of Chaline (1972) was based upon a return to a traditional concept. Miller's "traditional" concept of 1896 lasted 16 years, until he published his monograph on western European mammals (1912).

Chaline also stated that he followed the specialists of central and eastern Europe—Ognev (1950) and Kretzoi (1958), who had returned to the concept of Miller (1896). Ognev did use an all-inclusive genus (hardly that of Miller, however, but defended by the 1896 usage of Miller; Ognev, Vol. VI, 1948); but Kretzoi (1958) only said (emphasis added), "**if** groups as *Pitymys* or *Phaiomys* are only subgenera of *Microtus* (a very extended opinion among recent mammalogists)," and he did not advocate the usage in the cited report, although a year later (Kretzoi, 1959) he claimed that he did.

As has been mentioned, neither Ognev nor Chaline mentioned that Miller himself abandoned his 1896 classification in his 1912 monograph on the mammals of western Europe, or that essentially all students of microtine rodents followed the classification of Miller (1912) until 1966.

Following Miller (1912), later workers (including Hinton, 1926) recognized many of Miller's 1896 subgenera as separate genera. Ognev (1950), followed by Chaline (1972), eliminated many of the genera by placing them into *Microtus*, but by this time the list of subgenera included in *Microtus* bore little resemblance to that of Miller (1896). The distinctive character used to unify these genera as subgenera under *Microtus* was the same: *Microtus* has rootless cheek teeth.

Miller's (1896) single exclusive character for *Microtus* was the presence of rootless cheek teeth in combination with a lack of the lemming position of the lower incisor. The popular depiction of these rodents as having "rootless cheek teeth" is, in a sense, incorrect; they differ from genera with "rooted teeth" only in that hypsodonty has evolved to the point where the animal dies before the teeth reach full maturity and form roots.

Rootless cheek teeth are no more diagnostic of lineage than are elongating dentine tracts. The increasing length of dentine tracts and the "rootless" condition are a single character; dentine tracts are a measure of hypsodonty and the rootless condition is simply the ultimate state of hypsodonty (Anderson, 1985). Young horses do not belong to a genus different than that to which old horses belong just because they have rootless cheek teeth. A classification that groups all microtines with no roots on their cheek teeth makes no more sense than a classification that groups all microtines that have dentine tracts. Hypsodonty is the diagnostic character; dentine tracts and rootless cheek teeth only help measure its development. Increasing hypsodonty is a feature that frequently evolved in many microtine lineages, as well as among other mammalian lineages.

Zazhigin (1980) has treated *Allophaiomys* as a separate genus in recognition of its biostratigraphic significance, which is different than that of *Microtus* (*sensu stricto*), and because of its distinct dental morphology. Some neomammalogists (such as Corbet, 1978), have separated *Pitymys* from *Microtus*, following Ellerman and Morrison-Scott (1951) and as a convenience in classification. Repenning (1983) has recognized *Allophaiomys*, *Pitymys*, *Microtus*, and a few smaller groups as separate genera because of their different histories as separate lineages; he has also recognized *Lasiopodomys* as an intermediate, phyletic genus between *Allophaiomys* and *Microtus* (Repenning and Grady, 1988). Pfaff (1990) also recognized *Microtus*, *Pitymys*, and *Pedomys* as full genera. Repenning (1983) further recognized two tribes to include the two major lineages derived from *Allophaiomys* and leading to *Microtus* and *Pitymys*: the tribe Microtini and the tribe Pitymyini. Many specialists continue to follow Chaline and include all of these, including the ancestral *Allophaiomys*, within the genus *Microtus*.

As noted by Chaline (1966), *Microtus* and *Pitymys* are separable on morphologic grounds; in this Chaline followed the diagnoses of Hinton (1923), except that Hinton considered them as separate genera. As also noted by Chaline (1966, 1972, and 1974), Fejfar and Horacek (1983), Repenning and Grady (1988), and in the present report, in the earlier stages of the evolution of these genera out of *Allophaiomys*, continuous gradation occurs in the morphologic variation of the dental patterns between these forms and *Allophaiomys*; this is the nature of evolution.

As discussed in the section, "Variability and evolution" (p. 12), separation of genera and species during the time of evolution between defined morphotypes can be made only on a statistical basis. Further, as in every case of complete morphologic gradation between taxa, there will be some individuals that are not certainly assignable to a taxon in any sample of two taxa in transition. Only the population can be so assigned on the basis of its modal morphology.

Whether punctuated or not, evolution is a gradual process; anagenesis produces no sharp morphologic boundaries. No individual is greatly different than its parent or its offspring. On the other hand, classification is based upon ordered categories defined by theoretically sharp morphologic boundaries. Taxonomic nomenclature is the language of classification but is intended to reflect evolution; an incompatibility is built into the procedure. The only recourse provided by the rules of nomenclature is the authority of the type, and, as pointed out in the present report, its population.

In the pages that follow, the definitions of the above-named genera are reviewed in terms of closeness to "typical" dental morphology. As has been explained, "typical" dental morphology is the most common morphology of the named species in the type population as sampled at the type locality. If the name *Allophaiomys pliocaenicus* is applied to any population other than the type population, it must include a similar range of variability, including a good percentage of individuals with recognizable pitymyinine characters; and about 3 percent of its individuals must have a *Terricola* morphotype, otherwise that population did not have the same genetic composition as the type population.

The concepts of both the most abundant individual morphology of the type sample and the limiting range of variation recognized in the type population are included in the word "typical." Both morphology and variability are needed to judge stage of evolution and identity of the taxon represented by the population sample. As will be illustrated, in species as individually variable as microtine rodents, it is difficult or impossible to positively identify named species from a single specimen; the nature of the population is critical.

An example will best illustrate the taxonomic significance of variability. The type population of *Allophaiomys pliocaenicus* from Betfia–2, Romania, discussed more fully in the following section, has wide variation in morphologic characters (fig. 3; the morphologic characters used are shown in figs. 3 and 10). The most common morphology is one that has a simple rounded Cap on the Anteroconid Complex of the first lower molar and two widely confluent Primary Wings (forming the "*Pitymys* rhomboid" or "Pitymyan rhombus" of authors), the Wings are also broadly confluent with the Cap. This is the morphology that most workers associate with the genus; it is the "typical" morphology.

The type population also includes some variants that are similar to the morphology of the living *Phaiomys leucurus* (also in the tribe Arvicolini). Because of these variants Martin (1989) placed the species "*pliocaenicus*" in the genus *Phaiomys* (his subgenus). But living *Phaiomys leucurus* has this morphology in a great majority (all?) of its individuals, whereas the type population of *Allophaiomys pliocaenicus* has only 7 percent of its individuals showing this morphology.

Similarly, the type population of *Allophaiomys pliocaenicus* has a small minority of individuals with a reduced Dimension B–B′, constricting or closing the confluence between the Primary Wings and the Cap. A few weakly suggest a developing Dimension A–A′. These are the character states of the genus *Terricola* (tribe Pitymyini), and in one individual the typical morphology of *Terricola arvaloides* is present in the type population. Kretzoi (1958) recognized this morphology and listed this species as being present in the Betfia–2 fauna (where it is still listed, as *Pitymys arvalidens*, in some records, for example, Maul, 1990). Van der Meulen (1973) recognized that this individual was simply an extreme variant of *Allophaiomys pliocaenicus* in the type population from Betfia–2 and that the fauna should not be listed as including *Terricola.* To include this genus in the faunal list from Betfia–2 would indicate a much younger age than otherwise indicated.

Because of the presence of these *Terricola* variants, the nomenclatorial reasoning of Martin (1989) would seem to say that the species *Allophaiomys pliocaenicus* also belongs in the genus *Terricola,* as this morphology is also present as an individual variation in Betfia–2. This, of course, cannot be done, and its inappropriateness illustrates the point that the "typical" morphology, not the morphology of minor variants, must be used in making taxonomic assignments. To identify the typical morphology some sort of statistical procedure must be applied to the type population; in many cases a visual inspection of the sample will be conclusive, but variability must be estimated, and that variability must be named as a character of the species. Without consideration of population variability, the less variable species *Allophaiomys deucalion* would have to be considered a synonym of *A. pliocaenicus.*

Thus the type population of *Allophaiomys pliocaenicus* is characterized both by a typical morphology, unique to the taxon, and by individual variability overlapping the morphology of living *Phaiomys* and living *Terricola.* However, *A. pliocaenicus* differs from both of these other genera in that only a small percentage of its type population has these atypical morphologies and the vast majority exhibits its unique typical morphology. From typical *Phaiomys* and *Terricola* it also differs in having a very great range of individual variability. These features of variability are obviously diagnostic.

The degree and direction of variability are genetic differences as surely as is the uniqueness of the "typical" morphology, and this difference should be considered in taxonomy. It is expressed by population characteristics and is not evident in the single type specimen. Different degrees and vectors of individual variability speak against synonymy. Thus the authority of the type specimen is extended to the type population.

Morphologic and directional limits to recognized taxa must be specified for the purposes of uniform classification. Thus the origin of a taxon is here defined as the geologically earliest appearance in more than 60 percent of a population of a character, or character state, that consistently separates it from its anagenetically related taxon. Again, population characteristics, not type specimen characteristics, are the primary basis for taxonomy in lineages showing great individual variability.

As discussed previously in the section on variability, the recognition of the evolution of a derived taxon begins with a hyphenated, double-taxon identification to indicate its intermediate position between populations of two defined morphotypic species (which may bridge two genera). This technique is intended to deter accidental broadening of the diagnosis of either ancestral or descendant taxa. The same form cannot be identified as different species of different genera in different fossil localities and still be expected to make any evolutionary or biochronologic sense.

The following discussion reviews some of the more significant localities showing morphologic intergradation between the taxa present, and of the logic for the recognition of these taxa. Although some examples are discussed which could be given new names, such as "*Allophaiomys* n. sp." from SAM Cave, New Mexico, no new generic or specific names are introduced; only existing, published nomenclature is used in an attempt to present a very complex history as simply as possible. New names can be introduced in more detailed discussions of specific faunas. A complete review of these taxa and lineages is not attempted here, and the discussion of several taxa that do not bear on the age of the Olyor Suite is brief. Nevertheless, they must be mentioned to illustrate the nature of the faunas discussed and the pattern of the evolution of *Allophaiomys.*

SYSTEMATICS: PHILOSOPHY, PROBLEMS, APPLICATIONS

TRIBE ARVICOLINI, KRETZOI, 1954

Revised dental diagnosis.—Genera of tribe Arvicolini (of subfamily Arvicolinae: Kretzoi, 1969; Repenning and Grady, 1988) have a first lower molar with posterior loop, preceded successively by three substantially closed and alternating triangles and terminated by an Anteroconid Complex with confluent, lingual and buccal Primary Wings and an uncomplicated, more or less globular Cap. Most genera have rooted cheek teeth, and dentine-tract elongation characterizes increasing hypsodonty.

Generic contents of the tribe.—Genera currently included in tribe Arvicolini are *Allophaiomys, Aratomys, Arvicola, Atopomys, Cromeromys, Hibbardomys, Mimomys* (including many subgenera), *Nebraskomys, Polonomys, Promimomys, Prosomys, Phenacomys, Phaiomys,* and *Villanyia.*

[Note: Because it has a complicated Anteroconid Complex in nearly all species, *Phenacomys* should not be included in tribe Arvicolini. A new tribe will not be introduced in this discussion, however. It is also not certain in the author's mind that *Hibbardomys* represents a single lineage, although the forms that have been assigned to this genus certainly belong in this tribe.]

By having a first lower molar with a posterior loop, three basic alternating triangles, and an Anteroconid Complex with a simple, single-cusped Cap and confluent Primary Wings; a last upper molar with two or three triangles and a simple posterior loop; and a lower incisor that passes beneath the cheek teeth, *Allophaiomys* belongs in tribe Arvicolini of subfamily Arvicolinae. This is where Kretzoi (1954, p. 355) placed the genus when he recognized and named the tribe; he also included *Phaiomys* and *Arvicola*. These three genera are the only rootless arvicolines. The rootless descendants of *Allophaiomys* compose the tribes Microtini and Pitymyini; the descendant *Phaiomys* remains in the Arvicolini.

Phaiomys and *Arvicola* are the only living, rootless members of tribe Arvicolini and belong in this tribe because of their diagnostic dental characters; they belong to neither the Microtini nor the Pitymyini, which have more complicated Anteroconid Complexes. As mentioned, they and extinct *Allophaiomys* are unique within the tribe Arvicolini in having advanced to the stage of hypsodonty at which they have "rootless" cheek teeth. When one accepts the minor significance of the lack of tooth roots, *Allophaiomys*, *Phaiomys*, and *Arvicola* are recognizable as typical arvicolines.

Enamel-thickness differentiation in the tribe Arvicolini may be of "*Mimomys*," intermediate, or "*Microtus*" types. The earliest genera and species of the tribe have either intermediate or "*Mimomys*" enamel-thickness differentiation; the youngest (living) genera and species of the tribe almost universally have "*Microtus*" enamel-thickness differentiation. Between these two points the nature of the enamel differentiation is variable.

GENUS *ALLOPHAIOMYS* KORMOS, 1932

Type species.—*Allophaiomys pliocaenicus* Kormos, 1932.

Revised dental diagnosis.—A genus of the tribe Arvicolini with rootless molars and length of first lower molar 3.0 mm or less; Dimensions A–A′, B–B′, and C–C′ never strongly constricted in over 40 percent of a population.

"TYPICAL" *ALLOPHAIOMYS*

ALLOPHAIOMYS PLIOCAENICUS KORMOS, 1932

(fig. 3)

Type locality.—Betfia–2, Romania (locality 3 in fig. 1).

Revised dental diagnosis.—A species of the genus *Allophaiomys* with the Cap of the Anteroconid Complex uncomplicated by posterolingual corner or other modifications in the "typical" morphology but having a posterolingual corner in about 7 percent of the type population. Reduction of Dimension C–C′ lacking, Dimension B–B′ greatly reduced in 3 percent and some reduction evident in about 30 percent, and Dimension A–A′ noticeably reduced in 20 percent of the population; these variations result in about 3 percent of the population having a *Terricola* morphotype. There is no *Microtus* morphotype or character state tending toward the Microtini.

Discussion.—The dental pattern of *Allophaiomys pliocaenicus* is similar to that of the ancestral genus *Mimomys*, but *A. pliocaenicus* has rootless cheek teeth. *Allophaiomys* is also similar to the significantly larger genus *Arvicola*, as noted by Kormos (1932), but *Arvicola* evolved out of *Mimomys* much later than *Allophaiomys* (von Koenigswald, 1973), actually after *Allophaiomys* had become extinct.

The first lower molar of the type species, *Allophaiomys pliocaenicus*, is rootless and well cemented; it consists of a posterior loop, three basic alternating triangles, and an Anteroconid Complex composed of two prominent, confluent Primary Wings and a smoothly rounded Cap with moderate variability (fig. 3). The Cap is often skewed lingually (fig. 3*B*, *C*) and in a few individuals shows weak indentations marking the position of reentrants that separate Secondary Wings in more derived genera (fig. 3*G*); these indentations also mark the beginning of a Dimension A–A′ (well developed and marked in fig. 10). Dimension C–C′ (marked in fig. 3*A*), between the apices of the reentrant posterior to the lingual Primary Wing and anterior to the buccal Primary Wing, is wide to only slightly narrowed so that the dentinal confluence between the buccal and lingual Primary Wings is complete to great. Dimension B–B′ (marked in fig. 3*E* and *I*), across the neck between the Primary Wings and the Cap, is moderate to broad. Enamel differentiation is primarily intermediate. The length of the first molar usually is 3.0 mm or somewhat less.

The last upper molar of *Allophaiomys pliocaenicus* is "simple" and consists of an anterior loop, two to three alternating triangles, and a posterior loop that may or may not be extended posteriorly, but never develops a hook at its posterior end.

Population variability.—Kormos (1932) described two species from the type locality, *Allophaiomys pliocaenicus* (the type species) and *Allophaiomys laguroides*; but the present author follows van der Meulen (1973) and considers them synonymous.

With the exception of the last upper molar of "*Allophaiomys laguroides*" in figure 3 (fig. 3*L* copied from Kormos), the illustrations of this species from the type population of *Allophaiomys pliocaenicus*, from Betfia–2, Romania (10 M/1), were provided by O. Fejfar of Prague. Van der Meulen (1973) illustrated 20 first lower molars from this population, and others are published by Kormos and by others. These illustrations form the basis for statements regarding population variability; the type population has not been reviewed.

Based on this "sample" of about 30 first lower molars (some of the previously published illustrations are obviously duplicates of the same specimens), typical *Allophaiomys*

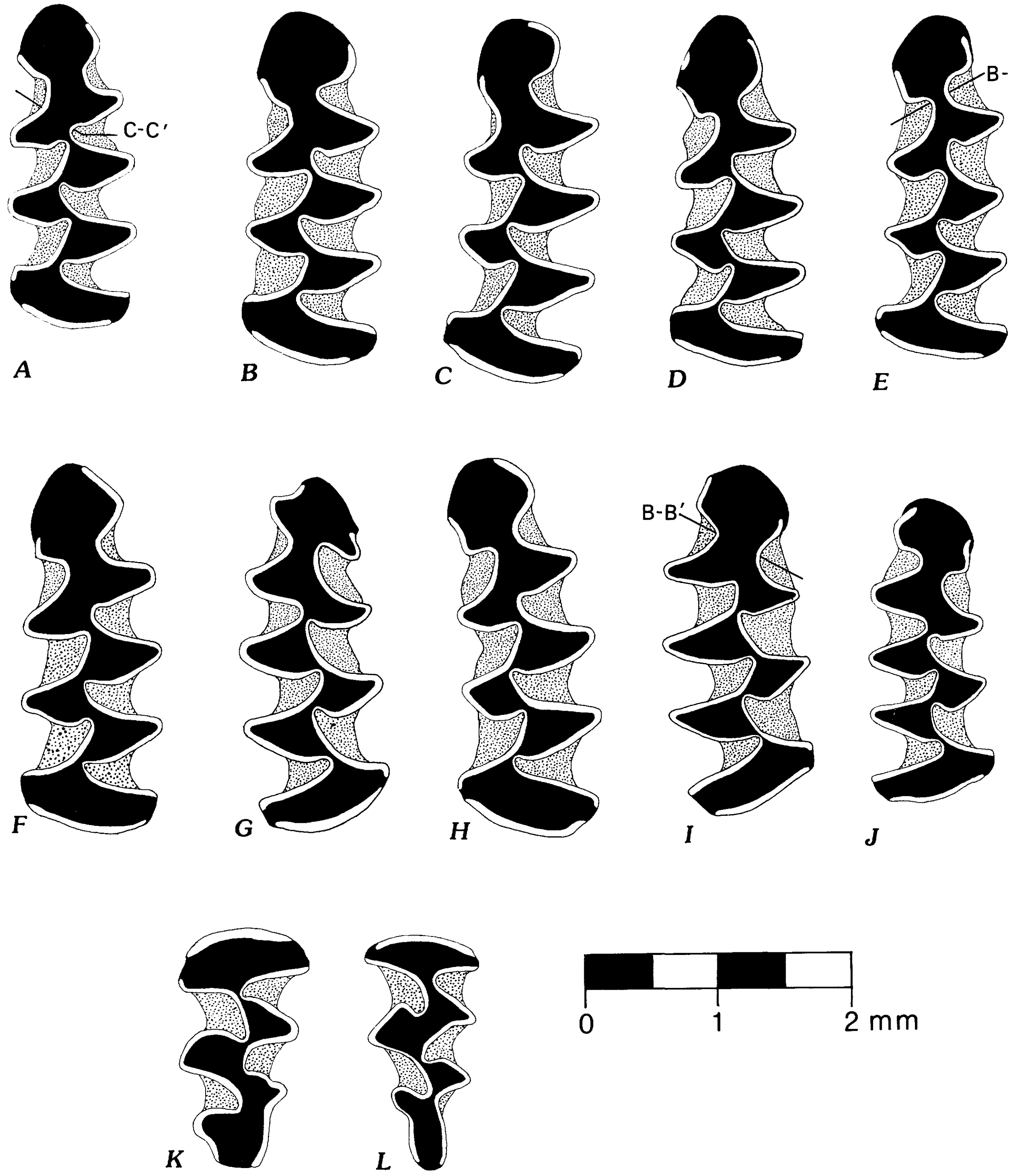


Figure 3. *Allophaiomys pliocaenicus* Kormos from Betfia–2 (Puspokfurdo), Romania. *A–J* are first lower molars; *K* and *L* are last upper molars; all are occlusal views and anterior is upward. The posterior loop of the first lower molars extends lingually; the posterior salient angle of the last upper molars extends lingually. Dentine is black, enamel is white, and cementum is stippled. *K* is a "rhomboid" M\3 of *A. laguroides* redrawn from Kormos (1932). All figures except *K* were made from drawings provided by Oldrich Fejfar. C–C′, Dimension recording degree of closure of confluence between Primary Wings, is indicated on *A*. B–B′, Dimension recording closure of confluence between Cap and Primary Wings, is shown on *E* and *I*; it is narrow on *E* and wide on *I*. Other named features of tooth morphology are shown in figure 10. Specimens *A*, *D*, and *E* were marked "*Allophaiomys laguroides*" in Kormos' handwriting. Note individual variation in the Cap. HNHMB specimens.

pliocaenicus has little modification of the Cap. It lacks a high percentage of individuals with weak development of Secondary Wings or shortening of Dimension B–B′. At least 63 percent show no modification at all; the Cap is a simple circular or rounded structure. In most individuals there is a wide confluence between the Cap and the Primary Wings, but in about 30 percent Dimension B–B′ is noticeably reduced (partly a factor of less wear), and in 3 percent this dimension is essentially closed—a *Terricola* character state. In about 7 percent of the specimens, an angularity at the posterolingual corner of the Cap is developed, similar to that in several North American advanced populations and in living *Phaiomys leucurus*. Thirteen percent have an angularity at the posterobuccal corner of the Cap, a condition that is less common in advanced North American populations but is rather frequent in some Eurasian populations that are approaching *Terricola*.

In about 20 percent of the type sample, a weak development of Secondary Wings coupled with a minor reduction of Dimension B–B′ suggests the *Terricola* morphotype, and one specimen clearly is of this morphotype (3 percent). Kretzoi (1941) listed this specimen as *Pitymys arvaloides* (until quite recently *Terricola* was included in *Pitymys*), but van der Meulen (1973) noted that it was only an extreme variant of *Allophaiomys pliocaenicus*, an opinion that is obvious from the above inventory of variations. However, the name is still carried in faunal lists, as *Microtus* (*Pitymys*) *arvalidens* (Maul, 1990).

Specific preoccupation of *Pitymys arvaloides* by *Microtus arvaloides* came into effect with the inclusion of the genus *Pitymys* in the genus *Microtus* by Ognev (1950), and *Pitymys arvalidens* was suggested as a substitute if this was done (Kretzoi, 1958). The recognition of *Pitymys* and *Terricola* as separate genera in the present publication requires the recognition of the name Kretzoi first applied to the Betfia–2 individual. There is now in use, as there was from 1923 until 1958, both *Microtus arvaloides* Hinton and *Terricola arvaloides* (Hinton), but *Terricola arvaloides* is not present in the Betfia–2 fauna, except as a rare morphotype variation of *Allophaiomys pliocaenicus*.

The individual variation of the type population of *Allophaiomys pliocaenicus* includes variations in the direction of the *Terricola* morphotype, and a small percentage of individuals (one individual) overlaps this morphology. There are no individuals in the sample in which Dimension C–C′ is reduced, a reduction that would suggest evolution toward the tribe Microtini.

Morphologic evolution.—Earlier records throughout Eurasia suggest that the Pitymyini, represented by *Terricola* (=*Pitymys* in former reports), is the first lineage to have evolved out of *Allophaiomys*.

If the age (during the Olduvai event) inferred by Repenning and others (1990) for the Kudun fauna south of Lake Baikal (Erbaeva, 1976) is correct, this record is an exception that is earlier than the oldest known *Terricola*.

Van der Meulen (1973) described an interesting sequence of faunas from the Monte Peglia locality of Italy which supports the earlier derivation of *Terricola* out of *Allophaiomys*. He divided the Monte Peglia collections into lower and upper faunas, herein called Monte Peglia–1 and Monte Peglia–2, respectively. Based upon his figured specimens, the lower faunas contain an advanced species of *Allophaiomys* that he called "sp. A" because he believed that the form was being named by Chaline (1972); the present author does not know which of the species subsequently named by Chaline was being considered by van der Meulen. "Sp. A" of van der Meulen (1973) contained 22 percent typical *Allophaiomys* variants, 44 percent pitymyinine-like variants with a weak but clear lingual Secondary Wing, and 34 percent *Terricola* morphotypes with a conspicuously shortened Dimension B–B′ and some development of both Secondary Wings. "Sp. A" is decidedly advanced over typical *Allophaiomys pliocaenicus* and showed the same direction of morphologic drift, toward the Pitymyini; the morphotype percentages just cited would indicate that it would be reasonable to assign "sp. A" to the genus *Terricola*. No individual showed a reduction of Dimension C–C′, leading toward the Microtini, in Monte Peglia–1.

A different condition is indicated in van der Meulen's illustrations of the species from the younger fauna samples of Monte Peglia–2, which he called "sp. B" in the belief that it might be synonymous with *Allophaiomys ruffoi* Pasa (1947). Half of these specimens showed a reduction of Dimension C–C′, which is leading toward the Microtini, and one-third had an acceptable *Lasiopodomys* morphotype. An exceptionally deep lingual reentrant angle 4 (between the lingual Primary Wing and the Cap) is present on nearly all specimens. One specimen (8 percent, only 12 specimens were illustrated) conformed to the "typical" *Allophaiomys pliocaenicus* morphotype. Based upon the illustrated sample from Monte Peglia–2, the population of *Allophaiomys* sp. B could be called "advanced *Allophaiomys-Lasiopodomys.*"

Allophaiomys sp. B from the Monte Peglia–2 fauna is decidedly advanced over typical *Allophaiomys pliocaenicus* and shows morphologic drift toward the Microtini, overlapping *Lasiopodomys* in one-third of the sample. None showed a complete reduction of Dimension B–B′ or the development of a weak buccal Secondary Wing, that would suggest *Terricola*. However, in the illustrated sample of *A.* sp. B, from Monte Peglia–2, 58 percent had a noticeable inflection of the anterolingual margin of the Cap (lingual reentrant 5), a feature which suggests the *Lasiopodomys-Microtus* transition in other faunas to be discussed, primarily in North America. Although not so in the closure of Dimension C–C′, the character state of this weak reentrant is more advanced than in "*Microtus* ex gr. '*oeconomus*'" described by Markova (1990) from the Karay-Dubina fauna of the Ukraine. This provides a suggestion that there may be a separate origin of the Microtini in the European fauna, marked by different rates in character change.

Considerable time would seem to separate "sp. A" and "sp. B" in the Monte Peglia faunas, and probably *Terricola* evolved during this time, although no recognized pitymyinine specimens were found with "sp. B." The lack of *Terricola* in the younger fauna could be related to latitudinal shifts in climate or unknown ecologic preferences of different populations of *Allophaiomys*. Like *Allophaiomys*, *Terricola* avoided colder climates that were tolerated by *Microtus* and *Lasiopodomys*.

Identification.—The microtine rodent genus *Allophaiomys* was named by Kormos (1932) from an ample number of specimens collected at Betfia–2, known to Kormos as Puspokfurdo, southeast of Oradea in the Muntii Bihor, western Romania. Its name indicates that it is similar to the living genus *Phaiomys*, the type species of which is *Phaiomys leucurus* Blyth (1863). Kormos named several features of the skull and mandible that separate *Allophaiomys* from *Phaiomys leucurus* and also some features of the dentition. On the basis of dental similarity (7 percent of the type population have a posterolingual angularity on the Cap as does 100 percent of *Phaiomys*), the two genera have been considered synonymous by Martin (1989), but Martin did not discuss the diagnostic characters given by Kormos or those in this report; in fact, he made no attempt to explain why he considered them identical.

The sample of the living *Phaiomys leucurus* examined for this study (six specimens from the type region of Ladak, Kashmir) was not large enough to define population characteristics, but all living individuals seen have the following:

1. "*Microtus*" enamel-thickness differentiation (the enamel on the anterior wall of the triangles of the lower cheek teeth is thicker than that on the posterior wall), whereas "intermediate" enamel-thickness differentiation (enamel thickness equal on anterior and posterior walls of the triangles) is by far the most common condition in "typical" *Allophaiomys pliocaenicus*.

Many advanced populations of *Allophaiomys* have dominant "*Microtus*" differentiation; van der Meulen (1974) hinted that the primitive *Allophaiomys deucalion* has "*Mimomys*" enamel-thickness differentiation in more than 50 percent of his sample (he said the specimens "more often" have "*Mimomys*" differentiation, but it is not absolutely clear that he referred only to the *A. deucalion* sample; he might have meant "more often" than the type population of *A. pliocaenicus*); *A. deucalion* was not examined for the present study.

2. A persistent posterolingual angularity on the Cap of the Anteroconid Complex of the first lower molar (M/1) in all individuals; this is in the position of the lingual Secondary Wing of more advanced genera, and this feature is present only in a small minority (7 percent) of individuals of typical *Allophaiomys pliocaenicus*. In certain populations of advanced *Allophaiomys* in both Eurasia and North America, however, the posterolingual angularity of the Cap is a dominant character state.

3. No third buccal salient angle at the anterior end of the third lower molar (M/3), as is present in some typical *Allophaiomys* (largely or entirely those smaller specimens that Kormos assigned to *Allophaiomys laguroides*). The significance of this difference is uncertain.

4. A posterior loop on the last upper molar (M\3) that is consistently reduced from the condition in most individuals of *Allophaiomys*, whether advanced populations or not.

And most significantly, as mentioned previously:

5. A dental pattern variability that is conspicuously less than that of either typical or advanced *Allophaiomys* (fig. 4).

These differences all seem explainable as the result of genetic polarization in living *Phaiomys*, a polarization not seen in the nearly 2 million-year-old typical *Allophaiomys* or any known population of this genus. It is not argued whether such polarization can be considered as significant in specific or in generic separation, but it is stated that it has resulted in character differences that clearly separate *Phaiomys* from *Allophaiomys*. The primitive condition of some of these characters persisted in younger populations of *Allophaiomys*, and others evolved toward the condition of living *Phaiomys*.

Note that continued reduction of the posterior loop of the last upper molar would produce the most distinctive character of the Chinese genus *Proedromys* (Hinton, 1926, fig. 33; Zheng and Li, 1990, fig. 21). However, this genus is in the tribe Microtini because the structure of the first lower molar is advanced relative to either *Allophaiomys* or *Phaiomys*.

A confusing and not fully explainable misconception of the identity of *Phaiomys* was adopted by Ognev (1950). With his inclusion of the genus *Phaiomys* in the genus *Microtus*, as well as many other former genera, the species *leucurus* became the junior homonym of *Microtus leucurus* (included in *M. nivalis* by Corbet, 1978). The name *Phaiomys blythi* (= *Arvicola blythi* Blanford) was then applied to the type species. In addition, modifying Ellerman (1940–1941) but apparently before the emendations of Ellerman (1949) were seen, Ognev also included species in *Phaiomys* (his subgenus of *Microtus*) that had been placed in *Lasiopodomys* or *Neodon* by some others (*brandtii* Radde, *vinogradovi* Fetisov, *carruthersi* Thomas, and *juldaschi* Svertsov). Although *carruthersi* and *juldaschi* had earlier been assigned to *Phaiomys* by other authors and are included in the tribe Pitymyini herein, Ognev appears to have been the first to assign *brandtii* and *vinogradovi* (=*mandarinus* in Corbet, 1978) to the genus (his subgenus) *Phaiomys*, and they are herein returned to *Lasiopodomys* and the tribe Microtini (Corbet, 1978, returned them to this lineage as species of *Microtus*).

Ognev's assignment of *brandtii* and *mandarinus* (=*vinogradovi*) to *Phaiomys* was not followed by Gromov and Polyakov (1977), who returned these species to

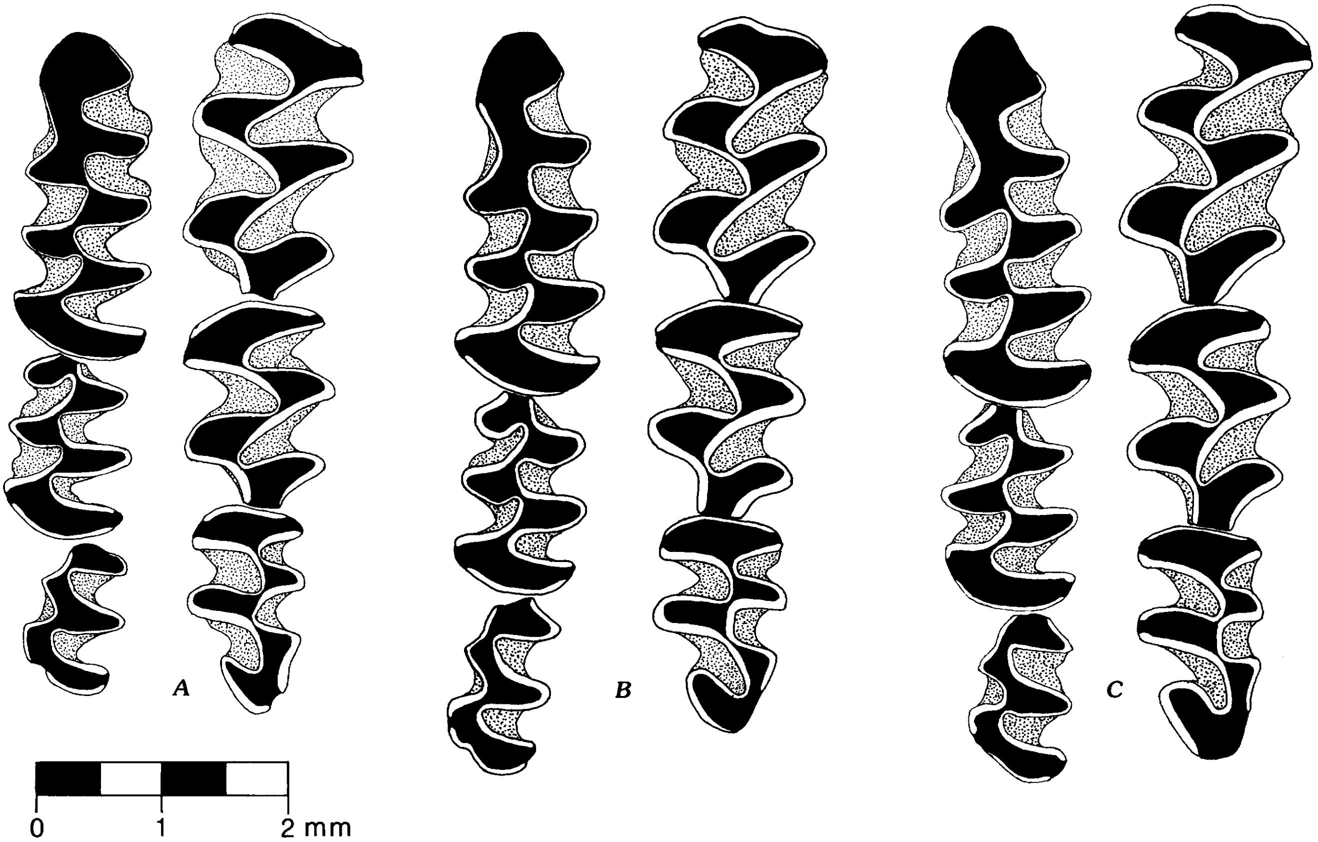


Figure 4. *Phaiomys leucurus* Blyth from the region of Ladak, Kashmir. Left lower dentition illustrated on the left side of each specimen; right upper dentition on the right. *A*, USNM 198541. *B*, USNM 84033. *C*, USNM 84034. Note weak posterolingual angle on Cap of first lower molar and reduction of the posterior loop of last upper molar. Also note slight individual variability.

Lasiopodomys, which they recognized as a full genus. These authors, however, were uncertain of the definition of *Phaiomys*, and placed the type species, *Phaiomys leucurus*, in the subgenus *Neodon* of the genus *Microtus*. Their uncertainty may reflect some feature of the Moscow collections, as the specimen they illustrated (1977, fig. 39) is not *Phaiomys leucurus*, but is a form belonging in the tribe Microtini and in the genus *Lasiopodomys* of the Oriental faunal region (which includes part of the former U.S.S.R.); they did not indicate where it came from, and the individual could represent either of the two living species of *Lasiopodomys*. (Compare with this report, fig. 11*N* and *O*.) If this error reflects an error in the Moscow collections, it may explain Ognev's confusion.

Phaiomys leucurus Blyth has a simple, rounded Cap and completely confluent Primary Wings; it belongs in the tribe Arvicolini (Kretzoi, 1954). *Lasiopodomys brandtii* (Radde) has a cap with Secondary Wings and complete closure between the Primary Wings and belongs in the tribe Microtini. The genus *Phaiomys* does not occur in the former U.S.S.R., although a number of specialists believe that it does (Ognev, 1950; Chaline, 1974).

As mentioned on page 25, two species from Betfia–2 were named by Kormos: *Allophaiomys pliocaenicus*, the generic type species, and *A. laguroides*, a slightly smaller species that differs in some dental characters from the sample of *A. pliocaenicus* (fig. 3). Chaline (1966) found morphotypes of both species in the French localities of Balaruc and Mas Rambault and reported individual variation in dental-pattern morphology that bridged the differences between the two morphotypes. He therefore placed the species *A. laguroides* into synonymy with *A. pliocaenicus*.

No consideration was made by Chaline of a possible bimodal distribution of the characters that might have separated the two species; it thus remains possible that two species existed in these French populations and that these were united by overlapping individual morphologic variation in a minor number of individuals (as in the type population). Chaline (1974) later resurrected *P. laguroides* on the basis of its M\3, but Chaline's 1966 synonymy is here followed because van der Meulen (1973) could not separate the two species in the topotypic material from Betfia–2—and they are very similar (fig. 3). In the sample of the type population in Budapest, the specimens are labeled in Kormos' handwriting, indicating which species is represented.

Chaline's later (1974) reinstatement of *laguroides*, as a subspecies of *Allophaiomys pliocaenicus*, was on the basis of Kormos' type having a "rhomboid" M\3. Chaline did not indicate whether individuals from Betfia–2 other than the type specimen had this "rhomboid" M\3. The "rhomboid" M\3 (a "simple" M\3; this report, fig. 13*K*) is an individual variant found in many populations of *Allophaiomys* throughout the Northern Hemisphere as well as in derived species; it is a variable character of the southern species of European *Terricola*, some of which have a "rhomboid" M\3, and, in North America, it is typical of *Pitymys* and *Pedomys*. In the present study, it was not determined whether the "rhomboid" M\3 was consistent in *Allophaiomys laguroides* and, as was done by Chaline (1974), the M\3 of "*A. laguroides*" is illustrated in figure 3 by redrawing the figure published by Kormos (1932).

Temporal correlation.—As noted in the Introduction, the oldest dated records of *Allophaiomys* are from Zone IV deposits of China (Zheng and Li, 1990). These records are dated as older than the Olduvai Normal-polarity Subchron (more than 1.9 Ma). Other records in Asia may be older, but are not dated by age control external to faunal interpretations; none seem as old as the Gauss Chron (ending 2.48 Ma; present report, fig. 14).

The age of the Betfia–2 locality is not known by evidence external to the nature of the fauna and its inferred biochronologic significance. The fauna is usually considered as being an early Biharian fauna in Europe, but not the earliest Biharian fauna (Fejfar and Horacek, 1983). Earliest Biharian faunas of Europe (considered latest Villanyian by some authors) include Kamyk (Poland), Villany–5 (Hungary), Betfia–13 (Romania), and Zuurland (Holland); these contain a typically Villanyian fauna except that they also contain *Allophaiomys*.

The differing assignment to European micromammal stages (latest Villanyian or earliest Biharian) derives from differing approaches to the biochronologic definitions. Some authors rely upon the total composition of the fauna and so refer these faunas to late Villanyian because, other than *Allophaiomys*, the faunas are typical of advanced Villanyian faunas; other authors conceive the Biharian as beginning with the first appearance of a Biharian immigrant (*Allophaiomys*—the first microtine with rootless teeth other than the lemmings) and are more influenced by the time of immigration than by the overall faunal composition.

Defining the Biharian Stage as beginning with the earliest immigrant that is characteristic of that stage (*Allophaiomys*), regardless of the nature of the rest of the fauna, is followed in this report. This definition is believed to be a more precise time signal than is the gradual change in general faunal composition. In the United States the first Irvingtonian immigrant also is *Allophaiomys* and also appears at the beginning of the Olduvai event (1.9 Ma), but other faunal elements have a strong Blancan V (next older age) composition until at least 1.4 million years ago. In addition, the same earliest appearance of *Allophaiomys* occurs in other places around the world, apparently close to the same time, so that the beginning of this small-mammal stage is easily recognizable in many places by the "oldest *Allophaiomys*."

In North America the correlative age boundary, the Blancan-Irvingtonian boundary, can be dated either at 1.9 million years ago, if the first Irvingtonian immigrant (*Allophaiomys*) is the criterion (Repenning, 1987), or at about 1.4 million years ago, if the last prominently Blancan faunal assemblage is the criterion. The first North American record of *Allophaiomys*, at the beginning of the Olduvai event in southern Colorado, is remarkably similar in age to that in Europe (Holland; van Kolfschoten, 1988). However, endemic faunal change in Europe may have progressed faster than in the United States, where the Blancan aspect of faunas persisted at least 500,000 years after the arrival of *Allophaiomys*. The difference in philosophical concept is of little significance, but the difference in use as a correlation tool is great and requires a statement of usage to avoid confusion in discussion.

Allophaiomys may have disappeared before the Jaramillo Normal-polarity Subchron in northern Europe. In Holland the youngest records of *Allophaiomys* are approximately late Eburonian in age (van Kolfschoten, 1988). This age termination has not been dated more closely than between the Olduvai and the Jaramillo events (1.67 to 0.97 Ma). However, T. van Kolfschoten (written commun., 1991) has indicated that *Allophaiomys* morphotypes have been found, with the first appearance of *Microtus*, in the Bavelian fauna of Holland (during the Jaramillo event). These morphotypes of *Allophaiomys* may (or may not) represent variants in populations of *Terricola*, as in the Karay-Dubina fauna of the Ukraine. *Allophaiomys* is not often associated with *Microtus* as herein defined, as the two genera represent much different stages in evolution as well as different environmental tolerances.

Because of the habit of listing morphotype variations of one population as individuals of a different species and different genera, the youngest record of *Allophaiomys* in Europe is not certainly known, and cannot be used to estimate the age of Betfia–2. More faunal populations need to be evaluated in the manner of Fejfar and Horacek (1983).

The Karay-Dubina fauna of the Ukraine (Markova, 1982, 1990) has been cited as a late record of *Allophaiomys;* however, its inferred age is based only upon the base of the Brunhes Chron some 8 m (26 ft) higher in the section, and the magnetic polarity of the fossil horizon itself is unknown, as is its position within the Matuyama Reversed-polarity Chron. Figure 6 of Markova (1982) and figure 16 of Markova (1990), in combination with figure 1 of Velichko and others (1983), indicate from three to five erosional unconformities in the section between the base of the Brunhes Chron and the underlying Karay-Dubina fauna of unknown paleomagnetic polarity.

In addition, to judge from Markova's (1990) excellent illustrations, *Terricola hintoni* and *Allophaiomys pliocaenicus* morphotypes intergrade and appear to constitute a single variable population (of *Terricola*). Twenty-three specimens are illustrated by Markova (1990), of which *Terricola* morphotypes represent 60 percent, intermediate morphotypes represent 14 percent, and *Allophaiomys* morphotypes (lacking any sign of Secondary Wings and having a relatively large Dimension B–B′) represent 17 percent of the illustrated population sample.

From published information only, it would appear that *Allophaiomys* should not be recognized in the Karay-Dubina fauna and that the entire population should be considered a primitive population of *Terricola hintoni* with individual variants overlapping the morphology of *Allophaiomys*. The same logic that would recognize *Allophaiomys* in the Karay-Dubina fauna would recognize *Allophaiomys* in the Trout Cave No. 2 fauna of West Virginia (Pfaff, 1990; about 725,000 years old, to be discussed) and in the living populations of *Pedomys ochrogaster*.

In summary, the youngest populations of *Allophaiomys* known from Europe probably are of an age intermediate between the ages of the Jaramillo and the Olduvai Normal-polarity Subchrons, approximately of latest Waalian age, which is inferred to be about 1.4 million years ago (Repenning and Brouwers, 1992). In the United States, as will be discussed, *Allophaiomys* survived until about 70,000 years after the Jaramillo event. Records this young in Europe, insofar as they have been presently evaluated, appear to be *Allophaiomys* morphotypes that are variants from populations of more advanced genera, primarily *Terricola*; in the United States such variants are found in populations of *Pitymys* and *Pedomys*, and include the living *Pedomys ochrogaster*.

The oldest records in western Europe appear to be at the base of the Olduvai event and may be slightly older in the Black Sea area, where the oldest *Allophaiomys* appears to be pre-Olduvai. In the People's Republic of China the genus is demonstrably this old. By faunal approximation, the type locality, Betfia–2, is presumed to be about as old as the end of the Olduvai event (fig. 14), or at the Pliocene-Pleistocene boundary.

Allophaiomys pliocaenicus differs from living *Phaiomys leucurus* in its much greater individual variation, in only occasional angularity on the posterolingual portion of the Cap, and in enamel differentiation. It differs from its derived genera by the lack of closure of Dimension C–C′ (*Lasiopodomys*, *Lemmiscus*, *Proedromys*, and *Microtus*), the lack of Secondary Wings on the Anteroconid Cap (*Pitymys* and *Pedomys*), or the lack of either the lingual or both Secondary Wings and closure of Dimension B–B′ (*Terricola*).

Evolution into derived genera is accomplished primarily by direct drift of morphologic variation into the defined morphology of the descendant taxa but can also occur through the development of bimodal distribution of dental characters, a polymorphism recording two closely related taxa in the population sample. Evolutionary extinction through linear morphologic drift into a derived taxon morphology is accomplished in single, provincial populations and does not occur everywhere at the same time. These statements will be illustrated on the following pages.

North American record.—The record of *Allophaiomys* from North America is very similar to that in Eurasia. It begins with nearly typical *Allophaiomys* that evolved progressive individual variability, overlapping the definitions of derived genera that are somewhat different than those in Eurasia. In North America *Lasiopodomys* is an immigrant and cannot be traced back to *Allophaiomys* as it can in Eurasia. In addition, *Microtus* (with one exception) and *Terricola* also appear as immigrants in North America; these appear much later than the immigration of *Allophaiomys*.

All evidence of evolution out of *Allophaiomys* in North America is toward the endemic genera *Lemmiscus*, *Pitymys*, and *Pedomys*. In some faunas these events are well dated. The earliest records of both *Microtus* and *Lasiopodomys* in North America indicate that more and earlier evolution of genera out of *Allophaiomys* is yet to be discovered in Eurasia or recognized by better external dating.

Allophaiomys is known in North America only to the east of the Rocky Mountains, although both *Lasiopodomys* and *Microtus* are known, at different times, both east and west of this mountain range. *Terricola* is also known to the west of these mountains, but appears to have arrived there by dispersing southward from Beringia down the east side of the mountain range, westward around its south end, and then northward up the Pacific Coast (Repenning, 1983).

Provincial differences in degree and direction of individual morphologic variation, as well as of dispersal patterns, exist in North America and could confuse age interpretations based only on the stage of evolution within the genus *Allophaiomys* as now known. These differences suggest that caution be used in inferring the history in Asia only from the recorded events of Europe and North America. An extreme example of provincial differences in the timing of evolution is discussed later in the section titled "Provinciality."

The oldest record of *Allophaiomys* in North America may be slightly more ancient than that in Holland. This record is a single, rootless tooth, a third lower molar (fig. 7), recovered from a core drilled at the foot of Hansen Bluff, south-central Colorado, in the eastern part of the Rocky Mountains. As will be discussed, the foot of Hansen Bluff is in reversed deposits of the Matuyama Reversed-polarity Chron below the Brunhes Normal-polarity Chron and above the Jaramillo Normal-polarity Subchron (Rogers and others, 1985). The core passed through the Jaramillo event and continued down through the Olduvai Normal-polarity Subchron and bottomed in the Gauss Normal-polarity Chron (Rogers and others, 1992).

At 240 ft (73.1 m) depth in this core, a single microtine tooth was recovered (fig. 7*E*). The first polarity sample upcore from the tooth, at 237 ft (72.2 m) depth, was normal and represented the lowest record of the Olduvai event; the first polarity sample downcore was reversed and at 241 ft (73.4 m) depth. Therefore, the microtine tooth was deposited either during the oldest part of the Olduvai event or just before it (Rogers and others, 1992); it came from a 4-ft (1.2-m) section between the polarity determinations.

The tooth cannot be certainly identified as being that of *Allophaiomys*, but its age and dental pattern make it very difficult to imagine that it represents any other rootless microtine rodent; none but the lemmings had evolved before the Olduvai event, and the tooth does not belong to a lemming. It could belong to nearly any member of the tribes Microtini or Pitymyini, but the existence of these at such an early date is unbelievable. Other dated records of *Allophaiomys* in North America are younger than the Olduvai event.

In North America, the youngest dated record of a population that can be assigned to *Allophaiomys* is about 830,000 years old and is of an evolved form that has been described as *Allophaiomys guildayi* (van der Meulen, 1978). *Allophaiomys* morphotypes are known in many younger North American faunas including the population of *Pedomys llanensis* from Trout Cave No. 2, West Virginia (perhaps 725,000 years old; about 34 percent *Allophaiomys* morphotypes) and the living *Pedomys ochrogaster* (a very small percentage). These will be discussed in following sections.

ALLOPHAIOMYS FROM THE JAVA FAUNA

(fig. 5; locality 10, fig. 1)

The Java fauna, from north-central South Dakota, U.S.A. (Martin, 1989), is of early Irvingtonian age. External age control has not been established, but the fauna includes holdover late Blancan microtines, including *Mimomys*, *Pliophenacomys*, *Guildayomys*, and a primitive *Ondatra* (Martin, 1989). Holdover microtines of the Blancan V age (*Mimomys parvus*, *Mictomys vetus*, and *Ondatra idahoensis*) are known in older Irvingtonian faunas as young as (or younger than) about 1.4 million years ago (Vallecito Creek faunal sequence in the Anza-Borrego Desert, California; Zakrzewski, 1972; author's unpub. data, 1990). The Java fauna also includes the Irvingtonian immigrant microtines *Phenacomys* and *Allophaiomys*, the earliest records east of the Rocky Mountains (except *Allophaiomys* from Colorado). *Phenacomys* first appears in Idaho later than the Olduvai event, with Blancan holdovers (Froman Ferry faunas, Idaho, also containing *Mimomys parvus*, *Mictomys vetus*, and *Ondatra idahoensis*; author's unpub. data). Climatic constraints cited by Repenning (1990; it is a very warm and wet fauna) seem to indicate that the Java fauna is older than 1.7 or younger than 1.5 million years because this period of time was relatively cool in the Northern Hemisphere (Repenning and Brouwers, 1992). Therefore the Java fauna is considered as being between 1.9 and 1.4 million years old—during the early part of the Irvingtonian I microtine age in the United States but probably excluding the time between 1.7 and 1.5 million years ago (fig. 14). It was deposited either during or after the Olduvai event; a magnetic polarity determination would greatly help to narrow this possible age range.

The sample of *Allophaiomys* from the Java fauna is large; Martin (1989) listed well over 100 first lower molars. However, the assignment to a species is difficult and involves theoretical considerations. Only a small portion of the sample (*n*=9) was examined for this study. The population characteristics are as follows.

Martin (1989) noted that various dental dimensions and ratios do not plot in a bimodal distribution; the population does not seem to be diversifying. No individuals of *Allophaiomys* are known from North America that have "*Mimomys*" enamel-thickness differentiation; about 80 percent of the Java fauna sample has "*Microtus*" enamel-thickness differentiation (about 20 percent intermediate), suggesting advancement over typical *Allophaiomys pliocaenicus* from Betfia–2. Some populations of more advanced *Allophaiomys* in North America, such as of *Allophaiomys guildayi*, have only "*Microtus*" differentiation.

In the Java sample the range of individual variability does not include *Pitymys* morphotypes, unlike most later populations in the United States that overlap the morphology of *Pitymys* or *Pedomys*, whereas a small percentage of the type population from Romania is of a *Terricola* morphotype. Thus the Java sample of *Allophaiomys* differs from typical *Allophaiomys pliocaenicus* of the Betfia–2 fauna in having considerable "*Microtus*" differentiation of enamel thickness, and in having a range of individual variation that does not overlap descendant genera (North American). Individuals showing these variation modes and extremes are illustrated in figure 5.

The Betfia–2 and Java faunas are on opposite sides of the Northern Hemisphere, and the oldest dated record of *Allophaiomys* is in China, suggesting an Asian, possibly east Asian, earliest origin of the genus. A reasonable speculation is that the European and North American populations belong to different, as well as widely separate, lineages of the genus and that both may have originated in eastern Asia but developed somewhat different characteristics as they dispersed westward to Europe and eastward to the United States. They may express somewhat different evolutionary directions, although neither is greatly removed from the hypothetical common ancestor. The different subsequent vectors of evolution in Europe and North America certainly seem to support this inference. Considerable additional evaluation of Asian populations is needed before this suggestion can be judged, but one implication is that the specific name *pliocaenicus* may be inappropriate in North America. The name *Allophaiomys* sp. cf. *A. pliocaenicus* is here applied to the Java population, accordingly.

As a consequence of this difference in individual variation in the morphotypes of early *Allophaiomys*, the Java fauna cannot be confidently equated by stage of evolution with the type population from Betfia–2. It is considered as only "about" the same age, but, to judge from the broad record of evolution of the genus throughout the world, it could easily be as much as 100,000 years different in age.

The Java population appears to have much less individual variability than many of the described *Allophaiomys* populations of Europe. It seems less advanced than the Balaruc fauna of France, described by Chaline (1972), and certainly less than the Mas Rambault fauna, which appears to have more than 50 percent of its individuals with a posterolingual corner on the Cap (Chaline, 1972, fig. 20). Younger European faunas have even greater individual morphologic variation, for example, the Valerots fauna of France.

Surprisingly, both American and French faunas with advanced *Allophaiomys* morphotypes (as described by Chaline, 1972) contain no primitive variants of tribe Microtini and do not include morphotypes typical of *Lasiopodomys*, from which *Microtus* evolved, as will be described. *Lasiopodomys* morphotypes are known from Central Europe eastward throughout Asia, and, as immigrants, in North America. But apparently the genus *Microtus* did not evolve in France. The same suggestion is evident in Holland where *Allophaiomys* probably became extinct before the immigration of *Microtus* (van Kolfschoten, 1990).

Mention has been made of the *Allophaiomys/Lasiopodomys* transition in the younger Monte Peglia faunas of Italy, and other faunas of the Paratethyian region contain *Allophaiomys* variations in *Lasiopodomys* populations. As will be discussed in connection with the microtine fauna of Beringia, *Allophaiomys* and *Terricola* had (and *Terricola* still has) warmer environmental preferences than did fossil *Lasiopodomys* and *Microtus*. Thus the first appearance of *Microtus* during the Jaramillo polarity event in France and Holland, a date later than farther north or inland in Europe, suggests that the North Atlantic Ocean before this time was markedly warm, and so was coastal Europe.

ALLOPHAIOMYS FROM THE SAM CAVE FAUNAS

(fig. 6; locality 15, fig. 1)

SAM Cave is in the valley of the Rio Grande in northernmost New Mexico, U.S.A. The cave is at 8,900 ft (2,728 m) elevation. It contains a number of imbricated as well as isolated sedimentary deposits that include at least nine localities containing *Allophaiomys*. Three additional localities are more recent in age, containing *Microtus* cf. *M. montanus* of Beringian or Asian source, but no *Allophaiomys*. Only one of these SAM Cave localities has been examined in any detail for this discussion; it is called BOT–4, and 62 first lower molars of *Allophaiomys* have been recovered (fig. 6). BOT–4 also contains a primitive form of *Lemmiscus*, *Mictomys kansasensis*, and two rooted teeth questionably assigned to *Phenacomys* sp. The history of the cave is under study by K.L. Rogers and the cave has not been described in publication.

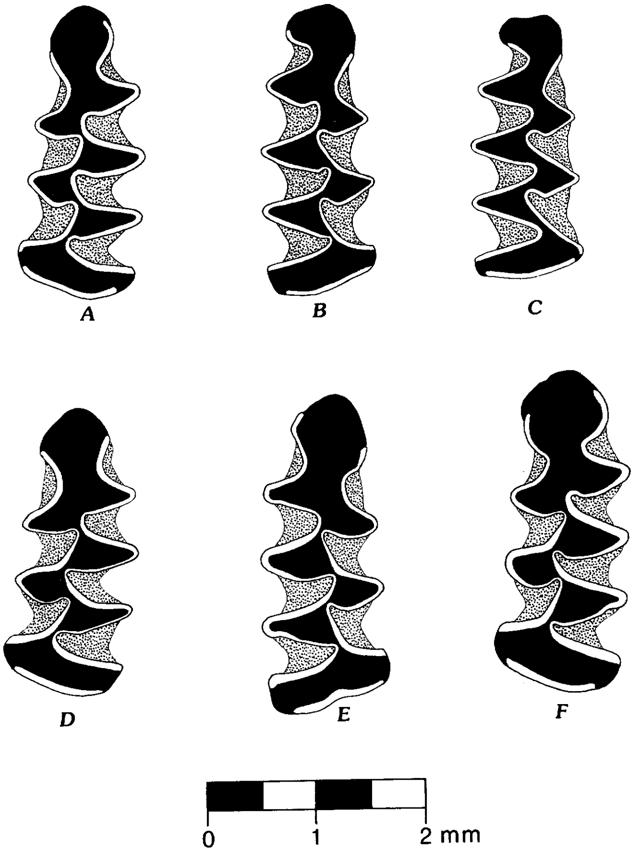


Figure 5. *Allophaiomys* sp. from Java fauna, South Dakota. *A*, *B*, and *C* have "intermediate" enamel-thickness differentiation (about 20 percent of the fauna sample); *D*, *E*, and *F* have "*Microtus*" enamel-thickness differentiation (about 80 percent of the fauna sample).

Preliminary and contradictory paleomagnetic studies of the sediments in SAM Cave seem to indicate an older normal polarity, a reversed middle part of the deposits, and a younger normal section. *Allophaiomys* appears to be confined to the older and middle deposits. The presence of *Microtus* cf. *M. montanus* in the younger normal-polarity deposits indicates that the later part of the Brunhes Chron is represented. Locality BOT–4 lies in the reversely magnetized deposits, thus representing the Matuyama Chron following the Jaramillo event; the advanced state of the populations of *Allophaiomys* in SAM Cave precludes the possibility that the oldest normal magnetism might represent the Olduvai event.

Lasiopodomys and *Terricola* immigrated to the United States about 850,000 years ago (Repenning, 1987; this report, p. 63), and neither is present in the several localities containing *Allophaiomys* in SAM Cave. As will be discussed later, *Lasiopodomys* is a genus derived from *Allophaiomys* in the Old World, and is ancestral to *Microtus*; *Terricola* represents the immigrant group of the tribe Pitymyini in North America (the "*quasiater* species group" of Repenning, 1983) and has been called *Pitymys* in all reports prior to Chaline and others (1988).

In the nearby (39 mi, 63 km) Hansen Bluff faunal sequence of Colorado, also in reversed deposits of the latest Matuyama Chron and dated as 820,000 years old (Rogers and others, 1985; possibly only 30,000 years younger than BOT–4), both immigrant lineages are represented, although *Lasiopodomys* is represented by its derivative *Microtus paroperarius*. The BOT–4 fauna from SAM Cave existed before this immigration but also after the Jaramillo event of the Matuyama Chron. The possible range in age is before 850,000 and after 900,000 years ago; an averaged age of 875,000 years is arbitrarily assigned (fig. 14).

The population of *Allophaiomys* from Locality BOT–4 (actually from all older SAM Cave localities containing *Allophaiomys*) is distinctly different, in several features, from the type material from Betfia–2, Romania. Rather than having a typical globular Cap on the Anteroconid Complex of the first lower molar (figs. 5, 6, and 8), about 83 percent of the sample from BOT–4 has a posterolingual angularity, or corner, on the Cap (in the position of lingual salient angle 5 or lingual Secondary Wing or Triangle 7) (fig. 6*D*). However, 79 percent of the individuals show no suggestion of Triangle 6, the buccal Secondary Wing.

The enamel pattern on 83 percent of the first lower molars of *Allophaiomys* from SAM Cave, New Mexico, is more similar to that of living *Phaiomys leucurus* (fig. 4 and fig. 6*D*) than to that of typical *Allophaiomys pliocaenicus*, but it is immensely more variable than in the living *Phaiomys*. A similar typical morphologic pattern and population variability range are found in *Allophaiomys guildayi* from the Hanover Quarry Fissure of Pennsylvania (fig. 9), and in the Cumberland Cave fauna of Maryland (see van der Meulen, 1978, figs. 7E, G, and H), both to be discussed. These are younger faunas, and, for reasons also to be discussed, it seems probable that the SAM Cave population of *Allophaiomys* became locally extinct before *Allophaiomys guildayi* evolved. In addition, unlike the *Allophaiomys* from SAM Cave, individual variation within populations of *Allophaiomys guildayi* overlaps, in percentages varying with the advancement of the population, the morphology of *Pedomys*. Therefore, the name *Allophaiomys guildayi* is not used for the SAM Cave faunas, and the species is left unnamed. Giving it a name in this synthesis is inappropriate and this action is postponed until the SAM Cave faunas are fully described.

The great individual variation in the morphology of the first lower molar of the *Allophaiomys* population from SAM Cave includes individuals with the morphology of *Allophaiomys pliocaenicus* from Betfia–2 (fig. 6*A*, *B*) as well as with the morphology of *Lemmiscus* (usually treated as a subgenus of *Lagurus* in North America; fig. 6*F*, *G*, and *J*). However, typical morphotypes of *Allophaiomys* represent less than 4 percent of the sampled population while *Lemmiscus* morphotypes (13 M/1 and 4 M\3) comprise 21 percent, and the sample is weakly bimodal. The dominant mode is that of *Allophaiomys* with a moderate development of a posterolingual corner on the Cap (fig. 6*D*).

Although the sample from Locality BOT–4 of SAM Cave suggests that *Lemmiscus* evolved from the population of *Allophaiomys* (45 first lower molars), the *Lemmiscus* morphotype was noted in the older populations from other localities in SAM Cave. As the interpretation of an origin of North American *Lemmiscus* out of North American *Allophaiomys* would be of considerable significance in classification, no firm conclusions are here drawn, pending consideration of the other populations from SAM Cave. Current classification derives *Lemmiscus* from Old World lagurines. These are very similar forms but have recognizable differences, such as the lack of cement in the cheek teeth.

The original examination of the BOT–4 samples recognized the *Lemmiscus*-like morphology of the last upper molars, but it was Alexy Tesakov (Moscow), who, in reviewing an earlier version of this report, questioned the assignment of the first lower molars to a *Microtus*-like morphotype, and he correctly suggested that they also might be *Lemmiscus*.

The *Lemmiscus* sp. morphotypes from BOT–4, SAM Cave, appear to differ from the living *Lemmiscus curtatus* in that the confluence between the lingual Primary Wing (T.5) and the Cap (Dimension B–B′) is usually open and contains a moderately wide neck of dentine (fig. 6*F*; this neck is unusually narrow in fig. 6*G*, which also has a lingual Secondary Wing). The buccal Secondary Wing (T.6) is always present and the lingual Secondary wing (T.7) is not always present, as in living *Lemmiscus curtatus*; this development of T.6 in preference to T.7 is opposite to the early trends in *Microtus* in which the lingual Secondary Wing (T.7) appears first. Enamel differentiation is of the "*Microtus*" type. The SAM Cave localities are unquestionably the oldest record of the genus. The next oldest record is from Porcupine Cave, Colorado (Barnosky and Rasmussen, 1988), and is believed to be about 450,000 years old. *Lemmiscus* was not reported from the Hansen Bluff faunal sequence (Rogers and others, 1985).

Barnosky and Rasmussen (1988), based on the history of sedimentation in Porcupine Cave, have suggested that the following dentinal features of *Lemmiscus* may be primitive: (1) small size, (2) less constriction of Dimension A–A′, and (3) a broader Cap anterior to Dimension A–A′. This interpretation appears to be confirmed by the condition of *Lemmiscus* sp. from the older SAM Cave BOT–4 fauna, which has (1) smaller average size (mean length M/1=2.43 mm) than six of the samples compared by Barnosky and Rasmussen (1988; their table 4), but not smaller than all samples, (2) less constriction of Dimension A–A′, and (3) a broad Cap anterior to A–A′ (fig. 6*G*, but not *F*—in part a result of less wear).

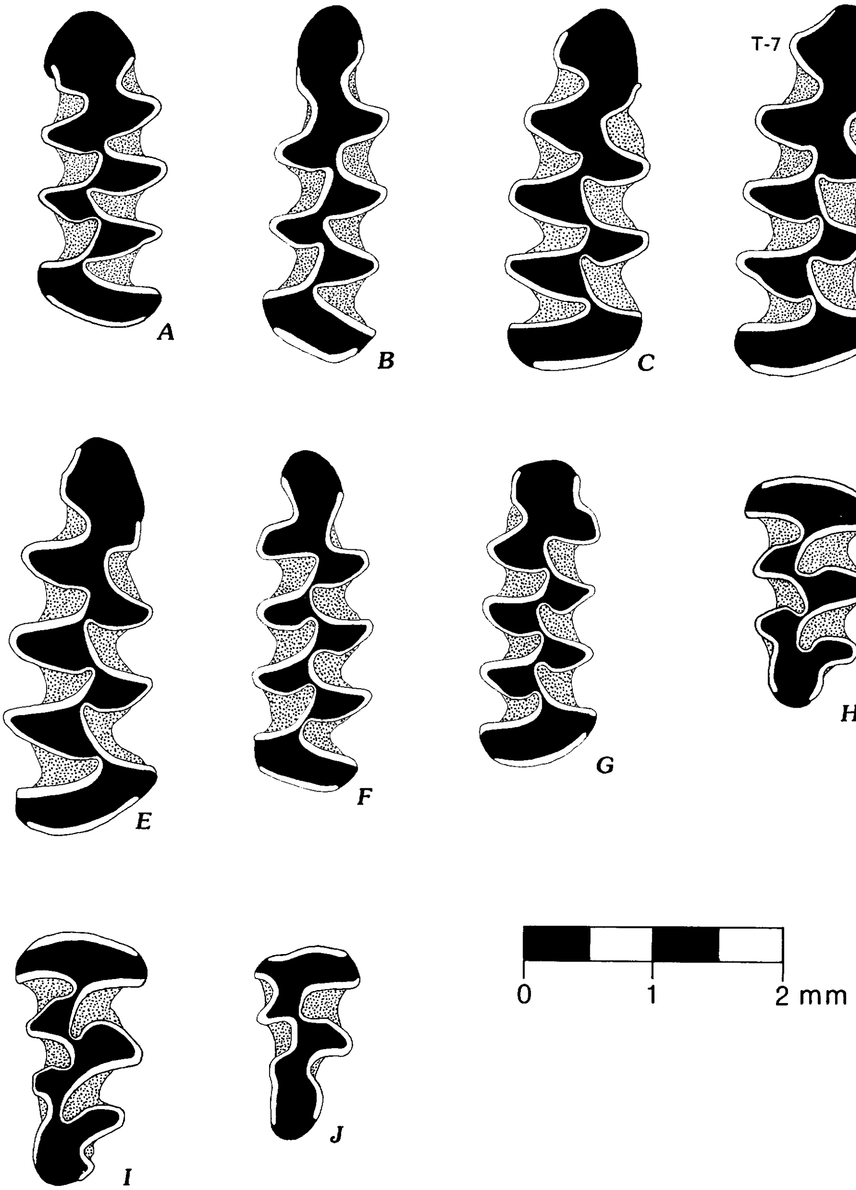


Figure 6. *Allophaiomys* n. sp. (*A–E, H, I*) and *Lemmiscus* n. sp. (*F, G,* and *J*) from SAM Cave, New Mexico: Locality BOT–4. *A–C,* "intermediate" differentiation (34 percent of the sample); *D, E,* "*Microtus*" differentiation (66 percent); *D,* the modal morphotype in the fauna (83 percent of the sample), with a posterolingual angularity on the Cap (T. 7); *F, G, Lemmiscus* n.sp. first lower molar morphotypes. *H, Allophaiomys* n. sp. M\3 with "simple" morphotype (87 percent); *I, Allophaiomys* n. sp. M\3 with weakly "complex" morphotype (the most complex in the sample; 13 percent); *J, Lemmiscus* n. sp. last upper molar. *A, D,* and *E* have a posterolingual angle on Cap (83 percent of sample). Advancement in variability of the Anteroconid Complex of *Allophaiomys* n. sp., from the condition of typical *Allophaiomys pliocaenicus* is comparable to that of *Allophaiomys nutiensis* from Valerots, France, except for the *Lemmiscus* morphotypes.

About 66 percent of the SAM Cave sample of *Allophaiomys* has "*Microtus*" enamel-thickness differentiation, also differing from *Allophaiomys guildayi,* which has this type of enamel-thickness differentiation in **all** individuals. Enamel-thickness differentiation appears to have evolved independently of other morphologic characters, and is difficult to equate in detail with evolution.

Last upper molars from the BOT–4 sample of *Allophaiomys* are of varied morphology (fig. 6*H–I*); 88 percent are "simple" and 12 percent are somewhat advanced and have a rudimentary posterior hook (fig. 6*I*). Eighteen percent of the sample of last upper molars have a great elongation of the posterior loop and are assigned to the *Lemmiscus* sp. morphotype (fig. 6*J*). Many of these *Lemmiscus* last upper molars have a reduced anterobuccal reentrant (fig. 6*J*) as do many individuals of the living *Lemmiscus curtatus*.

The SAM Cave, BOT–4 population of *Allophaiomys* is distinctly more advanced than others that have been considered thus far and is considered a separate species. Although similar to the species *A. guildayi* in having a large majority of individuals with an angle developed on the posterolingual corner of the Cap, the SAM Cave population is not completely converted to "*Microtus*" enamel-thickness differentiation and shows no overlap of individual characters with the genus *Pedomys*, as do the samples of *A. guildayi* from Cumberland Cave and Hanover Quarry Fissure. Figure 6*E* shows the closest approach to pitymyinine characters in the examined sample, and it is not very close.

Indication of a buccal Secondary Wing is totally lacking in the BOT–4 sample except for the few individuals (21 percent) assigned to the *Lemmiscus* morphotype; the *Lemmiscus* variants are clearly not *Pitymys* by virtue of the closure between the dentine fields of the Primary Wings (closure of Dimension C–C′, fig. 6*F* and *G*). And they are not *Microtus* because the SAM Cave *Lemmiscus* variants show the development of primarily the buccal Secondary Wing, whereas *Microtus*, *Pitymys*, *Pedomys*, and *Terricola* show development of the lingual (or both) Secondary Wings (figs. 10, 12, and 13).

The SAM Cave *Lemmiscus* morphotypes are different than those of *Microtus*. They shortly predate the arrival from Beringia of *Terricola* and *Lasiopodomys*, perhaps only by 25,000 years. *Microtus*, which evolved from immigrant *Lasiopodomys*, and *Terricola* were present in the same part of the Rio Grande basin as SAM Cave 820,000 years ago, as indicated by the records from the Hansen Bluff faunas 39 miles (63 km) to the north and east (Rogers and others, 1985). Extinction of *Allophaiomys*, possible modernization of *Lemmiscus*, immigration of *Terricola* and *Lasiopodomys*, evolution of *Microtus* out of *Lasiopodomys*, and climatic change to introduce the Nebraskan continental glaciation to North America all happened in this Colorado–New Mexico basin of the Rio Grande between the time of the BOT–4 fauna of SAM Cave and the oldest faunas of the Hansen Bluff faunal sequence; between an interpolated 875,000 years and a rather well controlled date of 820,000 years ago. This region is in the eastern belt of the Rocky Mountains.

Surprisingly, no variations in the SAM Cave population resemble *Lasiopodomys*. This was a very common variation of advanced *Allophaiomys* throughout Eurasia, where it preceded the evolution of *Lasiopodomys*. The genus *Lasiopodomys* resulted from the great reduction of Dimension C–C′, separating the two Primary Wings, without the development of Dimension A–A′ and Secondary Wings that define *Microtus* and *Lemmiscus*.

The *Lasiopodomys* morphology is completely avoided in the individual variability of the BOT–4 population of *Allophaiomys* by the simultaneous development of a closed Dimension C–C′ and the appearance of a single, **buccal** Secondary Wing, forming the *Lemmiscus* morphotype (fig. 6*F*, *G*). North American *Lasiopodomys* was an immigrant.

All available records indicate that the development of a lingual Secondary Wing marks the origination of *Microtus*; the *Lemmiscus* morphotypes of *Allophaiomys* from the SAM Cave do not conform to this pattern. The origins of *Lasiopodomys* and, with one exception, *Microtus* are in the Old World. Also, there is only very slight suggestion of the variation that led to the Pitymyini in the SAM Cave population (fig. 6*D*, *E*), in which the Secondary Wings alone developed and Dimension C–C′ remained unreduced; in the SAM Cave sample a few individuals of *Allophaiomys* have a slightly reduced Dimension B–B′, suggesting the Pitymyini. Greater variation toward the Pitymyini is found in all other *Allophaiomys* populations of the United States soon after the SAM Cave fauna lived. Thus the SAM Cave population is unique in North America in its direction of variation toward the *Lemmiscus* morphotype, as well as in avoiding an intermediate *Lasiopodomys* morphotype leading to *Microtus* or significant morphologic gradation toward the Pitymyini.

The unique individual variation forming the *Lemmiscus* morphotype in *Allophaiomys* from SAM Cave, New Mexico, emphasizes the fact that different populations of *Allophaiomys* had different evolutionary patterns. SAM Cave is now well south of the range of living *Lemmiscus*, and this distribution and the modern colder summer preferences of *Lemmiscus curtatus* prompt the suggestion that the fauna may represent a high elevation (8,900 ft; 2,728 m) province; the next younger record, Porcupine Cave, Colorado (Barnosky and Rasmussen, 1988), is higher (9,500 ft; 2,900 m) and half as old (perhaps 450,000 years old), and lies half as far from the modern range of the genus beginning in high plains at the northern boundary of Colorado.

ALLOPHAIOMYS FROM THE WELLSCH VALLEY FAUNA

(fig. 7; locality 9, fig. 1)

The Wellsch Valley fauna is in southern Saskatchewan, Canada (Churcher, 1984). Although earlier paleomagnetic studies indicated deposition during the Olduvai event, recent restudy (Barendregt and others, 1991) indicates that the Jaramillo and Olduvai normal events are not present in the section. The fossil locality was deposited before the beginning of the Brunhes Chron in reversely magnetized beds of the Matuyama Chron; its position within the Matuyama is uncertain, although the faunal horizon is reversely magnetized and cannot correlate with the Jaramillo event. The age of the fauna may be very close to, or the same as, the age of BOT–4 of SAM Cave, New Mexico.

The fauna represents a warm climate (Churcher, 1984) and cannot be contemporaneous with the Nebraskan glaciation (the locality was indeed covered by this ice sheet): therefore it must be older than 850,000 years. This conclusion is also suggested by the absence of both *Lasiopodomys* and *Terricola,* both of which appear to have entered the United States from Beringia at the beginning of Nebraskan glaciation.

The Wellsch Valley fauna contains one Blancan holdover, the canid *Boraphagus.* An advanced form of *Microtus* is present in the fauna, and the history of Beringian *Microtus* suggests that the fauna is the age of or younger than the Jaramillo event; its reversed polarity eliminates the possibility of an equivalent age. Biogeographic considerations suggest that the Wellsch Valley *Microtus* probably is not as old as 1.5 million years; no record is known of this genus that is older than this age, and Wellsch Valley is on the east side of the Rocky Mountains where there is no record of *Microtus* so old in the United States.

The sample of *Allophaiomys* from the Wellsch Valley fauna is very small, consisting of only four first lower molars (fig. 7); no evaluation of individual variation is possible. Three of the four specimens known are of typical morphology, but have "*Microtus*" enamel-thickness differentiation and show a remarkably great size variation (fig. 7). The fourth first lower molar is an individual variant with a posterolingual angularity on the Cap, overlapping the morphology of *Allophaiomys guildayi* and the species from SAM Cave.

The few last upper molars from the Wellsch Valley fauna are of a "simple" structure and presumably are assignable to *Allophaiomys.* The associated first lower molar of *Microtus* is too advanced to be considered as having a simple last upper molar.

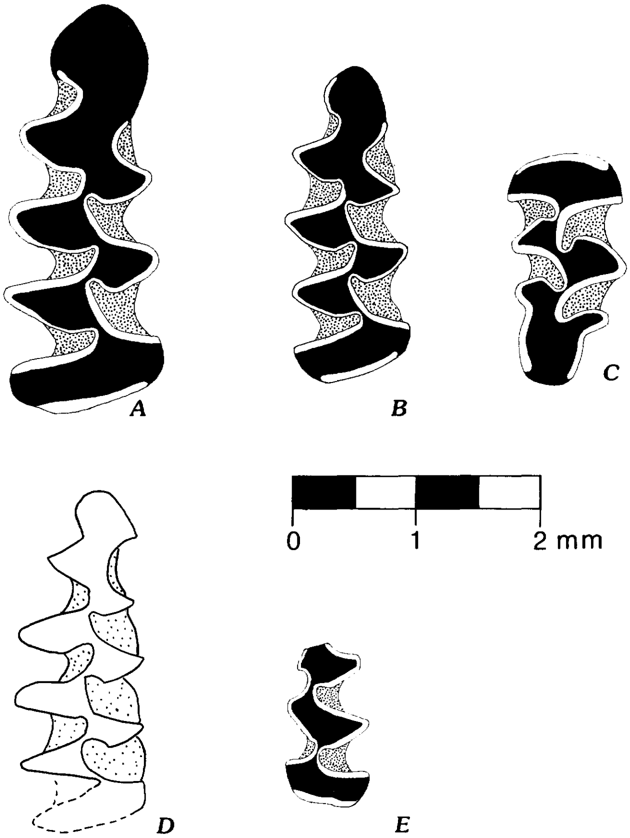


Figure 7. *Allophaiomys* sp. and *Microtus* sp. from the Wellsch Valley fauna, Saskatchewan; M/3 from the Hansen Bluff core, Colorado. *A* and *B, Allophaiomys* sp. first lower molars; note size variation. *C, Allophaiomys* last upper molar. *D, Microtus* sp., NMC 17848—first lower molar, reproduced from a manuscript by C. S. Churcher. *E,* Last lower molar, assigned to *Allophaiomys* on basis of great age and rootless state, from the base of the Olduvai event in Hansen Bluff core, Colorado. NMC specimens except for *E,* which is in Adams State College, Alamosa, Colorado.

In the Wellsch Valley fauna the association of *Allophaiomys* with a rather advanced species of *Microtus* is of great interest. The single specimen of *Microtus* has a first lower molar that is morphologically similar to the most advanced morphotypes of *Microtus paroperarius* from its type locality, the 610,000 year-old Cudahy fauna of Kansas. It has a fully closed Dimension C–C′ (separating the two Primary Wings), a fully closed Dimension B–B′ (between the lingual Primary Wing and the Cap) and well-developed Secondary Wings (fig. 7*D,* reproduced from a manuscript by C.S. Churcher). This is the only association in North America, possibly in the world, of *Allophaiomys* with so advanced a *Microtus* morphotype.

In the latitudinal confines of the United States east of the Rocky Mountains, the presence of a species of *Microtus* with an advanced first lower molar in a late Matuyama fauna is unknown. East of the Rocky Mountains, no *Microtus* is known before 830,000 years ago and those that are known before the Brunhes have recently evolved out of the immigrant *Lasiopodomys.* They are primitive and have only very weak development of Secondary Wings. It was not until about 700,000 years ago, well into the time of the Brunhes Normal-polarity Chron, that *Microtus paroperarius* in the United States evolved to the point where some individuals were as advanced as the *Microtus* specimen from the Wellsch Valley fauna. *Allophaiomys* became extinct in the United States before this time, but the Wellsch Valley fauna is from reversely polarized deposits.

In addition, in faunas east of the Rocky Mountains in the United States, the earliest records of *Microtus* are associated with *Terricola* or *Lasiopodomys,* which immigrated to the United States 850,000 years ago. Neither *Lasiopodomys* nor *Terricola* is known from the Wellsch Valley fauna, suggesting that this Canadian fauna is older than their immigration, and older than the first primitive *Microtus* of the United States east of the Rocky Mountains.

In Beringia the oldest record of *Microtus* (Krestovka Sections) is of a more primitive morphotype (fig. 16) and predates the Jaramillo event by 200,000 years. In eastern Beringia (northwestern Canada) both advanced and primitive *Microtus* morphotypes were present during the Jaramillo Normal-polarity Subchron (fig. 14). *Lasiopodomys* was associated with these varied *Microtus* types in Beringia, but *Allophaiomys* was extinct in this region long before this time. As will be discussed later in this report, it appears that *Allophaiomys* became extinct in the Arctic region during the Olduvai event, probably before 1.7 million years ago. Its extinction appears to have been climatically regulated, as *Allophaiomys* was present in Beringia only during an extremely warm period.

The varied morphotypes of *Microtus* that lived during the Jaramillo event in eastern Beringia are known from Locality CRH–47 of the Old Crow basin of northern Yukon Territory (R.E. Morlan, oral commun., 1986). Two apparently younger faunas from the Old Crow basin also are normally magnetized and contain *Lasiopodomys* (CRH–11 and CRH–64); these have a greater assortment of *Microtus* morphotypes (Morlan, 1984). The Old Crow localities (locality 25, fig. 1) are about 100 miles (160 km) south of the Arctic Ocean.

A much older *Microtus*, perhaps 1.4 million years old, is known from the Anza–Borrego Desert of southern California, west of the Rocky Mountains (Zakrzewski, 1972; this report, fig. 10; locality 21, fig. 1). This record is the oldest dated *Microtus* in the world. The species, *Microtus californicus* (an advanced living species), is also known from the Irvington fauna of central California, which is older than the Brunhes Chron—possibly about 870,000 years old. The history of advanced *Microtus* is much longer west of the Rocky Mountains than it is east of them in the United States.

In addition, one fragmentary specimen of *Lasiopodomys* exists from the Anza-Borrego Desert of California that also predates the Jaramillo event and is about 1.2 million years old (fig. 11*A*); it is much older than the time of its dispersal to the United States east of the Rocky Mountains.

Because of these age relationships, *Microtus californicus* to the west of the Rocky Mountains, as well as the species in the Wellsch Valley fauna, must represent immigrants from Beringia; they cannot be related to *Microtus paroperarius*, which evolved out of *Lasiopodomys* east of the Rocky Mountains after the first Nebraskan ice advance (850,000 years ago).

Although apparently never present in the area west of the Rocky Mountains and extinct in Beringia long before the Jaramillo event, *Allophaiomys* survived east of the Rocky Mountains in the United States until about 830,000 years ago, during the early part of the Nebraskan ice advances. The *Allophaiomys* from Wellsch Valley must represent a northward extension of the then-surviving populations in the United States.

Thus the unique association of *Allophaiomys* with an advanced morphotype of *Microtus* in the Wellsch Valley fauna of southern Saskatchewan must have been the result of its intermediate latitudinal position between the Beringian and the eastern United States faunal regions. At the time that this fauna lived, *Allophaiomys* had been extinct for about 850,000 years in Beringia but still survived in the United States. *Microtus* was not known to the east of the Rocky Mountains in the United States until 30,000 years later, and even then was of a much less advanced morphology. However, the variety of *Microtus* morphotypes, some advanced, known from Beringia during the earlier Jaramillo event indicates that the Wellsch Valley locality was far enough south to support *Allophaiomys* from the populations still living in the United States and far enough north that it included *Microtus* from Beringian populations, where *Allophaiomys* was extinct.

Based on (1) its reversed polarity (>790,000 years old and not Jaramillo); (2) the presence of an advanced *Microtus* morphotype (not related to *Microtus* of the U.S.A., which evolved later and did not develop an advanced morphology before the Brunhes Chron, 790,000 years ago); (3) the presence of *Allophaiomys* (extinct to the south in the Great Plains before the Brunhes Chron and apparently extinct to the north in Beringia during the Olduvai Subchron); (4) the lack of both *Lasiopodomys* and *Terricola* (immigrants to the Great Plains to the south about 850,000 years ago); (5) the lack of abundant Blancan holdovers (less than 1.4 Ma); and (6) based on evidence of a warm climate, older than the first Nebraskan glacial advance 850,000 years ago, the Wellsch Valley fauna is here presumed to be between 850,000 and 900,000 years old. Some possibility remains that the Jaramillo event, missing in the Wellsch Valley polarity section, is younger than the fauna and that the fauna may be between 1.0 and 1.4 million years old (fig. 14). One Californian locality (Anza Borrego) contains an advanced *Microtus* that is this old, but this form appears less advanced and is associated with many Blancan holdovers.

ALLOPHAIOMYS FROM THE CHEETAH ROOM FAUNA

(fig. 8; locality 17, fig. 1)

The Cheetah Room fauna is from Hamilton Cave, West Virginia, and contains a large variety of microtine rodents. These include a population of the southern bog lemming *Synaptomys cooperi* with a remarkable individual variation overlapping that of the northern bog lemming *Mictomys borealis*, a primitive subgenus of *Phenacomys*, and a very late record of the genus *Mimomys* of the tribe Arvicolini, as well as *Allophaiomys*, *Lasiopodomys*, and *Pitymys*. In the original description of the Cheetah Room fauna (Repenning and Grady, 1988), *Microtus paroperarius* was also listed, but this identification was based upon a minority of extreme variants in the population of *Lasiopodomys deceitensis* and not upon a bimodal distribution of morphotypes; the identification is here withdrawn, although the specimens are very primitive *Microtus* morphotypes.

No external control of the age of the Cheetah Room fauna exists, but overlapping biochronologies identify its age closely. Based upon the emergence of the southern bog lemming *Synaptomys* out of the northern bog lemming *Mictomys* in the Cheetah Room fauna, the fauna is older than the Brunhes Normal-polarity Chron (beginning about 790,000 years ago); *Synaptomys* is known elsewhere before the Brunhes. Based upon the presence of the immigrant genus *Lasiopodomys*, the Cheetah Room fauna is younger than the dispersal event that introduced Irvingtonian II microtine rodents to the faunas of the United States (about 850,000 years ago; Repenning, 1987; Repenning and others, 1990). The presence of *Lasiopodomys* indicates that the Cheetah Room fauna is older than the oldest faunas of the Hansen Bluff faunal sequence in Colorado (820,000 years old; Rogers and others, 1985), which contain immigrant, primitive *Terricola* and *Microtus paroperarius*, but not immigrant *Lasiopodomys*, from which *Microtus* evolved, as will be discussed.

The Cheetah Room fauna is thus older than 820,000 years and younger than 850,000 years. Other faunas, to be discussed, are also of this age range but younger than the Cheetah Room fauna, making it seem that the Cheetah Room fauna must be closer to 850,000 than to 820,000 years old; it is considered to be about 840,000 years old (fig. 14).

Although additional material is available at USNM, the examined sample of *Allophaiomys* from the Cheetah Room fauna comprises 30 first lower molars. Separation of the immigrant genus *Lasiopodomys* from *Allophaiomys* presents no problem, but the gradation between *Allophaiomys* and *Pitymys* (representing the native "*pinetorum* species group" of Repenning, 1983) is complete and distinctly bimodal.

Fifty-two first lower molars assigned to *Pitymys hibbardi* are in the examined sample, and individual variation not only overlaps that of *Allophaiomys* but also overlaps the typical morphology of *Pitymys cumberlandensis* ("intermediate" enamel differentiation) and the type species of the genus, *Pitymys pinetorum* (fig. 13*A*, *B*, and *C*; see also Repenning and Grady, 1988). It had been suggested in earlier publications that North American *Pitymys* evolved provincially out of endemic *Allophaiomys* (van der Meulen, 1978; Repenning, 1983).

The 30 first lower molars of *Allophaiomys* from the Cheetah Room fauna (exemplified in fig. 8) differ considerably from the sample from SAM Cave (fig. 6). Although the great majority (83 percent) of first lower molars from SAM Cave show a posterolingual angularity on the Cap, only 10 percent of the *Allophaiomys* from the Cheetah Room fauna can be considered as possibly showing this character, and in these individuals the suggestion is weak.

In addition, in the Cheetah Room sample the configuration of the last upper molar is like that of the type population: the sample lacks a substantial percentage of individuals with a greatly extended (*Lagurus*-like) posterior loop and lacks any suggestion of the development of a posterior hook. The *Lemmiscus* morphotypes present in the sample from SAM Cave are completely lacking in the Cheetah Room fauna. Individual variation in the morphology of the first lower molar does not overlap that of either *Lemmiscus* or *Microtus*, but grades into that of *Pitymys*. The distribution of *Allophaiomys* and *Pitymys* morphologies is distinctly bimodal in the Cheetah Room sample.

Clearly, the first lower molars and the last upper molars of *Allophaiomys* from the Cheetah Room fauna are more similar to teeth of the type population of *Allophaiomys* from Betfia–2 (fig. 3) than to these teeth in the SAM Cave fauna of New Mexico. However, enamel-thickness differentiation is not greatly different from that of SAM Cave and, as in that sample, "*Microtus*" differentiation is present in half the individuals from the Cheetah Room fauna. This approximate proportion of "*Microtus*" differentiation is equal in both *Allophaiomys* and *Pitymys* modes of this bimodal population. The *Pitymys* mode is referred to *Pitymys hibbardi* (Repenning and Grady, 1988).

Although younger than the SAM Cave population, that from the Cheetah Room fauna is not considered to be a new species, but an advanced condition of *Allophaiomys* sp. cf. *A. pliocaenicus* first seen in the Java fauna. It is not so advanced in the modal morphology of the *Allophaiomys* part of the population as is *Allophaiomys guildayi*. Its apparently more "conventional" morphology also suggests that the older SAM Cave population, overlapping the *Lemmiscus* morphology, was an isolate population, some characters of which parallel those seen in *Allophaiomys guildayi*.

The Cheetah Room population of *Allophaiomys* grades into the morphology of *Pitymys*, and the bimodal population has a much higher percentage of pitymyinine morphotypes than the type population of *Allophaiomys pliocaenicus* (Betfia–2). The differences in the population structure between SAM Cave and the Cheetah Room suggest not only separate lineages but also a more advanced condition toward a descendant generic group in the Cheetah Room population. A separate species name would seem justifiable, but is neither applied nor endorsed here. Conceivably, one could apply a new name to every population in this rapidly evolving lineage to the disadvantage of comprehensible nomenclature.

It seems best, in the present state of knowledge, to advocate the application of whatever specific name is applied to the Java form with the notation that the Cheetah Room population is the same but much more advanced. Hence, "*Allophaiomys* sp. cf. *A. pliocaenicus*, advanced" is used in the present report. The population is, however, bimodal and thus must further be described as "*Allophaiomys* sp. cf. *A. pliocaenicus-Pitymys hibbardi,*" which far exceeds the usual length of a binomial and is quite cumbersome. The sooner that a new name is applied to the Java fauna form of *Allophaiomys* the better. The Cheetah Room species is replaced, in perhaps 5,000 years, by a new name, *Allophaiomys guildayi* from the Hanover Quarry Fissure

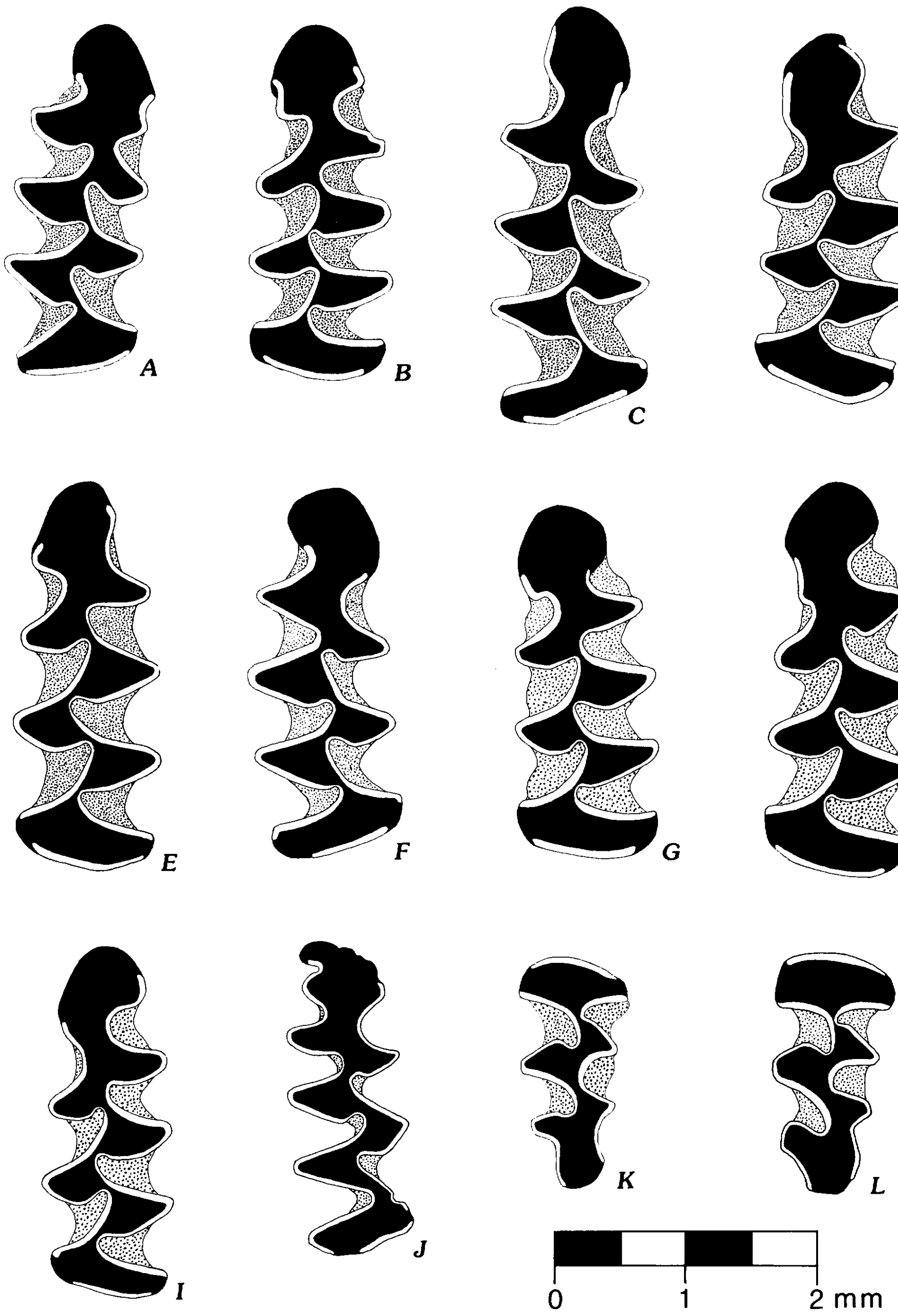


Figure 8. *Allophaiomys* sp. cf. *A. pliocaenicus* (advanced): first lower molars from the Cheetah Room fauna, Hamilton Cave, West Virginia. *A–E*, intermediate enamel differentiation. *F–H*, "*Microtus*" enamel differentiation. *I*, *J*, little-worn teeth showing that differentiation is not obvious with little wear. *K*, simple M\3 with long posterior loop. *L*, simple M\3 with short posterior loop. USNM specimens.

fauna, so the snowballing of qualifiers ends here, and begins again.

The differences in *Allophaiomys* tooth morphology variation between the SAM Cave fauna of New Mexico and the slightly younger Cheetah Room fauna of West Virginia, faunas that are possibly less than 35,000 years different in age, suggest that provincialism may have a significant effect on population morphology. Certainly, the total population from SAM Cave is more derived in terms of character changes than that from the Cheetah Room fauna. It also seems evident that the SAM cave form is evolving into *Lemmiscus* whereas the Cheetah Room form has branched a new genus called *Pitymys*. Lacking other age control, this could have been interpreted as an age-significant difference, in a sense that is opposite to that evident from the rest of the fauna: the more "derived" *Allophaiomys* from SAM Cave is older than that from the Cheetah Room fauna on several counts.

ALLOPHAIOMYS FROM THE HANOVER QUARRY FISSURE FAUNA

(fig. 9; locality 16, fig. 1)

The Hanover Quarry Fissure locality was exposed in Bethlehem Steel Corporation's limestone quarry at Hanover, Pennsylvania. The fauna contains *Allophaiomys guildayi* (fig. 9), ?*Lasiopodomys* sp. (fig. 11), and *Pitymys cumberlandensis* (fig. 13). The original designations by Guilday and others (1984) were *Pedomys guildayi*, *Microtus paroperarius*, and *Pitymys cumberlandensis*. The locality does not seem to contain a mixed fauna.

Allophaiomys guildayi is clearly advanced over the type species, *A. pliocaenicus*; the sample is of good size, consisting of 44 first lower molars. In the prevalence (64 percent) of an angular posterolingual corner of the Cap (incipient lingual Secondary Wing), *A. guildayi* from the Hanover Quarry is similar to the older population of *Allophaiomys* n. sp. from SAM Cave (83 percent with a posterolingual corner) and to the apparently younger type population of *A. guildayi* from Cumberland Cave (32 percent; van der Meulen, 1978, fig. 7E, G, and possibly H). None of the Hanover Quarry sample overlaps the characters of the Microtini (*Lemmiscus*) as does a small percentage (21 percent) of the SAM Cave sample.

In that only a minor number of individuals (7 percent) have developed both Secondary Wings, the Hanover Quarry sample is less advanced than the type sample from Cumberland Cave (16 percent). This development (of both Secondary Wings) overlaps the characters of *Pedomys*, thus accounting for the original assignment of the type sample to *Pedomys guildayi* by van der Meulen (1978). However, in his type description, van der Meulen stated that the species fit the definition of *Allophaiomys*, and Repenning (1983) placed it in this genus, followed by Martin (1987) and Pfaff (1990).

In the more advanced population from Trout Cave No. 2, West Virginia, the *Pedomys* morphotype represents 66 percent of the sample, and Pfaff (1990) logically assigned the population to *Pedomys llanensis*, even though a minor percentage of the population still retained a typical *Allophaiomys* morphotype (Pfaff, 1990, fig. 5C, D, and E).

Pedomys llanensis was defined by Hibbard (1944) from the Cudahy fauna of Kansas, and at most five topotypic specimens have been mentioned in publication. The sample is much too small to establish individual variation of the type population, and Pfaff's (1990) referral of the Trout Cave No. 2 population to this species thus provides proxy population characteristics by reference.

Although van der Meulen (1978) recognized the gradation from *Allophaiomys* to *Pedomys* in the Cumberland Cave fauna, the addition of the faunas from Hanover Quarry and from Trout Cave provides a sequence of populations with increasing percentages of *Pedomys* morphotypes leading, from *Allophaiomys guildayi*, through *Pedomys llanensis*, to the living *Pedomys ochrogaster*. This sequence with the increasing proportions of the *Pedomys* morphotypes in evolving populations of advanced *Allophaiomys* (Hanover–7 percent, Cumberland Cave–16 percent, and Trout Cave–66 percent) is here considered as strong evidence of age relationship. Martin (1987) mentioned that some individuals of living *Pedomys ochrogaster* still have an *Allophaiomys* dental morphology, although they must represent a very small percentage of the population.

Other aspects of the *Allophaiomys* population from Cumberland Cave, however, as well as features of the Cumberland Cave population of *Microtus*, are not in complete agreement with this interpretation of an evolutionary sequence. These other aspects are discussed in later sections.

The Hanover Quarry Fissure fauna is considered younger than the SAM Cave fauna because of this variation in *Allophaiomys* that overlaps the Pitymyini rather than a lineage of the Microtini (*Lemmiscus*) in SAM Cave, and because of the presence of the immigrant lineage represented by ?*Lasiopodomys* that is not present in the SAM Cave faunas. All specimens of *Allophaiomys guildayi* from the Hanover Quarry Fissure have "*Microtus*" enamel differentiation, further suggestion of advancement beyond the species from SAM Cave and, also, beyond the species of *Allophaiomys* from the Cheetah Room fauna.

The sample of *Pitymys cumberlandensis* from Hanover Quarry appears to be the same as in the type locality, Cumberland Cave, Maryland. It is represented by 21 first lower molars, of which 86 percent have "intermediate" enamel-thickness differentiation; but otherwise this population sample is very similar to the living *Pitymys pinetorum*, which has "*Microtus*" enamel-thickness differentiation in most(?) of its population. *Pitymys cumberlandensis* evolved out of *Allophaiomys* earlier, the process being recorded in the Cheetah Room fauna.

The lack of difference between *Pitymys cumberlandensis* of the Hanover Quarry population and that of the Cumberland Cave fauna is continued into the younger Trout Cave No. 2 fauna (Pfaff, 1990) and strongly suggests that this lineage had polarized its morphologic variation after diverging from *Allophaiomys* in the Cheetah Room fauna.

It is assumed, from their strong similarity, that this species leads to the living *Pitymys pinetorum*, but to 1992 no fauna has been described in which variability in enamel-thickness differentiation increases, leading to the dominant "*Microtus*" differentiation of the living species. This is the principal difference between the species, and the increase in variability of the enamel-thickness differentiation may be recorded only in the living populations. There is no reason to

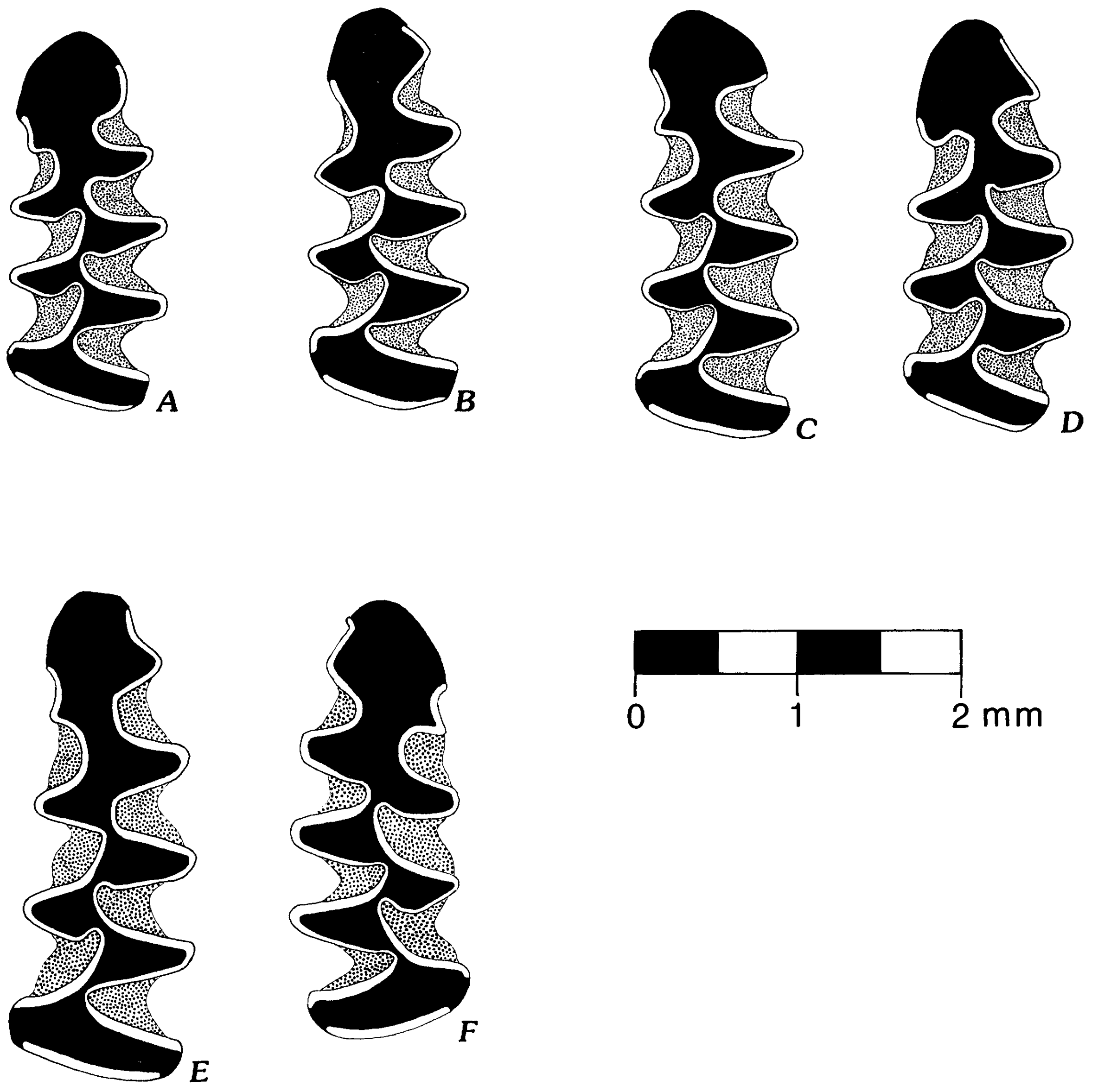


Figure 9. *Allophaiomys guildayi* from Hanover Quarry Fissure fauna, Pennsylvania. First lower molars. All have "*Microtus*" enamel-thickness differentiation. *B*, no posterobuccal angle, or corner, on Cap (29 percent; this morphotype is comparable to living *Phaiomys leucurus*). *A, C, D*, posterobuccal angle on Cap (64 percent). *E, F*, individuals overlapping *Pedomys* morphotype (7 percent). CMNH specimens.

think that these variations, characterizing progressing evolution, should not be found in the living fauna.

ALLOPHAIOMYS FROM THE CUMBERLAND CAVE FAUNA

(locality 11, fig. 1; illustrated in van der Meulen, 1978)

Cumberland Cave was exposed during excavation for a railway cut in nearly vertical Paleozoic limestone at the south side of the town of Corriganville, 4 miles (6.4 km) northwest of Cumberland, western Maryland. Study of the vertebrate fossils from the cave was begun in 1912 (Gidley and Gazin, 1938) and has continued intermittently since then, the most recent detailed work being that of van der Meulen (1978). The fauna contains a good variety of microtine rodents including *Allophaiomys guildayi*, *Pitymys cumberlandensis*, and the most primitive known population of *Microtus paroperarius*, which, because of its very primitive condition, is herein referred to as *Microtus paroperarius*-*Lasiopodomys deceitensis*, as has been mentioned and will be further discussed.

The Cumberland Cave population of *Allophaiomys guildayi*, the type population, is represented by a good sample of 37 first lower molars (available for this study;

van der Meulen cited 200 in his complete study). Of these, 51 percent have a typical *Allophaiomys* morphotype (van der Meulen, 1978, fig. 7A to D, and F; compared to 29 percent in the Hanover Quarry sample), 32 percent have an advanced *Allophaiomys* morphotype in which a posterolingual corner is evident on the Cap (van der Meulen, 1978, fig. 7E, G, and H; compared to 64 percent in the Hanover Quarry sample), and 16 percent have a *Pedomys* morphotype with weak but evident Secondary Wings on both sides of the Cap (van der Meulen, 1978, fig. 7I; compared to 7 percent in the Hanover Quarry sample).

In other faunas, a higher percentage of primitive morphotypes seems to correlate with older faunas (and a higher percentage of advanced morphotypes seems to correlate with younger faunas), and the increase in individuals with a *Pedomys* morphotype would seem to correlate with a younger fauna. But the percentages of *Allophaiomys* morphotypes from Cumberland Cave, just cited, do not seem to agree with the increase in *Pedomys* morphotypes.

Both localities—Cumberland Cave and Hanover Quarry—have been described in such a way that contamination from unknown faunas by stream action appears unlikely to have biased the samples. Guilday and others (1984) specifically stated this unlikelihood at the Hanover Quarry Fissure. Gidley's (1913) preliminary report on the Cumberland Cave fauna indicates that although there may have been other entrances to Cumberland Cave in the past, they would all have been near the crest of a prominent ridge, and introduced sand or gravel in the fossil deposit was almost totally lacking. The main entrance to Cumberland Cave appears to have been destroyed in digging the railway cut. The differences so far considered between this fauna and that of the Hanover Quarry Fissure may relate to unknown environmental differences. Possibly the concept of a suitable sample size used herein is too small. In addition, no information is available regarding how the Cumberland Cave sample of 37 M/1s of *Allophaiomys guildayi* that was available for this study was selected from the 200 that van der Meulen indicated was the total sample.

As will be discussed, the greater-than-50-percent proportion of *Microtus* morphotypes in the Cumberland Cave population of intergrading *Microtus* and *Lasiopodomys* also suggests a fauna younger than the Hanover Quarry Fissure fauna, although in this case the Hanover sample is very small. However, the suggestion is in agreement with the greater percentage of *Pedomys* morphotypes, and this age inference is adopted here. In either case, the Hanover Quarry and Cumberland Cave faunas appear close in age.

As has been discussed, the Cumberland Cave fauna contains *Pitymys cumberlandensis*, whose origin out of *Allophaiomys* appears to be recorded in the Cheetah Room fauna of Hamilton Cave, West Virginia, that is estimated to be about 840,000 years old. The population of *Microtus paroperarius* from Cumberland Cave, intergrading with abundant *Lasiopodomys deceitensis* morphotypes, is much more advanced than the *Lasiopodomys* population of the Cheetah Room fauna, containing at most 25 percent individual variants of the *Microtus* morphotype. In addition, the origin of *Synaptomys* out of *Mictomys* is recorded in the Cheetah Room fauna, and both of these lemmings are present in the Cumberland Cave fauna with no reported morphologic intergradation. Thus, the Cumberland Cave fauna appears to be younger than the Cheetah Room fauna.

The presence of primitive *Microtus paroperarius* (morphologically comparable to 59 percent of the individuals of the *Microtus-Lasiopodomys* population from Cumberland Cave) in the oldest Hansen Bluff faunas, Colorado, without any associated *Lasiopodomys* morphotypes (41 percent of the Cumberland Cave population) indicates that the Cumberland Cave fauna is older than the oldest Hansen Bluff faunas (820,000 years old). The age of the Cumberland Cave fauna is consequently approximated at 830,000 years (fig. 14). This age is very similar to that which was suggested by van der Meulen (1978, fig. 14).

OTHER NORTH AMERICAN LOCALITIES

Other faunas containing *Allophaiomys* in North America add little more to the history of the North American evolution of this genus. In the Great Plains region these include the Wathena, Kentuck, Nash, Courtland Canal, and Aries faunas of Kansas, and the Sappa fauna of Nebraska (Zakrzewski, 1985). These faunas are of an age between those of the Java and Cheetah Room faunas but are otherwise not dated (the Sappa fauna underlies, by some distance, the Sappa Ash dated at 1.2 Ma). The samples of *Allophaiomys* from these faunas show a comparable variability and similarity to the Java *Allophaiomys* sp. cf. *A. pliocaenicus*. Most were originally described as *Pedomys llanensis*, but Martin (1975) called attention to their similarity to *Allophaiomys pliocaenicus*. When Chaline (1966) first described the evolution of *Allophaiomys* into *Microtus* and *Pitymys*, no one was aware that *Allophaiomys* had existed in North America for over a million years.

Allophaiomys appears to have become "extinct" in the United States about 825,000 years ago (between Cumberland Cave and Trout Cave No. 2 faunas), by evolving a mode in its individual dental morphology that is characteristic of living *Pedomys ochrogaster*. The latest appearance of *Allophaiomys* morphotypes may be individual variants of *P. llanensis* in the Trout Cave No. 2 fauna of West Virginia (Pfaff, 1990); or occasional variants of living *P. ochrogaster*. In addition to pointing out its close relationship with *A. guildayi*, Pfaff also suggested that *P. llanensis* may be synonymous with *ochrogaster*—this was not a contradiction, but an expression of close similarity and of a difference between the species of *Pedomys* that expresses, primarily, differences in the range of individual variability.

The lineage of *Pitymys pinetorum* appears to have evolved its characteristic mode slightly earlier, beginning in a bimodal association with *Allophaiomys* in the Cheetah Room fauna, continuing with the polarized morphology of *Pitymys cumberlandensis* in several faunas, and apparently culminating in the living species by increasing the predominance of "*Microtus*" enamel-thickness differentiation.

Pfaff (1990), in an otherwise very specific report on Trout Cave No. 2, West Virginia, was rather vague about the separation between *Pitymys cumberlandensis* and living *P. pinetorum*. He suggested that the fossil species appears less variable than the living on the basis of examination of specimens of the living species from the central Appalachian Mountains. This seems reasonable, and only increasing variability marks the evolution of the living species. This would be a trend that was duplicated in the past by *Allophaiomys pliocaenicus* prior to diversification into *Lasiopodomys*, *Lemmiscus*, *Terricola*, *Pitymys*, and *Pedomys*, and by *Lasiopodomys* prior to evolution into *Microtus*. In a real sense, present evidence seems to indicate that the type species of *Pitymys* is only now evolving out of *P. cumberlandensis*, an ancestor with more strongly polarized dental characters than its living descendant.

With the exception of SAM Cave, New Mexico, the individual variations of *Allophaiomys* in North America are in the direction of *Pitymys* and *Pedomys*. The ancestry of native *Microtus* in the eastern half of the United States lies not in immigrant *Allophaiomys*, but in immigrant *Lasiopodomys*. Three hundred eighty thousand years later, native *Microtus* was replaced by immigrant *Microtus* from Beringia and Asia. The presence of this Asian-Beringian population to the north is indicated by two localities in California, one possibly 1.4 million years old and the other probably about 850,000 years old; by Locality CRH-47 of Yukon Territory about 900,000 years old; by the Wellsch Valley fauna of Saskatchewan older than 850,000 years; and in the wave of immigration of Beringian *Microtus* to the United States about 450,000 years ago (Repenning, 1987).

TRIBE MICROTINI, SIMPSON, 1945

Basis of diagnosis.—Hinton, 1923 (for genus *Microtus*): "M$_1$ with posterior loop followed by five (or four) substantially closed and alternating triangles and terminated by an anterior loop of variable form."

Revised dental diagnosis.—Genera of the tribe Microtini (subfamily Arvicolinae) lack dentinal confluence between the Primary Wings of the Anteroconid Complex (Dimension C–C′ substantially closed); Cap of the Anteroconid Complex simple or complex (Secondary Wings may be present); cheek teeth are rootless with cementum in the reentrants.

Generic contents of the tribe.—*Lasiopodomys*, *Lemmiscus*, *Microtus*, and *Proedromys*. (Many more genera seem potentially recognizable, but are here retained as subgenera of *Microtus* for lack of data to defend their removal.)

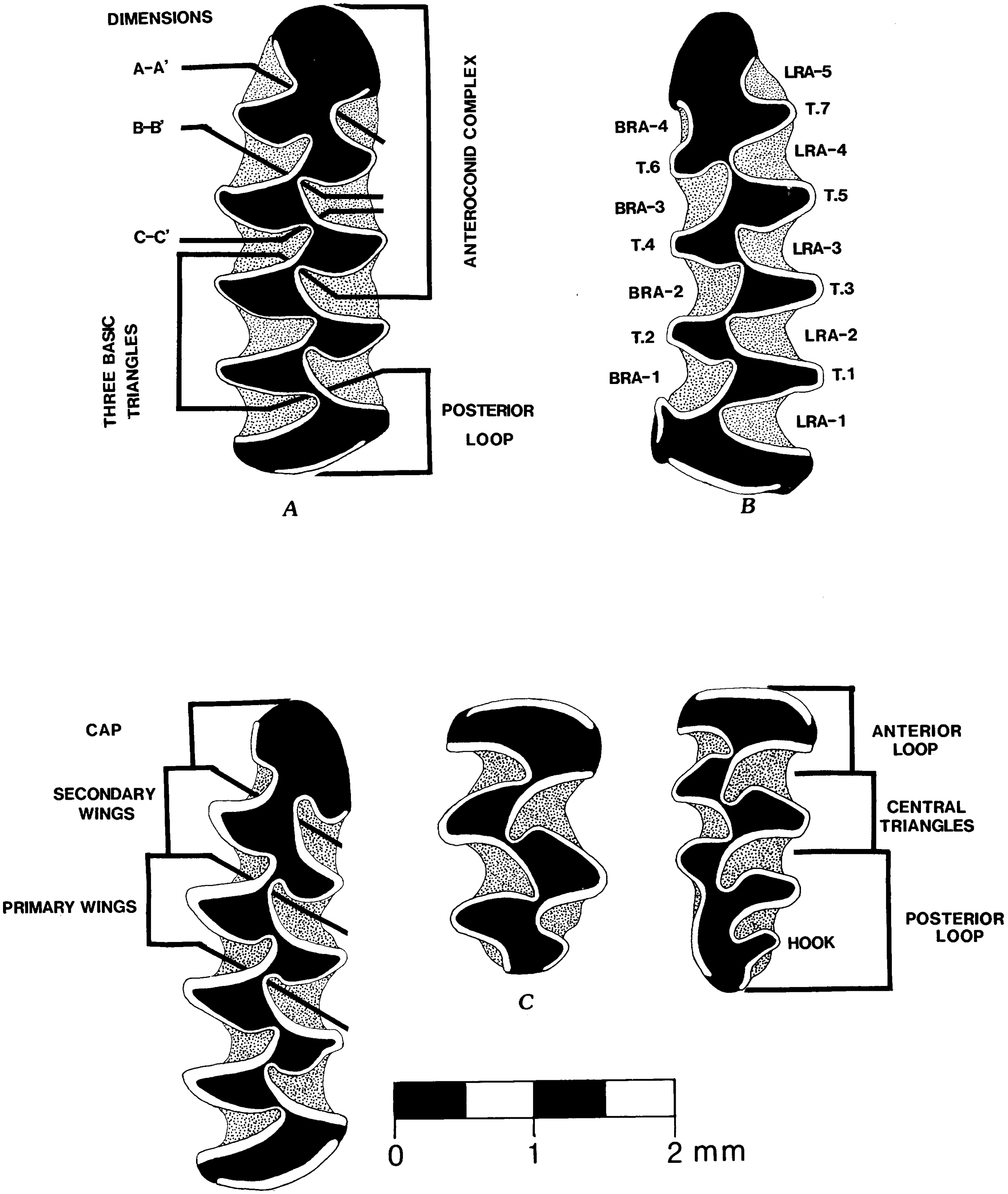
Discussion.—In the tribe Microtini, Dimension C–C′, between the Primary Wings of the first lower molar (fig. 10), is greatly shortened and separates (or nearly separates) the two Primary Wings; the buccal wing forms Triangle 4. Dimension B–B′ may remain the same as in *Allophaiomys* or may be greatly shortened, closing the dentinal confluence between the lingual Primary Wing and the Cap, thus forming Triangle 5. Dimension A–A′ may equal the width of the Cap (no sign of Secondary Wings) or be greatly reduced, creating a lingual or both Secondary Wings. M\3 is simple or complex, but is complex in the majority of living species.

Note that the above diagnosis is simplified and not universally accepted. If Dimension C–C′ can be shortened in an *Allophaiomys* morphotype to produce a member of the tribe Microtini, there seems to be no reason why this dimension could not also be shortened in a member of the tribe Pitymyini more derived than *Allophaiomys*, thus producing a species of the Microtini from a species of the Pitymyini. This is not evident in the North American record, and thus may be not fully appreciated by the author.

Chaline (1972, p. 300) was possibly the first to defend such a suggestion with illustrations, and he implicated the *gregalis*, *agrestris*, and *arvalis* groups of *Microtus* in an origin out of more ancient species of *Terricola* (his *Pitymys*), such as *T. hintoni*. He provided no population data. It is the present author's impression that such concepts are based on very small samples and upon the configuration of the Cap of the Anteroconid Complex, the most variable part of the first lower molar. However, the present author has not had opportunity to review the pertinent faunas, and Chaline's opinion still persists among many authorities, particularly regarding the *gregalis* group (subgenus *Stenocranius*).

"*Mimomys*" enamel-thickness differentiation is very rare (but see fig. 16*A*), intermediate differentiation is usual in many fossil forms, and all living species have "*Microtus*" enamel differentiation, with the exception of

Figure 10 (facing page). *Microtus* and *Terricola* with illustrations of dental terms. *A*, *Microtus californicus* (LACM 24540 from Locality LACM 6683) and *B*, *Terricola meadensis* (LACM 24828 from Locality LACM 68123), first lower molars from the Anza-Borrego Desert of California. *C*, *Microtus californicus* (UCMP 71258), first lower and second and last (third) upper molars (UCMP 71257) from the Irvington fauna, California (Locality UCMP V-3604). Second upper molar (center) shows incipient additional posterior dentine field typical of the species. Note that the Secondary Wings on the first lower molars of *M. californicus* are confluent; this has led some to place these specimens in the genus *Pitymys*; the Primary Wings are, however, separated by a closed Dimension C–C′ and the specimens conform to the morphology of *Microtus*. Explanation of dental morphologic terms used throughout text: T., triangle; BRA, buccal reentrant angle; LRA, lingual reentrant angle. Anterior is up; posterior is down. Lingual is to left in left-hand drawings, to right in right-hand drawings and *C*. Posterior loops extend lingually.


DIMENSIONS
A-A'
B-B'
C-C'
THREE BASIC TRIANGLES
ANTEROCONID COMPLEX
POSTERIOR LOOP
A
LRA-5
T.7
BRA-4
LRA-4
T.6
T.5
BRA-3
T.4
LRA-3
BRA-2
T.3
T.2
LRA-2
BRA-1
T.1
LRA-1
B
CAP
SECONDARY WINGS
PRIMARY WINGS
C
ANTERIOR LOOP
CENTRAL TRIANGLES
POSTERIOR LOOP
HOOK
0
1
2 mm

Microtus xanthognathus that usually has intermediate differentiation. Martin (1987) has noted that the poorly known Central American *M. oaxacensis* also has intermediate enamel-thickness differentiation and that *Herpetomys guatemalensis* and *Orithriomys umbrosus* have "*Mimomys*" differentiation.

Those North American faunas containing *Allophaiomys* that are younger than 850,000 years show varying degrees of morphologic shift away from typical *A. pliocaenicus* and toward living North American *Pitymys* and *Pedomys*. In none of these is there a morphologic overlap in individual variability between *Allophaiomys* and *Microtus*. In North American faunas that are older than 850,000 years, a direction of variation toward the Microtini is known only from SAM Cave, New Mexico; this is the unique population with a trend of *Allophaiomys* toward the North American microtine genus *Lemmiscus*. Otherwise, the origins of the tribe Microtini are in the Old World.

The genus *Lasiopodomys* has been used for more than 10 years by the author to indicate an evolutionary grade between *Allophaiomys* and *Microtus*. This usage was first made by Repenning in 1978, was defined by Repenning in 1983, defined in more detail by Repenning and Grady (1988), and is restated in the present report. The concept of what should be called *Microtus* is the same for the present author and V.S. Zazhigin (who placed *Lasiopodomys* in *Allophaiomys*), but their usage is more restricted than that of many authors, including Markova (1990), who include *Lasiopodomys* in *Microtus*. As discussed in the preceding section, "Classification," the majority of current students of microtine rodents would place all genera discussed in the present report in the genus *Microtus*.

The less specifically varied and more provincial genera *Proedromys* and *Lemmiscus* are also mentioned under the tribe Microtini.

GENUS *LASIOPODOMYS* LATASTE, 1887

(fig. 11)

Type species.—*Arvicola brandtii* Radde, 1861.

Type locality.—Northeast Mongolia, P.R.C.; locality 30, in fig. 1.

Revised dental diagnosis.—A genus of the tribe Microtini with no development of Secondary Wings or of Dimension A–A′ on the Cap of the Anteroconid Complex of the first lower molar, except in living and some fossil forms of the Oriental faunal region, and having a simple last upper molar (see discussion).

"TYPICAL" *LASIOPODOMYS*

Revised dental diagnosis.—As for the genus.

Selection of "typical" morphology.—As defined in the living and fossil fauna of the Oriental faunal region (Transbaikalia, Mongolia, and the People's Republic of China with minor extensions following topography through the Himalaya), *Lasiopodomys* is a genus of the tribe Microtini with a Dimension B–B′ on its first lower molar that is reduced to the point of closure at the confluence between Triangle 5 and the Cap. It also has slight to moderate reduction of Dimension A–A′, forming a weak Secondary Wing or Wings (fig. 11*N*, *O*). These conditions describe the most advanced morphology of the first lower molar in the genus and this morphology is known only in the Oriental faunal region. Universally, the genus has a simple last upper molar.

As *Lasiopodomys* is known in the fossil record of the rest of the Northern Hemisphere (fig. 11), Dimension B–B′ usually is wide or only moderately constricted, Triangle 5 is not fully formed and is confluent with the Cap, and Dimension A–A′ is not evident although a posterolingual angularity may appear on the Cap. One exception is noted herein of a very advanced form from the Hanover Quarry Fissure fauna of Pennsylvania (fig. 11*L*, *M*).

In the Oriental region, *Lasiopodomys brandtioides* is known from mammal zone VI of Zheng and Li (1990; Gongwangling age), which is close to being the oldest record for the genus (mid-Matuyama age; ≈1.3 Ma); and it is more advanced than the specimens from the Hanover Quarry Fissure fauna (≈0.83 Ma). The oldest record for the genus, *Lasiopodomys praebrandtii* from the Kudun fauna of Buryat south of Lake Baikal, is of the more simple and primitive form (see Repenning and Grady, 1988, fig. 4*B*) and is similar in structure to the specimens of figure 11*B–G*; the individual variation of this species overlaps the morphology of *Allophaiomys* (Erbaeva, 1976). The fauna is believed to be about the age of the Olduvai event on faunal grounds (Repenning and others, 1990). Buryat is in western Transbaikalia, the northwesternmost part of the Oriental faunal region as herein defined.

In all areas other than the Oriental faunal region, the appearance of dimension A–A′ on the Cap of the first lower molar marks the morphologic beginning of *Microtus*, and this condition appears before the last upper molar becomes complex, as indicated by one associated upper and lower dentition from the oldest faunas of the Hansen Bluff faunal sequence in Colorado (fig. 12*A*), or as indicated by several living species of *Microtus*. The last upper molar is simple in living and fossil forms of *Lasiopodomys*. As a generalization, typical *Lasiopodomys*, known from abundant fossil records throughout the Northern Hemisphere, differs from *Allophaiomys* only by the closure of Dimension C–C′. Some workers have assigned such fossils to either *Allophaiomys* or to *Microtus*, as has been noted. This different usage has caused many erroneous biochronologic correlations, as has also been noted.

Thus we have the somewhat awkward situation in which the living species of the genus are very advanced forms living only in the Oriental faunal region. Most of the fossil species in this region are similarly advanced. Elsewhere, from Maryland to California, from northern Canada to northern Yakutia across Beringia, across Siberia to the Ural Mountains and westward through Kazakhstan and the Ukraine to central Europe (but not to France or Holland), a common early Pleistocene form of *Lasiopodomys* was present that is much less advanced toward *Microtus* than most fossil or living species of the Oriental faunal region. If the remains of living *Lasiopodomys brandtii* were found in the United States, they would be thought to be a primitive species of *Microtus* and possibly more than 800,000 years old. Compare figure 11*N* (living *Lasiopodomys brandtii*) with figure 12*A* (820,000 year old primitive *Microtus paroperarius* from Colorado) and with figure 12*C* (a fossil representative of the living *Microtus nivalis* from Czechoslovakia). Both of these examples of *Microtus* can have a simple last upper molar; that of the illustrated specimen of *Microtus paroperarius* (a gigantic individual) is also illustrated (fig. 12*A*).

In view of the "atypical" morphology of most *Lasiopodomys* species from the Oriental faunal region (where the genus exclusively lives today), the present author has taken the liberty of declaring the more primitive form known in the fossil record of the rest of the Northern Hemisphere as having the "typical" first lower molar morphology of the genus (fig. 11*B–G*).

The extinct fossil species *Lasiopodomys deceitensis* (Beringia and North America) and (or) *L. ratticepoides* (Eurasia exclusive of Beringia) are considered typical for the genus. *L. deceitensis*, described (as *Microtus deceitensis*) from the Cape Deceit fauna of Alaska (Guthrie and Matthews, 1971), has more frequent posterobuccal angularities on the Cap than do some. (See figs. 11, 15, 16, and 17.)

L. ratticepoides was described (as *Microtus ratticepoides*) from the Upper Freshwater Bed at West Runton, England, by Hinton (1923). It is considered by many to be ancestral to those living species of *Microtus* that have a relatively simple first lower molar, such as *M. oeconomus*. This may be so, but *M. oeconomus* has a complex last upper molar, and *Lasiopodomys* does not. The last upper molar of *Microtus* (or *Lasiopodomys*) *ratticepoides* has never been identified, and may not be cited in defense of the generic assignment. It is, therefore, possible that the form from European late Biharian faunas (Koneprusy C–718 and Upper Freshwater Bed) may indeed have a complex M\3 and may be ancestral to *M. oeconomus*, while middle Biharian faunas (Holstejn, Chlum 6, and Valerots) may have a simple M\3 and might be called "*L. preratticepoides.*" This possibility cannot be confirmed without further examination of the collections. Lacking this, one cannot say when *Lasiopodomys* became extinct in Europe.

The distinctively different history of evolution of *Lasiopodomys* in the Oriental faunal region is one of several examples illustrating the relative isolation of this region, indicating its provincial faunal nature. Other examples among the microtines will be mentioned, and Flynn and others (1991) have suggested a similar provincial isolation because of other and older aspects of the Chinese fossil fauna.

The recognition of a separate genus *Lasiopodomys* is a compromise: It provides a name for intermediate forms that have been assigned either to the more primitive *Allophaiomys* or to the more advanced *Microtus*. The evolutionary history, dispersal patterns, and environmental preferences of *Lasiopodomys* are different than those of the genera to which it has been elsewhere assigned. Therefore, its recognition as a distinct taxon is informative. This recognition permits the definition of *Allophaiomys* as limited to an open Dimension C–C′ and that of *Microtus* as beginning with the presence of Dimension A–A′. The morphologic limits of these two genera, respectively the ancestor and the descendant of *Lasiopodomys*, have been too vague in previous delineations of these genera.

Erbaeva (1976) was the first to assign "typical," primitive fossil forms to the genus *Lasiopodomys*; advanced fossil forms from China, assigned to the genus much earlier (Young, 1934), differ little from the living species and indicate a different, but parallel, history in the Oriental faunal region. Repenning (1980) followed Erbaeva's usage of 1976.

Character evolution.—"Intermediate" enamel-thickness differentiation is most common in fossil populations of *Lasiopodomys*, although "*Mimomys*" differentiation is known (fig. 16*A*) and most, but not all, advanced forms have "*Microtus*" differentiation.

Evolutionary advancement of the genus is marked by increasing percentages of "*Microtus*" enamel-thickness differentiation, increasing prominence of either or both lingual and buccal posterior angularities on the Cap (eventually leading to Secondary Wings in *Microtus*), and narrowing of Dimension B–B′ (fig. 11). These changes lead to the living species of *Lasiopodomys*, and to the genus *Microtus*.

The most primitive described morphotype of *Lasiopodomys* is found in the species *Lasiopodomys praebrandtii*, described by Erbaeva (1976) from the Kudun fauna of Buryat A.S.S.R., south of Lake Baikal. In this species, reduction of Dimension C–C′ is evident only in some individuals. Reduction is never complete, never completely closing the buccal Primary Wing to form Triangle 4 (Repenning and Grady, 1988, fig. 4*B*). The generic assignment has been questioned (M.A. Erbaeva, oral commun., 1987). Depending upon morphotype percentages within the sample, the species might be more appropriately considered an advanced species of *Allophaiomys*, but population characteristics are not available. As the species is not in question, the intermediate arbitrary name might be "*Allophaiomys-Lasiopodomys praebrandtii.*"

Lasiopodomys praebrandtii is a small species, having a first lower molar that is little more than 2 mm long. The small size may be a provincial character, as Zheng and Cai (1991) have recently described *Lasiopodomys probrandtii* from Weixian County, Hebei Province, P.R.C., that is morphologically similar to *Lasiopodomys deceitensis*, but smaller. The sample was of fairly large size. Zheng and Cai have considered *L. probrandtii* to be as old as about 1.2 million years, roughly the same age as older records of the derived *L. brandtioides,* which suggests the existence of two lineages of *Lasiopodomys* in China, one of which is smaller and has an evolutionary rate more comparable with that of extra-Chinese *Lasiopodomys*.

The age of the Kudun fauna has not been determined by external evidence. It is here believed to be about the age of the Olduvai event on the basis of the associated fauna. No other record of *Lasiopodomys* is thought to be as old.

"Typical" forms have been described from central Europe to China, but have been listed as *Allophaiomys* or *Microtus*; some of these clearly show an individual variation of morphotypes overlapping that of *Allophaiomys*, but none show a mode so apparently intermediate as that from the Kudun fauna, and none are securely dated.

When and where *Lasiopodomys* first evolved out of *Allophaiomys* is not at all clear. One is impressed with the suggestion of mosaic evolution, but frustrated in the effort to recognize a possible center of origin by the lack of external time control.

By the diagnosis here used, the living species of *Lasiopodomys* (*L. brandtii* and *L. mandarinus*) and some advanced Chinese fossil species, such as *Lasiopodomys brandtioides* (Young, 1934), have primitive *Microtus* first lower molar morphotypes; they have a weak development of at least the lingual Secondary Wing on the Cap of first lower molar (fig. 11*N*, *O*). The presence of a simple last upper molar is not universally exclusive of *Microtus*, as the earliest forms of this genus had simple last upper molars and some living lineages retain them. The living species of *Lasiopodomys* could be considered as primitive species of *Microtus* as here defined.

As here defined, based on the character states of fossil species included in the genus, *Lasiopodomys* is a genus intermediate between ancestral *Allophaiomys* and derived *Microtus*. With the exception of *Lemmiscus*, which evolved directly out of *Allophaiomys* in the United States, and *Proedromys*, whose derivation is not yet known, *Lasiopodomys* initiates the lineage of the tribe Microtini and leads to the obviously polyphyletic genus *Microtus* (fig. 14).

Although overlapping individual variability correctly indicated to Chaline (1972) that *Microtus* evolved from *Allophaiomys*, a conclusion that this evolutionary sequence is documented in France is not indicated by the faunas Chaline considered. He described no fauna with a population of "typical" *Lasiopodomys*, although he illustrated advanced forms of *Lasiopodomys* (with prominent lingual and buccal posterior angularities on the Cap) under the name *Microtus nivalis*, from the localities Combe Grenal, Regourdou, and Hortus (Chaline, 1972, figs. 58 and 59). Only one individual variant described by him is a "typical" morphotype; it is from Regourdou (no. 10 of his fig. 58).

To judge from the illustrations of Chaline (1972), *Lasiopodomys* (or the *Lasiopodomys* morphotype in primitive *Microtus* populations) was an immigrant to France at a late date, possibly middle to late Biharian, and at an advanced stage; the beginning of the tribe Microtini took place elsewhere.

Discussion.—That the application of names to forms here included in the genus *Lasiopodomys* varied greatly led directly to the misunderstanding of the age of the Olyor Suite in Yakutia, which stimulated this discussion. It also led to the invalid conclusion that the age of the Olyor Suite was comparable to that of the Karay-Dubina fauna of the Ukraine. It was not realized that what was called *Allophaiomys* in the Olyor faunas was called *Microtus* in the Karay-Dubina fauna. Each misunderstanding, based as it was upon acceptance and use of names that appeared in published lists rather than upon comparison of specimens, led to erroneous interpretations of the paleomagnetic patterns and thus to errors in temporal correlation nearly as great as a million years.

As here used, the morphologic point of first discrimination of *Lasiopodomys* of tribe Microtini from *Allophaiomys* of tribe Arvicolini is the essential closure of Dimension C–C′ (fig. 10), separating the Primary Wings of the Anteroconid Complex and producing Triangle 4 in an otherwise typical *Allophaiomys* first lower molar (fig. 11). This is the only consistent dental character that defines the morphologic beginning of *Lasiopodomys* and the tribe Microtini. It is a character completely lacking in the type population of *Allophaiomys pliocaenicus* and, hence, in the genus.

Except in the Oriental faunal region, the first point of discrimination of *Microtus* from *Lasiopodomys* lies in the development of one or both Secondary Wings on the Cap of the Anteroconid Complex of the first lower molar of *Microtus* (Repenning and Grady, 1988). This is the only consistent

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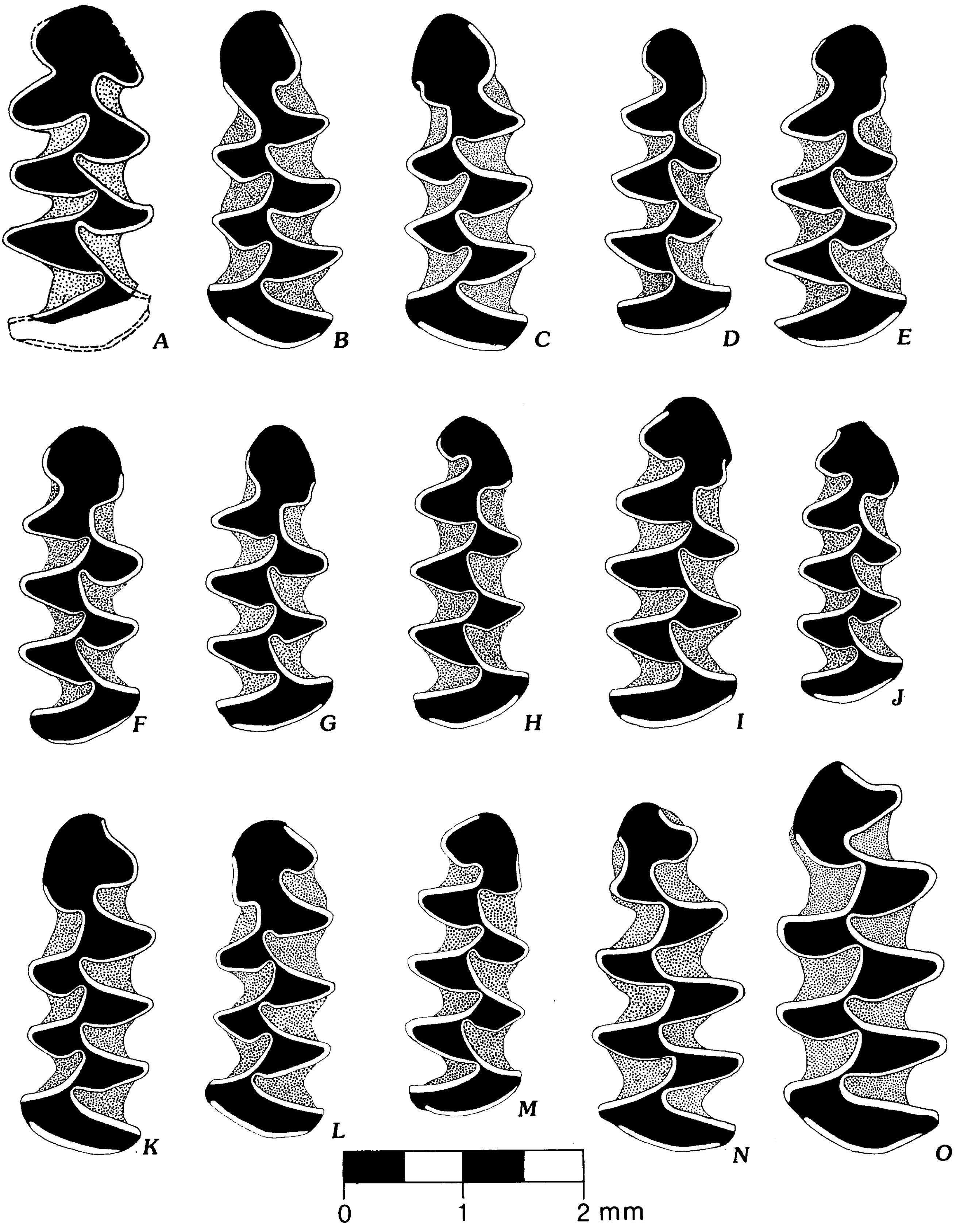
Figure 11 (facing page). *Lasiopodomys*. *A*, *Lasiopodomys* sp., Anza-Borrego Desert, California; LACM specimen; outline dashes indicate incomplete parts of specimen. *B*, *Lasiopodomys ratticepoides*, Locality C718, Czechoslovakia. *C–K*, *Lasiopodomys deceitensis* from: *C*, County Line, Illinois; ISM specimen. *D–I*, Cheetah Room fauna, West Virginia; USNM specimens. *J*, *K*, Cheetah Room fauna, individuals overlapping *Microtus* morphology; USNM specimens. *L*, *M*, ?*Lasiopodomys* sp., advanced morphology from Hanover Quarry Fissure, Pennsylvania (sample consists of three specimens); CMNH specimens. *N*, *Lasiopodomys brandtii* from Inner Mongolia, P.R.C., living species; USNM specimen. *O*, *Lasiopodomys mandarinus* from Korea, living species; USNM specimen.


A
B
C
D
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2 mm

dental character that defines the morphologic beginning of *Microtus*, as here defined, and even this character state is violated by the advanced state of living *Lasiopodomys* and similarly advanced fossil forms of eastern Asia.

In the consideration of the earliest records of *Microtus paroperarius* that follows, the development of Secondary Wings in the living *Lasiopodomys* species of eastern Asia is regarded as independently derived, and *Microtus* is recognized in the United States and Eurasia (excluding the Oriental region) with the first modal development of one or both of these wings. Although not always developed, a great reduction in Dimension B–B′, forming Triangle 5 on the first lower molar, and the development of a complex last upper molar are also indicative of *Microtus*.

In the introductory section on Conventions, it was stated that the system of diagnostic dimensions followed that of van der Meulen (1973) with one significant addition called Dimension A–A′, the distance between the reentrants anterior to the secondary wings of the present report (fig. 10). Van der Meulen (1973; 1978) actually recorded this dimension, naming it dimension D–D′—the width of the Cap. He considered it to be present in *Allophaiomys*, in which no reentrants are present on the Cap, and to be present in morphologically advanced forms with Secondary Wings, such as are shown in figure 10 of the present report. In these advanced forms van der Meulen's dimension D–D′ does not show the width of the Cap, but rather the narrowness between the reentrants on the Cap anterior to the Secondary Wings. When reentrants are present (making Secondary Wings), van der Meulen's dimension D–D′ is always less than the width of the Cap (van der Meulen, 1973, fig. 22) and it corresponds to the Dimension A–A′ of the present report; when reentrants are not present, van der Meulen's dimension D–D′ is the width of the Cap (van der Meulen, 1978, fig. 3), but the Dimension A–A′, as herein used, does not exist.

To avoid possible confusion in usage, a Dimension A–A′ (an alphabetical symbol not used by van der Meulen) is used in the present report and it is not considered the same as van der Meulen's dimension D–D′. The Dimension is considered to be present only when reentrants have developed anterior to the Secondary Wings; it is not present in *Allophaiomys* or typical *Lasiopodomys*, whereas van der Meulen's dimension D–D′ is.

The transition of *Microtus* out of *Lasiopodomys* or *Lasiopodomys* out of *Allophaiomys* is understood to take place within the modal morphology of the population; it may not be represented in individual variants of low abundance in populations. An *Allophaiomys-Lasiopodomys* transitional fauna, showing this origin of the Microtini, is not known from North America. *Lasiopodomys* evolved from *Allophaiomys* in Eurasia, and both genera dispersed to North America, but at greatly different times.

Little difference in the morphology of different North American populations of *Lasiopodomys* has been recognized, and nearly all are assigned to *Lasiopodomys deceitensis* (Guthrie and Matthews) (1971), named (as *Microtus deceitensis*) from the Cape Deceit fauna of Alaska. (See fig. 17.) The present author is currently unable to separate *L. deceitensis* from Eurasian *Lasiopodomys ratticepoides* (Hinton) (fig. 11*B*), but retains the separate names until further study can be made. It is considered possible that the genus *Lasiopodomys* is not represented by the type population of *Microtus ratticepoides* Hinton, as the last upper molar has not been described. If it were complex, the species *ratticepoides* should remain in the genus *Microtus*.

LASIOPODOMYS FROM THE ANZA-BORREGO DESERT

(fig. 11*A*; locality 21, fig. 1)

In the Anza-Borrego Desert of southernmost California (lat 33°10′ N.), 39 miles (62 km) north of the border of Mexico, west of the Salton Sea and on the western flank of the Imperial Valley, lies an extensive and continuous exposure of sediments extending upward from the marine Imperial Formation, of late Miocene and early Pliocene age, essentially to the top of the lower Pleistocene (Downs and White, 1968). The section has paleomagnetic control from the Nunivac Normal-polarity Subchron of the Gilbert Reversed-polarity Chron to what has been assumed to be the Jaramillo Normal-polarity Subchron of the Matuyama Reversed-polarity Chron (Johnson and others, 1984), but which must represent the beginning of the Brunhes Normal-polarity Chron.

Sedimentation rates have been calculated throughout this section and, in that part between the Olduvai and the purported Jaramillo events, there appears to have been very little variation (Johnson and others, 1984). *Terricola meadensis* (fig. 10*B*) was found in this part of the Anza-Borrego Desert section (the Vallecito Creek fauna; LACM Locality 68123, specimen number LACM 24828) below the youngest normal magnetic interval in a continuous part of the section with other faunas used in characterization of the late Vallecito Creek mammalian fauna (J.A. White, written commun., 1990). There is no record of *Terricola meadensis* in the United States that is as old as the Jaramillo event and this immigrant indicates an age younger than 850,000 years. Thus the youngest normal-polarity zone represents the Brunhes Chron, and sediment rates must be less than was calculated on the basis of this polarity being the Jaramillo event. More importantly, at least one period of nondeposition is indicated by the lack of a record of the Jaramillo event in the section. This decreasing depositional rate, with gaps of no deposition, is more consistent with the subsequent record of orogenic activity that resulted in elevation and the cessation of all deposition in the Anza-Borrego part of the former basin (Johnson and others, 1984).

Although microtine rodents are not common in the Anza-Borrego Desert deposits because of the southern location, a few of some significance to the present discussion have been recovered: *Microtus*, *Lasiopodomys*, and, as just mentioned, *Terricola* (figs. 10*A* and *B*, and 11*A*). Figure 11*A* shows the only tooth with a *Lasiopodomys* morphotype from the Vallecito Creek faunal sequence in the Anza-Borrego Desert. It is a very damaged specimen, but what is preserved clearly indicates that it is a *Lasiopodomys* morphotype. It is the only microtine tooth from LACM Locality 1942 (ANZA–2 on fig. 14), which is 540 feet (164.6 m) below the Brunhes Chron and 1,000 feet (304.8 m) above the Olduvai normal event (J.A. White, written commun., 1990). Assuming the uniform depositional rates that have been calculated (Johnson and others, 1984), it is about 1.10 million years old. This is older than the Jaramillo event, which was not recorded in the section, and therefore the age should be older than this calculation by at least the duration of this event (70,000 years) or about 1.17 million years. An age of about 1.2 million years is thus assumed for the specimens of *Lasiopodomys*, although it is not possible to judge what other irregularities in deposition are present in the long reversely polarized section. Although quite speculative, this approximate interpolated age is quite close to a Northern Hemisphere cold period (Repenning and Brouwers, 1992) that climaxed just before the Cobb Mountain Normal-polarity Subchron (1.10 Ma), suggesting a correlation between the southward dispersal of *Lasiopodomys* from Beringia and climate change.

Although imperfectly preserved and inadequate as a representative sample of the population, what is preserved (fig. 11*A*) is clearly a *Lasiopodomys* morphotype; and it seems probably older than the oldest immigrant *Lasiopodomys* to the east of the Rocky Mountains (about 840,000 years old). It provides some suggestion of the possible age of the genus and also a suggestion of differing dispersal and evolutionary histories on either side of the Rocky Mountains of North America. The last suggestion has been discussed in consideration of the *Allophaiomys* and *Microtus* from Wellsch Valley, Saskatchewan, and is discussed again in the section, "Provinciality." This is the only known specimen of *Lasiopodomys* from west of the Rocky Mountains.

LASIOPODOMYS FROM THE CHEETAH ROOM FAUNA

(fig. 11*D–K*; locality 17, fig. 1)

The Cheetah Room fauna of Hamilton Cave, West Virginia, was discussed previously in connection with its *Allophaiomys* population. It is believed to be about 840,000 years old on the basis of its fauna (Repenning and Grady, 1988). The ample sample of *Lasiopodomys deceitensis* (36 M/1s in the sample seen; as noted previously, the entire sample was not seen) is apparently the oldest record south of Beringia on the east side of the Rocky Mountains of North America; it is younger than the specimen of *Lasiopodomys* from California and from Beringia.

One specimen of *Lasiopodomys deceitensis* from the Cheetah Room fauna (USNM 264316) has associated upper and lower dentition, and is the only fossil record of physically associated upper and lower dentition of this genus known to the author. The last upper molar of the individual with associated first lower molars is simple, as is equally indicated by the isolated teeth from the fauna.

Nonbimodal (unimodal) morphologic overlap was described in the separation of *Microtus* morphotypes from the *Lasiopodomys* population of the Cheetah Room fauna (Repenning and Grady, 1988). The *Microtus* morphotype was very primitive and of minor proportion (25 percent) in this population, and thus it should have been viewed only as an extreme in the individual variation of *Lasiopodomys*. The strong single mode (75 percent) of *Lasiopodomys* in this fauna (fig. 11*D–I*) was counted by considering even the slightest suggestion of a lingual Secondary Wing (fig. 11*J*, *K*) as a *Microtus* morphotype; a much smaller number (perhaps 3 percent) were obvious morphotypes of *Microtus* (Repenning and Grady, 1988, fig. 4*E*). The presence of *Microtus* morphotypes in the *Lasiopodomys* population from the Cheetah Room fauna justifies a separate species name within *Lasiopodomys*, although none has been or is suggested.

The most *Microtus*-like individual in the Cheetah Room fauna was illustrated by Repenning and Grady (1988, fig. 4*E*). Except that it is smaller, it is quite similar to the specimen shown from the older part of the Hansen Bluff faunal sequence (this report, fig. 12*A*; Repenning and Grady, 1988, fig. 4*K*; these are left and right teeth of the same individual). This most advanced *Microtus* morphotype of *Lasiopodomys* from the Cheetah Room fauna resembles the primitive *Microtus paroperarius* morphotypes of Cumberland Cave (van der Meulen, 1978, figs. 11A, D, F, and G), and of Hansen Bluff (fig. 12*A*), and the more primitive variations of the typical population from the Cudahy fauna of Kansas (fig. 12*B*; also see Paulson, 1961, figs. 7A–D and H). It is unlike the *Lemmiscus* morphotypes in the variation of *Allophaiomys* from SAM Cave, New Mexico, which, as has been noted, show development of primarily the buccal Secondary Wing (fig. 6*F*, *G*).

Even these weak indications of the *Microtus* morphotype are not recorded in the very small sample from Hanover Quarry Fissure (fig. 11*L*, *M*), but this sample also has no typical morphotypes of *Lasiopodomys deceitensis*. The low variability of the population of *Pitymys cumberlandensis* from the Hanover Quarry Fissure fauna and the presence of *Allophaiomys guildayi* and typical *Synaptomys* indicate that the Hanover Quarry Fissure fauna is younger than the Cheetah Room fauna.

As discussed in the later section, the *Lasiopodomys* and *Microtus* morphotypes in the Cumberland Cave fauna, Maryland, also lack a bimodal distribution in this population. The single mode is within the *Microtus* morphotypes, although very close to the defined boundary between this genus and *Lasiopodomys*. Three situations indicate that the Cumberland Cave fauna is more derived than the Cheetah Room fauna: (1) the Cheetah Room fauna contains a *Lasiopodomys* modal morphology (rather than the *Microtus* modal morphology in the Cumberland Cave fauna), (2) morphologic gradation occurs between *Pitymys cumberlandensis* and *Allophaiomys* in the Cheetah Room fauna (contrasting with the polarity of the *Pitymys* morphology in Cumberland Cave), and (3) the gradation between the lemmings *Synaptomys* and *Mictomys* in the Cheetah Room fauna (Repenning and Grady, 1988) contrasts with the morphologic polarity of these two genera in Cumberland Cave fauna.

?*LASIOPODOMYS* FROM THE HANOVER QUARRY FISSURE FAUNA

(fig. 11*L* and *M*; locality 16, fig. 1)

The Hanover Quarry Fissure fauna was discussed previously in connection with its population of *Allophaiomys guildayi*. Its age is close to that of the Cumberland Cave fauna, but it may be slightly older because, although very small, the sample of ?*Lasiopodomys* sp. contains no *Microtus* morphotypes, whereas over half the population in Cumberland Cave was of *Microtus* morphotypes, and in the Hanover population of *Allophaiomys guildayi* a lower percentage of individuals exhibit a *Pedomys* morphotype than in the Cumberland Cave population (Guilday and others, 1984, p. 121).

The few individuals (five were listed by Guilday and others, 1984, two more than were available for the present study) of ?*Lasiopodomys* were originally referred to *Microtus paroperarius* (Guilday and others, 1984) because they conform to morphotypes of *Lasiopodomys* that van der Meulen (1978) included in *Microtus paroperarius* when describing the Cumberland Cave fauna. Although not sufficiently derived to fit the morphologic definition of *Microtus*, the morphology of all three specimens is quite advanced for *Lasiopodomys* (fig. 11*L*, *M*). Salient angles are present at the positions of the Secondary Wings, but the Wings are not present; the anterior portion of the Cap is not enlarged so that the position, or existence, of Dimension A–A′ is not indicated. In addition, the separation of Triangle 5 (the lingual Primary Wing) from the Cap is complete in one individual (fig. 11*M*), and reduction of Dimension B–B′ is complete. ?*Lasiopodomys* from Hanover Quarry Fissure is very close to living *Lasiopodomys mandarinus* (fig. 11*O*), as are *Microtus* variants of *Lasiopodomys* from the Cheetah Room fauna (fig. 11*J*, *K*).

Strict adherence to the definition of *Microtus*, as forms first being recognized with the development of Secondary Wings and a Dimension A–A′, requires that these few individuals from Hanover Quarry Fissure be called advanced *Lasiopodomys* morphotypes. The morphology of these specimens is similar to some morphologies found in the Cumberland Cave samples that have been placed in *Microtus paroperarius*, but nearly half the Cumberland Cave population consists of *Lasiopodomys* morphotypes.

The Hanover Quarry Fissure fauna contains nothing that resembles the first lower molar of typical *Microtus paroperarius* or of typical *Lasiopodomys deceitensis*. Without a population sample of sufficient size, determining the modal morphology is impossible, and generic assignment is uncertain.

LASIOPODOMYS FROM THE CUMBERLAND CAVE FAUNA

(locality 11, fig. 1; illustrated in van der Meulen, 1978)

The Cumberland Cave fauna of western Maryland has been discussed in connection with its population of *Allophaiomys guildayi*. As just mentioned, it also contains a population that was referred to the species *Microtus paroperarius* by van der Meulen (1978). He showed an overlap in variability between the morphotypes of *Lasiopodomys* (his figs. 11B, C, and E) and *Microtus* (his figs. 11A, D, F, and G) in this sample, although he referred the entire sample to *M. paroperarius*.

Because van der Meulen did not consider Dimension A–A′, the development of which is indicated by the appearance of the Secondary Wing or Wings that define *Microtus*, and did not indicate what percentage of the Cumberland Cave population has these morphotypes, it is not clear from his report what genus should be recognized in the fauna.

A total of 178 first lower molars from the Cumberland Cave fauna are here assigned to *Microtus paroperarius-Lasiopodomys deceitensis*. These M/1s are composed of "typical" *Lasiopodomys deceitensis* (15 percent) and "advanced" *Lasiopodomys* morphotypes having a posterolingual corner on the Cap similar to figure 11*I–M* (26 percent). "Primitive" *Microtus*, with at least the lingual Secondary Wing in evidence (and often a weakly developed buccal one) similar to figures 11*O* and 12*B*, *C*, or *D*, constitutes the largest part of the population (42 percent). A smaller portion (17 percent) is made up of "unquestionable" but still primitive *Microtus paroperarius* similar to forms from the oldest faunas of the Hansen Bluff faunal sequence, to a few morphotypes from the Cheetah Room fauna, and to the more simple morphotypes from the type population of the Cudahy fauna. All *Microtus* morphotypes thus make up 59 percent of the population, although only 17 percent would be considered "typical" on the basis of the type population from the Cudahy fauna. There are no advanced, complicated *Microtus* morphotypes in the Cumberland Cave population as there are in the type population. "*Microtus*" enamel-thickness differentiation was present in 71 percent of *Microtus* morphotypes and in 56 percent of *Lasiopodomys* morphotypes.

The unimodal morphological variation has its mode very close to the diagnosed taxonomic boundary between the definitions of *Lasiopodomys* and *Microtus*. Diversification into two distinct species is not indicated; the anagenetic evolution of one population, grading from *Lasiopodomys* to *Microtus*, is. A slight percentage dominance of *Microtus* morphotypes suggests that the population might be called *Microtus paroperarius*, but it is very much a borderline situation, and the hyphenated name *Microtus paroperarius-Lasiopodomys deceitensis* is here assigned. It would be, and has been, very misleading to assign the entire population to either of these defined species and genera.

The Cumberland Cave fauna of Maryland records the evolution, in the United States, of *Microtus paroperarius* out of *Lasiopodomys deceitensis*. This independent evolution of one species of *Microtus* postdates many older records of *Microtus* species, which had evolved out of *Lasiopodomys* in regions other than the United States. It was not until about 450,000 years ago that species of these older lineages of *Microtus* first entered the United States east of the Rocky Mountains. The oldest record may be in the undated Porcupine Cave fauna of south-central Colorado, which contains both immigrant *Microtus* and native *M. paroperarius* (Barnosky and Rasmussen, 1988). With the immigration of Beringian-Asian *Microtus* to the United States, *M. paroperarius* appears to have become extinct, and no younger records exist.

Nearly half the population of *Microtus paroperarius-Lasiopodomys deceitensis* from Cumberland Cave consists of *Lasiopodomys* morphotypes, which should have been associated with simple last upper molars, and some of the simplest morphotypes of *Microtus paroperarius* also should have had associated simple last upper molars. Because **typical** *Microtus paroperarius* (from Cudahy, Kansas) has complicated last upper molars, van der Meulen (1978) assigned only complicated last upper molars from the collection to this species. No associated upper and lower dentitions appear to have been collected in Cumberland Cave. Of the total last upper molars collected, the number that he assigned to this species is reasonably proportionate to the number of first lower molars with *Microtus* morphotypes. It is probable, therefore, that some of the simple last upper molars from the Cumberland Cave fauna, which van der Meulen (1978) assigned to *Pitymys* and *Pedomys*, belong to more primitive morphotypes of the *Microtus-Lasiopodomys* population.

If the two first lower molar morphotypes from Cumberland Cave that van der Meulen included in *Microtus paroperarius* are not recognized as representing separate generic morphotypes, the use of the generic name *Microtus* would also be made acceptable for *Lasiopodomys deceitensis*. For example, Guilday and others (1984) identified the first lower molars of a *Lasiopodomys* morphotype (fig. 11*L*, *M*) from the Hanover Quarry Fissure fauna as *M. paroperarius* because they match the *Lasiopodomys* morphotypes that van der Meulen (1978) included in this species of *Microtus* from Cumberland Cave. Also, the single tooth of *Lasiopodomys* from the County Line fauna of Illinois was assigned to *M. paroperarius* on this basis (Miller and others, 1987).

It is generally agreed that the lineage leading to *Microtus* is *Mimomys*→*Allophaiomys*→*Lasiopodomys*→ *Microtus*. If *Microtus* is acceptable as the generic assignment for species with a *Lasiopodomys* morphotype, then, by extension, the same logic would be acceptable for *Allophaiomys* morphotypes in faunas of *Lasiopodomys* (possibly the Razdolie fauna). *Microtus* could thus become acceptable as the generic assignment of typical *Allophaiomys pliocaenicus*.

By further extension, primitive populations of *Allophaiomys*, with some individuals having less hypsodonty and rooted teeth, would then become acceptable as representatives of the genus *Microtus*. Ultimately the species now assigned to *Mimomys* and the subfamily Arvicolinae could have a history represented by the single genus *Microtus*. The purpose of taxonomy is to identify definable stages in a known history, and such treatment would identify very few. The majority of population morphotypes must conform to existing diagnoses.

Although this hypothetical possibility seems unlikely, it should be pointed out that Chaline (1972) has done exactly this, except in reverse, and has projected the generic name *Allophaiomys* well into the definitions of the genera *Microtus* and *Pitymys* by allowing nomenclature to follow gradation beyond the limits of diagnosis.

Chaline did not have complete gradation. *Microtus* did not evolve out of *Allophaiomys* in France any more than it did in North America; it originated elsewhere in faunas possibly older than any French localities considered by Chaline and immigrated to France and to North America. In nearby Holland, *Allophaiomys* became extinct before *Microtus* first appeared (van Kolfschoten, 1988).

In his treatment Chaline (1974) did nothing more, in fact, than did van der Meulen (1978) when he enlarged the definition of the species *Microtus paroperarius* to include atypical morphologies here called *Lasiopodomys deceitensis*. Van der Meulen had, in his study collection, specimens of Guthrie and Matthews' (1971) *L. deceitensis* (in the terminology of the present report), but apparently did not realize that part of his population of *M. paroperarius* was identical to *L. deceitensis*.

Although slightly more than 50 percent of the population from Cumberland Cave has a *Microtus* morphotype, the morphologic borderline condition of the population mode indicates that the identification *Microtus paroperarius-Lasiopodomys deceitensis* should be used in order to prevent creating the impression that all of the morphologies present are truly *Microtus*. As mentioned, several published references (Guilday and others, 1984; Miller and others, 1987, for example) identify typical *L. deceitensis* morphotypes as *M. paroperarius* on the strength of the name that van der Meulen gave to this Cumberland Cave population. The admittedly awkward device of a hyphenated name is here adopted to point out the morphologically intermediate nature of the population from Cumberland Cave and to avoid the inference that *Lasiopodomys* morphotypes can be included in the genus *Microtus*.

In addition to the lack of *Allophaiomys*, no *Lasiopodomys* morphotypes were present in the samples of *Microtus* from the oldest faunas of Hansen Bluff. These population conditions suggest that the Cumberland Cave fauna is older than the oldest faunas of Hansen Bluff (820,000 years) and older than was suggested by Repenning (1987); it is about the age that van der Meulen (1978, fig. 14) indicated.

As has been discussed, Cumberland Cave is younger than the Cheetah Room fauna (approximated at 840,000 years) on the basis of its having (1) a lack of individual variation in *Synaptomys cooperi* overlapping the genus *Mictomys*, as is present in the Cheetah Room fauna; (2) a very primitive *Microtus paroperarius* morphologic mode within a *Microtus-Lasiopodomys* population, rather than a *Lasiopodomys* population that overlaps *Microtus* in its variability; and (3) *Pitymys cumberlandensis* with no overlap of *Allophaiomys* in its morphologic variation. All these conditions are more progressive than has been documented in the Cheetah Room fauna (Repenning and Grady, 1988). The Cheetah Room fauna is less than 850,000 years old because it contains the Old World immigrant *Lasiopodomys*.

The Cumberland Cave fauna is here arbitrarily considered 830,000 years old, intermediate between the oldest part of the Hansen Bluff faunal sequence, which indicates a more advanced fauna, and the older Cheetah Room fauna. All these faunas lived shortly before the Brunhes Normal-polarity Chron, by the time of which *Microtus paroperarius* contained advanced individual variants, and after 850,000 years ago, when *Lasiopodomys* and *Terricola* immigrated into the United States.

LASIOPODOMYS FROM THE COUNTY LINE FAUNA

(fig. 11*C*; locality 20, fig. 1)

The County Line locality lies near the Mississippi River in central Illinois and is under study by Miller and others (1987). These authors have reported mollusks, insects, pollen, plant megafossils, and mammals from the locality, as well as reversed paleomagnetic polarity. A single first lower molar of a microtine rodent was found and was reported as *Microtus paroperarius* (Miller and others, 1987), an identification that is acceptable under the identification used by van der Meulen (1978), but not by morphologic definition as here explained. The tooth is typical of *Lasiopodomys deceitensis* (fig. 11*C*) and, as such, is in agreement with the inference that the reversed magnetic polarity represents the late Matuyama Chron.

Although the population characteristics of the single specimen from the County Line fauna are unknown, the morphotype from the County Line locality (fig. 11*C*) is that of typical *Lasiopodomys deceitensis*, rather than an advanced form of *Lasiopodomys* that could possibly be associated with some *Microtus* morphotypes. It could be an individual representing a very minor percentage of a population like that from Cumberland Cave (15 percent), but its "typical" morphology suggests that it more likely is from a more typical population of *Lasiopodomys*. Consequently, it is questionably referred to *L. deceitensis* until a larger sample might establish that the nature of the population differs from what is suggested by the single tooth. In such rapidly evolving and individually variable lineages, no certain identification of so small a sample is possible.

The age suggested by this tooth from the County Line locality is equal to or greater than that of the *Microtus-Lasiopodomys* fauna of Cumberland Cave (±830,000 years old). It could be as old as the *Lasiopodomys*-with-*Microtus*-variations fauna of Cheetah Room (±840,000 years old). It cannot be older than the approximated 850,000-year-old immigration of *Lasiopodomys* into the United States, and cannot be as young as the 820,000-year-old faunas in the Hansen Bluff sequence, which appear to postdate all *Lasiopodomys* morphotypes in the United States.

To 1992, further collecting of the locality has failed to produce additional microtine fossils (R.W. Graham, oral commun., 1990).

LASIOPODOMYS FROM THE LOCALITY CRH–47 FAUNA

(locality 25, fig. 1)

Locality CRH–47, along the Old Crow River in northern Yukon Territory, Canada, is near the Canada–Alaska border and about 100 miles (161 km) south of the Arctic Ocean in easternmost Beringia. The locality was discovered by C.R. Harington and contains a very large microtine rodent fauna that is under study by R.E. Morlan of the Archaeological Survey of Canada (R.E. Morlan, written commun., 1991). The sediments at the locality have normal magnetic polarity (Schweger, 1989). This fauna has been discussed previously in consideration of the affinity of the *Microtus* associated with *Allophaiomys* from the Wellsch Valley fauna of Saskatchewan (p. 38).

R.E. Morlan's examination of this fauna (written commun., 1991; work in progress) indicated that it contains *Phenacomys deeringensis*, named from the Cape Deceit fauna of Alaska (Guthrie and Matthews, 1971; age uncertain and to be discussed). Locality CRH–47 also contains a species of *Mimomys* (*Cromeromys*) similar to *M.* (*C.*) *virginianus* from the Cheetah Room fauna of West Virginia (Repenning and Grady, 1988; ±840,000 years old) and to *M. dakotaensis* (Martin, 1989) from the Java fauna of South Dakota (1.9–1.4 Ma); the subgenus is older than the Brunhes Chron in both North America and Eurasia.

R.E. Morlan (written commun., 1991) noted a shift in the dental pattern complexity of the collared lemming *Dicrostonyx* upsection at CRH–47, which appears to conform to the changes in pattern from *Dicrostonyx renidens* into *D. simplicior*, and, accordingly, he has referred the time-averaged sample to *D. renidens-simplicior.* This identification is in accord with an assignment of the normal polarity of the locality to the Jaramillo event, as *D. simplicior* was described from a middle Biharian fauna of Europe (Fejfar, 1966) and *D. renidens* is more primitive (Zazhigin, 1976). Zazhigin (in Sher and others, 1979) recognized the earliest *D. renidens* from Locality KLO–9 of the Krestovka Sections, in the uppermost part of the older member of the Olyor Suite (IIIa), to be discussed in the final section of this report, “Age of Krestovka Olyor and Cape Deceit faunas.” In that discussion, Locality KLO–9 is assigned an age of about 1.1 million years, 200,000 years older than the Jaramillo event.

The fauna from CRH–47 also contains *Lasiopodomys deceitensis* (also described from the Cape Deceit fauna) and an assortment of *Microtus* that includes morphotypes similar to *M. paroperarius* as well as forms that seem to be early representatives of several advanced living species (R.E. Morlan, written commun., 1991). *Lasiopodomys* became extinct farther south (in the United States) before the Brunhes Chron. It also became extinct in western Beringia before the Brunhes Chron (Sher and others, 1979, as *Allophaiomys*).

Of considerable significance in the Old Crow faunas, including CRH–47, is the total lack of *Allophaiomys* and of members of the Pitymyini; this lack in both eastern (Old Crow) and western (Krestovka) Beringia suggests a period of erosion, rather than deposition due to lowered sea level caused by the accumulation of ice on the continents. These genera were and are temperate-climate animals and they must have passed through Beringia during marked warm periods immediately following or preceding major continental glaciation. *Allophaiomys* passed through Beringia to North America just before the Olduvai event, no more than 100,000 years after a peak in continental glaciation extended south to the State of Iowa and during a remarkably warm period throughout the Northern Hemisphere. *Terricola*, of the tribe Pitymyini, entered the United States 850,000 years ago, just prior to the first of the glacial advances that have been called Nebraskan in North America (Repenning and Brouwers, 1992).

It now appears virtually certain that the normal polarity of Locality CRH–47, Old Crow basin of Yukon Territory, represents the Jaramillo Normal-polarity Subchron. This indicates that the fauna, containing no *Allophaiomys*, is of the same approximate age as the older faunas of SAM Cave, New Mexico, containing only *Allophaiomys*. Locality CRH–47 may be slightly older than the Wellsch Valley fauna of southern Saskatchewan that is intermediate in latitude and faunal composition, and contains both *Allophaiomys* (which still survived to the south) and *Microtus* (known at this time primarily to the north in Beringia), as has been discussed (p. 38).

The late derivation of *Microtus* in the Cumberland Cave fauna of Maryland (± 830,000 years old) is clearly an event uniquely occurring in the United States to the east of the Rocky Mountains, because in southern Canada east of the Rocky Mountains and at two localities in California, west of the Rocky Mountains, advanced *Microtus* lived during the reversed polarity before the Brunhes Chron, and even before the Jaramillo event in the Anza-Borrego Desert of California.

It does not seem that Locality CRH–47 can be as young as the Brunhes Chron; it contains *Lasiopodomys*, *Mimomys* (*Cromeromys*) sp. cf. *M.* (*C.*) *virginianus*, and *Dicrostonyx renidens* (R.E. Morlan, written commun., 1991) not known anywhere in the world as recently as the Brunhes Chron. Nor are these forms known from localities as old as the Olduvai event. But Locality CRH–47 is normally polarized; it can only represent the Jaramillo event.

This age interpretation is further supported by a consideration of the climate indicated by the plant remains from CRH–47 when compared with other records of the arctic region. These climatic factors are discussed in consideration of the age of the lower part of the Olyor Suite to follow, and by Repenning and Brouwers (1992).

Led by the similarities of parts of this fauna to the Cape Deceit fauna of Alaska, earlier reports by the present author (especially Repenning, 1984) correlated the normal polarity of Locality CRH–47 with the Olduvai event. This age assessment was reinforced by his misconception regarding the age of the Krestovka Olyor Suite (similar to that of the Cape Deceit fauna), as will be discussed. However, as further information was gathered about the little-known microtine historical sequence between the Olduvai and Jaramillo polarity events (the greatest lacuna in microtine biochronology), this opinion became increasingly questionable, as stated by Repenning and Grady (1988), for two reasons.

First came the realization that *Lasiopodomys deceitensis* had a rather long temporal range (Repenning and Grady, 1988). As has been discussed, *Lasiopodomys* lived until just before the Brunhes Chron in several faunas of the United States, and its oldest dated record is about 1.2 million years old, although some undated localities (especially the Kudun fauna of Buryat A.S.S.R.) may be as old as the Olduvai event.

Second, with his visit to Moscow in 1990, the author learned that his original concept of the age of the Olyor Suite of the Krestovka Sections was in error, as explained in the section, "Explanation of the problem." This information greatly strengthened the author's confidence in the biochronology of the collared lemmings, *Predicrostonyx* and *Dicrostonyx*, and required the revision of those correlations influenced by the previous interpretations of the age of the Krestovka Olyor, the Cape Deceit fauna and Locality CRH–47.

Critical to the correlation of faunal history, the fauna from Locality CRH–47 provides strong evidence of far greater diversification of *Microtus* than is known in considerably younger faunas of the United States. At the time when Locality CRH–47 was deposited, only *Allophaiomys* was present in the United States east of the Rocky Mountains; *Lasiopodomys* and *Terricola* were not introduced into the United States until 50,000 years after the Jaramillo event. And although *Microtus paroperarius* evolved out of immigrant *Lasiopodomys* in the eastern United States perhaps 80,000 years after CRH–47 was deposited, Beringian *Microtus* did not enter the United States to the east of the Rocky Mountains until about 450,000 years after the CRH–47 fauna lived, marking the beginning of the Irvingtonian III small mammal age (Repenning, 1987; as Rancholabrean I). Latitudinal provincialism is prominent in microtine history.

Lasiopodomys is an abundant part of the CRH–47 fauna and continued to be present in apparently younger faunas of the Old Crow basin (at Localities CRH–11 and CRH–64 as "*Microtus* sp. X" (Morlan, 1984, fig. 3)) coexisting with an increasing variety of advanced *Microtus* morphotypes.

Age relationships of the Old Crow basin faunas are still under study, but all these faunas that contain *Lasiopodomys* are in normally magnetized deposits. If *Lasiopodomys* became extinct in Yukon Territory before the Brunhes Chron, as it did in western Beringia (as *Allophaiomys*) and in the United States (where it is not known after about 825,000 years ago), all *Lasiopodomys*-bearing faunas of the Old Crow basin would appear to date from the Jaramillo event. However, at present no evidence suggests that *Lasiopodomys* became extinct in eastern Beringia at the same time that it did in the United States and Yakutia with the exception of those arguments presented above.

GENUS *MICROTUS* SHRANK, 1798

(fig. 12*E*; Germany; locality 32, fig. 1, exact locality uncertain)

Type species.—*Mus arvalis* Pallas, 1779; = *Microtus terrestris* Shrank, 1798.

Revised dental diagnosis.—A genus of the tribe Microtini with Secondary Wing or Wings and a Dimension A–A′. Last upper molar simple or complex.

"TYPICAL" *MICROTUS*

Revised dental diagnosis.—As for the genus.

Comment.—Living and some fossil *Lasiopodomys* from the Oriental faunal region overlap this diagnosis, as has been noted (p. 46). The generic name *Lasiopodomys* derives from this lineage, and the lineage appears to be unique to this province. Should further study indicate that these forms from the Oriental region are more properly considered as a separate lineage of *Microtus*, originating in this province at an early date, the use of *Lasiopodomys* for more simplified fossil forms of the Northern Hemisphere will become inappropriate.

This is not implausible, to judge from the present fossil record: an extremely early, advanced *Microtus* is known from the United States west of the Rocky Mountains (fig. 10*A* and *C*; California localities 21 and 22; fig. 1) which could have had its origin (fig. 14; ANZA–1 and Irvington) in such an early form of *Microtus* in the Oriental faunal region. These early Californian *Microtus* survive as the living *Microtus californicus* and have been mentioned in connection with the age of the Wellsch Valley fauna of Saskatchewan (p. 37). They will be further discussed in the major section, "Provinciality," which follows on page 74.

As here used, *Lasiopodomys* appears earlier than *Microtus* in most fossil records, and thus the generic distinction is biochronologically useful as well as morphologically definable. As has been discussed, the lack of recognition of this distinction has caused considerable variation in identification, with consequent errors in biochronologic interpretation.

Discussion.—The development of the first Secondary Wing is here considered to be marked by the first detectable indentation of the anterolingual surface of the Cap of the first lower molar, anterior to the posterolingual angularity, or corner, of the Cap found in advanced *Lasiopodomys*. The specimens of figure 11*J* and *K*, from the population of *L. deceitensis* in the Cheetah Room fauna, were counted as *Microtus* morphotypes although they hardly differ from some associated teeth counted as advanced *Lasiopodomys*. The most developed *Microtus* morphotype from this population (Repenning and Grady, 1988, fig. 4*E*) is very similar to the specimens of figures 12*A* and 16*D* of the present report.

The appearance of a complex last upper molar and, with minor exception, the extreme narrowing or closure of Dimension B–B′ are features not found in extinct morphotypes of *Lasiopodomys* (but see the living species in fig. 11*N*, *O*); they are also suggestive characters of *Microtus*, but are not always present in this genus.

Other advanced characters not always present in *Microtus* are: (1) narrowing or closure of Dimension A–A′, (2) prominent development of both Secondary Wings, (3) narrowing or closure of Dimension B–B′ (forming Triangle 5 out of the buccal primary wing), (4) closure of Dimension A–A′ (forming Triangles 6 and 7), and (5) complication of the last upper molar by development of a posterior hook and lingual third reentrant.

As here restricted the genus *Microtus* is large, complex, and unquestionably polyphyletic. The type species is *M. arvalis* (Pallas), and it incorporates all morphologic criteria (fig. 12*E*): Secondary Wings are well developed on the Cap of the Anteroconid Complex, the last upper molar is complex and has a posterior hook, and Dimension B–B′ is narrow to closed. But exceptions to these characters are common among the living species; only the presence of at least one Secondary Wing is universal. *M. oregonensis* (fig. 12*F*) and *M. nivalis* (fig. 12*C*) have an advanced M/1, but **usually** retain simple M\3s; *M. oeconomus* (fig. 12*D*) and its extinct

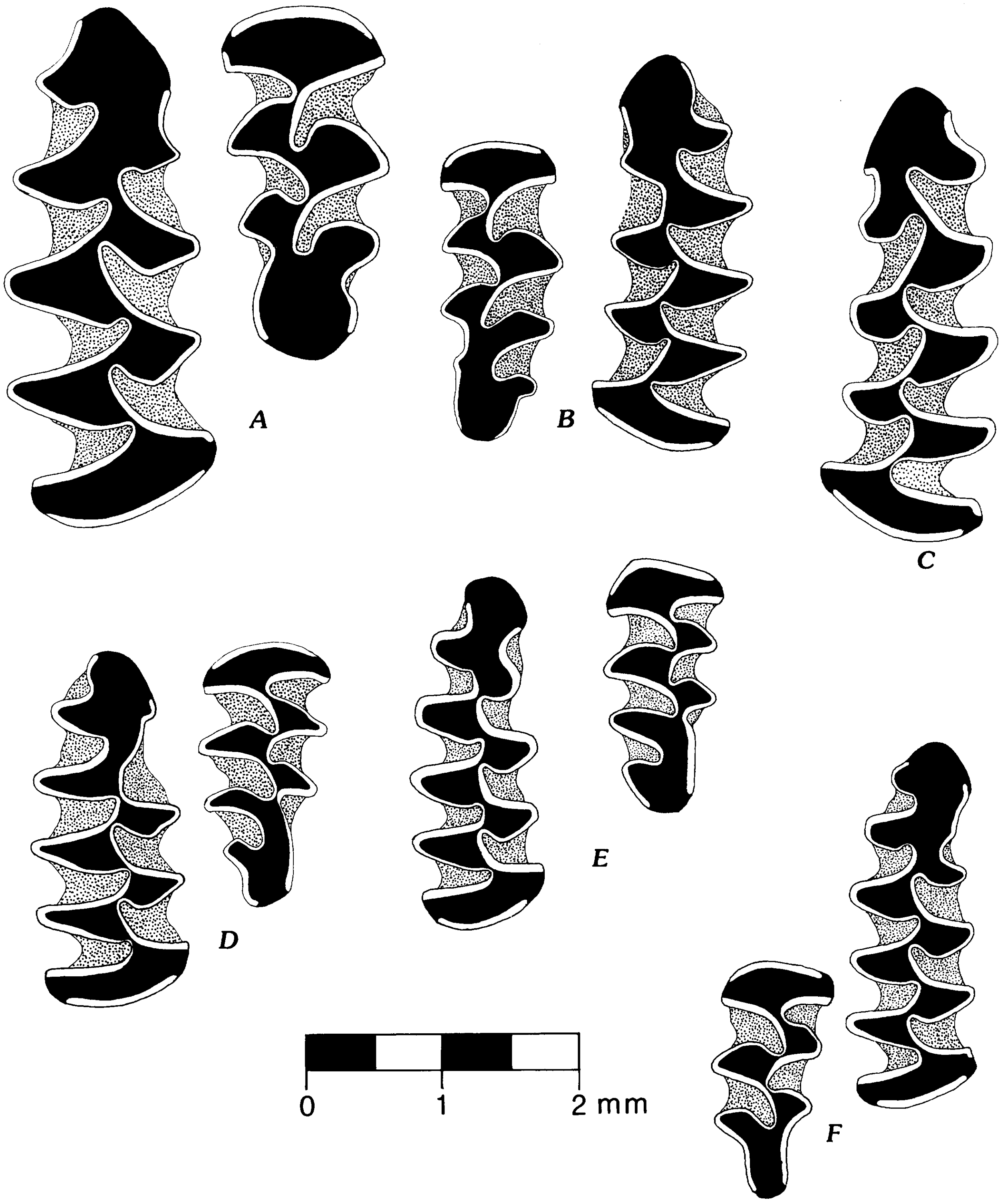

Figure 12. *Microtus. A, Microtus paroperarius*, locality CT–2, oldest fauna in the Hansen Bluff faunal sequence, Colorado, M/1 and M\3 of primitive and gigantic form. *B, Microtus paroperarius*, Cudahy fauna, Kansas, M\3 and M/1 of advanced form. *C, Microtus nivalis*, Dzeravaskala fauna, Czechoslovakia, M/1. *D, Microtus oeconomus*, living, Alaska, M/1 and M\3. *E, Microtus arvalis*, living, Belgium, M/1 and M\3. *F, Microtus oregonensis*, living, Washington, M/1 and M\3.

namesake, *M. paroperarius* (fig. 12*B*) (*M. operarius* is a junior synonym of *M. oeconomus*), have a complex M\3, but their M/1 often lacks any sign of a buccal Secondary Wing.

The separation of *Lasiopodomys* from *Microtus* identifies an ancestral trunk (at least double) from which the branches containing the many species of *Microtus* diverged, but this separation is only useful biochronologically and does little to help understand the phylogenetic interrelationships among the species of *Microtus*. Many attempts, based on morphology and genetic analysis (Chaline and Graf, 1988, among others), have been made to elucidate these interrelationships, and some seem obvious from the living fauna but biogeographically puzzling: for example, can *M. oregonensis* of the United States be closely related to *M. nivalis* of Europe and western Asia as their simple last upper molars would suggest?

Identification.—Attempts to define the general configuration of the Anteroconid Complex have resulted in specific, named terms for the major variations in pattern. (See van der Meulen, 1973, p. 54–55, for descriptions.) From this attempt such terms as "ratticepid," "nivalid," "gregalid," "arvalid," "hintonid," and others have originated. The terms are useful in description and, as their names indicate, are characteristic of the Anteroconid Complex in the majority of individuals in particular living species.

However, the Cap of the Anteroconid Complex is the most variable feature in the dentition of microtine rodents, and exceptions are common even in the living species, in which character polarization would seem to have had the greatest time to remove the variability that reflects ancestral morphologic features. The various patterns of the Cap of the Anteroconid Complex have been considered meaningful in species assignment and have been traced backward in time to try to establish the history of the living species lineages. This concentration on the configuration of the Cap of the Anteroconid Complex has led to neglect of other characters and to acceptance of variations in Cap configuration as probable evolutionary trends. The results, as published by competent authorities, have been extreme in their inferences of differing affinity; particularly in Europe the recognition of only one species of *Microtus* in fossil faunas is rare, and thoughtful population analysis is needed, as has been done by Fejfar and Horacek (1983), to recognize potential oversplitting.

Tracing Cap configuration **back** in time has caused a morphotype from the Karay-Dubina fauna of the Ukraine to be assigned to "*Microtus* ex gr. '*oeconomus*'" (Markova, 1990, fig. 17, nos. 23–34). This morphotype is identical to forms from the Olyor Suite, Krestovka Sections of Yakutia, that, by tracing Cap configurations **forward** in time, have been assigned to "*Allophaiomys* cf. *pliocaenicus*" (Zazhigin in Sher and others, 1979) or "*Allophaiomys pliocaenicus* (advanced form)" (Zazhigin in Sher, 1986). Specimens of the latter populations are first illustrated in figures 15 and 16 of the present report, and are compared with "*Microtus* ex gr. '*oeconomus*'" from the Karay-Dubina fauna, reproduced from Markova (1990), in figure 16. All are called *Lasiopodomys* spp. in the present report, and they provide no justification for the interpretation that the Krestovka Olyor Suite is the same age as the Karay-Dubina fauna on the grounds that they both contain the transition from *Allophaiomys* into *Microtus*—as neither actually does.

In arriving at these identifications, Markova would seem to have considered the lack of a fifth lingual reentrant on the first lower molar, always present in *Microtus oeconomus*, and the presence of a simple last upper molar, never found in *M. oeconomus*, as primitive features of the lineage. Zazhigin would seem to have considered the closure of Dimension C–C′, never found in *Allophaiomys pliocaenicus*, as an advanced feature of the *Allophaiomys* lineage. Both are reasonable assumptions, but neither considered the definitions of other related taxa, and both assumptions extended the morphologic definition of the named taxa into the morphology of other taxa as used by others. As a result, what Zazhigin called "*Allophaiomys pliocaenicus* (advanced form)" is the same morphotype that Markova referred to "*Microtus* ex gr. '*oeconomus.*'"

The morphotype from Karay-Dubina that Markova called *Allophaiomys* is in agreement with the present report, but is not present in the Olyor. The morphotype from the Olyor that Zazhigin called *Microtus* is in agreement with the present report, but is not present in the Karay-Dubina fauna. As herein defined, three generic morphotypes are recognized: (1) *Allophaiomys*, represented in the Karay-Dubina fauna but not present in the Krestovka fauna; (2) *Lasiopodomys*, called *Microtus* in the Karay-Dubina by Markova and called *Allophaiomys* in the Krestovka by Zazhigin; and (3) *Microtus*, represented in the Krestovka fauna but not present in the Karay-Dubina fauna (but present in younger faunas of that region).

Both authors listed an "*Allophaiomys* replacement by *Microtus,*" and the age of the Krestovka Olyor fauna was based on that of the Karay-Dubina fauna because of this replacement. But the "replacement" was not the same, and the correlation was incorrect. In the terminology of the present report, *Lasiopodomys* seemed to replace *Allophaiomys* in the Karay-Dubina fauna, and *Microtus* seemed to replace *Lasiopodomys* in the Krestovka fauna.

Actually the few *Allophaiomys* morphotypes present in the Karay-Dubina fauna appear, in Markova's illustrations, to be variants of *Terricola*, and were not replaced by "*Microtus*." Instead, these morphotypes no longer appeared in the younger faunas because they had been polarized out of the range of variability in the *Terricola* populations. Similarly, *Microtus* was an immigrant to the Krestovka fauna, as stated in Sher and others (1979), and *Lasiopodomys* did not disappear by evolution into *Microtus*, but presumably is missing in younger faunas because these are not well known—younger faunas of the Krestovka Sections are represented by very small samples (A.V. Sher, oral commun., 1990); the genus is known in younger faunas elsewhere in Beringia. In addition, the Krestovka *Lasiopodomys* morphotypes are "typical," and not advanced, they are not approaching a *Microtus* morphotype, as will be discussed in this report under the heading, "Age of Krestovka Olyor and Cape Deceit faunas."

Markova (1990) and Sher (1986) also assumed that the Karay-Dubina fauna was well dated by paleomagnetic control. In reality, no paleomagnetic control exists other than that the fauna is older than the Brunhes Chron; the paleomagnetic determinations ended well upsection of the horizon from which the described fauna was recovered (Velichko and others, 1983). The Karay-Dubina fauna could have lived after, during, or before the Jaramillo event. The section overlies Tertiary limestone (Markova, 1990), and the younger age constraint provided by the paleomagnetic study is simply "older than the beginning of the Brunhes Chron"; how much older the Karay-Dubina fauna may be is not constrained.

Configurations of the Cap of the Anteroconid Complex have been used in the hope of subdividing the Arvicolinae and in describing variations within their populations. These configurations of the Anteroconid Complex are very similar in the tribes Microtini and Pitymyini. At times, in the mind of the person looking for a pattern, consideration of the general configuration of the Anteroconid Complex supersedes the significance of Dimension C–C′, the dimension that determines whether Triangles 4 and 5 are confluent as in *Allophaiomys* and the Pitymyini or separated as in the Microtini. Lineages have been proposed of one Anteroconid Complex Cap configuration but include members of both the Microtini and the Pitymyini.

In this regard, workers may tend either to ignore the distinction between *Microtus* and *Pitymys* that Hinton (1923) specifically described, or to have trouble counting triangles forward from the posterior loop of the first lower molar. For example, in discussing *Microtus paroperarius* from the type locality, the Cudahy fauna of Kansas, van der Meulen (1978, p. 122) stated (bracketed material added in explanation):

> It is possible that Paulson included some five-triangled variants of *M. meadensis* [*Terricola meadensis*] in his counts [of *Microtus paroperarius*]. This is concluded from the presence of seven five-triangled *M. meadensis* variants in vial V40299 (evidently picked for *M. paroperarius*). *M. meadensis* is distinguished from *M. paroperarius* by the better developed anterior loop [Cap] of the former. On this criterion the *M. paroperarius* m1's of Paulson (1961: Figs. [7]F and [7]G) belong to *M. meadensis*. Neither Hibbard (1944) nor Paulson (1961) have described five-triangled variants of *M. meadensis*.

In the definitions by Hinton (1923) for *Microtus*, given previously (p.44), and for *Pitymys*, given later (p. 65), which were certainly followed by Hibbard and Paulson, *Terricola meadensis* is a species of the tribe Pitymyini and **cannot** have a five-triangled variant, or even a four-triangled variant; if it did it would be a member of the tribe Microtini. Dimension C–C′, as well as Dimension B–B′, must be closed to have either or both Triangles 4 and 5; and the specimen with these character states belongs in the tribe Microtini by definition. Members of the tribe Pitymyini have confluent Primary Wings in the position of Triangles 4 and 5.

Paulson's figures 7F and G show specimens in which the Primary Wings are separated by closure of Dimension C–C′; they are *Microtus*, as he indicated. Van der Meulen (1978) apparently forgot the difference between *Microtus* and *Pitymys* in his concern about the configuration of the Cap of the Anteroconid Complex; if he were considering the definitions of Hinton (1923), he could not have made these statements.

Paulson's figures 7F and G of *Microtus paroperarius* **do** have confluent Triangles 6 and 7 (**Secondary** Wings). These confluent Secondary Wings on the Cap of the Anteroconid Complex are well developed. **Both** the Microtini and the Pitymyini may have completely confluent **Secondary** Wings; it is the nature of the **Primary** Wings that separates the members of these two tribes (fig. 10). Because of the nature of the **Secondary** Wings on Paulson's figures, it seems plausible that van der Meulen assigned these specimens to *Pitymys meadensis*; that is, it seems possible that van der Meulen mistook confluent Triangles 6 and 7 for confluent Triangles 4 and 5 in these two specimens. The diagnostic Primary Wings (Triangles 5 and 6) are, however, not confluent, and the specimens are *Microtus*.

Van der Meulen (1978) did not explain how he defined *Microtus* and *Pitymys* (= *Terricola*): a strange situation in a paper naming new species of these genera. Paulson's figures 7F and 7G are *Microtus paroperarius* by the only available definition: Dimension C–C′, between Triangles 4 and 5, is closed. If one can count to Triangle 4, no similarity exists between these two specimens and *Terricola meadensis*.

Seldom is a late Pleistocene fauna described with only one species of *Microtus* or *Terricola*; the reason possibly lies more in the variability of the pattern of the Cap of the Anteroconid Complex, than in the congeniality of species of these genera. If any success results from consideration of the configuration of the Cap of the Anteroconid Complex, it will be on a statistical basis, as was accomplished by Fejfar and Horacek (1983). At present, no pattern is apparent other than the characters discussed herein.

Correlation.—In the Anza-Borrego Desert of California, *Microtus californicus* is presumably dated at about 1.4 million years old (locality 21, fig. 1; fig. 10*A*; ANZA–1 of fig. 14). The locality, LACM 6683, is 109 m above the Olduvai event and 360 m below the Brunhes Chron, but the rate of sedimentation was not constant. As discussed previously (p. 50) in the section on *Lasiopodomys* from the Anza-Borrego Desert, the date is approximate. The presence of *Terricola meadensis* in overlying deposits (fig. 14, Locality ANZA–3) suggests that the youngest normal polarity recorded represents the Brunhes Chron, rather than the Jaramillo event as inferred by those making the paleomagnetic study (Johnson and others, 1984), because *Terricola* does not appear elsewhere in the United States until after the Jaramillo event, both east and west of the Rocky Mountains (Repenning, 1983).

The specimens of *Microtus* from the Anza-Borrego Desert are the oldest dated record of the genus in the world, but the date is not consistent with the remainder of the history of *Microtus*; it seems too old (see fig. 14). If the beginning of the Brunhes is represented, as seems evident, the Jaramillo appears to be missing in the section, and possibly reversely polarized deposits older and (or) younger than the Jaramillo are also missing. If so, the age is quite uncertain. The association with several Blancan holdover microtines (*Mictomys vetus*, *Mimomys parvus*, and *Ondatra idahoensis*: Zakrzewski, 1972; Repenning, unpub. data) does suggest a rather early age following the Olduvai event, possibly as much as 1.4 million years ago, and still the oldest known *Microtus* in the world.

However, great age for an advanced *Microtus* morphotype indicated by the Anza-Borrego record is also indicated by the younger, and larger, sample from the Irvington fauna of central California (Savage, 1951). The age of the Irvington fauna is plausible in consideration of global records of the genus (figs. 10*C*, 14).

The record from the Irvington fauna includes 14 first lower molars and 5 last upper molars that indicate the presence of the advanced species *Microtus californicus*, with a morphologic variability that had polarized to a fixed, little-variable phenotype. Such an advanced morphotype did not become common east of the Rocky Mountains until the 610,000-year-old *M. paroperarius* of the Cudahy fauna of Kansas, and it is not apparent that *M. paroperarius* evolved a morphologically stable pattern before its extinction about 450,000 years ago. Yet the Irvington fauna of California is in reversely polarized deposits, clearly more than 790,000 years old.

As discussed previously (p. 50), the first *Lasiopodomys* known in the United States, also from the Anza-Borrego Desert (fig. 11*A*), is at least 1.2 million years old if the youngest normal polarity represents the Jaramillo event; and as discussed, if the youngest deposits with normal polarity represent the Brunhes, the record seems to be older. However, *Lasiopodomys* did not immigrate from Beringia to the area east of the Rocky Mountains until 850,000 years ago, and immigrant *Microtus* did not appear there until about 450,000 years ago. To the east of these mountains, *Microtus* reached southern Canada possibly 875,000 years ago in the Wellsch Valley fauna, as discussed, and its oldest record east of the mountains in the United States is approximated at 450,000 years ago in the Porcupine Cave fauna of Colorado (Barnosky and Rasmussen, 1988).

The evolution of *Microtus paroperarius* out of *Lasiopodomys* in the United States east of the Rocky Mountains is obviously a provincial event and does not correlate with dispersal patterns. Evidently, *Lasiopodomys* and *Microtus* (other than *M. paroperarius*) dispersed across Beringia to western North America between 1.4 and 1.2 million years ago, but the later dispersal of these microtines southward was at different times and followed different routes on either side of the Rocky Mountains (Repenning, 1990).

Allophaiomys is not known west of the Rocky Mountains, but it immigrated to the eastern three-quarters of the United States at the beginning of the Olduvai event. No data from the west suggest an immigration of any microtine at the beginning of the Olduvai event, but the genus *Phenacomys* dispersed south to Idaho (Froman Ferry, locality 33, fig. 1; Repenning, unpub. data) after the Olduvai event. The lack of *Allophaiomys* west of the mountains thus suggests that the genus was present in Beringia only during the Olduvai and that it was not present to participate in a southward dispersal west of the Rocky Mountains with *Phenacomys*. No paleomagnetic evidence exists in Beringia that suggests nonmarine deposition during the Olduvai event, so the suggestion cannot be supported by Beringian fossil records.

Later, 850,000 years ago, *Terricola* and *Lasiopodomys* entered the United States east of the Rocky Mountains. *Lasiopodomys* was by then a long-time resident of Beringia, but the lack of record of *Terricola* in Beringia again suggests that this genus had a very brief presence in this northern region after the Jaramillo event and before the Brunhes Chron. In this case, Beringian deposits believed to be of this age do exist, in the type section of the Olyor Suite of Yakutia (Virina and others, 1984), but *Terricola* is not reported from their faunas, which are represented by small samples.

Beringian *Microtus* is first recorded before the Jaramillo event (p. 84); the genus is abundant in Yukon Territory (eastern Beringia) during the Jaramillo event (p. 54); it is present in southern Canada before the Brunhes Chron (p. 36); and it first appears, as an immigrant, in the United States east of the Rocky Mountains during the middle part of the Brunhes Chron (≈450,000 years ago; Barnosky and Rasmussen, 1988).

These records of the distribution of *Allophaiomys*, *Terricola*, and *Microtus* suggest major ecological restrictions in the dispersal of these microtines through Beringia and to the south. Constraints on the use of a dispersal route to the west of the Rocky Mountains are, in part, related to uplift and erosion of coastal mountains in Canada and Alaska and to periods of intense glaciation in these mountains. Constraints on the use of a dispersal route to the east of the Rocky Mountains are only partially documented; these include subtropical climates in the Great Plains of the United States, forests in the Great Plains of Canada, and possibly continental ice before 2.0 million years ago and intermittently after 850,000 years ago (Repenning, 1990; Repenning and Brouwers, 1992).

The delay in southward dispersal of *Microtus* into eastern U.S.A. seems to follow climatic deterioration and requires that the provincial nature of latitudinal climatic zones, as well as east-west regional separation of microtine faunas by the Rocky Mountains, be considered in biochronologies. Correlations in North America based on the genus *Microtus* must be specific for at least four different regions: Beringian, Canadian, Eastern U.S.A., and Western U.S.A. It seems reasonable that a fifth, Mexican, region will be added when enough information is available.

These regional considerations are well illustrated by *Microtus*, but apply to most microtines. The regions of Eurasia are not well comprehended from this biohistorical point of view, but separate faunal regions and provinces would seem to be more numerous there than in North America. These are not yet well documented by differences in the distribution and composition of microtine faunas, although broad differences between Europe, western Asia, and eastern Asia are presently recognizable. As indicated in this discussion, there is ample reason to infer the presence of northeastern (Beringian) and southeastern (Oriental) Asian regions.

MICROTUS FROM THE HANSEN BLUFF FAUNAS

(fig. 12*A*; locality 15, fig. 1)

Hansen Bluff is in the broad valley of the Rio Grande of southern Colorado, U.S.A., a few miles north of the New Mexico State line in the eastern part of the Rocky Mountains. The bluff is at 7,546 feet (2,300 m) elevation; 1,400 feet (428 m) lower than, and about 39 miles (63 km) northeast of SAM Cave, New Mexico. Both localities are within deposits filling the uppermost basin of the Rio Grande. Hansen Bluff contains a succession of vertebrate and invertebrate faunas and pollen floras that range in age from possibly 840,000 to an approximated 700,000 years (Rogers and others, 1985).

Age control for most of the Hansen Bluff faunas is tightly constrained by paleomagnetic patterns, one identified tephra of known age, and climatic correlation with the early part of the Nebraskan glaciation of North America (Rogers and others, 1985). Rogers confirmed its position within the youngest reversed deposits of the Matuyama Chron after 1985 by digging to the Jaramillo event at the foot of Hansen Bluff, and by drilling a core through the Matuyama Chron to the Gauss Normal-polarity Chron at the same location (K.L. Rogers, oral commun., 1986; and Rogers and others, 1992). The faunal sequence was listed as "Alamosa, Colorado" in Repenning (1987), which was written earlier than Rogers and others (1985).

The oldest faunas of the Hansen Bluff faunal sequence (localities CT1–3 and PP2) are about 820,000 years old. The youngest (CG, TS, and FT) are estimated to be about 700,000 years old (Rogers and others, 1985).

The microtine fauna includes *Microtus paroperarius* (fig. 12*A*) and *Terricola meadensis* (fig. 13*G*; listed as *Pitymys meadensis* in Rogers and others, 1985). *T. meadensis* represents the immigrant group of the Pitymyini in North America (the "*quasiater* species group" of Repenning, 1983), and Hansen Bluff is the oldest record of this immigrant in North America. This species varies little from the oldest to the youngest faunas in Hansen Bluff (Rogers and others, 1985): its morphotype seems to have polarized, and it had not recently evolved from some more primitive ancestor like *Terricola arvaloides* of Eurasia. Dimension A–A′, however, is not as markedly constricted as it is in the type sample from the 610,000 year-old Cudahy fauna of Kansas.

In contrast, *Microtus paroperarius* varies from the oldest to the youngest Hansen Bluff faunas in the shortening of Dimension A–A′ and complication of the last upper molar. Its changing mode of variability indicates a recent evolution out of *Lasiopodomys* by its lack of polarization in dental pattern. Although no *Lasiopodomys* morphotypes are present, the oldest populations of *Microtus paroperarius* in the Hansen Bluff sequence have a relatively simple Anteroconid Complex on the first lower molar with little reduction of Dimension A–A′, and a fairly high proportion (40 percent) of simple last upper molars (fig. 12*A*).

These oldest faunas of the Hansen Bluff faunal sequence contain the only known association of upper and lower dentition of *Microtus paroperarius*. In this specimen a simple first lower molar is associated with a simple last upper molar, indicating that some of the simple last upper molars in the fauna belong to primitive *Microtus*, rather than all of them belonging to the pitymyinine *Terricola*. Relative proportions, based upon the count of lower first molars, suggest that 40 percent of *M. paroperarius* individuals in the oldest fauna of Hansen Bluff had a simple last upper molar. Simple last upper molars are unknown from the younger faunas of the Hansen Bluff sequence, and some of the first lower molars show well-developed reentrants anterior to the Secondary Wings and a conspicuous reduction of Dimension A–A′.

Microtus paroperarius from the older faunas of Hansen Bluff closely resembles: (1) *Microtus* variants of *Lasiopodomys deceitensis* from the Cheetah Room fauna (see Repenning and Grady, 1988, fig. 4); (2) *Microtus* morphotypes (primitive) in the population referred to as *Microtus paroperarius-Lasiopodomys deceitensis* from Cumberland Cave (see van der Meulen, 1978, fig. 11D, F); (3) the more primitive forms of *Microtus paroperarius* shown by Pfaff (1990; fig. 4 except 4D and G) from the Trout Cave No. 2 fauna in West Virginia; and (4) the simplest forms from the type population of *M. paroperarius* from the Cudahy fauna (see Paulson, 1961, fig. 7A–D). They do not resemble the *Lemmiscus* morphotypes found in the nearby but older population of *Allophaiomys* from SAM Cave (this report, fig. 6*F*, *G*).

The population described by Pfaff (1990; fig. 4) from Trout Cave No. 2 most resembles samples from the middle part of the Hansen Bluff sequence, but sample sizes from this part of the Hansen Bluff sequence are very small. In the youngest faunas from Hansen Bluff, approximated at

700,000 years old by the rate of deposition calculated in the lower part of the section (where age control is stronger), the populations of *Microtus paroperarius* are comparable to the typical form from the Cudahy fauna of Kansas (Paulson, 1961), but again are represented by very small sample sizes.

Although not far from the SAM Cave localities and in deposits filling the same valley, the Hansen Bluff faunal sequence contains no record of *Allophaiomys.* It has been noted previously in the discussion of *Allophaiomys* (p. 31) that in the core drilled at the foot of Hansen Bluff a single tooth that can only be attributed to *Allophaiomys* was collected 240 feet down core, very close to the base of the Olduvai event. A few teeth of *Allophaiomys* were also recovered higher in the core, above the Olduvai event. That the genus was probably a part of the local fauna until shortly after the Jaramillo event is indicated by the faunas from nearby SAM Cave, containing large samples.

It would appear that *Allophaiomys* became extinct in the upper part of the Rio Grande drainage basin shortly before 820,000 years ago. No records in the United States suggest that it survived later, although the *Allophaiomys* morphotype survives in the living fauna as a variation of *Pedomys* at lower elevations east of the Rocky Mountains.

There is a global pattern of province-by-province extirpation of *Allophaiomys* soon after the appearance of *Lasiopodomys*, or *Microtus* where the more primitive intermediate genus is not known. The pattern, repeated in many records throughout the Northern Hemisphere (Repenning, 1990), appears to reflect climatic change to an environment too cold for *Allophaiomys* but preferred by *Microtus*, or *Lasiopodomys*, as will be discussed. The pattern also suggests that the evolution of *Allophaiomys* into *Pedomys* in North America provided some advantage, as *Pedomys* persists in the presence of *Microtus*, but usually only in the more temperate parts of colder environments; its avoidance of higher elevations in the Rocky Mountains and of summer arctic air in northeastern North America is conspicuous in its modern distribution.

Possibly because of differing environmental constraints, no *Pedomys* are known from the high-elevation Hansen Bluff faunal sequence or the Porcupine Cave fauna farther north and at greater elevation in Colorado. *Pedomys* was, and is, widely distributed across the Great Plains; and the genus now lives westward to the eastern foot of the Rocky Mountains up to 5,000 to 7,000 feet (1,542-2,158 m) in elevation. It is not known in higher terrain. It seems possible that the 7,546-foot elevation of Hansen Bluff in the upper Rio Grande Valley has always been too high for this genus. Although *Pitymys cumberlandensis* is known from the Appalachian Mountains before the time of the Hansen Bluff faunas, the genus appears to have always remained distributed only in the eastern United States. *Terricola* did not enter this eastern province, although present in both high elevation localities, Hansen Bluff and Porcupine Cave, suggesting some reason other than high-elevation climate factors for its avoidance of the eastern United States.

The absence of both *Allophaiomys* and *Lasiopodomys*, and the transition upsection into typical *Microtus paroperarius* make the 820,000-year-old oldest faunas of Hansen Bluff appear younger than the Cumberland Cave fauna of Maryland, which is, accordingly, considered as being about 830,000 years old and intermediate in age between the Cheetah Room fauna (containing no *Microtus*) and the Hansen Bluff fauna (containing no *Allophaiomys* or *Lasiopodomys*) (fig. 14).

MICROTUS FROM THE CUMBERLAND CAVE AND LOCALITY CRH–47 FAUNAS

(localities 11 and 25, fig. 1)

The Cumberland Cave fauna of western Maryland has been discussed in connection with its *Allophaiomys* and *Lasiopodomys*. Locality CRH–47 fauna of easternmost Beringia in northern Yukon Territory, Canada, has been discussed in connection with the age of *Microtus* and *Allophaiomys* from the Wellsch Valley fauna of Saskatchewan and in connection with *Lasiopodomys* from CRH–47.

As just mentioned, Cumberland Cave seems to be about 830,000 years old. Locality CRH–47 was deposited during the Jaramillo polarity event between 970,000 and 900,000 years ago. Two younger localities in the Old Crow basin of Yukon Territory, CRH–11 and CRH–64, also contain *Lasiopodomys* and are normally magnetized (Morlan, 1984), suggesting that they also represent the Jaramillo event and that the fauna from CRH–47 may have lived fairly early during this event. This assumption is based upon the further assumption that *Lasiopodomys* became extinct in eastern Beringia before the Brunhes as it did in the United States and western Beringia.

Because of their latitudinal provinciality, the faunas of Cumberland Cave and Locality CRH–47 contrast greatly, even though they may be only 70,000 years different in age. In a single, intergrading population identified as *Microtus paroperarius-Lasiopodomys deceitensis*, Cumberland Cave contains both *L. deceitensis* and primitive *M. paroperarius* morphotypes. The species *M. paroperarius* evolved out of *Lasiopodomys* in the Cumberland Cave fauna.

The older Locality CRH–47 also contains *Lasiopodomys deceitensis*, but this fauna contains a large spectrum of *Microtus* morphotypes including forms resembling primitive *M. paroperarius* as well as forms that appear related to modern species (R.E. Morlan, oral commun., 1986-1987 and work in progress, 1991). *Allophaiomys* is present in the Cumberland Cave fauna but missing in the fauna of Locality CRH–47. No pitymyinines are present in Locality CRH–47, although they are abundant in Cumberland Cave. The effects of latitudinal provincialism are obviously great at this time, just prior to and during the Nebraskan glaciations (beginning 850,000 years ago).

Between the ages of these two faunas, about 850,000 years ago, the genera *Lasiopodomys* and *Terricola* dispersed southward from Beringia into the conterminous United States, as has been mentioned (p. 33). The complete lack of any *Terricola* in Locality CRH–47, or in other locality along the Old Crow River (Morlan, 1984), suggests that it was after the Jaramillo event that *Terricola* passed through Beringia on its way to the United States, in agreement with its earliest records in the U.S.A.

The original date for this dispersal was assumed to approximate the first of the Nebraskan glacial advances in North America, the age of which was first inferred from the age of stage 22 of the oceanic oxygen isotope record (Repenning, 1984). Most recognized microtine dispersal events can be associated with "cold" climatic events as suggested by the oxygen isotope record (Repenning and others, 1990).

Since that initial evaluation of the age of this dispersal event, the age of the Cumberland Cave fauna (about 830,000 years) and that of the older Cheetah Room fauna of West Virginia (about 840,000 years), both containing some of the immigrants, have reinforced the younger limit of this assumption. Among the SAM Cave faunas of New Mexico, Locality BOT–4 contains none of the immigrants but is younger than the Jaramillo Normal-polarity Subchron (younger than 900,000 years), supporting and further restricting the older limit of the assumption made from oxygen stage 22 and the Nebraskan glaciations. The author still considers as reasonable the interpretation, originally based on the inferred age of oxygen stage 22, that the dispersal of these microtines into the United States was about 850,000 years ago.

After this dispersal event, records east of the Rocky Mountains in the United States show *Lasiopodomys* evolving only into *Microtus paroperarius*; no other species of *Microtus* is evident until the next dispersal event, about 450,000 years ago, and these are of immigrants from Beringia, and presumably Asia. Despite evidence of much earlier (about 1.4 Ma) immigrant populations west of the Rocky Mountains, despite the great variety of *Microtus* morphotypes in Yukon Territory (co-occurring with *Lasiopodomys* before 0.97 Ma), and despite the southern Saskatchewan record (perhaps 0.87 Ma) of an advanced morphotype of *Microtus* from reversed deposits of the Wellsch Valley fauna (co-occurring with *Allophaiomys*), it seems that east of the Rocky Mountains *Microtus* did not enter the United States until about 0.45 million years ago, 1 million years after it was first present along the Pacific Coast of the United States (Repenning, 1984, 1987, and 1990).

These later immigrant *Microtus* are assigned to living species. *M. paroperarius* appears to have become extinct shortly after this late *Microtus* invasion; only in Porcupine Cave of south-central Colorado is *M. paroperarius* found in association with more advanced species of *Microtus* that were then newly immigrant from Beringia (Barnosky and Rasmussen, 1988).

These different but interrelated records have direct bearing on the age of *Microtus* in Beringia and the Olyor Suite of the Krestovka Sections. During the Jaramillo Normal-polarity Subchron, *Microtus* was abundant and diverse in Beringia, but unknown in the United States except west of the Rocky Mountains. In the discussion of the Wellsch Valley fauna of southern Saskatchewan, Canada, it was indicated that Beringian *Microtus* had a range that extended essentially to the northern boundary of the United States before 850,000 years ago; no record indicates that it moved southward across this international boundary to the east of the Rocky Mountains until about 450,000 years ago, although it has a record west of these mountains perhaps 1.4 million years old. The oldest record of *Microtus* to the east of the Rocky Mountains is in Cumberland Cave, Maryland, and is clearly the result of endemic evolution out of *Lasiopodomys* in the United States.

MICROTUS FROM THE TROUT CAVE NO. 2 FAUNA

(locality 17, fig. 1)

Trout Cave is in West Virginia, near Hamilton Cave, which contains the Cheetah Room fauna. The microtines from locality Trout Cave No. 2 were recently described by Pfaff (1990) and include *Microtus paroperarius*, *Pedomys llanensis*, and *Pitymys cumberlandensis*. The first two species were described as being more advanced than from Cumberland Cave, the last as being the same.

As indicated previously, the population characteristics of *Microtus paroperarius* from Trout Cave appear to fit in the upper part of the Hansen Bluff faunal sequence, probably correlative to the earliest part of the Brunhes Chron. No *Lasiopodomys* morphotypes are present, as there are in Cumberland Cave, and no simple last upper molars were assigned to *M. paroperarius*, as in the oldest faunas of Hansen Bluff. First lower molars from Trout Cave No. 2 include primitive forms like those from the oldest Hansen Bluff faunas as well as more advanced forms, but none are as advanced as are some from the type locality, the Cudahy fauna of Kansas (Paulson, 1961).

A conspicuous reduction of Dimension A–A′ seems indicated by Pfaff's figures 4D and G and may approximately correlate with his statement that 39 percent of the sample had cementum in buccal reentrant angle 4, the buccal side of this Dimension. Cementum is increasingly likely to be deposited in the reentrants as they become deeper transversely. Pfaff noted that cementum deposition is greater than that in the Cumberland Cave fauna and less than that in the type Cudahy fauna. The presence of such cement deposition indicates a stage of advancement beyond that of the oldest faunas of Hansen Bluff, as do the morphologies that Pfaff illustrated.

Pfaff also noted that *Pedomys llanensis* is more advanced than *Allophaiomys guildayi* from the Cumberland

Cave fauna, but still retains a wide range of individual variation, with a good percentage (34 percent) of *Allophaiomys* morphotypes (having no Dimension A–A′; Pfaff's figs. 5C, D, and E). In this respect the population may be less advanced than the type sample from the Cudahy fauna of Kansas, which is extremely small; it is clearly advanced over the condition of *Allophaiomys guildayi* from Cumberland Cave.

The population characteristics of *Pitymys cumberlandensis* from Trout Cave No. 2 are very similar to those of Cumberland Cave and Hanover Quarry Fissure. Again, these similarities suggest a persistence of the polarization of characters in this lineage. From its evolution out of *Allophaiomys* in the Cheetah Room fauna (about 840,000 years old) through Hanover Quarry Fissure (perhaps 835,000 years), Cumberland Cave (about 830,000 years), Trout Cave No. 2 (possibly 725,000 years), and possibly lasting until the living fauna, *Pitymys pinetorum* shows no change in the morphologic structure of its teeth other than in enamel-thickness differentiation (van der Meulen, 1978).

Although the opinion is based upon inadequate faunal samples from the upper part of the Hansen Bluff faunal sequence, it seems that Trout Cave No. 2 may be somewhat greater than 700,000 years old, but clearly younger than 820,000 years old, by comparison with this series of faunas. In agreement with Pfaff, it certainly seems older than the 610,000-year-old Cudahy fauna of Kansas. An arbitrary age of about 725,000 years is assigned.

GENUS *LEMMISCUS* THOMAS, 1912

(fig. 6*F*, *G*, and *J*; Mt. Magruder, Nevada; locality 37, fig. 1)

Type species.—*Arvicola curtatus* Cope, 1868.

Revised dental diagnosis.—A genus of the tribe Microtini with only the buccal Secondary Wing strongly developed on the Anteroconid Complex of the first lower molar; a weak lingual Secondary Wing may be present or absent; because of this arrangement of the cusps of the first lower molar, the Primary Wings (forming fully developed Triangles 4 and 5) are in a position more alternating than opposing, as is usual in the Microtini; the last upper molar has two alternating triangles and an elongate, uncomplicated posterior loop.

"TYPICAL" *LEMMISCUS*

Revised dental diagnosis.—As for the genus.

Comments.—*Lemmiscus* is a North American genus (largely U.S.A.) of the tribe Microtini. The genus now lives in the northwestern Great Plains of the United States (extending north a short distance into Canada) and in the northern Rocky Mountains. West of these mountains the range of *Lemmiscus* extends southward to the Inyo Mountains of California and down the Wasatch Plateau to Escalante, Utah; this far south it lives at much higher elevations (9,000 to 10,000 ft; 2,776–3,048 m).

The single species, *Lemmiscus curtatus*, has always been questionably considered a member of genus *Lagurus*, of tribe Lagurini, because of many similarities, but differences have been noted (see Carroll and Genoways, 1980). These differences have led to the separation of the American species from Eurasian ones by including *Lagurus curtatus* in a subgenus *Lemmiscus*. *Lemmiscus* is sometimes treated as a full genus within the tribe Lagurini; this is the first published treatment as a member of the tribe Microtini.

The direct origin of *Lemmiscus curtatus* out of North American *Allophaiomys*, discussed previously in connection with *Allophaiomys* from SAM Cave, New Mexico (p. 33–35; fig. 6*F*, *G*, and *J*), requires a separate generic, non-lagurinine identity for this lineage. It belongs in the tribe Microtini, and Thomas' term is here treated as a full genus within the tribe. The relationship with *Allophaiomys* will be further considered when the several faunas of SAM Cave are completely studied, but the relationship seems obvious in the sample from Locality BOT–4 of SAM Cave.

R.E. Morlan (written commun., 1991) has identified an apparently true lagurinine (more like living *Eolagurus* than *Lagurus*) from Locality CRH–47 in the Old Crow basin of Yukon Territory, Canada. Otherwise the tribe Lagurini seems not to have entered North America. Although SAM Cave, New Mexico, and Porcupine Cave, Colorado (containing the living species *Lemmiscus curtatus*; Barnosky and Rasmussen, 1988), are both well south of the modern distribution of *L. curtatus*, this is not the southernmost extent of its former range. Harris (1980) reported the species from Dry Cave, southeastern New Mexico, dating from a late Pleistocene glacial period.

This single-species lineage (ignoring the possibility that the material from SAM Cave may deserve a separate species name) has no bearing on the age of the Olyor Suite in the Krestovka Sections. The North American lineage differs from Old World lagurinines by the dominance of only the buccal Secondary Wing on the first lower molar, by only two alternating triangles between the anterior and posterior loops of the last upper molar, and by having cementum present in the reentrants angles of the teeth. Other differences have been noted by Davis (1939).

The morphotypes from SAM Cave, Locality BOT–4, differ from living *Lemmiscus curtatus* in having relatively wide Dimensions B–B′ and A–A′, more strongly resembling *Allophaiomys*. However, by about 450,000 years ago these dimensions have been reduced to the condition observed in the living species, *L. curtatus*, as documented in Porcupine Cave, Colorado (Barnosky and Rasmussen, 1988). The genus is unusual in that it appears to have originated in and not dispersed far from the Rocky Mountains. Hypothetically, its origin may have resulted because of high-elevation cooling before the Nebraskan glaciation, and out of subtropical to temperate *Allophaiomys*. Its present northward range retraction seems to be the result of post-glacial hot summers, of which it is intolerant. The modern northward range limit, essentially to the northern border of the United States, also suggests an intolerance of severe winter cold, and that the *Mictomys* and ?*Phenacomys* association in SAM Cave indicates a similar ecologic restriction to cool summers and relatively temperate winters.

Rogers and others (1985) recorded a relatively warm climate at nearby Hansen Bluff, Colorado, just before the time of the second advance of the Nebraskan ice in the United States, and *Lemmiscus* was not present in this fauna. Interestingly, a few specimens of *Mictomys kansasensis* were in this fauna, but these were all badly abraded, as though they had washed down into the valley of the Rio Grande from the surrounding mountains. Possibly cool-summer-, warm-winter-adapted *Lemmiscus* was first forced to withdraw northward (by virtue of its evolved adaptations) not long after it evolved out of the local population of subtropical to temperate *Allophaiomys*.

GENUS *PROEDROMYS* THOMAS, 1911

(Minchow, Kansu, People's Republic of China; locality 36, fig. 1)

Type species.—Proedromys bedfordi Thomas, 1911.

Revised dental diagnosis.—A genus of the tribe Microtini with a first lower molar like that of "typical" *Lasiopodomys*, having a closed Dimension C–C′ and a rounded Cap with no Dimension A–A' or Secondary Wings; but with a last upper molar having the posterior loop reduced to a single **buccal** Hook (illustrated in Repenning and Grady, 1988; fig. 4A).

"TYPICAL" *PROEDROMYS*

Revised dental diagnosis.—As for the genus.

Comments.—Proedromys is a Chinese genus of the tribe Microtini and has little or no distribution outside of that faunal region. Like *Microtus*, its fossil record goes back to before the Jaramillo event (Gongwangling fauna; An and Ho, 1989). The first lower molar appears identical to that of *Lasiopodomys deceitensis*, and an origin out of *Allophaiomys* or early *Lasiopodomys* seems apparent but is not as yet documented.

The genus is characterized by a reduction, rather than complication, of the last upper molar; the posterior loop is essentially lost even in its oldest recognized form, from the Gongwangling fauna of China (Zheng and Li, 1990). The genus shows little change to the living fauna and has no evident bearing on the age of the Olyor Suite of Yakutia. The unusual evolutionary vector of reduction, rather than complication, of the third upper molar has only been observed elsewhere in living *Phaiomys leucurus* (fig. 4), and in *Phaiomys* it has progressed only half as far in that direction.

TRIBE PITYMYINI, REPENNING, 1983

Basis of diagnosis.—Hinton, 1923 (for genus *Pitymys*): "M_1 with posterior loop, followed successively by three substantially closed and alternating triangles and a confluent pair of triangles, and terminated by an anterior loop of variable form."

Revised dental diagnosis.—Genera of the tribe Pitymyini (subfamily Arvicolinae) have dentinal confluence between the Primary Wings of the Anteroconid Complex (Dimension C–C′ open or substantially open); Cap of the Anteroconid Complex is complex (Secondary Wing or Wings present, Dimension A–A′ present and variously reduced); Dimension B–B′ often narrowed or closed; cheek teeth rootless with cement in the reentrants.

Generic contents of the tribe.—Herpetomys, Terricola, Neodon*, Orithriomys*, Pedomys, Pitymys*, and *Tyrrhenicola**.

[Note: The genera marked by an asterisk have not been examined in detail during this study and no opinions are offered. They have no bearing on the age of the Olyor Suite.]

Discussion.—In the tribe Pitymyini the Anteroconid Complex Dimension C–C′, between the Primary Wings of first lower molar, does not shorten and separate the two Primary Wings as in the Microtini; it remains as it was in *Allophaiomys*, and the Primary Wings (incomplete Triangles 4 and 5) remain partially to completely confluent. Narrowing of Dimension A–A′, to initiate the development of Secondary Wings on the Cap of the Anteroconid Complex, is the only criterion that separates all species of the tribe Pitymyini from *Allophaiomys*. Hinton's diagnosis of *Pitymys* separates it from *Microtus*, but not from *Allophaiomys*, which was not known in 1923, although the very similar *Phaiomys* was and has been considered a pitymyinine.

The interrelationships of tribe Pitymyini are as complex as those of tribe Microtini, and are in need of as much study. In North America the tribe is represented by two lineages. One is endemic and contains the type species of *Pitymys* as well as the genus *Pedomys*. The other is that of *Terricola*, and this lineage immigrated to North America from Asia 850,000 years ago (Repenning, 1983), with *Lasiopodomys* of the tribe Microtini.

Rather than become involved in a major revision of nomenclature, Repenning (1983) called the two lineages "species groups," each named after representative living North American species: the "*pinetorum* species group" for the native stock and the "*quasiater* species group" for the immigrants from Eurasia.

Ognev (1950) has discussed the problem of generic separation of the Eurasian species—the "*quasiater* species group"—from the separately derived *Pitymys* of North America—the "*pinetorum* species group" (he did not discuss the concept of these groups). He stated that *Terricola* Fatio (1867) was preoccupied by *Terricola* Fleming (1828), said to be a genus of mollusk. He suggested (Ognev, 1950, p. 345

of the English translation) that "it would be most reasonable to unite all Old World animals within the confines of the subgeneric name *Micrurus* to distinguish them from the American *Pitymys* s. str." His use of *Micrurus* as a subgenus reflects his inclusion of all genera of the Pitymyini and the Microtini in the genus *Microtus*.

Ognev (1950), however, did not recognize this taxonomic separation of the Old World forms included in *Pitymys* (although he did so in his classification of 1948), but continued using the genus *Pitymys* in the U.S.S.R. His suggested (1950) and substituted (1948) generic name was *Micrurus* Forsyth-Major (1877), a pitymyinine genus erected to hold a species from Sicily. *Micrurus* Forsyth-Major is preoccupied by *Micrurus* Wagler (1824), a coral snake. In addition, Ognev's statement that *Terricola* Fatio was preoccupied was in error; Fleming (1828) used the term "Terricola" in the Latin vernacular for land-dwelling mollusks as a group, and not as a genus. It, therefore, is available as a generic name (Chaline and others, 1988; K. Kowalski, written commun., 1991).

Terricola Fatio (1867) is the first available name and was originally applied as a subgenus to include both *Terricola savii* and *Terricola subterraneus* where their ranges overlap in Switzerland. There appears to be considerable variability in the development of the last upper molar in species of *Terricola*, which needs further study to explain.

Although many have, for many years, suggested that the two groups of Pitymyini should be separated, Chaline and others (1988) were the first to do so. There seems to be no reason for not doing so except for the reluctance to drastically revise the present nomenclature. With this separation the genus *Pitymys* ceases to exist in Eurasia, and some species of North America (the "*quasiater* species group") no longer belong in *Pitymys*. The usage of Chaline and others (1988) is here followed.

The endemic North American *Pitymys* and *Pedomys* usually have both Secondary Wings developed, although individual variation is great, reflecting the recency of their evolution out of *Allophaiomys*. The development of these Wings is not strong, however, and Dimension A–A′ is usually large (fig. 13*A–F*). Dimension B–B′, separating the confluent Primary Wings from the Cap and its weakly developed Secondary Wings, often is quite large but is extremely variable and may be quite narrow; the average condition probably is more reduced than in *Allophaiomys pliocaenicus*, but the variability is so great that it is not easily noticed. The presence of weak Secondary Wings remains the most reliable character to separate *Pitymys* and *Pedomys* from *Allophaiomys*.

The earliest Pitymyini of Eurasia often do not have both Secondary Wings. Many early *Terricola* have only a lingual Secondary Wing. By the time that *Terricola* had dispersed to North America, about 850,000 years ago, the development of both Secondary Wings (shortening of Dimension A–A′) had polarized as a generic character, at least in the dispersing lineage, as in the living Eurasia lineages.

Thus all North American Pitymyini, endemic or immigrant, have both lingual and buccal Secondary Wings. However, in North America the Secondary Wings in *Terricola* are much better developed than they are in endemic North American genera (fig. 13*G–K*; *J* and *K* are European). *Terricola* also differs from the North American *Pitymys* and *Pedomys* in its prominent shortening of Dimension B–B′, which easily distinguishes the genus from *Allophaiomys*.

In North America, the shortening of Dimension B–B′, as well as the shortening of Dimension A–A′, serves to separate the immigrant "*quasiater* species group" (*Terricola*) of the tribe Pitymyini from the native "*pinetorum* species group" (*Pitymys* and *Pedomys*), in which Dimension B–B′ may not be shortened or may be only moderately shortened on an individual basis and Dimension A–A′ is never shortened (Repenning, 1983).

In the Old World, early morphotypes, having only a lingual Secondary Wing but a greatly reduced Dimension B–B′, have been given names such as "*Pitymys hintoni,*" "*Pitymys arvaloides,*" and "*Pitymys gregaloides*" (based upon the configuration of the Cap). These are abundant in the early Pleistocene faunas of Eurasia. Some early Eurasian individuals with an extremely weak development of the lingual Secondary Wing are similar to advanced *Allophaiomys* (figs. 6*D* or 9*B*), except that Dimension B–B′ is much more constricted, and, of course, all of these early populations of *Terricola* include *Allophaiomys* morphotypes in their population variation. The retention of *Allophaiomys* morphotypes in early populations of *Terricola* persists much longer in evolving lineages than it seems to persist in early populations of *Lasiopodomys*.

An example of these primitive forms of *Terricola* comes from the Razdolie fauna, south of Barnaul in Western Siberia (Zazhigin, 1980, fig. 38; this report, locality 29 in fig. 1). Based upon figured specimens, this fauna contains intergrading morphotypes of moderately advanced *Allophaiomys* (72 percent) and *Terricola hintoni* (28 percent). Although the present author briefly examined this fauna in Moscow, the entire sample has not been counted to eliminate a few *Lasiopodomys* morphotypes (six were illustrated, one as *Microtus*) that were included in the count of, but that do not appear to intergrade with, *Allophaiomys*. A few last upper molars are complex (all included in *Terricola*), and the brief examination of the sample in Moscow showed that about 33 percent of the individuals have "*Microtus*" enamel-thickness differentiation. From the morphotype counts presented, a bimodal pattern does not appear evident, and it is not certain whether *Terricola hintoni* should be recognized in the fauna or whether a population of *Allophaiomys* is present with a strong *Terricola* variation.

The Razdolie fauna also contains *Cromeromys intermedius*, *Mimomys pusillus*, "*Villanyia,*" *Eolagurus*, *Prolagurus*, and *Clethrionomys*. From its composition, the fauna would seem to date from well before the Jaramillo event of the Matuyama Chron, but no paleomagnetic control is available. The Razdolie *Terricola* is much less advanced than that which dispersed to North America 850,000 years ago, after the Jaramillo event and before the Brunhes Chron.

Although *Terricola* in Eurasia and *Pitymys* and *Pedomys* in North America have separate origins out of *Allophaiomys*, they are retained in the single tribe Pitymyini. Because of the preliminary nature of the phylogeny of these descendants of *Allophaiomys*, suprageneric (tribal) groups are not treated as monophyletic in the present report. Basically the function of suprageneric categories is to subdivide bewildering arrays of taxa into comprehensible units. Thus, the separate origins of *Pitymys* and *Terricola* out of *Allophaiomys* (an unknown number of lineages in Eurasia and two in the United States) and the need for different dental diagnoses to distinguish them, are not here considered sufficient reason for the establishment of separate tribes. Nor are the two, and possibly more, origins of *Microtus* out of *Lasiopodomys* or the possible multiple origins of *Lasiopodomys* out of *Allophaiomys*. As the history of *Terricola* and *Microtus* is further revealed, tribal subdivision may become desirable for clarity in discussion.

GENUS *PITYMYS* M'MURTRIE, 1831

(fig. 13*A–E*; Georgia, U.S.A.; locality 28, fig. 1, exact locality uncertain)

Type species.—Psammomys pinetorum LeConte, 1830.

Revised dental diagnosis.—A genus of the tribe Pitymyini with weak Secondary Wings and a large Dimension A–A′; often with a large Dimension B–B′; and a simple M\3. Triangle 4 (buccal Primary Wing) of first lower molars projects posterobuccally—not normal to the tooth longitudinal occlusal midline (fig. 13). Enamel-thickness differentiation is of "*Microtus*" or intermediate type.

"TYPICAL" *PITYMYS*

Revised dental diagnosis.—As for the genus.

Comments.—Pitymys pinetorum has been recognized as belonging to a strictly North American lineage at least since van der Meulen (1978) and suspected as such prior to Ognev (1948). Both Secondary Wings on the Cap of the Anteroconid Complex are present, but they are poorly developed and Dimension A–A′ is large. M\3 is always simple. Enamel-thickness differentiation is of either the "*Microtus*" or the intermediate type; the enamel tends to be quite thick.

The genus is characterized by a moderate to wide Dimension B–B′ so that, like *Allophaiomys*, it usually has moderate to great dentinal confluence between the Primary Wings and the Cap of the Anteroconid Complex; however, this confluence has exceptions. Although only 6 of 44 first lower molars of *Pitymys pinetorum* from New Paris #3, Pennsylvania (Holocene), were judged to have Dimension B–B′ completely open, in the remainder the dimension was less than half closed. In none was the dimension closed, breaking the confluence between the Cap and the Primary Wings. On the other hand Paulson (1961) stated that he examined 91 specimens of *P. pinetorum* and counted 40 percent as being closed between the Primary Wings and the Cap. More examination of *P. pinetorum* would seem to be needed. Also, a more critical evaluation of uniformity in the use of the terms "open," "half closed," and "closed" would probably help reduce uncertainties. A question exists regarding the possibility of extreme differences between local populations.

In the population found in the Cheetah Room fauna of West Virginia, the genus can be seen to have evolved out of *Allophaiomys*. Judging from the sample seen from the Hanover Quarry Fissure fauna, from van der Meulen's description of the Cumberland Cave population, and from Pfaff's discussion of both Trout Cave No. 2 and Cumberland Cave populations, *Pitymys cumberlandensis* appears to be an evolutionary stage of the genus more fixed in its individual variability but differing from the living form by lacking "*Microtus*" enamel differentiation in a significant percentage of individuals.

Van der Meulen (1978) suggested that Dimension A–A′ of *P. cumberlandensis* is relatively wider than in *P. pinetorum* so that the reentrants created by its shortening are weaker and not filled with cement; that is, its Secondary Wings are less developed (fig. 13). This difference did not seem obvious in the sample of *P. cumberlandensis* from the slightly older Hanover Quarry Fissure here examined. *Pitymys cumberlandensis* from Cumberland Cave was not examined for the present evaluation, as its nature did not seem to be in doubt from published accounts; see van der Meulen (1978) for illustrations.

There appears to be little difference in the morphology of *Pitymys cumberlandensis* from the Hanover Quarry Fissure, from Cumberland Cave (van der Meulen, 1978), and from Trout Cave No. 2 (Pfaff, 1990). Viewed with the awareness of the distinct changes in morphotype modes in the *Allophaiomys*-to-*Pedomys* and in the *Lasiopodomys*-to-*Microtus* populations of these same faunas, this persistent lack of individual variability seems unusual. It strongly suggests that *Pitymys cumberlandensis* had achieved morphologic stability (polarization).

On the other hand, the difference between *Pitymys cumberlandensis* and the single living species of this genus, *Pitymys pinetorum*, is so slight (a change toward increased "*Microtus*" enamel-thickness differentiation) that it is difficult to believe that the living species does not derive from *P. cumberlandensis*. No other obvious source is known for the living species, and *Allophaiomys*, the ancestral root stock, appears to have become extinct, through linear evolution of

Allophaiomys guildayi into *Pedomys*, during the existence of *Pitymys cumberlandensis*.

After the time of the Trout Cave No. 2 fauna, the stability of the character polarization of enamel-thickness differentiation in *Pitymys cumberlandensis* must have decreased, but no fossil record of such has been demonstrated. Although an adequate number of populations have not been examined, many have reported the opinion that extreme variation characterizes living *Pitymys pinetorum*. It is suggested that this change in character stability may be happening today. This is a situation in which the identification of the decrease in polarization of enamel-thickness differentiation will require the determination of percentages of differentiation in large samples of the living species from many local populations. Half a dozen or fewer fossil species have been named (see Repenning, 1983) and they cannot be properly evaluated until the variability of the living species is better known.

Pitymys lives primarily near trees and has always had a distribution confined to open forests and the forest-prairie mosaic of the eastern United States. The possibility exists that it was competitive with immigrant *Terricola*, explaining their former mutually exclusive distributions.

GENUS *PEDOMYS* BAIRD, 1857

(fig. 13*F*; Fort Pierre, South Dakota; locality 29, fig. 1)

Type species.—Pedomys ochrogaster Baird, 1857.

Revised dental diagnosis.—A member of the tribe Pitymyini very similar to *Pitymys* but with Triangle 4 (buccal Primary Wing) projecting at right angles from the longitudinal occlusal midline of the first lower molar (fig. 13*F*).

Comments.—The type species has been considered by many as belonging in *Pitymys*. *Pedomys*, like *Pitymys* and *Allophaiomys*, has a moderate to wide Dimension B–B′ so that it has wide dentinal confluence between the Primary Wings and the Cap of the Anteroconid Complex. Both Secondary Wings on the Cap of the Anteroconid Complex are present, and, as in *Pitymys*, they are commonly poorly developed. Dimension A–A′ is large; the dimension does not seem to average quite as large, however, as in *Pitymys*. The M\3 is always simple. "*Microtus*" enamel-thickness differentiation is the rule, although in some individuals it is only weakly developed.

From dental characters, distinguishing individuals of *Pedomys* from those of *Pitymys* is difficult, as many who work with the teeth of these genera have stated. Martin (1974; enlarged in Martin, 1991) indicated that the first lower molars of *Pedomys* can be distinguished from those of *Pitymys* by the lateral projection of Triangle 4 (buccal Primary Wing), which projects nearly at right angles to the occlusal axis in *Pedomys*, rather than posterolaterally as in *Pitymys* (fig. 13). Pfaff (1990) agreed with this character but expressed it in terms of the angle formed by the anterior borders of the two Primary Wings (*Pedomys* >140°; *Pitymys* <135°); he also indicated that the reentrants of *Pitymys* are narrower and curved more to the anterior at their apices than are those of *Pedomys*.

Paulson (1961) examined 146 specimens of living *Pedomys ochrogaster* and counted 95 percent as being confluent between the Primary Wings and the Cap, differing in this great percentage from his observations of *Pitymys*, wherein only 60 percent were confluent. There is, however, reason to question this observation, as noted previously (p. 67). These characters may be useful in the identification of *Pedomys ochrogaster* populations for which a large sample is available, but are not without exception and are not positive in the identification of individual specimens.

Pedomys appears to have begun evolving from *Allophaiomys guildayi* in the Cumberland Cave fauna; it appears as a morphotype variant of *Allophaiomys* (7 percent) in the Hanover Quarry Fissure fauna. Van der Meulen (1978) stated that about 20 percent of the population from Cumberland Cave has the typical *Allophaiomys* morphotype, with no suggestion of the development of Secondary Wings. The remainder of the population has one or two rudimentary Secondary Wings according to his description. What van der Meulen's morphologic criteria were is not clear, but the present author's count of a part of the same sample indicates a different percentage, a condition that is bound to occur with different observers because of varying criteria for subdividing a morphologic continuum. Thirty-seven first lower molars were available for the present study, but van der Meulen stated that he had 200. How the sample available for the present study was separated from van der Meulen's is not known.

As previously discussed under *Allophaiomys* from Cumberland Cave (p. 42), 51 percent of the available sample of *Allophaiomys guildayi* has a "typical" *Allophaiomys* morphology, 32 percent has an "advanced" *Allophaiomys* morphology with a posterolingual angularity on the Cap, and 16 percent has a *Pedomys* morphology with both Secondary

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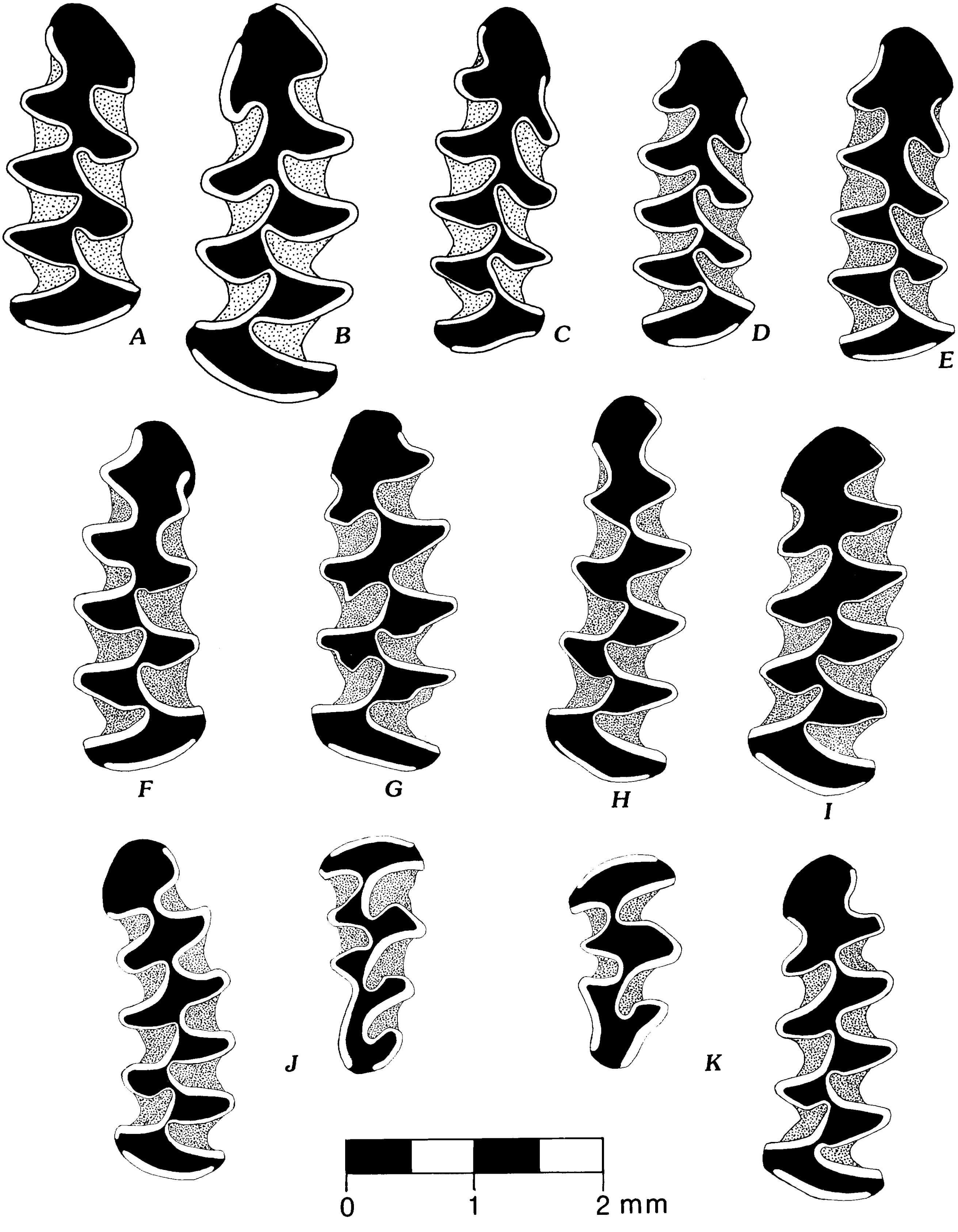
Figure 13 (facing page). *Pitymys* and *Terricola*, first lower and last upper molars. *A, Pitymys hibbardi*, Cheetah Room fauna, West Virginia, individual overlapping *Allophaiomys* morphotype; USNM specimen. *B, Pitymys hibbardi*, Cheetah Room fauna, West Virginia, typical individual; USNM specimen. *C, Pitymys hibbardi*, Cheetah Room fauna, West Virginia, individual overlapping *Pitymys cumberlandensis* morphotype; USNM specimen. *D, Pitymys cumberlandensis*, Hanover Quarry Fissure fauna, Pennsylvania; CM specimen. All the following (*E-K*) have "*Microtus*" enamel-thickness differentiation: *E, Pitymys pinetorum*, New Paris fauna, Pennsylvania (fossil). *F, Pedomys ochrogaster*, Kansas (living). *G, Terricola meadensis*, Locality CT–2, oldest faunas in Hansen Bluff faunal sequence, Colorado (fossil). *H, Terricola meadensis*, Cudahy fauna, Kansas (fossil). *I, Terricola quasiater*, Vera Cruz, Mexico, UCMVZ specimen (living). All the preceding have simple M\3s. *J, Terricola subterraneus*, Belgium, M/1 and associated complex M\3 (living). *K, Terricola duodecimcostatus*, Spain, M/1 and associated simple M\3 (living). The last is a "rhomboid" M\3.


A
B
C
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E
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0
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Wings in clear evidence, although never well developed. Such counts, of course, vary with the counter, and one may consider an enamel irregularity insignificant while another will consider it as certain evidence.

It seems probable that what is here considered as "advanced *Allophaiomys*" was considered as *Pedomys* by van der Meulen, and such a judgment could be defended by pointing to the variability observed in living *Pedomys*. But van der Meulen's method of judging would seem to eliminate half the type population from Betfia–2, and this is not justified. However, there remains the uncertainty of how the sample seen in the present study was separated from that examined by van der Meulen; the selection might have been biased.

To the extent that the present author has seen the type population from Cumberland Cave, *Allophaiomys guildayi* has a morphologic variation with 16 percent overlap of the *Pedomys* morphotype. Pfaff (1990) had access to the Cumberland Cave fauna and also referred the species to *Allophaiomys*. Earlier, Repenning (1983) made the same judgment from consideration only of van der Meulen's illustrations (1978, fig. 7), which contain only one *Pedomys* morphotype and eight specimens of "typical" and "advanced" *Allophaiomys* morphotypes.

Allophaiomys guildayi from Hanover Quarry Fissure fauna has the *Pedomys* morphotype in 7 percent of the sample; the minimum of 16 percent in the Cumberland Cave fauna (by the same counter) suggests advancement toward *Pedomys* and a somewhat younger age. The sample of *Lasiopodomys* from Hanover Quarry Fissure, though of inadequate size, suggests the same advancement. The possible age relationships are discussed under *Allophaiomys* from Cumberland Cave (p. 42).

PEDOMYS LLANENSIS HIBBARD, 1944

Discussion.—In 1944, Hibbard introduced the name *Pedomys llanensis* for a form from the Cudahy fauna of Kansas (610,000 years old). His illustration of the type specimen indicates a very weakly developed buccal Secondary Wing, and none is shown on the lingual side. As the lingual one is usually the first to form in this lineage and as it is suggested by an angular posterolingual corner on the Cap as illustrated, it seems probable that the lingual Secondary Wing had been present but was obliterated by wear of the tooth. Hibbard apparently had only one specimen, the type, although he mentioned a right and a left lower jaw. In 1961, Paulson illustrated a second left ramus from Cudahy and mentioned at least four individuals. He also noted the presence of slight fifth lingual and fourth buccal reentrants; these reentrants are those anterior to the Secondary Wings and their presence is necessary for the angular corners of the Cap to be called Wings.

Van der Meulen (1978) separated *Pedomys guildayi* from *Pedomys llanensis* on the basis of a wider Cap (relative to the width of the Primary Wings) and a longer Anteroconid Complex (relative to the total length of the tooth) in *P. llanensis*. These are features that result from the increase in the complexity of the Cap (or, in his ratios, result in a narrowing of the width across the Primary Wings), and thus their increase is a derived character relative to the condition in ancestral *Allophaiomys*. He also stated that the confluence between the Cap and the Primary Wings (Dimension B–B′) is less in *Pedomys llanensis*; this appears to be true of the specimen figured by Paulson (1961) but not of the type figured by Hibbard (1944).

Van der Meulen did not have an opportunity to study the type or other topotypic material from the Cudahy fauna; they also were not available for the present study. Published accounts seem to indicate that possibly only five individuals are known from the type locality—too few to know what the typical morphology might be.

The oldest unquestioned population of *Pedomys llanensis* is that from Trout Cave No. 2, West Virginia, which was described by Pfaff (1990). The sample of this population of the species includes morphotypes of *Allophaiomys pliocaenicus* (<10 percent), *A. guildayi*, and *Pedomys llanensis* (66 percent), and Pfaff noted that more than 90 percent have the development of at least one Secondary Wing (Pfaff, 1990, fig. 5A) and that 66 percent show the development of both (Pfaff, 1990, fig. 5). Less than 10 percent are described as having an *Allophaiomys pliocaenicus* morphotype (Pfaff, 1990, fig. 5E), and the sample apparently shows a *Pedomys*-mode with individual variation overlapping primarily the advanced *Allophaiomys* species morphotype.

This composition of the *Pedomys* population from Trout Cave No. 2 and the lack of *Lasiopodomys* variants in its sample of *Microtus paroperarius* indicate an age younger than Cumberland Cave, as concluded by Pfaff. The stage of advancement of the *Microtus* first lower molars (his fig. 4) is comparable to that known from the oldest faunas of Hansen Bluff, Colorado, but includes a few individuals with a more prominently reduced Dimension A–A′, and only complex last upper molars were assigned. The Trout Cave No. 2 fauna is thus considered to be somewhat younger than the oldest faunas of Hansen Bluff (820,000 years), but probably not as young as the youngest faunas of this Colorado faunal sequence (approximately 700,000 years). Pfaff noted that the fauna appears clearly older than the Cudahy fauna of Kansas (610,000 years), and it is here assigned an approximate age of 725,000 years.

The Trout Cave No. 2 fauna also contains *Pitymys cumberlandensis* in a population that seems no different than that of Cumberland Cave or Hanover Quarry Fissure, again suggesting a polarity of individual variation in this extinct species, as has been discussed.

The species *Pedomys llanensis* had been recognized in several other faunas (Wathena, Kentuck, and Sappa), until Martin (1975) pointed out that the fossils so identified were very similar to *Allophaiomys pliocaenicus*. Thus these other records do not help in the recognition of *P. llanensis*.

Pfaff (1990) noted the similarity of *Pedomys llanensis* to living *P. ochrogaster* and suggested that they might be conspecific, the principal difference being that older populations have, apparently, greater individual variability. But he also noted that considerable variability still exists in the living species. Graham (1972) reported the existence of about 30 additional first lower molars of *P. llanensis* from the Cudahy fauna and an equal number from Conard Fissure, Arkansas. The present author has not seen these and has not been able to confirm the existence of 30 additional first lower molars from Cudahy.

Living *Pedomys* is more of an open grassland animal than is *Pitymys* and has a distribution farther west, extending across the Great Plains westward to the foot of the Rocky Mountains. It does not live in the mountains and, as noted, it is not present in northeastern North America; its range appears to be exclusive of areas cooled in the summer by arctic air or higher topography. However, its modern range does not extend as far south as did that of *Allophaiomys*, and in contrast to *Allophaiomys*, it coexists with *Microtus* in the southern part of the range of the latter.

GENUS *TERRICOLA* FATIO, 1867

(figs. 10*B*, 13*G-K*; Lake Geneva, Switzerland; locality 35, fig. 1)

Type species.—Fatio did not designate a type species for *Terricola* but erected it as a subgenus to include both *Terricola savii* and *Terricola subterraneus*. The ranges of the two rather different species (this report, fig. 13*J, K*) overlap in the type area. *Terricola savii*, as grouped by Corbet (1978), is a southern European form that has a simple last upper molar in many populations (includes *T. duodecimcostatus*, this report, fig. 13*K*). *Terricola subterraneus* is a northern species with a complex M\3 (this report, fig. 13*J*). Many other living species have been named.

Revised dental diagnosis.—A genus of the tribe Pitymyini with strong Secondary Wings, wide to very narrow Dimension A–A', very narrow to closed Dimension B–B′, and "*Microtus*" enamel-thickness differentiation. Last upper molar complex or simple.

"TYPICAL" *TERRICOLA*

Revised dental diagnosis.—As for the genus.

Comments.—On the basis of the last upper molar alone, the genus *Terricola* appears in need of subgeneric subdivision. Kratochvil (1970) has examined many characters in an effort to subdivide and classify *Terricola*; Kratochvil and Kral (1974) have identified two major groups on the basis of karyotypes. Brunet-Lecomte and Chaline (1990) have examined European fossil and living species and have suggested a rather complicated, but nonetheless plausible evolutionary history. However, their analysis does not consider Asiatic and North American populations, nor the morphology of the last upper molar, which, in contrast with its significance in the tribe Microtini, appears so variable that it seems useless. No characters used in these attempts to subdivide *Terricola* of Europe and western Asia seem to match well with characters in the others; each attempt at subdivision seems to produce different geographic groupings, and in many populations individual variation appears to be great.

Discussion.—Unlike *Pitymys* and *Pedomys*, the genus *Terricola* has a very narrow to closed Dimension B–B′ resulting in little or no confluence between the Cap and the Primary Wings. Dimension A–A′ is also narrow in most living forms, and in most individuals Secondary Wings are strongly developed (fig. 13*G–K*). This character is much less prevalent in fossil species. In North America, *Terricola* has only "simple" last upper molars except for a few individuals of the living *Terricola quasiater* (east-central Mexico), which seem today to be developing a more derived last upper molar. This condition contrasts with many, but not all, Eurasian species (Repenning, 1983). Possibly a situation similar to that of the Mexican population may explain the variability reported in the Eurasian species, and it may be decipherable only on a "percentage of the population" basis. The Eurasian living *Terricola* populations have a variability in the complexity of the last upper molar comparable to that seen in *Microtus paroperarius* in the oldest faunas (820,000 years) of the Hansen Bluff faunal sequence; in some living *Terricola* lineages polarization to a complex last upper molar may only be in progress.

In Eurasia, species that have a simple M\3 are southerly in distribution (Miller, 1912), suggesting a distribution of more primitive relics. But the geographic pattern is not simple. Kratochvil (1970) recorded individual variation between simple and complex last upper molars in some species (such as *Terricola tatricus*) and tentatively identified five to seven geographic species groups; Miller (1912) also recognized many species groups by grouping them on the basis of last upper molar complexity.

With the possible exception of *Pitymys pinetorum nemoralis*, whose specific affinity (and now generic, with the separation of *Pitymys* from *Terricola*) Repenning (1983) questioned, North American *Terricola* appears to be now confined to central Mexico, although once widespread in the central and western United States.

The tooth shown in figure 10*B* is that of *Terricola meadensis* (Hibbard) from an undated locality in the Anza-Borrego Desert of California (LACM Loc. 68123). It is from a locality within the depositional sequence that was studied magnetically (J.A. White, written commun., 1990) and below the youngest normal polarity zone. Other records of *Terricola* in the United States, all west of the Mississippi River but both east and west of the Rocky Mountains (Repenning, 1983), indicate that this species is not known before the dispersal event 850,000 years ago.

These post-Jaramillo-event localities include Californian localities as far north as the San Francisco area and Cape Mendocino (localities 22 and 23, fig. 1). Thus the youngest normal polarity of the Anza-Borrego Desert study is not the Jaramillo event, as was supposed by Johnson and others (1984), but the Brunhes Chron. The oldest closely dated records of *Terricola meadensis* are in the 820,000-year-old faunas of the Hansen Bluff faunal sequence. The type is from the Cudahy fauna of Kansas, 610,000 years old.

It is believed that *Terricola meadensis* entered the United States, with *Lasiopodomys*, by way of the dispersal route on the east side of the Rocky Mountains and spread over the Great Plains between 850,000 and 610,000 years ago. At the time of its entry into the area of the United States, *Terricola* seems to have continued south past Hansen Bluff, Colorado, westward around the south end of the Rocky Mountains to southern California, and then northward up the Pacific Coast to nearly the northern limit of California. The genus is known from high in the Rocky Mountains (Hansen Bluff, 7,546 ft elevation, and Porcupine Cave, 9,500 ft elevation) and from sea level at the head of the Gulf of California (Anza-Borrego Desert) and at Cape Mendocino, northern California (Repenning, 1983; localities 15, 21, 22, and 23, fig. 1). This is a remarkable range in environment from what must have been subalpine meadows in Colorado to the northern fringes of subtropical coasts at the head of the Gulf of California. The obstacle preventing *Lasiopodomys* from also following this route was probably the presence of warmer climate around the south end of the Rocky Mountains, as other parts of the history of this genus indicate arctic to temperate climate preferences.

The immigrant *Terricola meadensis* was present only in the western areas of the United States (Cudahy, Hansen Bluff, Porcupine Cave, and other localities both east and west of the Rocky Mountains), and its absence in the Appalachian faunas (Cheetah Room, Hanover Quarry Fissure, Cumberland Cave, and Trout Cave No. 2 faunas) is a feature of the eastern United States; it has never been reported from east of the Mississippi River (Repenning, 1983).

Although an immigrant, with *Lasiopodomys*, from Beringia to the United States 850,000 years ago, *Terricola* is unknown in the Beringian fossil record. It is unknown from the several localities of the Old Crow basin in northern Yukon Territory, unknown in Alaskan fossil and living faunas, and unknown in northeastern Siberia, either fossil or living. Yet it certainly passed through Beringia and appears to have done so between 875,000 and 820,000 years ago.

Terricola meadensis does not appear to have stayed in Beringia very long, and unquestionably the coldest environments in which it has been found are those along the east edge of the Rocky Mountains of Colorado, at the Hansen Bluff locality (Rogers and others, 1985; 7,546 ft (2,300 m) elevation; during the Nebraskan glaciations) and Porcupine Cave locality (Barnosky and Rasmussen, 1988; 9,500 ft (2,900 m) elevation; possibly during the Kansan glaciation). At about the same time that it lived at Hansen Bluff, it also lived in hot subtropical wet climates near sea level at the head of the Gulf of California in the region of the modern Anza-Borrego Desert of California. Its known past range is broad in the region now occupied by the Temperate Zone but was mainly in warm-temperate to subtropical regions. The fossil record of *Terricola* does not speak for very intensive cold during the earlier glaciations of the United States (Repenning, 1983).

No southward dispersal from Beringia took place down the west side of the Rocky Mountains 850,000 years ago; a combination of rising coastal mountains in western Canada and southern Alaska and increased mountain glaciation, which flowed into the Pacific Ocean, appears to have obliterated a coastal plain environment suitable for dispersal as well as erecting walls of ice across the route (Repenning, 1990).

The lack of a record of *Terricola* in Beringia suggests that the genus did not linger there when dispersing to North America but moved southward ahead of the first Nebraskan ice sheet; nor does it live in arctic environments today. *Terricola* seems to have decided temperate preferences. The fact that it did disperse to North America thus suggests a period, probably brief, of temperate climate in Beringia just before the first Nebraskan ice advance. Scant evidence exists for such a Beringian warm period at this time, except that little record seems to exist of deposition during the 50,000 years between the Jaramillo event and the first Nebraskan ice sheet. Such a hiatus is known at least in Yakutia and Yukon Territory, as will be discussed in the section, "Age of Krestovka Olyor and Cape Deceit faunas" of this report.

Other than avoiding arctic climates, *Terricola* seems to have had great adaptability, from subtropical sea levels along the Mexican border in southern California to 9,500-ft subalpine valleys in the eastern parts of the Rocky Mountains. This adaptability seems to suggest that competition, rather than environmental constraints, caused the failure of the genus to occupy the United States east of the Mississippi River. It now exists as a relict population in the eastern slopes of the Sierra Madre Oriental in central Mexico.

SYSTEMATIC SUMMARY

(fig. 14)

Allophaiomys is a member of the tribe Arvicolini because it has a first lower molar with fully confluent Primary Wings and a Cap uncomplicated by Secondary Wings.

Dimension A–A′ equals the width of the Cap (that is, the dimension does not exist); Dimension B–B′ is wide and little reduced; Dimension C–C′ is wide and little reduced; M\3 is simple; enamel differentiation is primarily "intermediate"; and hypsodonty is advanced so that roots do not form on the cheek teeth.

The tribe Microtini.—The tribe Microtini formed out of *Allophaiomys* by complications of the Anteroconid Complex. The first complication is the separation of the two Primary Wings by the reduction of Dimension C–C′, forming Triangle 4. Further complications consist of (1) reduction of Dimension B–B′ to greatly narrow or eliminate the dentinal contact between the lingual Primary Wing and the Cap, ultimately forming Triangle 5; (2) establishment and reduction of Dimension A–A′ to develop Secondary Wings (Triangles 6 and 7); (3) complication of the posterior loop of the last upper molar; and (4) the development of "*Microtus*" enamel-thickness differentiation. These numbered further complications develop at rates that are independent of each other and define the genera of the tribe.

Lasiopodomys shows only separation of the Primary Wings and no further complications, although "*Microtus*" enamel-thickness differentiation may develop variably. Living species, in the Oriental faunal region of Asia, appear to be at about the same stage of evolution as were the first *Microtus* that evolved out of *Lasiopodomys*; they are believed to have developed in the Oriental region by evolution parallel to the other *Lasiopodomys* lineage present throughout the Northern Hemisphere. Multiple origins of non-Chinese *Lasiopodomys* (out of *Allophaiomys*) also seem possible.

Microtus shows further complication (2), establishment and reduction of Dimension A–A′ with the development of Secondary Wings; it may also show further complications (1), reduction of Dimension B–B′, and (3), complication of the posterior loop of M\3. Except for the earliest forms, further complication (4), "*Microtus*" enamel-thickness differentiation, is almost universal. Multiple origins out of different populations of *Lasiopodomys* on different continents at different times seem obvious.

The subgeneric and specific subdivisions of *Microtus* result from the variations in rates of these further complications and are not yet clearly documented. Better documentation of the fossil record of *Lasiopodomys* will assist understanding of the lineages of *Microtus*, for different lineages presumably evolved out of different populations of *Lasiopodomys* in different regions.

Proedromys is unique in that it shows a reduction, rather than complication, of the posterior loop of the last upper molar, but otherwise resembles *Lasiopodomys*. Its fossil and living records suggest no diversification or major dispersal, and it may have developed only in the Oriental region by evolution parallel to *Lasiopodomys*.

The present fossil record suggests that the North American genus *Lemmiscus* evolved directly out of *Allophaiomys* perhaps 870,000 years ago in the southeastern Rocky Mountains of New Mexico and that this lineage experienced no diversification after this time. Its unique characters are the presence of a last upper molar with an elongate posterior process but only two alternating triangles anterior to it, of only a buccal Secondary Wing on the first lower molar, and of cement in the tooth reentrants. Like *Proedromys* in China, *Lemmiscus* in western United States seems to have experienced no major (global scale) dispersal from its area of origin (Rocky Mountains), nor diversification.

Rather than being typical of either the eastern or the western regions of the United States, *Lemmiscus* appears unusual in that it appears to have originated within the Rocky Mountains and spread both east and west into both provinces. Its two oldest records are in Colorado within the eastern part of the Rocky Mountains.

The tribe Pitymyini.—The tribe Pitymyini developed out of *Allophaiomys* by complications of the Anteroconid Complex, the first of which is establishment and reduction of Dimension A–A′ to develop Secondary Wings (Triangles 6 and 7). Further complications consist of (1) reduction of Dimension B–B′ to narrow or eliminate the dentinal confluence between the Primary Wings and the Cap, (2) shortening of Dimension A–A′ to make the Secondary Wings more prominent, (3) complication of the posterior loop of the last upper molar, and (4) development of "*Microtus*" enamel-thickness differentiation. These numbered further complications develop at rates that are independent of each other, and their variations define the genera of the tribe. No subgenera are recognized, although they might be as justifiable as they are in *Microtus*.

Pitymys is variable in the presence of further complication (1), reduction of Dimension B–B′, and usually does not show it; the genus does not experience further complication (2), to produce prominent Secondary Wings, or further complication (3), to produce a complex last upper molar. Further complication (4), development of "*Microtus*" enamel differentiation, is variable and, because thick enamel is prominent in the genus, the differentiation is not always conspicuous; the genus may now be in the process of developing further complication (4) in the living fauna.

Pitymys evolved in North America out of *Allophaiomys* and appears always to have had an eastern distribution within the eastern region of the United States.

Pedomys usually does not experience further complication (1), reduction of Dimension B–B′, but otherwise has the same variability of further complications as does *Pitymys*. Triangle 4 usually projects normally from the tooth axis rather than posterolaterally as in *Pitymys*. *Pedomys* also evolved in North America out of *Allophaiomys*, but at a slightly later time than did *Pitymys*.

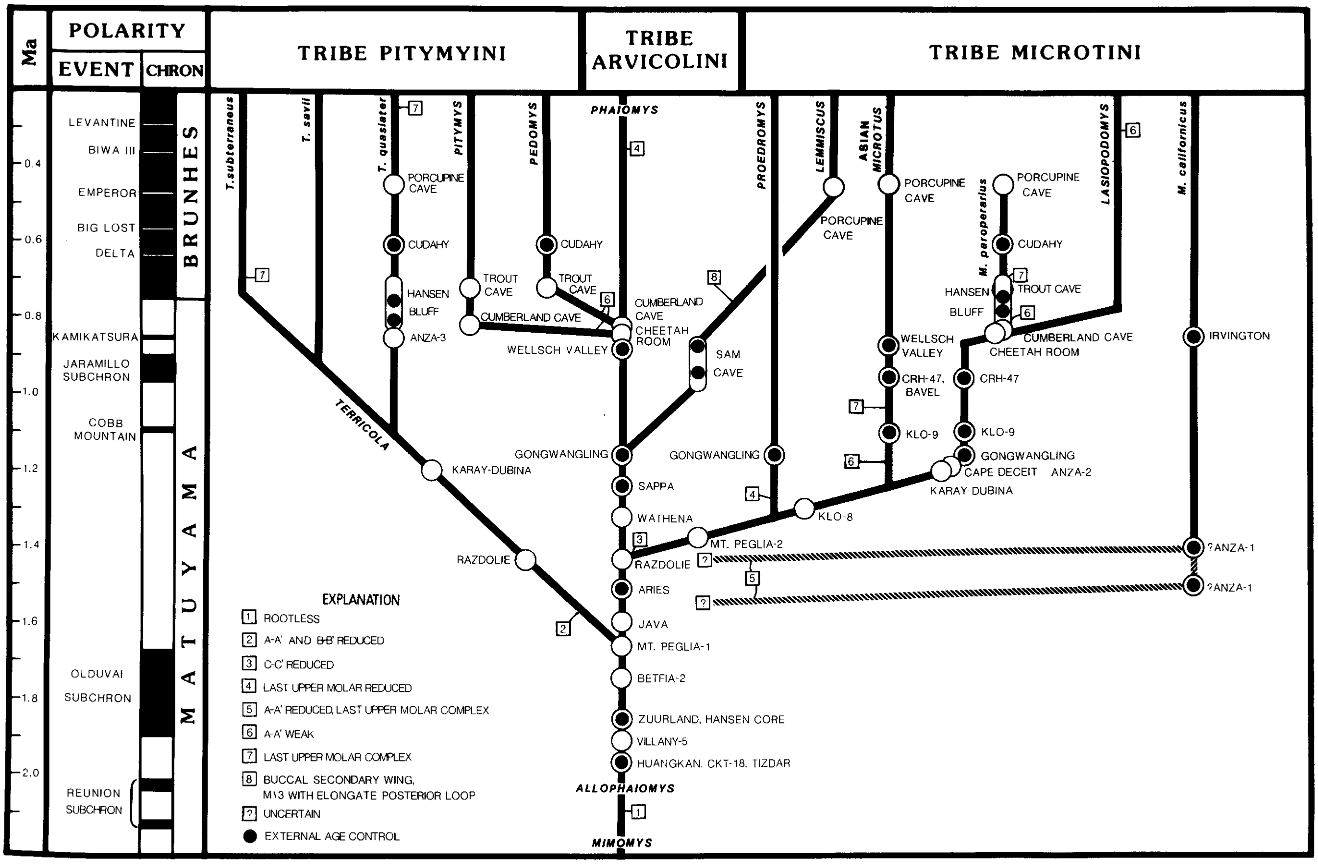

Figure 14. Phylogenetic diagram of genera of the Microtini and the Pitymyini herein discussed. Based upon present information. Geography is not indicated. Time and geopolarity are. Broken connecting lines at lower right, origin uncertain: possibly from Oriental faunal region.

Pitymys and *Pedomys* are not diverse and did not disperse to the Old World or west of the Rocky Mountains in North America.

Terricola experienced all listed further complications and evolved in the Old World. It dispersed to North America about 850,000 years ago at a stage when the dispersing lineage had not yet experienced further complication (3), complex M\3; the population of *Terricola* that immigrated to North America had already experienced further complications (1), shortening and closure of Dimension B–B′, and (2), shortening of Dimension A–A′. The North American population of *Terricola* may now be experiencing further complication (3), complex M\3. Like *Pitymys*, North American *Terricola* is not consistent and may or may not have "*Microtus*" enamel-thickness differentiation (further complication (4)).

The Eurasian species of *Terricola* appear to be divisible on the basis of whether or not further complication (3), complex M\3, has been experienced in their lineage, but the present record indicates current lack of polarity in many species. However, complicated last upper molars are a progressive character in all lineages of the subfamily Arvicolinae except that leading to *Proedromys*.

The genera *Herpetomys*, *Neodon*, *Orithriomys*, and *Tyrrhenicola* are of uncertain affinity, in the author's mind.

PROVINCIALITY

Among the descendants of *Allophaiomys*, differences in age of less than 10,000 years are inferred from progressive morphologic change within lineages; they are supported by other aspects of the fossil fauna as there are, currently, no age-determining methods which discriminate such brief time periods. The pattern of such rapid evolution cannot be calibrated with less accurate time control, and the age of stages of evolutionary change between times controlled by extrinsic (external) methods must be interpolated. Interpolation requires an estimate of proportionate change, and the assumption that the rate of change was uniform. A similar assumption, that the rates of deposition and evolution were uniform, is used to interpolate age in deep sea cores, possibly with less justification because it has often been demonstrated that the rate of deposition does change. Similarly, it is rather clear from the microtine fossil record that environmental change stimulates evolutionary change. These influences require that attention to depositional and environmental change be maintained.

Because of the rapid rates of morphologic change in microtine rodents, their provincial history must also be a consideration in interpreting their evolution. Over short periods of time, microtine populations can change greatly within a province, and these changes **need not resemble** those that took place in other provinces. Still, these changes **can be so similar** that they cloud recognition of provenance. Consequently, the integration of provincial histories around the world is impossible without an awareness of their differences and of interprovincial faunal exchanges. What came from Asia to Beringia as *Lasiopodomys* may have left Beringia for the United States as *Microtus*.

Without knowing the direction and rate of evolution, the constraints of climate and geography, the morphologic definitions of taxa, and without time control, one has no basis for interpreting microtine history; evolutionary paths would be assumed rather than demonstrated, and the magnitude of possible error in such an assumption increases with the rate of evolution. All factors are critical to understanding, and the neglect of any one leaves questionable any interpretation.

The record of microtine rodent history, at least in North America, is now known well enough to indicate that this history can be quite different in different faunal regions. It is as obvious in the past as it is today that the microtine fauna in the arctic region is not the same as that in Spain. It also is obvious that the distribution and composition of microtine faunas change with changes in climate. The appearance or disappearance of any taxon in Europe does not necessarily have the same temporal significance as it does in central Asia, or other areas. Faunal regions were no less distinct in the past than they are today, and the time and direction of evolution are determined by provincial ecosystems; microtine evolution is mosaic. This is illustrated by the polyphyletic origins of *Microtus*.

The following detailed demonstration illustrates the present lack of certainty regarding at what times and in what regions *Microtus* evolved out of *Allophaiomys* and the need to understand provinciality before inferring the origin of taxa and the timing of biochronology. This illustration has been mentioned repeatedly throughout this report, but serves as a summary of the preceding discussions of fossil faunas and their composition. And it is a significant consideration in the evaluation of the age of the Olyor Suite of the Krestovka Sections in Yakutia.

1. **SAM Cave, New Mexico** (first discussed in the present publication) contains several fossil faunas representing populations of *Allophaiomys* that are morphologically advanced from the condition found in the typical *Allophaiomys pliocaenicus* (figs. 3, 6). A few individuals overlap the morphology of *Lemmiscus* (fig. 6*F*, *G*). Absent are immigrant *Terricola* and *Lasiopodomys*, and native *Pitymys*, *Pedomys*, and *Microtus*, denoting a later age. Present are cool and moist climate indicators (primarily Canadian forests and prairies of today) of the Irvingtonian I microtine age, *Mictomys kansasensis*, ?*Phenacomys*, and the first *Lemmiscus*. This locality is at 8,900 ft (2,728 m) elevation, one of the highest fossil microtine faunas in the United States. Preliminary paleomagnetic determinations indicate that the BOT–4 fauna of SAM Cave lived shortly after the Jaramillo event—less than 900,000 years ago. The BOT–4 fauna is in reversed deposits above the Jaramillo event and is arbitrarily assigned the age of about 875,000 years; it is older than the immigration of *Lasiopodomys* and *Terricola* 850,000 years ago.

2. **The Hansen Bluff faunal sequence, Colorado** (Rogers and others, 1985) is 39 miles (62 km) northeast of SAM Cave and is from deposits within the same broad valley of the Rio Grande, which, for the most part, has been in its present valley for almost 5 million years (Repenning and May, 1986). This faunal sequence is at 7,546 ft (2,300 m) elevation, also one of the highest fossil microtine faunas in the United States. The oldest faunas of the Hansen Bluff sequence have no *Allophaiomys* or *Lasiopodomys*, but these faunas have primitive *Microtus* (fig. 12*A*) recently derived from immigrant *Lasiopodomys*. Immigrant *Terricola meadensis* (fig. 13*G*) and native *Mictomys kansasensis* are present in the fauna. Native *Synaptomys* is not present although it has a presumably earlier record (earlier because it does contain *Allophaiomys* morphotypes) from Fyllan Cave, Texas (A.J. Winkler, written commun., 1990). Lack of *Synaptomys* is believed to reflect the high elevation of Hansen Bluff and climatic conditions at the beginning of the glacial ages.

Paleomagnetic stratigraphy, dated tephra, and climatic correlations at Hansen Bluff date its oldest *Microtus* as having been alive shortly before the Brunhes Chron—about 820,000 years ago (Rogers and others, 1985). More advanced *Microtus* of Beringian-Asian origin is known earlier in northern and southern Canada (fig. 7*D*) and west of the Rocky Mountains in the United States (fig. 10*A*, *C*). The provincial age differences of the earliest *Microtus* are significant, but, thus far in this summary, the significance is unexplained.

In the Hansen Bluff faunal succession the primitive *Microtus* grades upsection into typical *Microtus paroperarius*, named from the 610,000-year-old Cudahy fauna of Kansas. Computation of sediment rates, based upon paleomagnetic and tephra age controls and climatic cycles in the lower part of the section, suggests that the youngest part of the Hansen Bluff sequence is about 700,000 years old (Rogers and others, 1985). Climatic changes through this section are interpreted in this same reference.

3. **The Cheetah Room fauna, West Virginia** (Repenning and Grady, 1988) contains three microtine populations pertinent to this summary:

A. Immigrant *Lasiopodomys deceitensis* with 25 percent of its individual variation overlapping primitive

Microtus paroperarius (fig. 11*J*, *K*). This fauna records a morphotype trend in *Lasiopodomys* toward that of *Microtus*; it is not the only fauna in the world to do so.

B. Nearly typical *Allophaiomys* (fig. 8) grading into a second morphologic mode that typifies endemic North American *Pitymys*, which, in turn, has individual variation that overlaps *Pitymys cumberlandensis* (fig. 13*A*–*C*). This fauna records the beginning of the genus *Pitymys*.

C. And a morphologic gradation from *Mictomys* into *Synaptomys*, endemic North American lemmings. The intergradation shows the origin of the living genus *Synaptomys*, and so indicates an age older than other records of this genus. In the present report the *Mictomys/Synaptomys* intergradation is of importance only in age considerations. No paleomagnetic control is available for the Cheetah Room fauna, but North American *Synaptomys* is known from pre-Brunhes faunas, as Fyllan Cave, Texas (A.J. Winkler, written commun., 1990), indicating that the *Mictomys*-to-*Synaptomys* diversification of the Cheetah Room fauna must be older than the Brunhes Chron (beginning 790,000 years ago).

The Cheetah Room fauna postdates the immigration of *Lasiopodomys* and *Terricola* to North America (about 850,000 years ago) because it contains *Lasiopodomys*. It is distinctly older than the oldest fauna of Hansen Bluff (820,000 years) in having *Lasiopodomys* and *Allophaiomys* present. It is older than the Hanover Quarry Fissure fauna and the Cumberland Cave fauna in lacking a polarized *Pitymys* population, in lacking polarized *Synaptomys* and *Mictomys* populations, and in having a lower percentage of *Microtus* morphotypes in its *Lasiopodomys* population.

Arbitrarily the Cheetah Room fauna is assigned an age of about 840,000 years (10,000 years after the immigration of *Lasiopodomys*; 10,000 years before the transition of *Lasiopodomys* into *Microtus* in Cumberland Cave; and 20,000 years before the extinction of *Lasiopodomys* and *Allophaiomys*, which are not present in the 820,000-year-old Hansen Bluff fauna).

4. The Hanover Quarry Fissure fauna, Pennsylvania (Guilday and others, 1984) contains three pertinent microtine populations:

A. *Pitymys cumberlandensis*, with no individual gradation into *Allophaiomys* as was found in the Cheetah Room fauna (fig. 13*D*). This species is also found in the Cumberland Cave fauna and in the Trout Cave No. 2 fauna, and may be changing into the living *Pitymys pinetorum* in the modern fauna.

B. *Allophaiomys guildayi* with individual variation overlapping *Pedomys* (fig. 9*E*, *F*). The same variation was found in the Cumberland Cave fauna, but with a significantly greater percentage of the *Pedomys* morphotypes. Still greater overlap toward *Pedomys* is found in the Trout Cave No. 2 fauna, where, because of its majority of *Pedomys* morphotypes, the population is assigned to *Pedomys llanensis* (Pfaff, 1990). The Hanover Quarry Fissure population is clearly almost all *Allophaiomys* morphotypes. Although assigned to a species of *Pedomys*, the Trout Cave No. 2 population retains a few individuals that are of the *Allophaiomys* morphotype.

C. ?*Lasiopodomys* of an advanced form (fig. 11*L*, *M*) similar to some of the morphotypes of this genus in the *Lasiopodomys-Microtus* population of Cumberland Cave, and as a variant of *Lasiopodomys* in the Cheetah Room fauna. But no *Microtus* morphotypes were found in Hanover Quarry Fissure, suggesting an age older than Cumberland Cave (a suggestion weakened by the small sample size). *Pitymys* did not grade into *Allophaiomys*, suggesting an age younger than the Cheetah Room fauna.

The Hanover Quarry Fissure fauna is younger than the Cheetah Room fauna and probably older than the Cumberland Cave fauna by virtue of these comparisons. However, these comparisons are only suggestive with respect to the Cumberland Cave fauna, and the two faunas are believed to be nearly the same age. Arbitrarily the Hanover Quarry Fissure fauna is assigned an age of 835,000 years.

5. The Cumberland Cave fauna, Maryland (van der Meulen, 1978) contains four pertinent microtine populations:

A. Immigrant *Lasiopodomys deceitensis* morphologically overlapping *Microtus paroperarius*. Both were called *Microtus* by van der Meulen (1978), but the population is almost exactly intermediate between the two genera. This is advanced over the condition found in the Cheetah Room fauna in which only a small percentage of *Microtus* morphotypes were present in a *Lasiopodomys* population.

B. *Allophaiomys* overlapping the morphology of living North American *Pedomys* (named *Pedomys guildayi* by van der Meulen, 1978). The population is advanced over the condition in Hanover Quarry Fissure fauna in its greater percentage of *Pedomys* morphotypes, but is considerably less in this percentage than Trout Cave No. 2. The major part of the population has an *Allophaiomys* morphotype and is assigned to this genus.

C. A primitive form of *Pitymys* inseparable from *Pitymys pinetorum* except for enamel-thickness differentiation (called *Pitymys cumberlandensis*). This is the further result of the *Allophaiomys/Pitymys* intergradation seen in the Cheetah Room fauna, but is the same as in Hanover Quarry Fissure and Trout Cave No 2.

D. And both *Mictomys* and *Synaptomys* but with no indication of morphologic overlap as in the Cheetah Room fauna (Repenning and Grady, 1988).

The Cumberland Cave fauna is clearly older than both the Cudahy fauna of Kansas (610,000 years) and the oldest Hansen Bluff faunas (820,000 years) because of the presence of a primitive stage in the *Microtus-Lasiopodomys* transition. It is younger than the Cheetah Room fauna (about

840,000 years) by virtue of the above comparisons, and its fauna suggests that it is younger than, but nearly the same age as, the Hanover Quarry Fissure fauna. Arbitrarily, the Cumberland Cave fauna is assigned an intermediate age of 830,000 years, 5,000 years younger than the similar Hanover Quarry Fissure fauna and 10,000 years older than the obviously more advanced oldest Hansen Bluff fauna.

6. **Trout Cave No. 2 fauna, West Virginia** (Pfaff, 1990) contains:

A. *Pedomys llanensis* containing a minor percentage of variants that overlap *Allophaiomys*, an advancement over Cumberland Cave.

B. *Pitymys cumberlandensis* apparently no different than that in Cumberland Cave or Hanover Quarry Fissure.

C. *Microtus paroperarius* lacking morphologic overlap with *Lasiopodomys deceitensis*, an advancement over Cumberland Cave.

Advanced morphologies of the first lower molar and the lack of simple last upper molars of *Microtus paroperarius* from Trout Cave No. 2 indicate an age younger than the oldest faunas of Hansen Bluff (820,000 years) but probably older than the youngest faunas of Hansen Bluff (about 700,000 years). The youngest faunas of Hansen Bluff seem nearly as advanced as the type population from the Cudahy fauna of Kansas, but these are very small samples from Hansen Bluff.

The Trout Cave No. 2 fauna is older than the Cudahy fauna (Pfaff, 1990), and, apparently, older than the youngest of the Hansen Bluff faunas, although the small samples from this part of Hansen Bluff sequence make this comparison uncertain. It is younger than the Cumberland Cave fauna and than the oldest faunas of Hansen Bluff by virtue of the above comparisons. Arbitrarily the Trout Cave No. 2 fauna is assigned an age of about 725,000 years.

These faunal compositions make it seem possible that in the faunas of eastern United States: (1) Cheetah Room fauna is perhaps 840,000 years old, (2) Hanover Quarry Fissure fauna is perhaps 835,000 years old, (3) Cumberland Cave fauna is perhaps 830,000 years old (compare van der Meulen, 1978, fig. 14, which places it at the same age as closely as the time scale can be read), and (4) Trout Cave No. 2 fauna is, uncertainly, in the vicinity of 725,000 years old.

Along the east side of the Rocky Mountains, (1) SAM Cave (BOT–4 locality) is perhaps 875,000 years old (other faunas in SAM Cave extend back in time into the Jaramillo event and forward into the Brunhes Chron), (2) oldest Hansen Bluff is about 820,000 years old, (3) youngest Hansen Bluff is perhaps 700,000 years old, (4) the Cudahy fauna, out on the Great Plains, has been known for some time to be about 610,000 years old, and (5) the age of the Porcupine Cave faunas, south-central Colorado, the highest fossil microtine faunas in the United States (9,500 ft), is not known, but the presence of immigrant *Microtus* (from Beringia) with the last of endemic *M. paroperarius* is believed to indicate an age of around 450,000 years.

Although the fossil microtine faunas of the eastern United States lack direct external age control, the integration of their evolutionary stages with those found in fossil faunas of the Great Plains and adjacent Rocky Mountains (that do have external age control) enables a plausible interpretation of the ages of these eastern faunas. Together, the microtine faunas of the United States, from the Rocky Mountains to the Atlantic coast, indicate and illustrate so explicit a history of change in several lineages that the entire region appears to be a single faunal region; and anomalous relationships, such as the failure of *Pitymys* and *Terricola* to coexist, raise the question of causes other than provincialism. It is difficult to consider greatly different age assignments for the faunas of the United States east of the Rocky Mountains.

The age of Porcupine Cave faunas is based entirely upon the presumed age of the immigration of Beringian *Microtus* (see Repenning and others, 1990). In terms of possible error for these "dated" faunas east of the Rocky Mountains, possibly the greatest uncertainty is in the age of the BOT–4 fauna of SAM Cave, which is certainly younger than the Jaramillo event and older than the immigration of *Lasiopodomys* and *Terricola*, believed to be about 850,000 years old. At first this immigration date was based on three premises: (1) the immigration came with the first Nebraskan ice; (2) the first Nebraskan ice correlates with oxygen isotope stage 22; and (3) oxygen isotope stage 22 is 850,000 years old. These assumptions appear to be in agreement with other evidence of the age of this climatic change around the Northern Hemisphere (Repenning, 1984; Repenning and others, 1990).

If the inferred age of the immigration is too old, the ages assigned to the Cheetah Room, Hanover Quarry Fissure, and Cumberland Cave faunas would be compressed against the 820,000 year age of the oldest fauna of Hansen Bluff. If the inferred age of the immigration is too young, it must be less than 50,000 years in error, as the age of the BOT–4 fauna of SAM Cave is clearly less than the 900,000 year termination of the Jaramillo event and the immigration clearly occurred more recently than the BOT–4 fauna. In theoretical averages, this would reduce to a margin of error of 10,000 years between the ages arbitrarily assigned to the Cheetah Room, Hanover Quarry Fissure, and Cumberland Cave faunas, and it would also deny what seems to be the most logical stimulus for the dispersal, the climatic change that brought on the Ice Ages. All these age assignments have the further qualification that they depend upon the accuracy of radiometric ages assigned to the paleomagnetic stratigraphy.

From the preceding comparisons and inferred ages, it would appear that to the east of the Rocky Mountains the last of immigrant *Lasiopodomys* evolved into a primitive *Microtus paroperarius* about 830,000 years ago (Cumberland Cave), which led to typical *M. paroperarius* between 700,000 (latest Hansen Bluff) and 610,000 years ago (Cudahy). The first *M. paroperarius* population without *Lasiopodomys* variants appears just before the Brunhes

Chron (820,000 years ago, oldest Hansen Bluff), and it is primitive in both first lower and last upper molars; not until well after the Brunhes had begun is an advanced *M. paroperarius* known (high Hansen Bluff, Cudahy, and Trout Cave No. 2).

7. The Anza-Borrego Desert, southernmost California, contains the Vallecito Creek faunal succession, from which two teeth shown in figure 10 were recovered. Figure 10*A* is clearly of an advanced species of *Microtus*, and the tooth appears inseparable from that of the living *Microtus californicus*, except that "*Microtus*" enamel-thickness differentiation is not so well developed; it has well-formed Secondary Wings and shortened Dimension A–A′.

This specimen, together with a toothless mandible whose alveolus indicates the same M/1, is from a locality in the Vallecito Creek faunal succession (LACM Loc. 6683). This locality is estimated, based on interpolation using a calculated constant sedimentation rate in a continuous section, to be 1.5 million years old (360 m (1,175 ft) below the base of the Brunhes Chron, 109 m (330 ft) above the Olduvai event). It may be the oldest "dated" record of *Microtus* in the world, but doubt has been raised about its age in preceding discussion (p. 59), and the age has been reduced 100,000 yr to allow for presumed hiatuses (Jaramillo not recorded).

The Irvingtonian I lemming *Mictomys anzaensis* (very similar to the latest Blancan *Mictomys vetus*) was described from this locality (Zakrzewski, 1972) and two other Blancan species, *Mimomys parvus* and *Ondatra idahoensis* (LACM specimens, unpublished), are also present in this and other faunas of this part of the section. These Blancan holdovers are typical of the Blancan V microtine age in the United States, which is between 2.6 and 1.9 million years old, but they are known to have lived into early Irvingtonian I faunas. (See section on correlation under the genus *Microtus*, p. 59–60.) All three are also present after the end of the Olduvai event (ending 1.67 Ma) in the Froman Ferry faunas (unpublished; present author's data) of the Glens Ferry Formation of Idaho (locality 33, fig. 1).

The *Microtus* from the Anza-Borrego Desert is remarkably advanced for so ancient a species of the Microtini. It is not possible to rationalize this oldest *Microtus* from the Anza-Borrego Desert of California in the perspective of the known history of the tribe Microtini in the Northern Hemisphere (fig. 14). It is perhaps 670,000 years older than the oldest possible appearance of the primitive *Microtus paroperarius* in the United States to the east of the Rocky Mountains (Cumberland Cave). It is nearly 800,000 years older than the first dated *M. paroperarius* with well-developed Secondary Wings (Cudahy fauna), and it is 1 million years older than the presumed date of the immigration of Asian-Beringian *Microtus* east of the Rocky Mountains.

A problem arises with the interpretation of the Anza-Borrego Desert records (see p. 59). Although all published descriptions of the paleomagnetic section over the last decade and more have presumed the youngest normal event to be the Jaramillo, this is an assumption. If the Jaramillo is absent in the section and the uppermost normal event represents the Brunhes Chron, as indicated by the presence of *Terricola meadensis* (p. 59–60; fig. 10*B*) the age of the oldest *Microtus* would be reduced to about 1.4 million years, depending upon how much of the record was missing in addition to the Jaramillo event. This would alter the age interpretation (fig. 14), but probably not very much.

Based on other records, the Blancan holdover species associated with this early *Microtus* may be as young as 1.4 million years. Tectonic history of the region indicates that the Anza-Borrego Desert was subjected to uplift that ended deposition after the youngest normal polarity recorded (Johnson and others, 1984). The specimen of *Terricola meadensis* was from the Vallecito Creek faunal sequence, and although the locality was not covered by the paleomagnetic study, it was along strike from deposits that were, and it was from the same horizon as several other faunas predating the youngest normal polarity of the magnetic section (J.A. White, written commun., 1991). It was not from an isolated deposit that might have accumulated later, after uplift of the Anza-Borrego Desert.

Microtus californicus is also known by a much better sample from the Irvington fauna near San Francisco, California: the type locality of the "North American" Irvingtonian mammal age (locality 22, fig. 1). Here, the species has associated complex last upper molars and more typical enamel-thickness differentiation (fig. 10*C*). This fauna is found in rocks of reversed polarity and is clearly older than the Brunhes Normal-polarity Chron, but is not certainly younger than the Jaramillo event (0.97 to 0.90 Ma). The Irvington fauna, although containing a good sample of *Microtus californicus*, completely lacks *Terricola meadensis*, although the species is known from other northern California localities, one quite near the Irvington locality (North Livermore Avenue locality; Repenning, 1983). This suggests that the Irvington fauna is older than 850,000 years and predates the immigration of *Terricola*.

Even if as young as 850,000 years, the **advanced** *Microtus californicus* from the Irvington locality would be 30,000 years older than the **very primitive** *Microtus paroperarius* from the lower part of the Hansen Bluff faunal sequence of Colorado (fig. 12*A*), 20,000 years older than the *Microtus-Lasiopodomys* from Cumberland Cave fauna of Maryland, and 10,000 years older than the *Lasiopodomys* with some *Microtus* variations from Cheetah Room of West Virginia, all with individuals having a **simple** last upper molar and a much less complicated first lower molar. The reversely polarized Irvington fauna cannot be as young as the *M. paroperarius* population from Trout Cave that is composed primarily of primitive morphotypes and which appears to be about the age of the beginning of the Brunhes Chron. It would be about 240,000 years older than the Cudahy fauna of Kansas, in which some individuals of *Microtus paroperarius* assume a morphology as advanced as *Microtus* *californicus* from the Irvington fauna; but the Cudahy population contains some individuals that are far more primitive than any individual from the clearly older Irvington sample, which has much less individual morphologic variation.

The sample of *Microtus californicus* from the Irvington fauna is of good size (65 specimens including several lower jaws) and shows very little individual morphologic variation in comparison with that shown by the Cudahy fauna. It is a population that has polarized its morphologic mode and is more removed in time from its ancestor than is the 610,000-year-old Cudahy population. Thus, more derived species of *Microtus* are known west of the Rocky Mountains from faunas that are at least 240,000 and possibly close to 1 million years older than *M. paroperarius* from the Cudahy fauna of Kansas, to the east of the Rocky Mountains.

This major interprovincial difference in the time of evolution of *Microtus* is significant, but has not yet been described outside the conterminous United States and adjacent southern Canada. As discussed in the consideration of *Allophaiomys* from the Wellsch Valley fauna of Saskatchewan (p. 36–38), the Californian records seem more in accord with the eastern Beringian records, which indicate that a large variety of both primitive and advanced *Microtus* morphotypes lived at Locality CRH–47 of the Old Crow basin during the Jaramillo event.

The Californian records, the Wellsch Valley record, and the east-Beringian records do not correlate with any record of the history of *Microtus* in the United States east of the Rocky Mountains before about 450,000 years ago when Beringian *Microtus*, assigned to several living species, first appeared in the eastern province of the United States (Repenning, 1984, 1987; Barnosky and Rasmussen, 1988).

Figure 11*A* illustrates a form of *Lasiopodomys* also from the Anza-Borrego Desert of California that is interpolated to be 1.2 million years old (LACM Loc. 1942; 165 m below the Brunhes Chron, 304 m above the Olduvai event). If the inferred date is correct, this would be the oldest dated record of *Lasiopodomys* in North America. *Lasiopodomys* is also dated as being older than the Jaramillo event in the Gongwangling fauna of Shaanxi Province, P.R.C. (An and Ho, 1989; Zheng and Li, 1990—as *Microtus*), and in the pages that follow some of the records from the Olyor Suite of the Krestovka Sections in Yakutia are shown to be probably this old or older. Older ages of *Lasiopodomys* in other Eurasian faunas are inferred by faunal composition, as mentioned previously (p. 46) in connection with *Lasiopodomys praebrandtii* from the Kudun fauna of Buryat A.S.S.R.

Finally, when, as well as where, *Microtus* first evolved out of *Lasiopodomys* is clearly uncertain; that it did so more than once in different regions of the world seems obvious. It is also probable that *Lasiopodomys*, the *Allophaiomys/Microtus* transitional genus, may also have a different age significance in these different provinces, and perhaps may not have looked quite the same.

The evolution of *Microtus paroperarius* out of *Lasiopodomys* to the east of the Rocky Mountains in the United States is clearly a provincial and late event. Before 450,000 years ago the absence of *Microtus* of Old World origin in the eastern province of the United States appears to result from climatic conditions (Repenning, 1990); not until the Kansan glaciation did this genus of Asian ancestry move south of southern Canada; its northern range before this time suggests that the eastern United States was too warm during the earlier (Nebraskan) glacial advances (Repenning, 1990).

The Rocky Mountain cordillera of North America has always been a barrier to the dispersal of microtine rodents. The fauna to the east of these mountains has always differed from that to the west, and, lasting until after the Olduvai event, two separate dispersal routes have been well documented on either side of the cordillera between Beringia and the United States (Repenning, 1987, 1990). No *Allophaiomys* is known west of the Rocky Mountains at any time, and its entry into the United States to the east of these mountains appears to have preceded, by nearly half a million years, the entry of advanced *Microtus* to the west. This has a bearing on the time of extinction of *Allophaiomys* in Beringia.

Topographically, the Rocky Mountains follow a great circle track across Alaska to the Bering Strait. Farther west they form the mountains of eastern and southeastern Siberia and extend past the Sea of Okhotsk southwest to the region of Lake Baikal. They fall in a nearly straight line on a polar projection such as used for figure 1.

Possibly *Microtus* evolved at an earlier date out of *Lasiopodomys* in China; its earlier evolution from that genus seems consonant with the distinctively advanced dental morphology of living and fossil *Lasiopodomys* in the Oriental faunal region. As noted earlier (p. 46), since before the Jaramillo event *L. brandtioides* of China was as advanced as morphotypes referred to *Microtus* in the rest of the Northern Hemisphere.

Possibly these forms dispersed through Beringia to North America south of the mountain barrier, without crossing it, thus ending in California still to the "south" of the mountain chain. Possibly Chinese *Lasiopodomys-Microtus* crossed the "Rocky Mountains" into northern and western Beringia later, and again moved southward in North America on the east ("north") side of the Rocky Mountains. Based upon present knowledge, it is equally possible that *Lasiopodomys* evolved into *Microtus* in Western Siberia later than in the Oriental region and moved eastward, north of the mountains, through northern Beringia and southward on the east side of the Rocky Mountains. The first record in the Krestovka Sections is a primitive form, although not the most primitive known morphotype, as might be expected in either model.

One is reminded that the single living North American species of *Microtus* that still retains a simple last upper molar in the majority of its individuals is *Microtus oregonensis*, which still lives in the Pacific Northwest, west of the Rocky

Mountains. This species has a first lower molar that is only modestly more advanced than living *Lasiopodomys brandtii* of Transbaikalia (compare fig. 12*F* with fig. 11*N*). That it could show so little change in perhaps 1.5 million years does not seem strange when one compares the 1.4 million-year-old *Microtus californicus* (fig. 10*A*) with the living species (not illustrated). Whatever the history was west ("south") of the Rocky Mountains and its topographic extensions, the rate of evolution in the descendants of *Allophaiomys* appears to have been much slower after developing a *Microtus* grade than it was in the United States to the east ("north").

Regardless of where speculation leads, more needs to be learned about provincial histories, dispersal routes, geographic and climatic constraints, and the age of specific faunas before it is known where and when *Microtus* originated. Determining the details of provinciality will explain the history throughout the Northern Hemisphere.

CORRELATION SUMMARY

The preceding summary of faunas (see also table 1), of the relationship of their faunal population elements to each other, and of external time controls associated with some, leads to the following interpretations of age. The interpretations are based on the assumption that the United States east of the Rocky Mountains has, for the most part, experienced faunal changes and faunal evolution as a single microtine faunal province.

Exceptions to this assumption have been noted, such as the restriction of native *Pitymys* to the eastern part of this province and the failure of the immigrant *Terricola* to colonize this area. The unique population characteristics of *Allophaiomys* from SAM Cave, New Mexico, at 8,900 feet (2,728 m) elevation, may have resulted from isolation by adaptation to higher elevations. It has been suggested that native *Pedomys* has had an environmental restriction that limited its distribution to areas below 7,000 feet (2,130 m) elevation in the western Great Plains and out of areas to the northeast that are dominated by arctic air. Little attempt is made to explain these exceptions, although possible reasons seem evident simply from the consideration of modern distribution patterns. The modern ecologic restrictions of *Pedomys* appear intermediate between those of *Microtus* and those inferred for *Allophaiomys*.

Despite these exceptions, the strength of the faunal similarity in most species from the Atlantic Coast to the eastern parts of the Rocky Mountains seems to indicate that this region did exist as a single faunal province within the United States. This similarity justifies the following integration of faunal records over this great area to produce a single biochronologic history. If true, within this region the following age relationships seem to be approximate but unavoidable conclusions. Their precision may raise some doubt in the mind of the reader; never before has such temporal precision been suggested.

However, as illustrated in the preceding section, faunal history is vastly different between the region to the east of the Rocky Mountains and that to the west. Faunas to the west clearly evolved within an entirely different time frame, essentially a million years earlier. As presently known and as discussed, the western time frame appears more in accord with the less known history of microtine faunas in Beringia and Asia, possibly China.

Outstanding in this review is the realization that the extinct species *Microtus paroperarius* of the United States is an endemic product of the eastern United States faunal province, equally as native to the region as *Pitymys pinetorum* and as unrelated to other species of *Microtus* elsewhere in the Northern Hemisphere as *P. pinetorum* is unrelated to *Terricola.*

Although clearly a provincial product of endemic evolution out of *Lasiopodomys* in the eastern two-thirds of the United States, early *Microtus paroperarius* is morphologically indistinguishable (in tooth morphology) from early *Microtus* in Asia and Europe, irrespective of the differences in age, ancestry, and geography that exist.

At present, information about the age of critical faunas from Eurasia, information based on evidence of age other than stage of evolution, is too weak to detect similarly different times and regions of evolution. Microtine biochronology has reached the point at which its time-sensitivity is more precise than the assumption of global synchroneity of evolutionary (or extinction) events.

The interpretation of evolutionary processes is also brought into question by this history. Debating whether evolution proceeds gradually or spasmodically seems pointless when demonstration of time is too weak to indicate the synchroneity of the evolutionary events compared. Additionally, systematic concepts that are based upon the fossil evidence of evolution available 200, 100, or even 25 years ago have been made inadequate by the acquisition of new evidence. In the present report the concept of a monophyletic species has been assumed, but not very well defended. The concept of a monophyletic genus, even as here recognized in unconventional detail, is, in reality, obviously impossible. And the conventionally used genus *Microtus*, including all taxa discussed in this report and represented in figure 14, has a very complex history, as has been repeatedly illustrated by Jean Chaline. If a genus is supposed to be monophyletic, *Microtus* cannot possibly include so many species and subgenera as Chaline has suggested; it cannot even include all the species here recognized in a greatly restricted sense. And the concept that a genus-group, or higher, taxon is monophyletic seems as archaic as the concept that species are diagnosable by sharply defined morphologic differences. Species boundaries, ultimately, must be drawn between parent and child.

Table 1. Inferred ages and significant faunal characteristics of fossil localities discussed; positioned in temporal sequence by evolutionary stages; and availability of external age control

[In taxa listed: / , bimodal overlap; two taxa, both named. > , variation overlap; one taxon, the first named. - , definition boundary mode, double name. ? , identification uncertain. In age control column: * , external age control, varying uncertainty. o , age interpreted from fauna. Dispersal events are shown between dashed lines (--)]

Locality and significant taxa	Age, in years B.P. (if Ma, so stated)	Age control (symbol)
United States east of Rocky Mountains		
Porcupine Cave, Colorado (last *Microtus paroperarius; Terricola*; immigration of Beringian *Microtus*).	450,000	o
Cudahy, Kansas (advanced *Microtus paroperarius*; *Terricola*; *Pedomys*).	610,000	*
High Hansen Bluff, Colorado (advanced *Microtus paroperarius*; *Terricola*).	700,000	*
Trout Cave No. 2, West Virginia (*Microtus paroperarius*; *Pitymys*; *Pedomys>Allophaiomys*).	725,000	o
Low Hansen Bluff, Colorado (primitive *Microtus paroperarius*; *Terricola*).	820,000	*
Cumberland Cave, Maryland (*Microtus-Lasiopodomys*; *Pitymys*; *Allophaiomys>Pedomys*).	830,000	o
Hanover Quarry Fissure, Pennsylvania (advanced ?*Lasiopodomys*; *Pitymys*: *Allophaiomys>Pedomys*).	835,000	o
Cheetah Room, West Virginia (*Lasiopodomys>Microtus*; *Allophaiomys/Pitymys*; *Synaptomys>Mictomys*).	840,000	o
County Line, Illinois (?*Lasiopodomys*).	840,000 to 850,000	*

Immigration *Lasiopodomys* and *Terricola*.	850,000	*

Wellsch Valley, Saskatchewan (*Allophaiomys*; Beringian *Microtus*; *Phenacomys*).	875,000	*
SAM Cave (BOT–4), New Mexico (*Allophaiomys>Lemmiscus; Mictomys; Phenacomys*).	875,000	*
Wathena, Kentuck, Aries, Kansas; Sappa, Nebraska (*Allophaiomys*).	1.6 to 1.0 Ma	o
Java, South Dakota (*Phenacomys*; *Allophaiomys*; many Blancan holdovers).	1.6 Ma	o
Hansen Bluff core, Colorado (*Allophaiomys*).	1.9 Ma	*

Immigration *Allophaiomys* and *Phenacomys*.	1.9 and 1.4 Ma	* and o
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United States west of Rocky Mountains		
Cape Mendocino, Livermore, and Anza-Borrego, California (*Terricola*; no *Lasiopodomys*).	<850,000	*
Irvington, California (advanced *Microtus*; no *Allophaiomys* or *Terricola*).	850,000+	*
Anza-Borrego, California (one of two oldest dated *Lasiopodomys*).	?1.2 Ma	*
Anza-Borrego, California (oldest dated *Microtus* [advanced]; many Blancan holdovers.	?1.4 Ma	*
Froman Ferry, Idaho (*Phenacomys*; many Blancan holdovers).	1.4 Ma	*

Immigration of *Microtus* and *Phenacomys* to West Coast, U.S.A.	?1.5 Ma	*

Beringia		
Olyor IIIb, Yakutia (west Beringia) (*Microtus*; no *Lasiopodomys* or *Terricola*).	<750,000	*
Old Crow Loc. CRH–47, Yukon Territory, east Beringia (*Lasiopodomys deceitensis*; diverse *Microtus*; *Phenacomys*; *Dicrostonyx renidens* to *D. simplicior*; no *Allophaiomys* or *Terricola*).	950,000	*
Olyor IIIa, Yakutia, west Beringia: Locality KLO–9 (to be discussed) (*Lasiopodomys deceitensis*; *Microtus*; *Dicrostonyx renidens*; no *Allophaiomys* or *Terricola*).	1.1 Ma	*
Cape Deceit, Alaskan Beringia (to be discussed) (*Lasiopodomys deceitensis*; *Predicrostonyx hopkinsi*; no *Allophaiomys*, *Terricola*, or *Microtus*).	1.3 to 1.6 Ma	o
Olyor IIIa, Yakutia, west Beringia: Locality KLO–8 (to be discussed) (*Lasiopodomys* sp., *Predicrostonyx compitalis*; no *Microtus*, *Allophaiomys*, or *Terricola*).	1.3 to 1.6 Ma	*
Other records mentioned		
Gongwangling, P.R.C. (one of two oldest dated *Lasiopodomys; Allophaiomys*).	1.2 Ma	*
Karay-Dubina, Ukraine (*Lasiopodomys*, *Terricola/Allophaiomys*).	?1.3 Ma	*
Razdolie, Western Siberia (*Mimomys*, *Lasiopodomys*, ?*Terricola*; *Allophaiomys*).	≈1.3 Ma	o
Mt. Peglia–2, Italy (*Allophaiomys>Lasiopodomys*).	≈1.5 Ma	o
Mt. Peglia–1, Italy (*Allophaiomys>Terricola*)	≈1.6 Ma	o
Betfia–2, Romania (*Allophaiomys pliocaenicus/Terricola*).	≈1.7 Ma	o
Zuurland, Holland:		
first *Microtus*	≈970,000	*
last *Allophaiomys*	≈1.5 Ma	*

Table 1. Inferred ages and significant faunal characteristics of fossil localities discussed; positioned in temporal sequence by evolutionary stages; and availability of external age control—Continued

Locality and significant taxa	Age, in years B.P. (if Ma, so stated)	Age control (symbol)
Zuurland, Holland—Continued first *Allophaiomys*	1.9 Ma	*
Huangkan, CKT–18: Beijing, China; Tizdar: Krasnodar, Russia (oldest dated *Allophaiomys*).	2.0–2.3 Ma	*

AGE OF KRESTOVKA OLYOR AND CAPE DECEIT FAUNAS

OLYOR FAUNA, WESTERN BERINGIA

Sher and others (1979) subdivided the Olyor Suite of the Krestovka Sections, Kolyma Lowlands, Yakutia (locality 31, fig. 1), into lower and upper members. These they called IIIa and IIIb, respectively. They have found four microtine faunas in the older Olyor IIIa, at localities KLO–8, KLO–7, KLO–10, and KLO–9, listed in increasingly younger order. One quarter of a meter above KLO–9, the reversed polarity of Olyor IIIa changes to normal (fig. 2). The identity of the normal polarity is the basic question in the difference of opinion about the age of the Olyor Suite. Repenning (1984) thought it probably represented the Reunion event; Sher and others (1979) thought it represented the base of the Brunhes Chron. The two interpretations were more than 1.1 million years apart.

KLO–8, 5.25 m (17 ft) below the base of normally magnetized deposits, and KLO–9, 0.25 m (10 in.) below the normal beds, contain the largest fossil microtine faunas and are discussed herein.

KLO–7, 2 m (6+ ft) below the normal beds, is younger than KLO–8 but consists in part of reworked fossils. The reworked fossils include *Hypolagus* and *Predicrostonyx hopkinsi*(?); both are otherwise unknown in the Krestovka Sections (Sher and others, 1979). Teeth of *Plioctomys* are also found in the older parts of Olyor IIIa, apparently reworked from the older Kutuyakh Beds, in which they are abundant.

Throughout the world *Hypolagus* is replaced by *Lepus*, and this replacement was about 2.0 million years ago in North America. *Lepus* is known from the oldest Olyor fauna (KLO–8) as well as younger Olyor faunas. *Predicrostonyx hopkinsi*, named from the Cape Deceit fauna of Alaskan Beringia, is the most primitive known member of the collared lemmings. The oldest locality, KLO–8, contains the more advanced *Predicrostonyx compitalis*. The genus is unknown from the older Kutuyakh Beds, and *P. hopkinsi*? from KLO–7 is presumed to have been derived from unknown depositional units missing in the unconformity separating the Kutuyakh Beds from the Olyor Suite. KLO–7 also contains *Lasiopodomys* sp. and *Cromeromys* sp. cf. *intermedius* (= *Mimomys* sp. cf. *savini*) that probably represent contemporaneous faunal elements. *Lasiopodomys* is not known in deposits older than the Olyor, and the form of *Cromeromys* (*C. intermedius*) is more advanced than that found in the Kutuyakh Beds; but both genera have a long temporal range through much of the European Biharian (about 1.9 Ma to 850,000 years old; *Lasiopodomys* is probably no older than 1.5 Ma in Europe). *Cromeromys* (or *Mimomys*) *intermedius* (or *savini*) has about the same time range in the Oriental faunal region, probably not surviving so long, and different species of the genus have about the same temporal range in North America, although they are known from only three localities, Java, South Dakota (Martin, 1990), CRH–47 in the Old Crow basin (R.E. Morlan, written commun., 1991), and the Cheetah Room fauna, West Virginia (Repenning and Grady, 1988).

KLO–10 (1.25 m (4 ft) below the normal beds) contains *Predicrostonyx compitalis* with an advanced last upper molar that appears to be transitional into the younger *Dicrostonyx renidens* (Sher and others, 1979). *D. renidens* was found 1 m (3 ft) higher in KLO–9. As described by Zazhigin (1976), the Olyor Suite of the Krestovka Sections contains nearly the full record of the evolution of collared lemmings from the earliest known form of *Predicrostonyx* into the living genus *Dicrostonyx*. It has been suggested that the lineage originated and evolved in arctic Asia, possibly farther north in regions now covered by the Arctic Ocean (Repenning, 1984).

LOCALITY KLO–8

As listed by Sher and others (1979), the small mammal fauna of Locality KLO–8 in Olyor IIIa of the Krestovka Sections contains *Lepus* sp., *Ochotona* sp., *Lemmus* cf. *obenus* (=*L.* cf. *sibericus*), *Predicrostonyx compitalis*, *Cromeromys intermedius*, *Clethrionomys* ex gr. *rutilus*, and the form that is illustrated in figure 15 of the present report. The last two taxa listed for KLO–8 are reported from faunas of Western Siberia as old as the Odessan age (Zazhigin, 1980). The form unnamed above was called *Allophaiomys* in Sher and others (1979) and is called *Lasiopodomys* in the present report.

Although KLO–8 is a large fauna by the standards of the Krestovka Sections, its sample of the tribe Microtini is not sufficiently large to confidently evaluate statistically. Five first lower molars are shown in figure 15. These have a Dimension C–C′ greatly reduced so that the dentinal confluence between the Primary Wings is almost eliminated: they are members of the tribe Microtini. Dimension B–B′, between the Primary Wings and the Cap, varies from

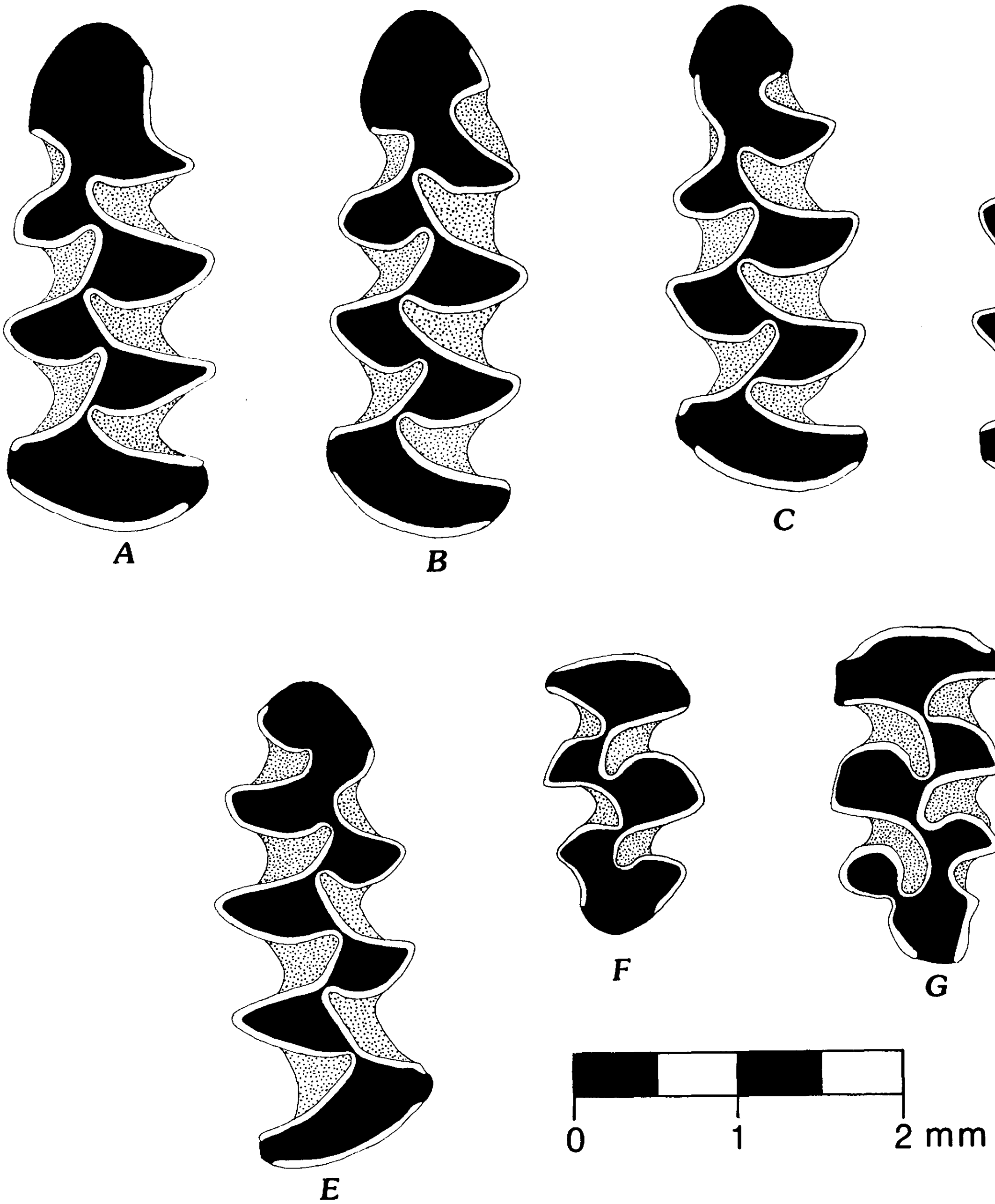

Figure 15. *Lasiopodomys* sp. from the Olyor Suite, member IIIa, Locality KLO–8, Krestovka Sections, Yakutia. Dimension C–C′ is nearly closed in all first lower molars (*A–E*). Dimension B–B′ is not reduced in *A* and *D*. There is no Dimension A–A′. M\3s are simple (*F*, *G*). Note that the Posterior Loop on *F* is reduced as in living *Phaiomys leucurus* (fig. 4). GIN specimens.

unreduced to moderately reduced; and Dimension A–A′, producing Secondary Wings, is not evident: they are members of the genus *Lasiopodomys*. All last upper molars in the sample are simple, and "intermediate" enamel-thickness differentiation is dominant.

Nothing in the sample resembles *Allophaiomys pliocaenicus*, nor *Allophaiomys* from other faunas described above. All individuals from KLO–8 belong in the tribe Microtini, as they have a significant reduction of Dimension C–C′. The specimens in figure 15 appear identical to those referred to as "*Microtus* ex gr. *oeconomus*" by Markova (1982) from the Karay-Dubina fauna of Ukraine (illustrated in fig. 16*F–H*, which are reproduced from Markova, 1990), and the genus *Lasiopodomys*, as herein defined, is obviously indicated. There is no suggestion of a posterolingual angularity on the Cap as found in advanced species of *Lasiopodomys*, nor is there any indication of a complex last upper molar in the sample.

The morphology of *Lasiopodomys* found in Locality KLO–8 includes individuals with a very large Dimension

B–B′ (fig. 15*A*, *D*). This condition is not a frequent character of known populations of *Lasiopodomys*, although a few individuals in some populations may show a very wide Dimension B–B′; three (1.7 percent) are present in the Cumberland Cave population of *Microtus-Lasiopodomys*, apparently the youngest record of "typical" *Lasiopodomys* morphotypes.

In typical *Allophaiomys pliocaenicus* from Betfia-2, the modal condition of Dimension B–B′ is narrower. Nearly all the specimens shown in figure 11 have a greater reduction of Dimension B–B′ than do two of the five first lower molars from KLO–8 that are shown in figure 15. Comparison with *Lasiopodomys deceitensis*, shown in figure 17, suggests that the less marked reduction of Dimension B–B′ of *Lasiopodomys* from KLO–8 may be significant, as it is not found in the Alaskan sample.

Although the significance of this large Dimension B–B′ is not certain, it suggests a primitive condition, and that possibly this sample should not be assigned to *Lasiopodomys deceitensis*. It is here referred to *Lasiopodomys* sp. The changes upsection into *Lasiopodomys* of Locality KLO–9 of the Krestovka Sections are in the direction of *Lasiopodomys deceitensis*.

Largely because of its stratigraphic position below KLO–9 (whose age is discussed next), and because of the apparent change of *Lasiopodomys* toward a morphotype more typical of *Lasiopodomys deceitensis* in the younger KLO–9 locality, the KLO–8 fauna is believed to be younger than the Olduvai event (younger than the Kudun fauna of the Lake Baikal area) but older than KLO–9. It is inferred to be between 1.3 and 1.6 million years old. At present, there is insufficient evidence to be more precise.

LOCALITY KLO–9

As listed by Sher and others (1979), Locality KLO–9 of Olyor IIIa, 5 m (16 ft) higher in the Krestovka Sections than KLO–8 and 1/4 m (10 in.) below the normally magnetized deposits, contains essentially the same fauna as Locality KLO–8 except that *Dicrostonyx renidens* replaces *Predicrostonyx compitalis* and a species with a *Microtus* morphotype is present.

Again, the genus *Lasiopodomys* is present, as indicated by the closure of Dimension C–C′; this dimension is slightly more closed than in the sample from KLO–8. Dimension B–B′ is consistently reduced in comparison with the sample from KLO–8, and the use of the species name *Lasiopodomys deceitensis* seems justified at Locality KLO–9. Not only did the lineage of *Dicrostonyx* undergo evolutionary advancement between the localities KLO–8 and KLO–9 of Olyor IIIa in the Krestovka Sections, but so did the lineage of *Lasiopodomys*.

No specimen has a suggestion of the presence of Dimension A–A′, and all last upper molars, with one exception, are simple; an advanced stage of *Lasiopodomys* evolution toward the *Microtus* morphotype is not indicated. In contrast, an individual with "*Mimomys*" enamel-thickness differentiation was in the sample of *Lasiopodomys* (fig. 16*A*); but the variability of this character is such that it is difficult to decide the significance of the occurrence.

The surprising addition to the fauna from KLO–9 is five first lower molars with a *Microtus* morphotype, noted by Sher and others (1979). Like *Lasiopodomys deceitensis* from the fauna, these have Dimension C–C′ closed, but Dimension B–B′ is either narrow or essentially closed, and the teeth also have a moderate development of Dimension A–A′ on the first lower molar (fig. 16*D*). These five first lower *Microtus* molars also contrast with those of *Lasiopodomys* in that they alone have "*Microtus*" enamel-thickness differentiation. The sample of Microtini from KLO–9 may be the only one in the world that has all three variations of enamel-thickness differentiation.

One complex last upper molar (fig. 16*E*) was in the sample and is presumed to belong with the first lower molars that have a *Microtus* morphotype. This is not the most primitive *Microtus* morphotype included in the genus as here defined, and it is reasonable to suppose that all individuals of *Microtus* had a complex last upper molar.

Unlike the *Lemmiscus* morphotypes from the SAM Cave faunas of New Mexico, the *Microtus* first lower molars from KLO–9 resemble those of primitive *Microtus paroperarius* populations from the older faunas of Hansen Bluff, Colorado (fig. 12*A*), and the most advanced morphologies of *Microtus paroperarius-Lasiopodomys deceitensis* from the Cumberland Cave fauna of Maryland (van der Meulen, 1978, his fig. 11D). The *Microtus* morphotypes from KLO–9 would be an expectable variation of advanced *Lasiopodomys*, such as shown from the Hanover Quarry Fissure fauna, Pennsylvania (fig. 11*L*, *M*), and they are similar to simple *Microtus* morphotypes from Locality CRH–47 of the Old Crow basin of Canada. In Europe such *Microtus* first lower molars would be referred to as "nivalid" or "arvalid" morphotypes and would be named on the basis of their morphologic similarity to a better known taxon, such as *Microtus nivaloides* or *Microtus arvalidens*, names based upon the similarity of their Anteroconid Complexes to those of the living species *M. nivalis* and *M. arvalis*. Such an identification would be made with the reservation that the taxon might not be identical or closely related.

The preceding comparisons indicate that the simple *Microtus* morphotype cannot be identified as a particular species without a much better understanding of the provincial history represented by the compared examples. Nor can they be identified without an analysis of the populations. The morphotypes of primitive *Microtus* look very similar whether they have evolved in North America or Eurasia. Most certainly, the simple morphotypes from the Olyor Suite are not primitive *M. paroperarius* on biogeographic

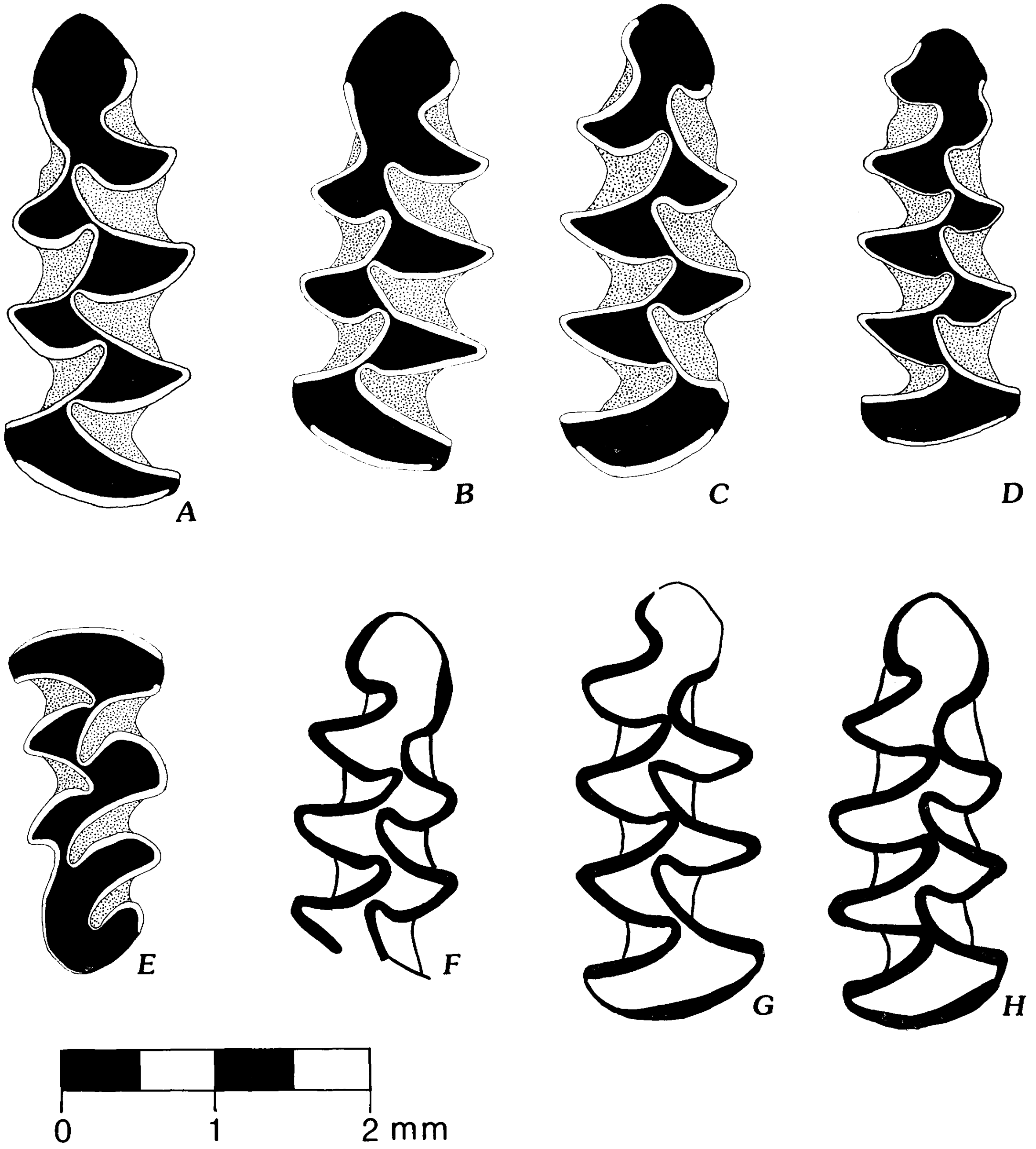

Figure 16. *Lasiopodomys* and *Microtus*. *A–C*, first lower molars of *Lasiopodomys deceitensis* (referred to as "*Allophaiomys* cf. *pliocaenicus*" in Sher, 1986) from Olyor IIIa Locality KLO–9, Krestovka Sections, Yakutia. *F–H*, *Lasiopodomys ratticepoides* referred to as "*Microtus* ex gr. *oeconomus*" in Markova, 1982, and in Sher, 1986) from the Karay-Dubina fauna, Ukraine. *D, E, Microtus* sp. from KLO–9, first lower and last upper molars. Dimension C–C′ is closed or substantially closed in all first lower molars. Dimension B–B′ is variably reduced in all individuals. Dimension A–A′ is weakly present in *D*, and this is a *Microtus* morphotype. All M\3s from KLO–9 are simple except that shown as *E*, which presumably is also *Microtus*. *A* has "*Mimomys*" enamel-thickness differentiation. *D* has "*Microtus*" enamel-thickness differentiation. *A* through *E* are GIN specimens. *F*, *G*, and *H* are reproduced from Markova (1990).

grounds, although on morphologic grounds they could be matched with individuals of this species. It would be reasonable, on biogeographic grounds, to consider them as the same species as similarly primitive forms from the Old Crow basin of Canada, but these have yet to be described and named by R.E. Morlan (written commun., 1991).

The associated *Lasiopodomys* from KLO–9 is not advanced; the limited sample shows no variation toward a

Microtus morphotype such as is seen in the Cheetah Room fauna of West Virginia (fig. 11*J*, *K*; also Repenning and Grady, 1988, fig. 4*E*). It appears to equal the advancement of *Lasiopodomys deceitensis* from the Cape Deceit fauna of Alaska, and could be described as "typical," with no individual variation approaching the morphology of either *Microtus* or *Allophaiomys*. No morphotype similar to those few from Hanover Quarry Fissure, Pennsylvania (fig. 11*L*, *M*), or to the advanced *Lasiopodomys* morphotypes of *Microtus-Lasiopodomys* from Cumberland Cave, Maryland (van der Meulen, 1978, fig. 11A, F, and G), is present in the Olyor Suite.

The sample size from KLO–9 is too small to statistically state that the *Microtus* morphotypes of the population either have or do not have overlap of dental morphology within the population of *Lasiopodomys deceitensis*; nor can the presence of one or two genera be statistically demonstrated. However, the morphotypes of *Lasiopodomys* from the KLO–9 fauna show no suggestion of gradation between *Lasiopodomys* and *Microtus*. The presence of a Dimension A–A′ is not suggested on any specimen of *Lasiopodomys*, as it is in a few individuals of typical *Lasiopodomys deceitensis* from Cape Deceit, Alaska (fig. 17*A*) or in 25 percent of the population from the Cheetah Room fauna, West Virginia (fig. 11*I*–*K*). And the associated *Microtus* morphotypes, although primitive, are not borderline, and have no individuals that approach a *Lasiopodomys* morphotype.

In the *Microtus paroperarius-Lasiopodomys deceitensis* population from Cumberland Cave fauna, Maryland, in which the morphologic mode of the first lower molar falls very close to the defined boundary between *Lasiopodomys* and *Microtus*, 68 percent of the individuals are morphologically intermediate between the conditions shown by the *Lasiopodomys* and the *Microtus* morphotypes from Locality KLO–9. It would seem, if the KLO–9 sample was of an intergrading population, that some specimens would show a suggestion of having an intermediate morphology.

In addition, "*Microtus*" enamel-thickness differentiation is unknown in *Lasiopodomys deceitensis* from KLO–9; in fact, one specimen has "*Mimomys*" differentiation. But 35 percent of the *Lasiopodomys* morphotypes from the Cheetah Room population have "*Microtus*" differentiation and, in the "borderline" population from Cumberland Cave, 56 percent of the *Lasiopodomys* morphotypes and 71 percent of the *Microtus* morphotypes have "*Microtus*" enamel-thickness differentiation.

Although the evolution of enamel-thickness differentiation is difficult to interpret, it does seem to parallel the development of other characters, while maintaining wide individual variability. Therefore, because the *Lasiopodomys* morphotypes lack (1) "*Microtus*" differentiation and (2) overlap of *Microtus* dental morphology, and because the *Microtus* morphotypes lack (3) "intermediate" enamel-thickness differentiation and (4) overlap of *Lasiopodomys* dental characters, it is difficult to believe that a single, endemic population, intergrading between *Lasiopodomys* and *Microtus*, is represented in Locality KLO–9.

Thus, the conclusion of Zazhigin (in Sher and others, 1979, p. 49) seems reasonable: the appearance of *Microtus* in KLO–9 represents an immigration of true, but primitive, *Microtus* from some other Asian area, and does not represent variation within a single, endemic population of *Lasiopodomys*.

Although the *Lasiopodomys* fauna of Beringia is still not well known, there is no evidence that it evolved into *Microtus* in this region; and primitive *Microtus* seems to have immigrated from elsewhere in Asia into western Beringia just before the recorded normal polarity of the Olyor Suite. The question of where *Microtus* came from is not yet answerable, although the Oriental faunal region had been suggested (p.79).

More can be said about the question of what polarity event is represented by the normal deposits closely overlying the immigrant *Microtus* sp. and endemic *Lasiopodomys deceitensis*. *Allophaiomys* is not present in the Olyor fauna, nor in any known Beringian fauna, but it dispersed to North America at the beginning of the Olduvai Normal-polarity Subchron; consequently the beginning of normal polarity in the Olyor Suite seems not to be the beginning of the Olduvai event; the associated fauna contains no *Allophaiomys* but does contain its descendants *Lasiopodomys* and *Microtus*, both of which have no certain record as old as the Olduvai. Furthermore, the beginning of the Olduvai was a very warm period in the Northern Hemisphere and the beginning of the normal polarity in the Krestovka Sections was the coldest period recorded in that section (Repenning and Brouwers, 1992).

Faunal considerations also do not favor correlating the oldest normal polarity of the Krestovka Sections with the base of the Brunhes Chron. These considerations include the lack of *Terricola* in the Olyor, a genus that dispersed to North America (through Beringia) less than 100,000 years before the Brunhes began. *Microtus* is abundant (with *Lasiopodomys*) during the Jaramillo event in the Old Crow basin of eastern Beringia, but not present in the oldest fauna of the Olyor and present only as a primitive form in the youngest reversely polarized Olyor 25 cm below the polarity change; if the first normal polarity were the Brunhes, one would expect a more diverse *Microtus* fauna. *Lasiopodomys* was the abundant microtine of the Olyor, yet it became extinct about 35,000 years before the Brunhes Chron in the United States. Finally, Sher and others (1979) reported the change from *Predicrostonyx compitalis* to *Dicrostonyx renidens* within 1.25 m (4 ft) below the polarity reversal in the Olyor, and R.E. Morlan (written commun., 1991) reported the evolutionary change from *D. renidens* into *D. simplicior* during the Jaramillo event in Locality CRH–47 of the Old Crow basin. The evolution of *D. simplicior* out of *D. renidens* during the Jaramillo event seems to eliminate the possibility that *P. compitalis* could evolve into *D. renidens* after the Jaramillo and just before the Brunhes Chron.

Faunas in the Old Crow basin other than CRH–47 that also contain *Lasiopodomys* and an even greater diversity of *Microtus* than Locality CRH–47 (Morlan, 1984) appear to be stratigraphically younger, but are also in normally magnetized deposits. These suggest that the fauna of Locality CRH–47 may have lived early during the Jaramillo event.

Particularly if Locality CRH–47 represents the older part of the Jaramillo event, it is difficult to imagine that the normal polarity 25 cm (10 in.) above Locality KLO–9 is the beginning of the Jaramillo event. In the record of the United States east of the Rocky Mountains, *Microtus paroperarius* took at least 290,000 years to evolve from a stage of evolution comparable to that in Locality KLO–9 (in the Cumberland Cave fauna) into an advanced condition (in the Cudahy fauna of Kansas), comparable to the *Microtus* population found in the Old Crow Locality CRH–47, in early Jaramillo deposits. The Jaramillo event was only 70,000 years long, and, from this comparison, the stage of evolution represented by *Microtus* from KLO–9 would suggest that the overlying normal polarity was perhaps 130,000 years older than CRH–47, deposited during the Jaramillo event—perhaps during the earliest part of the Jaramillo.

Although not consistent with other hemispheric records, the earliest record of *Microtus* from southern California indicates that a dispersal of this genus through Beringia must have taken place possibly 1.5 million years ago, 500,000 years before the Jaramillo event. The record does not indicate that the dispersing *Microtus* passed, en route, through the Kolyma Lowlands, where the Krestovka Sections are located, to be present in Locality KLO–9. Dispersal at this time is recorded only west of the Rocky Mountains in the United States, and it may also have been restricted to Magadan, in the lowlands east of the Kolyma Range, the "west side of the Rocky Mountains" as they project into Asia. Possibly this region was the source of the first *Microtus* in Locality KLO–9, via crossing the Kolyma Range.

The greatest objection to a correlation of the first normal polarity in the Krestovka Olyor Suite, 25 cm (10 in.) above the first *Microtus*, with the Jaramillo event comes from the consideration of the climatic record. Sher and others (1979) reported a major decrease in arboreal pollen ("almost absent") and an increase in pollen of grass and cold, dry-climate plants in the horizon of Locality KLO–9. The cold and dry period continues upward into the normally polarized deposits. The flora of KLO–9, continuing through the change to normal polarity, indicates a steppe-tundra environment, and the coldest climate recorded in the Krestovka Sections. The locality is now in boreal forest, a less severe climate than indicated in this part of the Olyor Suite.

An inconsistency is evident when this increase in climatic severity in the Krestovka Sections is compared with the pollen record of the type Olyor Suite, 150 kilometers (93 mi) to the north. Unlike the Krestovka Sections, the type section of the Olyor Suite is now in full and widespread tundra. The type section begins below the Jaramillo event and continues into reversed deposits above this event (Virina and others, 1984).

During the period of normal polarity that is assigned to the Jaramillo event in the type section, the percentage of shrub and arboreal pollen was no lower than 20 percent and was mostly well above this figure (Giterman and others, 1982); the pollen spectrum changes little throughout the type section. The lack of evidence of a severe cold and dry climate just before and during the Jaramillo event in the type section casts considerable doubt on the correlation of this event to the normally polarized deposits, containing pollen indicating climatic severity, recorded in the first normally polarized deposits of the Krestovka Sections 150 km to the south.

The inconsistency is present in other records in addition to the type section of the Olyor Suite. The eastern Beringian Locality CRH–47 of the Old Crow basin, which contains diverse morphotypes of *Microtus*, also dates from the Jaramillo event; like the type section of the Olyor Suite, its pollen record indicates a climate like that of today or possibly slightly warmer (J.V. Matthews, Jr., oral commun., 1987). In Holland, Zagwijn and de Jong (1984) described the Bavelian floral age, a warm age that begins just before the Jaramillo event and ends shortly after it. (*Microtus* first appears in Holland during the Bavelian according to van Kolfschoten, 1990.) In southern Canada, Churcher (1984) inferred that the Wellsch Valley fauna lived in a warm climate, and, as discussed previously (p. 37), this fauna probably lived shortly after the Jaramillo event. In core 644 in the Norwegian Sea (Jansen and others, 1988) and in CESAR core 14 on the east end of the Alpha Cordillera of the central Arctic Ocean (Scott and others, 1989), the Jaramillo event is marked by a warm period. The author is aware of no records during the Jaramillo event that indicate pronounced cold.

About a half meter (1½ ft) above the base of the normally polarized deposits in the Krestovka Sections, Sher and others (1979) reported a thin interval of reversed polarity. This was initially indicated by a single determination in uncleaned samples but appears, in Sher and others (1979, fig. 6), to be indicated by three samples after cleaning. These polarity determinations suggest the possibility that the deposits having the oldest normal polarity and the coldest climate in the Krestovka Sections may be only about one-third meter thick. The presence of these higher reversed samples has not been considered significant, but it seems possible that the oldest normal polarity of the Krestovka Sections represents a brief event before the Jaramillo Subchron.

The Cobb Mountain Normal-polarity Subchron was identified by Mankinen and others (1978) and may be the most securely dated short polarity reversal of the late Matuyama and Brunhes Chrons (Champion and others, 1988); it is 1.10±0.02 million years old (Mankinen and Grommé, 1982). Although possibly lasting less than 10,000 years (Champion and others, 1988), but possibly as much as 25,000 years (Clement and Kent, 1986), the Cobb Mountain is a completely normal event within the Matuyama Chron and, where found, is unambiguous. According to Mankinen and Grommé (1982) it has been identified in the Caucasus region of southern Russia (Kvemonataneby excursion), in the Melanesian region of equatorial Pacific, in Japan (Komyoike event), across the East Pacific Rise ("A" event), in the eastern Caribbean, and in California, U.S.A.

Although they did not report detecting the Cobb Mountain event, Jansen and others (1988) reported that at site 644 in the Norwegian Sea a transition to major glacial activity of the Scandinavian Ice Sheet began 1.2 million years ago, and they showed a pronounced peak in activity at 1.12 million years ago. This peak would have occurred during the Menapian cold flora of Holland, before the warmer Bavelian flora that centers on the Jaramillo event.

Also, in CESAR core 14 at the east end of the Alpha Cordillera in the Arctic Ocean, Scott and others (1989) reported a major change to periods of perennial ice cover (with one brief exception more than 2 million years ago, their first record of perennial ice in the Arctic Ocean) beginning with a pre-Jaramillo normal-polarity event. These periods of perennial ice cover decreased dramatically during the Jaramillo and then increased again after this event. Scott and others (1989) assigned the normal polarity at the beginning of the intermittent perennial ice record to the Gilsa event (about 1.64 to 1.63 Ma), but this assignment results in unusually rapid rates of sedimentation between the normal event and the Olduvai. An assignment to the Cobb Mountain event would reduce inferred sedimentation rates between the event and the Olduvai to within the limits they calculated for the entire core. In addition, assignment of the event to the Cobb Mountain would correlate the beginning of periodic perennial ice cover on the central Arctic Ocean with the beginning of major Scandinavian glacial activity.

The first brief period of deposition (0.3–0.5 m; 12–19 in.) during normal polarity in the Olyor Suite of the Krestovka Sections, included within that part of the section having evidence of the most severe climate recorded in the Krestovka Sections, is here correlated with the beginning of intermittent perennial ice cover of the Arctic Ocean reported in CESAR core 14, with the beginning of intense activity of the Scandinavian Ice Sheet reported in the Norwegian Sea at Site 644, with the Menapian cold flora of Holland, and with the Cobb Mountain Normal-polarity event (1.10 million years old) (Repenning and Brouwers, 1992).

The normal-polarity event recorded in the 0.3–0.5-m-thick part of the Krestovka Sections is assigned to the Cobb Mountain event and not the Jaramillo event, which is not marked by evidence of extreme cold in the type section of the Olyor Suite, nor in other areas of the Northern Hemisphere. This interpretation of the polarity of the section is also in agreement with the difference between the low-variety *Microtus* fauna of Locality KLO–9 in western Beringia and Jaramillo-aged, high-variety-of-*Microtus*-morphotypes fauna at Locality CRH–47 in eastern Beringia, as judged by the rate of morphologic change of *Microtus paroperarius* in the United States.

The beds with normal polarity in the uppermost part of the Olyor Suite of the Krestovka Sections (above the three reversed samples and assigned to Olyor IIIb) may represent the Jaramillo event or the Brunhes Chron, or both; the small samples (A.V. Sher, oral commun., 1990) of the microtine faunas present in Olyor IIIb are not diagnostic of population characteristics, but they contain *Microtus* and *Dicrostonyx* (Sher and others, 1979).

If this correlation of the short normal interval in the Krestovka Sections, containing the coldest flora of the Krestovka Sections, is correct, then the climatic disagreement between it and the oldest normal polarity of type Olyor Suite (and with Canadian Locality CRH–47) no longer exists, and the interpretation is in agreement with evidence of increasing cold at that time in the central Arctic Ocean, in the Norwegian Sea, and in the fossil flora of Holland. The age of Locality KLO–9 of Olyor IIIa would then be very close to 1.10 million years.

By polarity control, the age of the oldest fauna of the Krestovka Olyor, KLO–8, would be then older than 1.10 Ma, and, by biochronologic control, younger than *Lasiopodomys praebrandtii* in the Kudun fauna south of Lake Baikal; that is, Locality KLO–8 is younger than the Olduvai Normal-polarity Subchron ending 1.67 million years ago based on the age of the Kudun fauna inferred from faunal composition, and on the lack of normal polarity in the oldest part of Olyor IIIa.

THE CAPE DECEIT FAUNA, ALASKA

The Cape Deceit fauna of the Seward Peninsula, Alaska, was described by Guthrie and Matthews (1971). The locality is on the east side of Cape Deceit about 1.8 miles (3 km) northwest of the village of Deering. It was found in bluffs exposed along the shore of Kotzebue Sound of the Chukchi Sea. The locality is near lat 66° N. and now has a shrub tundra flora. Matthews (1974) has reviewed the fluctuating environments represented in the deposits, which were, alternately, both colder and warmer than today. The fauna contains *Lasiopodomys deceitensis*, *Predicrostonyx hopkinsi*, *Phenacomys deeringensis*, and *Lemmus* sp. cf. *L. sibericus* and was found in deposits recording the coldest environment recognized by Matthews. Matthews (1974) has inferred that deposition ended with a warm spell much warmer than today. Permafrost in the deposits thawed, with resulting erosion.

No external evidence of the age is available, and the fauna has been considered as being about the same age as Olyor IIIa from the Krestovka Sections, because of faunal similarity. Accordingly, its age is revised along with that of the Olyor.

The Cape Deceit fauna has a fair-sized sample of *Lasiopodomys deceitensis* (29 M/1), as well as some other types of microtines, and the fauna appears large enough to have included some *Microtus* if they were present in the area. Neither the Cape Deceit fauna nor the KLO–9 fauna has a *Lasiopodomys-Microtus* population as does the Cumberland Cave fauna, nor do they contain individuals of *Lasiopodomys* with a variation approaching a *Microtus* morphotype; *Microtus* was not evolving out of these Beringian populations. Although both are in the Beringian faunal province, Locality KLO–9 of the Krestovka Sections contains immigrant *Microtus*, which is missing in the Cape Deceit fauna, and a more advanced collared lemming than in the Cape Deceit fauna; both indicate that the Cape Deceit fauna is older than Locality KLO–9.

A contradiction may exist regarding the correlation of the Cape Deceit fauna of Alaska with the KLO–8 fauna of Olyor IIIa in Krestovka Sections. As has been noted, Locality KLO–8 contains some individuals of *Lasiopodomys* sp. (fig. 15) that are possibly more primitive than *L. deceitensis* from the Cape Deceit fauna (fig. 17) in that the KLO–8 sample has a Dimension B–B′ that is conspicuously large. However, *Predicrostonyx compitalis* from KLO–8 is more advanced than *Predicrostonyx hopkinsi* from Cape Deceit.

The inconsistency may indicate a dispersal delay of collared lemmings from western to central Beringia, or it may indicate too small a sample of the *Predicrostonyx* population from KLO–8, as specific identification depends upon the average condition of the population (Zazhigin, 1976; Agadzhanyan, 1976; Gromov and Polyakov, 1977). Conversely, the suggestion of the inferred primitive nature of *Lasiopodomys* from KLO–8 may not be correct. Both arguments are weak because of small samples and resulting misinterpretation.

Tentatively, the Cape Deceit fauna is considered to be of about the same age as KLO–8, but because of the uncertainty of the two conflicting interpretations the fauna is assigned an age span, rather than a specific age approximation. It is inferred that its age is between 1.3 and 1.6 million years—the same age range that is inferred for KLO–8. The Kudun fauna of the Lake Baikal area has a more primitive species of *Lasiopodomys* and is believed to date from the Olduvai event (ending 1.67 Ma). A more precise age interpretation is not possible without a better record of microtine history in Beringia and adjacent Asian faunal regions. If the deposits containing the Cape Deceit fauna have a normal polarity, this could only represent the Olduvai event, and the inferred age of *Lasiopodomys praebrandtii* from the Kudun fauna would have to be considered either the age of the early part of the Olduvai event, or older, unless greater detail is learned of the provincial histories involved.

CONCLUSION

Global history has been ignored in the previous use of the biochronology of microtine rodents. Similar evolutionary and extinction events, that in fact were local in extent, have been considered synchronous around the world. This has resulted in frequent errors in age interpretation. Such errors cannot be avoided without the aid of dated provincial histories and without knowledge of interprovincial dispersals.

The number of errors has been increased by the use of different taxonomic systems by various researchers, and by reliance on faunal lists for correlation without consideration of the classification system of the person who compiled the faunal list. By no means the only example, but as discussed in this report and shown in figure 16, what Markova called *Microtus*, Zazhigin called *Allophaiomys* and Repenning called *Lasiopodomys*. The present author had assumed that these specialists were in agreement on their classification; the offices of Zazhigin and Markova are little more than a long stone's throw apart.

The present author also thought that he could infer relationships on the basis of Markova's (1982) illustrations of her specimens and Zazhigin's listing of taxa (Sher and others, 1979). Thus the author's 1984 assessment of the age of Olyor IIIa of the Krestovka Sections was based upon the erroneous assumption that the same taxonomy was being used by the two different authors; this same erroneous assumption was made by Sher and others (1979) and Sher (1986), and seemed (in the past) to the present author to confirm his opinion.

The present report was written to illustrate how the biochronology of the microtine genus *Allophaiomys*, and those genera derived from this genus, is complex and asynchronous on a global scale, and also to demonstrate how the interpretation of the age of any fossil locality that is based upon this biochronology cannot be convincingly made across provincial boundaries without knowledge of the history of these lineages within each province of concern. However, with this knowledge or within a single faunal region, it is shown that a biochronology can be developed with a temporal resolution that approximates a precision of 5,000 years.

The greatest weakness of this precision is that currently there is no known external method of determining geologic age that could be used to check such temporal resolution. It must be emphasized that between points of external age control the age assignments given are interpolations. Because they are applied to single lineages over short time periods, these interpolations are less likely to incorporate greater error than other methods of geologic age interpolation between dated events, such as between control points in geopolarity stratigraphy.

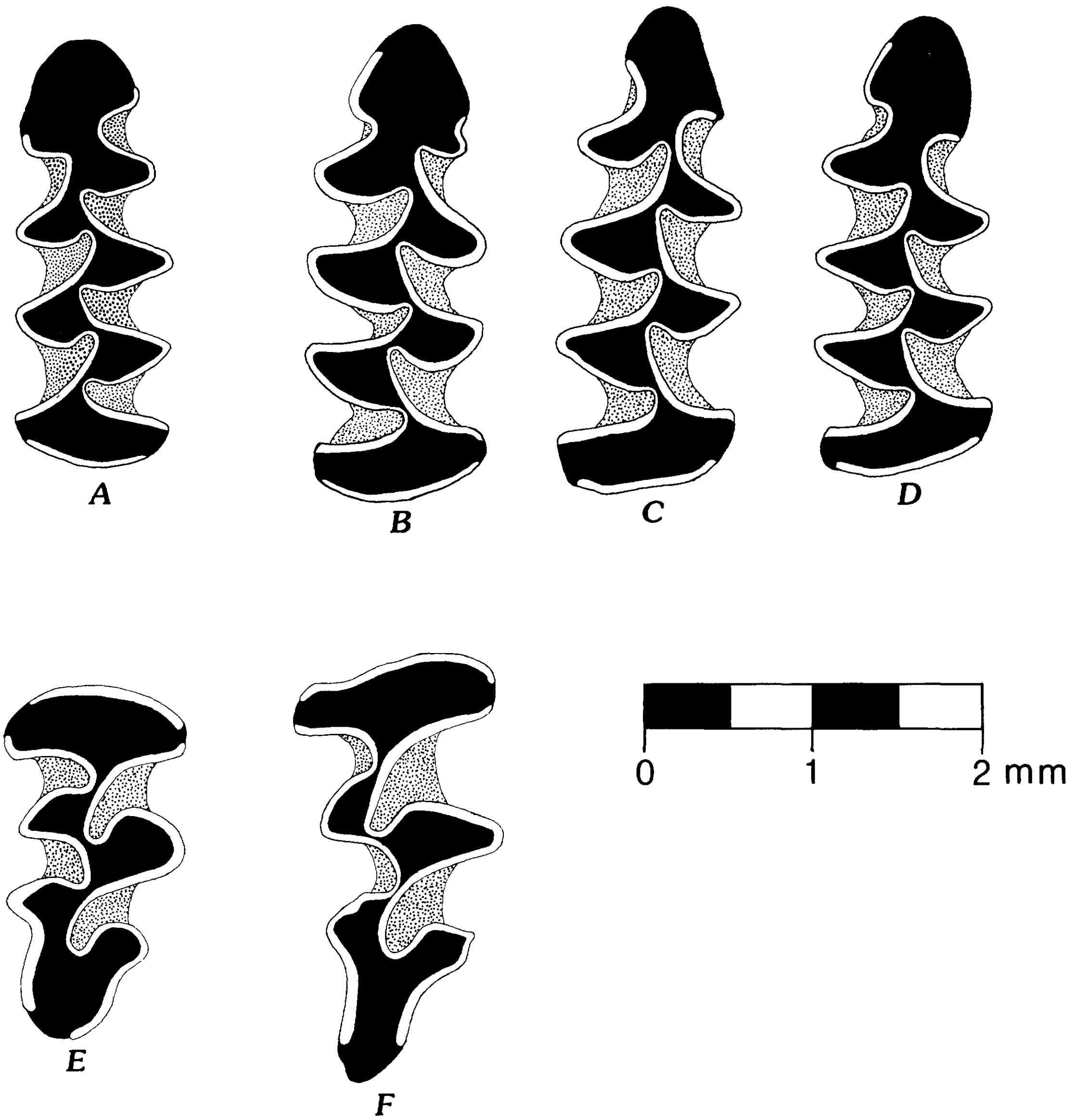

Figure 17. *Lasiopodomys deceitensis* from Cape Deceit fauna, Alaska. *A* through *D* are first lower molars; *E* and *F* are last upper molars. Dimension C–C′ is closed or nearly so in all first lower molars. Dimension B–B′ is reduced in all individuals. Dimension A–A′ is not present, although *B* shows a weak suggestion of a buccal Secondary Wing. M\3s are simple and *F* is little worn. This population of *Lasiopodomys* is considered "typical," and *B* most nearly approaches a *Microtus* morphotype. None approach a *Pitymys* or *Terricola* morphotype as Dimension C–C′ is closed.

However, that rates of evolution are more constant than rates of sediment deposition has not been established. The example of the history of what all concerned would call *Microtus* on either side of the Rocky Mountains in the United States illustrates the point that a single lineage must not be assumed because the taxa look alike and have been assigned to the same genus. Mention has been made (p. 78) of the slight change in *Microtus californicus* between the earliest record of the genus about 1.4 million years ago and living *Microtus californicus* on the west side of the Rocky Mountains; and of the evolution of the "same" genus from a *Lasiopodomys* morphotype to a characteristic *Microtus* morphotype in 220,000 years on the east side of this mountain barrier. These must be considered different lineages even though they are placed in one genus; obviously the two lineages have different biochronologic significance. And this is but the first clue to the diversity of *Microtus* on a worldwide basis.

In addition, the accuracy of the *Allophaiomys*-and-descendant biochronology, when used across regional faunal boundaries, depends upon the interpreter's familiarity with the global history of the organisms involved.

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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. The 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; the 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 USGS Map Distribution, Box 25286, Building 810, Denver Federal Center, 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 microfiche.

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