

Chapter 17

Mimomys in North America

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ABSTRACT

The earliest record of the microtine rodent genus *Mimomys* is from West Siberia, where, over 5 million years ago, it evolved from *Promimomys*. From western Asia, early *Mimomys* dispersed both east and west (to North America and to Europe), arriving at about the same time in both areas as a slightly larger and more evolved form that is essentially identical in both continents. Different species names are applied, as they obviously represent the beginnings of geographically separate lineages.

The immigration of *Mimomys* to North America marks the beginning of the Blancan Mammal Age by original definition. The earliest dated North American record is the Upper Alturas Fauna of California, which is well dated by paleomagnetic stratigraphy, tephra “fingerprinting”, and potassium–argon dating at 4.8 Ma. Lindsay et al. (1999) have supported this age by paleomagnetic stratigraphy in two areas of Nevada. One other known fauna, the Maxum fauna of Contra Costa County, California, contains immigrant *Mimomys* that may be slightly older, but is not dated.

Dispersal of the temperate-climate genus *Mimomys* between Eurasia and North America was through the Beringian Faunal Region, near the latitude of the Arctic Circle, and later intercontinental continuity of the genus was severely restricted by climate, not water. Other microtine rodents, more tolerant of cooler latitudes, were able to cross the Bering land area and thus integrate the biochronologies of the two continents, but the genus *Mimomys* is of little use in intercontinental correlation during most of the Pliocene.

Eurasia and North America contain many faunal regions, and the temperate United States comprises at least two, separated by the Rocky Mountains. Each faunal region has, to an extent limited by its isolation, unique faunas and a different historic biochronology. Although the first *Mimomys* immigrants to North America and Europe were very similar, the genus evolved independently on the separate continents for the next 3.4 m.y., producing species, subgenera, and ultimately, new genera dramatically different in the two areas. During this isolation, separate lineages in the United States resulted in the subgenus *M.* (*Cosomys*) and the genus *Ophiomys* in the Western Faunal Region and in the subgenus *M.* (*Ogmodontomys*) and the genus *Hibbardomys* in the Eastern Faunal Region.

Although also climatically constrained, the barrier to dispersal between these two faunal regions of the United States was much less rigorous than in Beringia. Several times taxa dispersed along two documented routes between the Eastern and Western Faunal Regions of the United States: through Yellowstone Pass in western Wyoming and around the southern end of the Rocky Mountains through Arizona and New Mexico. These faunal interchanges are useful in correlating the two regional biochronologies, and times of exchange correlate with the climate changes that made the Rocky Mountains, or the region to the south of it, habitable by temperate *Mimomys*.

About 1.3 Ma, global warming again permitted *Mimomys* to disperse through Beringia. At or slightly before this second immigration of *Mimomys*, the descendants of the first immigration had become extinct or had evolved into forms no longer conforming to the diagnosis of *Mimomys*. The new immigrants are assigned to the Eurasian subgenus *Mimomys* (*Cromeromys*) and they are known to have lived well into the Irvingtonian mammal age, less than 0.78 Ma. Present records thus indicate that the genus *Mimomys* and derived forms lived in the United States for over four million years before they became extinct.

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INTRODUCTION

Differences in the microtine faunas on either side of the Rocky Mountains persisted throughout their history and led Fejfar and Repenning (1992) to recognize Eastern (EFR) and Western (WFR) Faunal Regions in the conterminous United States (separated by the Rocky Mountains, which were an up-slope part of the Great Plains leading to the elevated Colorado Plateau during the history of North American *Mimomys*). Also recognized were a Beringian² Faunal Region in Alaska and adjacent northeastern Siberia as well as several faunal regions in Eurasia and North America.

Barriers to microtine dispersal are either mountains or latitude. Microtines occupy drainage basins and are reluctant to cross major divides; they are temperate to arctic animals and have specific climatic tolerances.

For at least 68 years, differing opinions have been published regarding the presence or absence of the genus *Mimomys* in North America. During this time their known Holarctic fossil record mushroomed. The question remaining is "Should an animal be placed in a new genus because it disperses through Beringia to North America?" With the exception of one species, *Mimomys* was an animal of warm, temperate climate. Lack of continuous contact between North American and Eurasian populations resulted from climate changes that made the high latitude Beringia inhospitable to warm-temperate animals. With loss of population continuity, evolution proceeded in independent ways.

The morphologic dissimilarities caused by population isolation are reduced with restoration of contact between separated populations. This happened once in the history of

immigrant *Mimomys* in North America; more frequently it happened between the two faunal regions of the USA. The EFR and WFR have their own distinct faunal histories that are as well, or better, illustrated by the history of *Mimomys* as by any other mammal. The same is true of the Beringian, Canadian, and Mexican faunal regions of North America, but these are less well known by fossil records, and few immigrants that could reach Beringia were adapted to Mexican environments; there is no record of *Mimomys* there.

In the discussion to follow it is important to remember that the history, the evolved forms, and the immigration of *Mimomys* differed in the Eastern and Western Faunal Regions of the United States. These differences are evident in the entire record of *Mimomys* in North America. It is also important to remember that the microtine rodents are the most rapidly evolving mammals yet known and, for this reason, many of the problems of their classification, and of the nature of their populations, are unique. This uniqueness makes their history sensitive to time and their biochronology more precise. In no other mammal group are there found so many populations with individual variation spanning the morphotypes from the most recent ancestor of the population to its direct descendant. The typically high intrapopulation individual variation makes insecure the identification of species from one or a few individuals; a population sample of at least 30 is considered minimal for positive identification.

TERMS: FORMAL AND INFORMAL

INFORMAL NAMES: In this report all cricetid rodents with distinctly hypsodont, triangularly prismatic cusps on the molar teeth are referred to as "microtines", a vernacular term having no ancestral connotation and based upon this condition. This informal name has been in use since Miller (1896) and includes *Dicrostonyx*, *Ondatra*, and *Prometheomys* as well as *Mimomys* and its relatives.

Sixty-six years later (starting with Kretzoi, 1962), the vernacular term "arvicolines" (sometimes "arvicolid") began to be used synonymously, but is herein restricted to the subfamily Arvicolinae, which has *Mimomys* as its common ancestor and excludes such

² Beringia is that part of northwestern North America and northeastern Siberia that was never covered by continental ice sheets; it extends from the Arctic Ocean near the delta of the Mackenzie River, Canada, westward to the eastern limits of Eurasian continental glaciation at the Taymyr Peninsula in Siberia. The southern limits are arbitrary. During periods of major continental ice accumulation and lowered sea level, vast areas of the East Siberian Shelf and the continental shelf from the Gulf of Alaska to Seattle were emergent, and the area of Beringia was nearly double what it is today and over 1,000 mi wide, north to south, in Asia. When emergent, southern Beringia was warmer than today due to a warm North Pacific Ocean.

microtine genera as *Dicrostonyx*, *Ondatra*, *Pliophenacomys*, and *Prometheomys*, whose ancestors are different and mostly uncertain. In the higher taxonomic rank, the family Cricetidae is recognized following Simpson (1945) rather than McKenna and Bell (1997), who placed both Cricetidae and Muridae of Simpson's usage in their family Muridae.

The monophyletic origin of arvicolines is strongly supported by the fossil record, as is the polyphyletic origin for all microtines (Repenning et al., 1990). The arvicolines and the microtines are, thus, different things, even in vernacular usage.

The classification of the microtine rodents used herein is that of Repenning et al. (1990: 392–393) with minor revisions of no concern here (see also Repenning, 1992, and Fejfar and Repenning, 1998, for these revisions).

FORMAL NAMES: No attempt is here made to introduce new specific or generic names; all discussed taxa were named previously, some several times. To more clearly express ancestry, however, some named species have been assigned to different subgenera, but all taxa discussed herein are *Mimomys* or were derived from it. Any system of interpreting ancestry that is based upon the principle of parsimony is frustrated by the complex microtine history of dispersal and regional isolation; ancestry is herein based on this history and morphologic advancement.

As a generality herein, genera transcend regions, subgenera usually express regional and/or lineage distinction within the genus, and species express diagnostic differences. Subspecies represent morphologically distinct contemporaneous (coeval) forms within one region or in adjacent regions, and are not used because determination of contemporaneity in geologic settings is uncertain.

Each taxon has its defined morphologic, as well as temporal and possibly biogeographic, distinction; species that appear morphologically identical but clearly represent different lineages on biogeographic grounds are considered different. Thus, the recognition of faunal regions is required in the classification used, at least in a group so well known as *Mimomys*.

The Old World subgenus *Mimomys* (*Cromeromys*) is used for North American forms because this immigrant arrived late in

the North American history of the genus and it does not show sufficient morphologic difference to alter the subgeneric assignment used (by some) in Eurasia. This subgenus obviously had subarctic adaptations so that isolation from Eurasian populations is difficult to prove. Because of its adaptation, it is the only *Mimomys* that has been found in Beringia. The earlier and more temperate immigrant is believed to have entered North America along the southern shore of Beringia, which is now below sea level.

ANATOMICAL NAMES: Terms for dental morphology appear on the figures and are derived from Repenning (1968: fig. 10; Repenning, 1992: fig. 10; Repenning et al., 1995: fig. 8). Many different names for the same morphologic feature have been proposed and those used here preserve the earliest terminology. Most date back to Hinton (1926); those not used by Hinton were added entirely because they name morphologic features that seem significant in diagnosis and evolution; their use also attempts to apply the rule of priority to morphologic terminology. The fewer new terms and formal names introduced, the better.

DESCRIPTIVE TERMS: Measurements of the length of the first molar (used in size considerations) were made on the occlusal surface of the tooth from the outer edge of the enamel walls. Extremely worn or slightly worn teeth were not measured, as these conditions can cause significant differences in length due to tapering of the tooth.

Schmelzmuster (enamel [rod] arrangement), like most tooth characters, developed differently in different microtine lineages (Koenigswald, 1980). During the first m.y. of the Pliocene in all areas of the Northern Hemisphere, the enamel of the cheek teeth of *Mimomys* was simple, consisting of a "radial" arrangement of enamel rods. The first immigrant to North America, *Mimomys sawrockensis*, and to Europe, *M. davakosi*, and the ancestral Asian *M. antiquus* all had radial Schmelzmuster (von Koenigswald, personal commun., 1991). A little more than 4 million years ago, two other patterns of enamel-rod arrangement developed, "tangential" and "lamellar". Because the position and degree of development of these Schmelzmuster types within the tooth enamel appears to be

diagnostic of lineages, it thus tends also to reflect the faunal region in endemic forms.

Koenigswald and Martin (1984) examined the Schmelzmuster of four species of *Mimomys* from the United States (the oldest being at least a million years younger than the earliest immigrant *Mimomys*). They found it to differ from that of the genus in Europe, and concluded that *Mimomys* did not exist in North America because the Schmelzmuster patterns did not match those of the European faunal regions. This conclusion was based upon two misconceptions: (1) that enamel Schmelzmuster is of greater significance than other characters, and (2) that a dichotomy into two lineages from a common ancestor should be recognized at the generic level.

Later discussion with von Koenigswald makes evident that no difference exists in our concept of *Mimomys* evolution (of American and European lineages evolving from the primitive Asiatic *Mimomys antiquus*); the only conceptual difference is the belief that the developing lineages in Europe and in the United States should have different generic assignments. The problem with this assumption is that it leaves unanswered the question of proper generic assignment of older species from Europe, Asia, and the United States that have (as far as has been checked) the primitive radial enamel inherited from their critetid ancestors.

TIME CALIBRATION: The temporal calibration of paleomagnetic stratigraphy used is basically that of Mankinen and Dalrymple (1979), with a few minor changes. These changes are given in Berggren et al. (1995). The dates from column 11 of their table 2 are used to the ending of the Réunion events (the conclusion of the Olduvai event is not listed in this column and the age of 1.76 Ma is used as an approximation that differs from the "preferred" age assignment in column 11 by about 10,000 years, about the limit of microtine biochronology resolution with adequate samples). Older than the ending of the Réunion events, column 8 is used to the beginning of the Mammoth event; and column 1 to the base of the Gilbert. Column 1 shows the original ages of Mankinen and Dalrymple (1979). They did not show an age for the beginning of the Gilbert Chron in their publication but about 5.35 Ma is used to ap-

proximate the Miocene/Pliocene time boundary (Berggren et al., 1995: fig. 4). Were they to extend the term Gilbert Reversed-polarity Chron into older deposits, it would appear to begin about 5.89 Ma in the late Miocene.

Direct radiometric calibration of polarity stratigraphy is what I have used since it was first published, and I continue to use it for consistency in my own statements. Berggren et al. (1995) revise radiometric age determinations in their table 2, columns 8 and 11. There are advantages to the use of radiometric calibration alone. Radiometrically dateable rocks associated with a fossil locality can be integrated with a magnetic polarity stratigraphy only if it is calibrated by radiometric methods. It is impossible to evaluate an associated radiometric date with the astronomical and marine evidence used by Berggren et al. (1995: table 2, columns 3, 4, 5, 10, 12) to adjust and "improve" the calibration of the polarity stratigraphy. These differences in age calibration of the polarity stratigraphy are real and can result in the appearance of conflicting evidence. For example, a radiometric date stratigraphically above the fossil horizon may be older than the "improved" age of the paleomagnetic reversal found below the horizon. This result leads to repeated radiometric measurements to discover possible error, but the error may lie in the "improved" calibration of the age of the polarity reversal. A single line of evidence avoids such apparent contradictions.

Repenning (1987) divided mammal ages on the basis of microtine evolution and dispersal. Blancan mammal age was divided into Blancan I, II, III, IV, and V; Irvingtonian mammal age into Irvingtonian I, II, and III (as later revised in Repenning et al., 1990). These divisions are used herein. Only occasionally do these faunal subdivisions, based on evolution and dispersal of microtine rodents, coincide with changes in other mammal types, but the microtine ages are grouped according to their position within the standard mammal ages.

ABBREVIATIONS

INSTITUTIONAL ABBREVIATIONS:

CAS	California Academy of Sciences
CIT	California Institute of Technology

DMNH	Denver Museum of Nature and Science
F:AMNH	Frick Collection, American Museum of Natural History
IMNH	Idaho State University, Museum of Natural History
KUMVP	Kansas University, Museum of Vertebrate Paleontology
LACM (CIT)	California Institute of Technology collection, now in the Natural History Museum of Los Angeles County
MNA	Museum of Northern Arizona, Flagstaff
MSU	Midwestern State University, Wichita Falls, Texas
NAU	Laboratory of Quaternary Paleontology, Northern Arizona University, Flagstaff
SDSM	South Dakota School of Mines and Technology Museum of Geology
UALP	University of Arizona Laboratory of Paleontology
UCMP	University of California Museum of Paleontology
UMMP	University of Michigan Museum of Paleontology
UNSM	University of Nebraska State Museum
UO	University of Oregon, Museum of Natural History (Condon Museum)
USGS	United States Geological Survey, former Branch of Paleontology and Stratigraphy
USNM	National Museum of Natural History, Smithsonian Institution
UTA	University of Texas, Austin
UW	University of Washington, Thomas Burke Memorial Washington State Museum

DENTAL FEATURES:

ACC	Anteroconid complex (“protoconid complex” of Russian authors)
DT	Dentine tract (“ <i>linea sinuosa</i> ” or “basal enamel margin” of some authors)
T#	Alternating triangle number, numbered from posterior loop forward on lower teeth; from anterior loop backward on upper teeth
B#	Buccal reentrant number on first lower molar, numbered from rear of tooth
L#	Lingual reentrant number on first lower molar, numbered from rear of tooth
MK	“ <i>Mimomys</i> ” Kante

OTHER TERMS:

WFR	Western Faunal Region of the USA
EFR	Eastern Faunal Region of the USA
FR	Faunal Region (preceded by name)
Ma	Million years, million years ago, or million years old
VPR	Vertebrate paleontology locality register, USGS, Menlo Park Office
TMR	Tertiary nonmarine mollusk locality register, USGS

RECOGNITION OF *MIMOMYS* IN NORTH AMERICA

In 1932, R.W. Wilson described *Cosomys primus* from the Coso Mountains of southern California. The locality is very close to 3.0 Ma (Bacon et al., 1979, and C.R. Bacon, personal commun., 1980). Wilson noted the great similarity of his species to Forsyth-Major’s genus *Mimomys* but reasoned that the few differences and the great geographic separation from Europe suggested that the use of *Mimomys* might not be appropriate for the Coso Mountain microtine.

Immediately after Wilson’s report, Hinton (1932) expressed the opinion that Wilson’s *Cosomys primus* was a species of *Mimomys*, and most later authors have followed this opinion. In 1934, Wilson described rodents from Idaho and he recorded *Mimomys (Cosomys) primus* (Wilson) from Hagerman, thus agreeing with Hinton’s opinion but retaining the name “*Cosomys*” as a subgenus, as is herein done. He also described a new species “*Mimomys? parvus*” from Jackass Butte, Idaho. The question mark recognized that this species did not greatly resemble known European species of that genus. However, neither Wilson nor Hinton seemed to be aware of the striking similarity of the m1 with that of European *Pliomys episcopalpis* Méhely (1914), a primitive muskrat. Hesse (1934) described another occurrence of *Mimomys primus* found in a Californian well core. Next, the Wood Committee (Wood et al., 1941: 13) defined the Blancan mammal age as being marked by the first appearance of *Mimomys* (and many other mammals) in North America, primarily the USA.

Hibbard (1949) described a microtine from the Saw Rock Canyon fauna of Kansas as *Cosomys primus*. He made no mention of

Mimomys. Later (1952) he again referred the Saw Rock Canyon material to *Cosomys primus* but noted without explanation that *Cosomys* was preferred to the genus *Mimomys*; and that the Saw Rock material was not certainly *Mimomys*. Still later Hibbard (1957) decided that the Kansas material and *Mimomys (Cosomys) primus* differed enough to merit different generic assignments, and made the Saw Rock Canyon form a new species in his genus *Ogmodontomys* Hibbard, 1941, *Ogmodontomys sawrockensis*. He then (1957: 41, 43) clearly recognized that Wilson's species had been referred to *Mimomys*, but denied it, suggesting that *Cosomys primus* was derived from *Ogmodontomys sawrockensis*, and thus was not *Mimomys*. However, he made no suggestion of the possible origin of the Saw Rock Canyon species of *Ogmodontomys*. It was not until much later that older, ancestral species of *Mimomys* were found in Eurasia (van de Weerd, 1979, and Zazhigin, 1980); Hibbard died in 1973 and never had the opportunity to revise his opinion.

The differences of *O. sawrockensis* that separated it from *M. (C.) primus*, as noted by Hibbard (1957), were few and were recognized as being primitive. They are related to lesser hypsodonty in *O. sawrockensis*. His generic assignment was based upon similarity to the genus he had described earlier from younger deposits in Kansas and had named *Ogmodontomys poaphagus* (Hibbard, 1941), an obvious derivative of *O. sawrockensis* in the Great Plains (Zakrzewski, 1967). Although Hibbard still made no suggestion of the ancestry of *O. sawrockensis*, he did suggest that *Mimomys* in Europe may have been derived from *O. sawrockensis* (Hibbard, 1964: 124). At that time nothing was known from Eurasia that suggested otherwise.

Hibbard's belief in the derivation of *Mimomys (Cosomys) primus* from his *Ogmodontomys sawrockensis* is accepted here. As inferred by Repenning (1987: 254), the Saw Rock Canyon fauna is possibly 1.8 Ma older than *Mimomys (Cosomys) primus* at its type locality (1.1 m.y. older than the oldest known occurrence of *M. (C.) primus*). Because of this greater age, *O. sawrockensis* should show the differences Hibbard noted.

Repenning (1987) returned the species *O.*

sawrockensis to the subgenus *Cosomys* where Hibbard (1949, 1952) had first put it (as a genus), and to the genus *Mimomys* following Hinton (1932) and Wilson (1934). However, referral of *Ogmodontomys sawrockensis* to the subgenus *Cosomys* is not followed in the present report, as will be discussed.

Mimomys sawrockensis is believed to have evolved into *Mimomys (Cosomys) primus* in the WFR, west of the Rocky Mountains. As seems obvious from Zakrzewski (1967), the species appears to have evolved into *Mimomys (Ogmodontomys)* in the Great Plains of the EFR. But the origin of the lineage is in the genus *Mimomys* of the Old World.

Hibbard's species, *Mimomys sawrockensis* (present usage), is also known in the WFR: from the Maxum fauna of the San Francisco area and from the Upper Alturas faunas of northeastern California (Repenning, 1987: 254), both presumably older than the type locality at Saw Rock Canyon, Kansas, and much older than the records of *Mimomys (Cosomys) primus*. Both Californian localities permit an invasion from Asia down the Pacific Coast of North America (discussed later) as well as derivation of *M. (C.) primus* in the WFR. Other records in the WFR are here recognized as representing *Mimomys sawrockensis*.

Claude W. Hibbard worked primarily on faunas from the Great Plains and could unambiguously see evolutionary changes that took place with time in that region. During the Pliocene, these changes were in a few persistent lineages largely confined to the Great Plains. New immigrants that abruptly appeared in the Great Plains (from west of the Rocky Mountains) could, in many cases, be considered of unknown origin and then observed to evolve in later faunas of the Great Plains. This led Hibbard to believe in a North American origin of the Great Plains microtines and explains his use of new genera, as *Ogmodontomys* and *Ophiomys*, and denial of a *Mimomys* ancestry.

This must have been done with very strong conviction because it was in the face of his knowledge that other mammalian types had dispersed from Asia to North America. By 1964 (Hibbard: 124) and 1967 (Hibbard and Zakrzewski: 268–269) the U.S.

history of microtines had assumed a Ptolemaic pattern to Hibbard and seemed to center around the Great Plains. This opinion of Hibbard's was firm and was instilled in his many students.

In about 1965, I received, from G. Dallas Hanna, of the CAS, some fossil microtine teeth collected from a diatomite deposit near Alturas, in northeastern California (fig. 17.3A, B). The material contained the teeth of a small and primitive microtine that could not, at that time, be separated from earliest *Mimomys* then known from Europe (*Mimomys gracilis* Kretzoi, fig. 17.2D, E; the great significance of DT development was yet to be realized). This suggested a possible immigrant to North America. It was, in fact, the most primitive species of *Mimomys* then known in the world and later proved to be older than *M. gracilis* from Europe. In the present report, I place the California specimens in *M. sawrockensis*, although it has taken me 35 years to come to this conclusion. Hibbard was immediately told by telephone of the suggestion that *Mimomys* had dispersed to North America; his reply was typically exact and direct: "That's impossible!" Neither of us stopped to think that it equally supported his interpretation of a Great Plains origin for Old World *Mimomys* and dispersal in the opposite direction to Europe. Fifteen years later an equally primitive *M. davakosi* van de Weerd, around 5 Ma, had been found in Europe and an even more primitive species, *M. antiquus* (Zazhigin), possibly 5.5 Ma, was described from western Asia.

NORTH AMERICAN DISPERSAL ROUTES

During the Pliocene, immigrant microtines and other mammals followed a route from Beringia down the Pacific Coast of North America. When they first arrived in the Pacific Northwest of the United States they most resembled their Eurasian ancestors. By the time that they dispersed to the Great Plains through the "Yellowstone Pass"³ or

³ Yellowstone Pass is the summit of a long ramp of the Great Plains in Wyoming that rises westward to the continental divide in western Wyoming and then drops into the Snake River drainage of Idaho or the Great Salt Lake basin in Utah, both in the WFR. This has been a

around the south end of the Rockies, they often had evolved into morphologically distinct forms, less easily recognizable as Old World genera. Dispersal in the opposite direction, from the Great Plains to the WFR, was also along these routes across or around the Colorado Rocky Mountains (Repenning, 1998: 45).

Late Tertiary uplift of the Canadian Rockies narrowed the Pacific Coast route and forced the immigrant mammals westward toward the sea; what is left of this dispersal route is now below sea level, covered by later glacial till as elevation of the mountains supported permanent mountain glaciation.⁴ This activity began to restrict dispersal along the Pacific Coast route in late Blancan faunas (Blancan V; beginning ca. 2.65 Ma). The uplift presumably formed a rain shadow in Canada to the east of the Rocky Mountains that permitted grasslands to develop. Through these passed the earliest microtines to disperse directly to the Great Plains of southern Canada and the USA, without first passing through the WFR (Repenning, 1990). About 1.5 Ma, the Pacific Coast route became permanently closed (Repenning, 1990; Repenning et al., 1995). Later microtine invasions were down the eastern side of the Rockies to the Great Plains, a route used by immigrant *Mimomys* only during its second invasion of North America after the beginning of the Pleistocene (1.76 Ma).

favored route between the east and west sides of the Rocky Mountains and Wasatch Range for meteorologic patterns, native Americans, wagon trains, railroads, highways, and dispersing mammals at least since the Colorado Front Range began rising during the Laramide Orogeny.

⁴ At times these glacial barriers existed as far south as Seattle. The ancient coastal plain route is now below sea level between Seattle and the Aleutian Islands. This coastal plain is cut by fjords and buried by nonmarine glacial deposits on the sea floor (Josenhans, 1997). Two and a half million years ago was the time of the first developing Northern Hemisphere continental glaciation (Boellstorff, 1978) due to global warming. The Pacific was abnormally warm, sea level was dropping, and cloud cover was great in northern North America and provided sufficient moisture for glaciation. Continental ice reached its peak by 1.2 Ma, reflecting so much solar radiation back into space that global cooling began, evaporation of sea water declined, skies became clear, and the continental glacier abruptly starved under clear winter skies and melted under clear summer skies (Repenning, 2001).

The Bering Land area was largely present between Asia and North America during more than the first half of the history of microtine rodents. During this part of their history, the periodicity of microtine dispersal events was entirely controlled by environmental constraints. During the latter part of their history, both the emergence of the Bering Land area and microtine dispersal events were controlled by climate change (Repenning and Brouwers, 1992; Repenning, 2001). A warmer climate in Beringia (needed for temperate microtines to disperse northward to Beringia and North America) and continental glaciations (needed to expose the submerged land area) were required for intercontinental dispersal. Climatic change seems to have been the regulator of most mammalian dispersal from Asia to North America; the presence of the Bering Strait during interglacials was similarly controlled and was no barrier except to very Arctic-adapted forms like the woolly rhinoceros.

The microtine dispersal route along the Pacific Coast persisted (probably intermittently because of varying sea levels) at least from late Miocene time⁵ until (and including) the early Pleistocene, a period of over 4 Ma. But about 2.65 Ma, with the beginning of the cyclic continental glaciation of the Pleistocene, the first known immigration down the east side of the Canadian Rockies occurred (Repenning, 1987: 247). These intercontinental dispersals, as well as those between the faunal regions of the United States, are discussed in Repenning (1998, 2001); the present discussion indicates more fully the many faunas, which are the defense of these routes.

THE FIRST ARVICOLINE IMMIGRANT

Species of *Mimomys*, similar in most characters to *M. davakosi* van de Weerd of Europe and to *M. sawrockensis* (Hibbard) in the WFR of the USA, are known across Asia, but their history of dispersal and provinciality is poorly known. The only species of *Mimomys* older and more primitive than *M.*

davakosi and *M. sawrockensis* is from Western Siberia, just north of Kazakhstan, and is *Mimomys antiquus* (Zazhigin 1980: 96; as *Promimomys antiquus*). This is believed to derive from a more primitive arvicoline often placed in Kretzoi's (1955) genus *Promimomys*. In Eurasia, there is a graded series of *Promimomys* species that evolved gradually into *Mimomys*, although no gradation of morphotypes occurs in single populations (Fejfar et al., 1990). Two of these earliest forms (fig. 17.1) and Eurasian forms resembling *Mimomys sawrockensis* (fig. 17.2) are illustrated.

In the United States, *Promimomys* (*Prosomys*) *mimus* (Shotwell) is known from late Hemphillian deposits in both the WFR and the EFR (Repenning, 1987: 253). Although there are faunas of later Hemphillian age in both regions of the USA, there are no records of younger species of *Promimomys* or of older species of *Mimomys*, as are found about this time in Eurasia. Thus, the fossil record does not support the belief that North American *Mimomys* had an independent origin from the same Holarctic genus, suggesting that *Mimomys sawrockensis* was an immigrant from Asia.

South of Canada there were two primary routes of dispersal from the Pacific Coast eastward within the WFR: they were along the ancient Columbia River (not then connected to the Snake River that led from Yellowstone Pass) and along the Sacramento River, which then emptied into an inland sea in the position of the Central Valley of California and connected to the Pacific possibly 100 mi to the south of the modern Sacramento mouth at San Francisco. There were thus two faunal subregions or provinces in the WFR which, in part, had separate histories. These histories merge into one with the diversion of the Snake River to the Columbia basin about 4 Ma, a million years after *Mimomys* dispersed to North America (Repenning et al., 1995).

From the inland sea in California, the immigrants dispersed both up the Sacramento Basin northward and then eastward up the old Snake River (before its rerouting to the Columbia) and eastward south of the then young Sierra Nevada and very old Laramide Rocky Mountains (essentially the modern

⁵ Microtines evolved in the late Miocene; the Bering Land area was permanently present at least since the end of the Cretaceous and until the first Bering Strait, whose age is still under study.

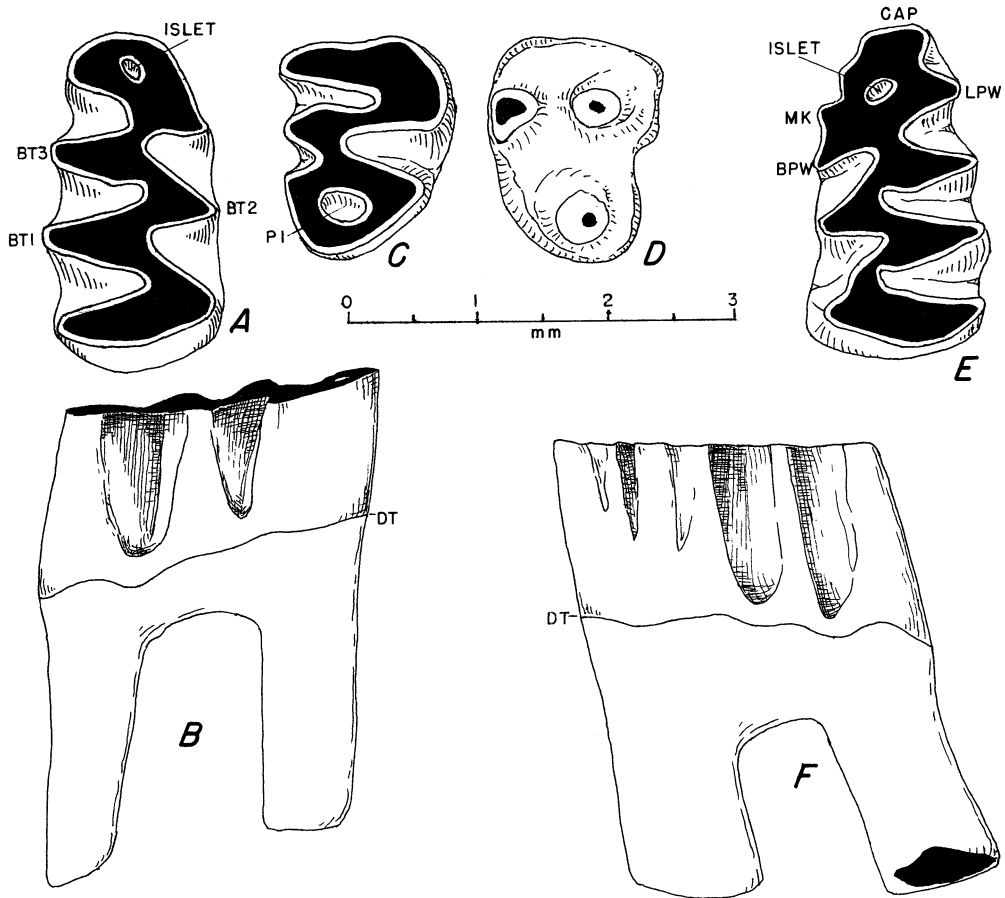


Fig. 17.1. Early arvicoline microtines. **A–D**, *Promimomys mimus* (Shotwell), late Hemphillian age, Christmas Valley fauna, Lake County, Oregon. **E, F**, *Mimomys antiquus* (Zazhigin), late Pavlodaran age (Novostanica stage), Peshniovo fauna, southernmost West Siberia, Russia (100 km north of Petropavlovsk, Kazakhstan). **A, E**, Occlusal views of m1s. **B, F**, Buccal views of m1s. **C**, Occlusal view of M3. **D**, Radicular view of M3. *Symbols*: BT1 = basic triangle 1; BT2 = basic triangle 2; BT3 = basic triangle 3; PI = posterior islet on M3; BPW = buccal primary wing; LPW = lingual primary wing; MK = *Mimomys* Kante; DT = dentine tract. All figures to the same scale, unlike the following figures.

Colorado Front Range but then penneplained to low relief) to the Great Plains of the EFR. The known localities of *Promimomys* suggest that it moved eastwards only up the Columbia River; the records of early *Mimomys* suggest that it went eastward from both the Columbia and from central California.

In the Columbia basin, the gradation *M. sawrockensis* → *M. sawrockensis-taylori* → *M. taylori* → *M. meadensis* and → *Ophiomys parvus* of the WFR is strikingly displayed in the Glens Ferry and Ringold Formations of Idaho and Washington. No such record is known in the southern part of the WFR,

where it was usually (but not always) too warm for the genus. In the EFR on the Great Plains, the gradation *M. sawrockensis* → *M. (Ogmodontomys)* → *Hibbardomys* is almost as well recorded as that in the Columbia basin, and *M. sawrockensis* appears to have dispersed to the Great Plains from California, with populations of derived forms from the Central Valley, northern Mojave Desert, southern Nevada, and the Great Plains.

GENUS *MIMOMYS* FORSYTH-MAJOR

The genus *Mimomys* was introduced by C.I. Forsyth-Major (1902) for a fossil micro-

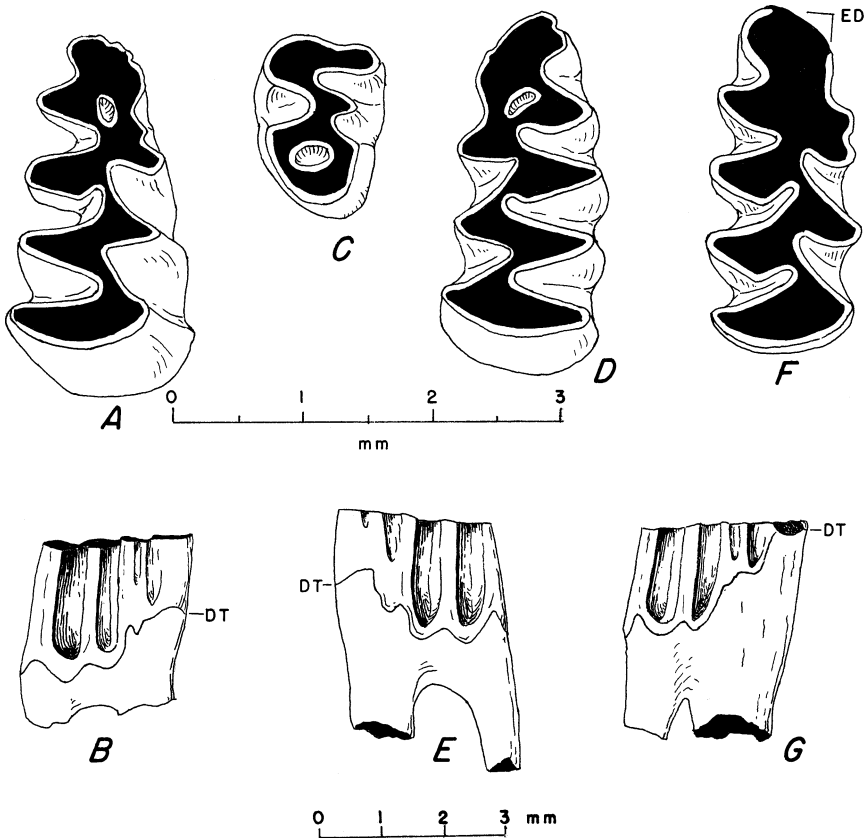


Fig. 17.2. Eurasian look-alikes. A–C, *Mimomys (Aratomys) bilikeensis* (Qiu and Storch), Yushean age, Bilike fauna (about 4 Ma), Inner Mongolia, China; drawings of a cast. D, E, *Mimomys (Cseria) gracilis* (Kretzoi), Csarnótan age, Weże fauna (about 4 Ma), Poland. F, G, *Mimomys (Aratomys) kashmiriensis* (Kotlia), latest Pliocene (in the Olduvai event, about 1.8 Ma), Kilar, Kashmir, India. A, D, F, Occlusal views of m1s. C, Occlusal view of M3. B, E, G, Buccal views of m1s. ED = enamel discontinuity where DT has been cut by occlusal surface. The subgenus *Mimomys (Aratomys)*, here proposed, appears to be a branch of the Oriental FR (and adjacent Kashmir) characterized by normal development of DT but retention of a primitive dental pattern and lack of cement, and slow to lose three roots on M3.

tine rodent from northern Italy (*Mimomys pliocaenicus*) that he had placed in the genus *Arvicola* 20 years earlier. He also included in *Mimomys* two species from Britain that Newton (1882) had placed in *Arvicola (Evotomys)*, but he neglected to select a type species. Of these three species, Méhely (1914) selected *Mimomys pliocaenicus* (Major) as the type species, as it was this form that Forstth-Major had personally described.

Generic rank followed from the opinion that the presence of roots on the molar teeth was a significant morphologic difference from *Arvicola*. It was also recognized that

many species of *Mimomys* showed a “*Mimomys* Kante” (= “prism-fold” of Hinton, 1926), as well as an enamel islet in the ACC, and that some older species of *Mimomys* in Europe lacked cement in the tooth reentrants, characters not present in *Arvicola*.

More recent studies and collections (Hinton, 1926, to Koenigswald, 1973), however, have shown that *Arvicola* did evolve from *Mimomys* (as have much more than half of the living genera of microtine rodents) by the loss of these characters with increasing hypsodonty. Most recently, discovery in western Germany of a lineage that had evolved from

Mimomys indicated that the lemming genera *Lemmus*, *Mictomys*, *Myopus*, *Pliocitomyia*, and *Synaptomys* all derive from *Mimomys* through early Pliocene *Tobienia*. This discovery eliminated the subfamily Lemminae and placed the tribes Lemmini and Synaptomyini in the subfamily Arvicolinae (Fejfar and Repenning, 1998).

Mimomys is a microtine genus of the tribe Arvicolini of the subfamily Arvicolinae (see Repenning, 1992: 24–25 for diagnoses). Calling it an arvicoline microtine separates it from other microtines, such as an ondatriine microtine. That *Mimomys* derives from *Promimomys* is not disputed. The origin of *Promimomys* out of the low-crowned cricetid *Microtodon* is also undisputed, but it is difficult to select among possible ancestral species within the *Microtodon* group, and, indeed, there may have been more than one.

DIAGNOSIS AND DISCUSSION: The genus *Mimomys* has high-crowned, rooted teeth, a first lower molar with three alternating triangles (“basic triangles” of Repenning, 1992), and an anteroconid complex with well-developed primary wings. Most individuals have a *Mimomys* Kante on the buccal primary wing, and an enamel islet within the ACC, diminishing in relative depth with evolution. Roots diminish slightly in number with evolution, and are absent in immature individuals of the most advanced Eurasian species (*M. savini*). All species have limited complexity of the ACC, and it becomes less complex in younger species as the genus approaches the rootless descendants *Allophaiomys* and *Arvicola*. Increasing tooth hypsodonty was the primary evolutionary trend [increasingly prominent dentine tracts, relative shallowing of the islet, reduction and ontogenetically later development of tooth roots, and (mainly in Eurasian species) development of cement in the reentrants all progressed with hypsodonty]. The principal characters diagnosing the genus are retention of roots and the three basic triangles, with a simple trefoil anteroconid on the m1. The M3 remains simple, more or less as in *Promimomys* except that it also increases in hypsodonty and reduces the number of its roots.

The complexity of the ACC, especially primary wings (sensu Repenning, 1983: 474; two sides to the prism), is lacking in the an-

cestral genus *Promimomys* (fig. 17.1). Derived genera differ in having a more complex ACC or in loss of roots; the complexity of the ACC in derived genera develops from the modification of the primary wings into triangles (approximating three sides to the prism). In descendants, the secondary, and in a few even the tertiary wings, also become triangles.

The “*Mimomys* Kante” (MK), or “angle” or “ridge”, is a lesser salient angle on the anterior face of the buccal primary wing of the ACC. In some subgenera it is shifted forward (fig. 17.9). In some it may be shifted “backward” toward, or to, the tip of the buccal primary wing producing a “doubled” salient angle (examples shown on fig. 17.7C, G). It may be absent in some individuals.

Usually in *Mimomys*, the MK is separated from the apex of the buccal primary wing by a weak reentrant adjacent and distal to the Kante that Hinton (1926: 111, 362) called a “prism-fold”. A recognizable MK is sometimes present without a prism-fold (see Repenning, 1968: fig. 10). When a definable prism-fold was not present but there remained a weak MK, Hibbard sometimes referred to the MK as an “enamel ridge” (see Hibbard and Zakrzewski, 1967: 263).

The MK is lost during the evolution of the buccal primary wing into a developed triangle (T4) on the ACC (fig. 17.6H or Repenning et al., 1995: fig. 8D), but this change and the loss of roots exceed the diagnosis of the genus *Mimomys*.

The configuration of the enamel pattern on the occlusal surface of m1 varies considerably with tooth wear, as in most hypsodont rodents with rooted cheek teeth, and a dentine tract (DT), extending up the buccal face of the ACC, varies from absent in the most primitive species of *Mimomys* to very high in the most advanced. With the loss of roots, DTs also become “ever-growing”, in which case their length (but not position) ceases to be important. When the occlusal surface wears to a point below the highpoint of the tract, the tract interrupts the enamel rim and makes a gap in the enamel pattern.

DTs are varyingly developed on other parts of m1 and on other teeth and can be specifically distinctive. The height of DTs is individually variable to some degree and dif-

ferences in development are best evaluated on those tracts that are most elongate, minimizing variability. The most elongate DT is on the buccal side of the ACC, although in advanced genera tracts develop on the salient angles of the posterior loop of m1; if these are significantly elongate they also can be used in diagnosis. In some genera, notably some lemmings, continuous tracts develop on all salient angles.

The last upper molar of *Mimomys* is universally "simple" (Repenning, 1992: 11, for definition) with an anterior loop, two alternating triangles, and a posterior loop. In early species of the genus, the posterior loop may be joined to the posterior alternating triangle, leaving only one triangle and an enlarged "posterior loop" with an enamel islet representing the reentrant that would separate the "true" posterior loop from the posterior (lingual) alternating triangle of later species or other individuals. This posterior islet is inherited from the ancestral *Promimomys*, and is not always present even in the most primitive species of *Mimomys*, but persists as an individual variant for at least a million years in *Mimomys* species before being completely lost.⁶

The M3 has three distinct roots in early species of *Mimomys* throughout the Northern Hemisphere, a feature also inherited from *Promimomys*. With evolution of the genus, the anterior two roots fuse, making the M3 two-rooted. The loss of some roots on other teeth (primarily upper) also occurs with evolution.

The loss of all roots in all individuals of a population, or (in the few descendant lineages retaining roots) an increased complexity of the M3 and/or the m1 (by the development of more alternating triangles), marks the transition to more advanced genera. Also, cementum is present in the more advanced species of Eurasian *Mimomys*, but does not develop in North American species. It is, however, introduced to the North American

Mimomys fauna east of the Rockies by re-invasion (from the Old World) of *Mimomys* shortly after the beginning of the Pleistocene, perhaps 1.3 Ma.

Earliest species of *Mimomys* have a simple radial Schmelzmuster on all continents, but later species develop lamellar and tangential patterns additionally and differently on different continents and in different lineages (Koenigswald, 1980). Apparently, interregional variation of this character is no less than that of any other character, but is not completely documented. Many different subgenera of *Mimomys* have been recognized throughout the Northern Hemisphere and these, apparently, develop their Schmelzmuster patterns differently. Even isolation close to the European mainland on the island of Sardinia has caused differences in the evolution of Schmelzmuster and other dental morphologic characters (Mezzabotta et al., 1995). The nature of Schmelzmuster development is incompletely determined and many questions remain.

Mimomys sawrockensis (Hibbard)

(First North American *Mimomys*; Western then Eastern Faunal Regions)

Figures 17.3; 17.4A, B, C, D; 17.5A, B, C, D, E, F

Cosomys primus Wilson, Hibbard, 1949, 1952.

Cosomys cf. primus Wilson, Hibbard, 1950: fig. 17.

Ogmodontomys sawrockensis Hibbard, 1957; Zakrzewski, 1967.

Ophiomys mcknighti Gustafson, 1978, 1985.

Mimomys (Ophiomys) mcknighti (Gustafson), Repenning, 1987 to Repenning et al., 1995.

Mimomys (Ophiomys) magilli (Hibbard), Repenning, 1987: 256 under "Panaca, Nevada" (incorrect identification).

Mimomys (Cosomys) sawrockensis (Hibbard), Repenning, 1987 to Repenning et al., 1995.

?*Mimomys panacaensis* Mou, 1997 (inconsistent Schmelzmuster therein).

NOT: *Mimomys davakosi* van de Weerd, 1979, or the similar *M. vandermeuleni* Fejfar et al., 1990, from Europe (western Paratethyan and Tethyan FRs) and early members of a different geographic lineage.

TYPE SPECIMEN: UMMP 28166, palate with most teeth.

TYPE POPULATION: 11 m1s and 6 to 10 M3s (Hibbard, 1957; Zakrzewski, 1967).

TYPE LOCALITY: Saw Rock Canyon, Sew-

⁶ The M3 of some individuals of ancestral *Promimomys* (see Repenning, 1968: fig. 9, drawing 7a) have a separation of the anterior loop and anterior triangle from the posterior triangle-posterior loop with islet, showing that these two parts of the last upper molar of the microtines derive from a basic mammalian trigon and talon (or hypocone).

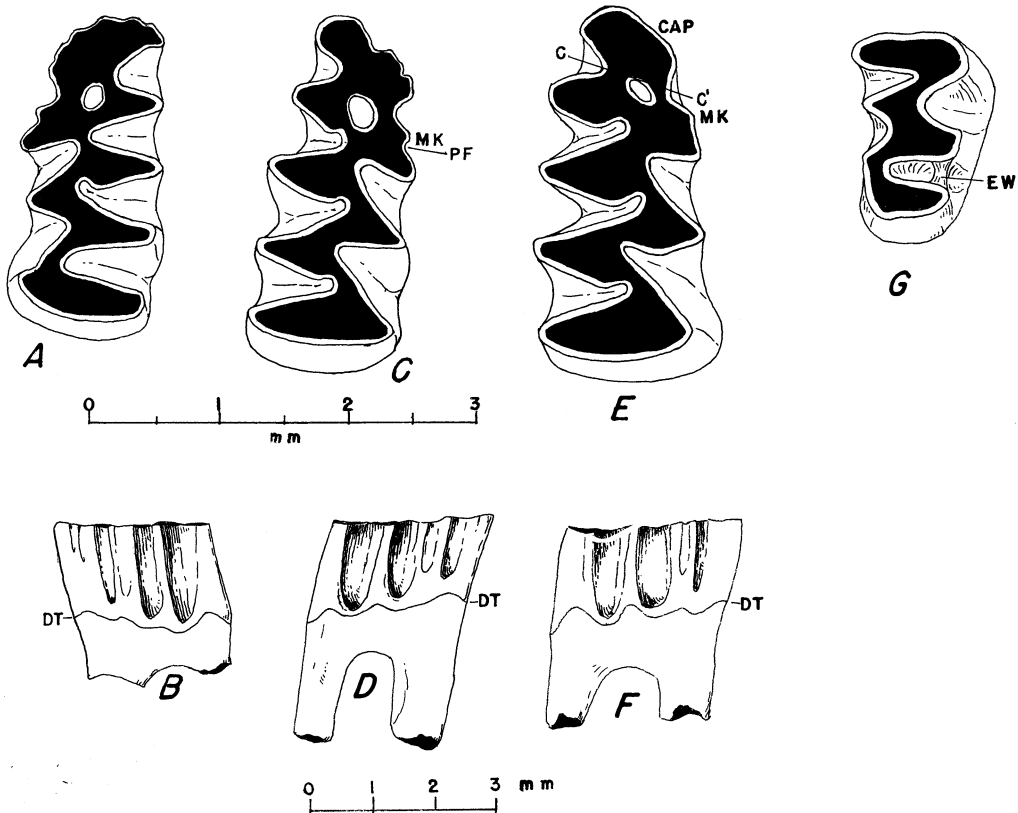


Fig. 17.3. *Mimomys sawrockensis* from the Upper Alturas fauna, Modoc County, California; early Blancan I (4.8 Ma). All are m1s, except G, which is an M3. Top row, occlusal views; bottom row, buccal views. A, B, From USGS locality M-1505 (Barnes Grade); CAS specimen. C, D, From USGS locality M-1506 (Canby). E, F, From USGS locality M-1507 (South Alturas). G, M3 UO 26913 (Barnes Grade). EW = enamel wall that would produce a posterior islet if the tooth were more worn; PF = prism fold; C-C' = constriction between the cap and the primary wings.

ard County, Kansas (KUMVP, UMMP), Blancan I age, probably late Blancan I.

REFERRED LOCALITIES: 1.—*Upper Alturas fauna: Barnes Grade, Modoc County, California* (see Repenning, 1995, for this and other localities), USGS, VPR M-1505 (transferred to the Denver office in 1985) (= CAS locality 36805, collected for diatoms by G.D. Hanna, C. Chesterman, and C. Jennings in Sept. 1959; = UO locality 26916 collected by J.A. Shotwell in the late 1950s). Along Barnes Grade of the Crowder Flat road leading up to Big Sage Reservoir, north of US 299 and 4 mi west of Alturas, California; about 72 ft below a capping basalt (dated 4.7 ± 0.5 Ma by M.L. Silberman, personal commun., 1978: sample no. FY-78-5, same results on three separate samples, collected far

apart to detect effects of lightning strikes), 6 ft below prominent white, diatomaceous tephra deposit dated 4.8 Ma by "fingerprint" correlation to a marine biochronology core off the California Coast (A.M. Sarna-Wojcicki, personal commun., 1985), and 5 ft above the Thvera event of the Gilbert Chron in a paleomagnetic section measured up Barnes Grade to the capping basalt by S.R. May and myself in 1984, SE margin SW quarter, Section 6, T. 42N, R. 12E, Modoc County, CA. This was the original discovery locality of the Upper Alturas fauna.

2.—*Upper Alturas fauna: Canby, Modoc County, California*, USGS M-1506 (VPR), 2 mi SW of Canby (18 mi west of Alturas) in first road cut west of Canby along US 299; 15 ft of section containing fish, ostracods,

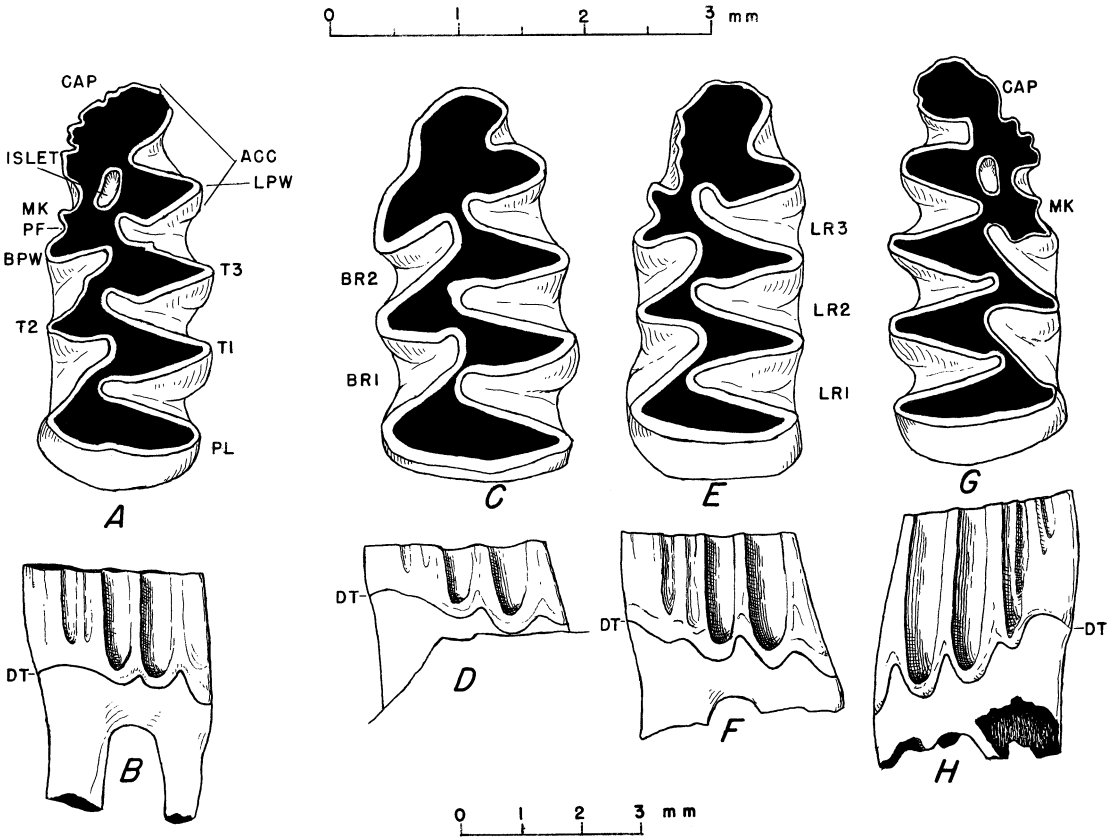


Fig. 17.4. First lower molars of *Mimomys sawrockensis*, *Mimomys* (*Ogmodontomys*) *transitionalis*, and *Mimomys* (*Cosomys*) *primus*. **A, B**, Largest individual of *M. sawrockensis* (Hibbard) from Upper Alturas fauna (locality M-1507; 4.8 Ma). **C, D**, Worn specimen of *M. sawrockensis* (Hibbard) from Saw Rock Canyon, Kansas (cast of UMMP 24344; ± 4.5 Ma). **E, F**, *M. (Ogmodontomys) transitionalis* (Zakrzewski) from Fox Canyon, Kansas (cast of UMMP 56691; 4.2+ Ma). **G, H**, *M. (Cosomys) primus* (Wilson) from Hagerman, Idaho (3.5 Ma). Top row, occlusal views; bottom row, buccal views. ACC = anteroconid complex; BPW, LPW = buccal, lingual primary wing; PL = posterior loop; T1, T2, and T3 = basic triangles 1, 2, and 3; BR1 and BR2 = buccal reentrants 1 and 2; LR1, LR2, and LR3 = lingual reentrants 1, 2, and 3.

and diatoms; same tuff bed is at top of exposure. Diatoms are the same flora as at USGS M-1505 14 mi to the east, and differ, in both localities, from those farther down section (in the Thvera event). NE quarter Section 36, T. 42N, R. 9E, Modoc County, CA. Collected by D.P. Adam in the early 1980s. The same stratigraphic horizon is indicated by the tuff and associated diatoms, and this locality is considered as part of the Upper Alturas fauna.

3.—*Upper Alturas fauna: South Alturas, Modoc County, California, USGS M-1507 (VPR), 7.5 mi south of Alturas along US 395*

on top of a prominent road cut with white tuff bed exposed in it; ant hill above tuff about midway through the road cut on east side and back 5–10 ft from the cut. This is the same tuff as that exposed at USGS M-1505 and M-1506 (A.M. Sarna-Wojcicki, personal commun., 1983), and the only locality where the fauna is known to overlie the tuff bed. NW quarter Section 24, T. 41N, R. 12E, Modoc County, CA. Fragments of large mammals found at this locality, including horse, camel, and proboscidean, were not identifiable to genus.

4.—*Upper Alturas fauna: Near South Al-*

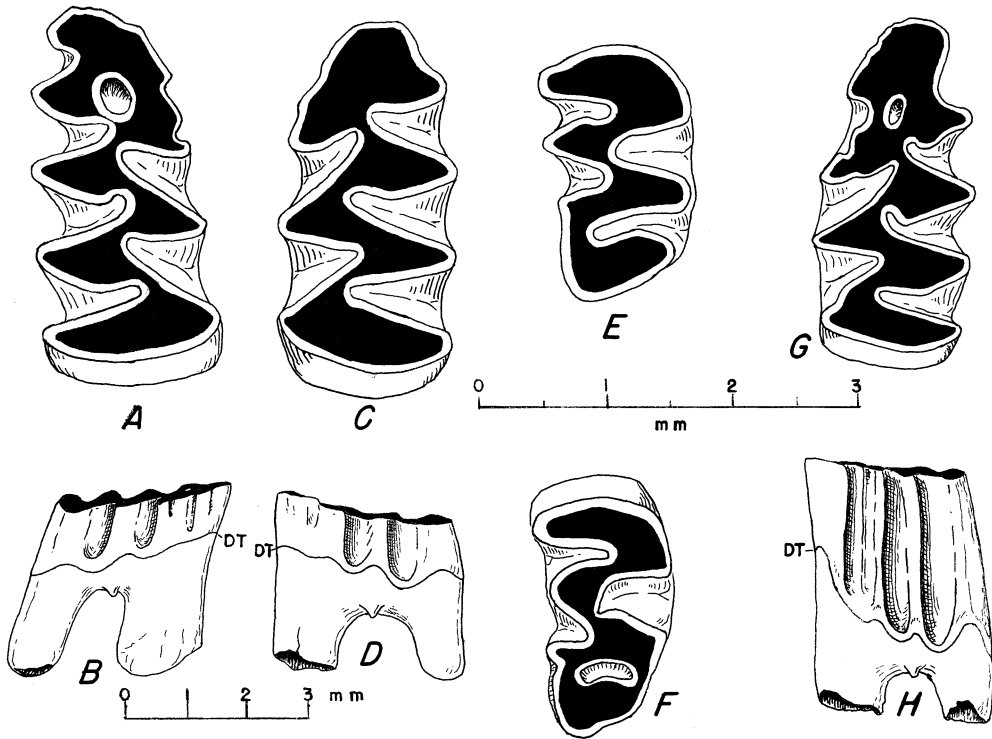


Fig. 17.5. *Mimomys sawrockensis* and *Mimomys meadensis*. A–F, *Mimomys sawrockensis* (Hibbard); two m1s and two M3s (from casts), Limestone Corner locality, Panaca, Lincoln County, Nevada (these are *Mimomys panacaensis* Mou). A, B, Less worn (UALP 21104) M1s. C, D, More worn (UALP 18000) M1s. E, F, M3s with (UALP 21081) and without (UALP 17980) posterior islet. G, H, *Mimomys meadensis* (Hibbard), Sand Draw fauna, Brown County, Nebraska (cast of type of “*Ophiomys magilli*” Hibbard, UMMP 57187, $2.8 \pm$ Ma).

turas, Modoc County, California, UCMP V95030. In the area near South Alturas locality fossil salvage operations done by Wagner & Associates of Redding, California, obtained additional material of *Mimomys sawrockensis*, including about 10 m1s (1 was found near Canby) and 5 M3s, 1 (UCMP 142436) with an islet and the two anterior roots fused together, 4 with three roots but no islet. This locality is near the South Alturas locality (USGS loc M-1507) but below the tuff (Hugh M. Wagner, personal commun., 1996). The material, accessioned by UCMP, enlarges the “population” size from the Upper Alturas faunas and helps eliminate some uncertainties.

The above four localities are referred to as the “Upper Alturas Fauna” in contrast to the Alturas fauna lower in the section in, roughly, the same depositional basin and of Hem-

phillian (late Miocene) age (Wood et al., 1941; Axelrod, 1944; Evernden et al., 1964). All Upper Alturas localities are in Modoc County, CA, and earliest Blancan I age following the “first appearance” characters of Wood et al. (1941).

5.—*White Bluffs fauna*, Franklin County, Washington, UW A5927 (type locality of *Ophiomys mcknighti* Gustafson), Ringold Formation. All microtines are from a thin zone ($15 \pm$ ft thick), below the “White Bluffs Tuff” and low in the fossiliferous section as described by Gustafson (1978, 1985). The material from locality UW A6503, 7 mi to the north of the type locality, contained no first lower molars and was about 80 ft stratigraphically above the horizon of the type locality; assignment of these specimens to this species was hypothetical, as was the statement that the species ranged through the en-

tire thickness of the fossiliferous section (see Gustafson, 1978: 30). Late Blancan I age, possibly between the Nunivak and Sidufjall events of the Gilbert Chron (ca. 4.25 Ma; Gustafson, 1985; Repenning, 1987).

6.—*Maxum fauna, Danville, Contra Costa County, California*, UCMP V6869, Tassajara Formation, Blancan I age, but without external age control. In the backyard of Dr. Bernard Maxum (Repenning, 1987: 254; May, 1981; material not seen since about 1978).

7.—*Panaca lake beds, bluffs east of Panaca, Lincoln County, Nevada*, F:AMNH locality PAN 139–79 and several other sites in the same area; several UALP localities. Repenning (1987: 256) misidentified and assigned too young an age to this occurrence. Age Blancan I; University of Arizona studies by Yun Mou (1997, 1998) in the Panaca area indicate that the oldest occurrence of *Mimomys* is in reversed polarity deposits a short distance above the Thvera Event (C3n.3r) and very close to the age of the Upper Alturas faunas, about 4.8 Ma by the calibration here used.

Mou (1997) assigned this material to the new species, *Mimomys panacaensis*, and described its Schmelzmuster (Mou, 1998), which is more advanced than the condition of *Mimomys sawrockensis* from Alturas, California, and different from that of *M. (Ogmodontomys) poaphagus*. In addition, the dental pattern of *Mimomys panacaensis* is more advanced than *M. sawrockensis* from Alturas (fig. 17.5A–F). Because of this, she suggests a separate invasion from Eurasia, a possibility, but an Old World ancestor is not known and would be recognizable only by different enamel structure. More examination of the Schmelzmuster of many Eurasian species is needed.

DIAGNOSIS: A species of *Mimomys* with lower dentine tracts than any other North American species of *Mimomys*. First lower molar with a large and persistent islet on the ACC of populations from the WFR, but small and shallow in the type material from Kansas, and a well-developed MK. Dentine tracts are stronger than in west Asian *Mimomys antiquus*, about the same as in Macedonian *Mimomys davakosi*, and less developed than in European *Mimomys (Cseria) gracilis* (see fig. 17.2D, E, fig. 17.3, fig.

17.4B, D). Size, as determined by the length of the first lower molar, is greatly variable in western populations of *Mimomys sawrockensis*, but comparable to that of the similar species from Paratethyan FR of Europe (*Mimomys davakosi*, van de Weerd, 1979).

DISCUSSION: The species *M. (Cseria) gracilis* from Weże, Poland, and other European localities, appears closer to *M. taylori* of North America (fig. 17.2D, E), including the DT. The species *Kilarcola kashmiriensis* Kotlia (1985) from Kilar, Kashmir (fig. 17.2F, G; here referred to *Mimomys (Aratomys) kashmiriensis*) is much more advanced in DT development (with associated loss of an enamel islet in the ACC) than is any earlier North American or European species of *Mimomys*, but it retains a more or less typical occlusal pattern on the first lower molar. The age assignment for the Kashmir species (about 1.8 Ma, during the Olduvai event, Kotlia, 1985) seems remarkably young for this occlusal pattern, but not for the DT development. Unlike contemporary European species, however, it has no cement in the reentrants, thus paralleling conditions in North America.

A possible Oriental FR subgenus, *Mimomys (Aratomys)*, is suggested by similar, but less advanced, characters of an older species from Bilike, Inner Mongolia (fig. 17.2A–C) named *Aratomys bilikeensis* Qiu and Storch (2000). Its characters include DT development while retaining a primitive enamel pattern and lacking cement. The third root on M3 of *Mimomys (Aratomys)* is lost at about the same time as in the WFR of the United States; it is variably present or fused in the species *M. (Aratomys) multifidus* (Zazhigin) (Gromov and Polyakov, 1992: 308) from Chono-Khariakh, western Mongolia, and apparently only two-rooted in *M. (Aratomys) bilikeensis* (Qiu and Storch, 2000: 195). It is two-rooted in the late species *M. (Aratomys) kashmiriensis* (Kotlia).

On one M3 of *Mimomys sawrockensis* (UO 26913 from Alturas, Barnes Grade locality, fig. 17.3G) the posterior of the two buccal reentrants is closed off to form an isolated enamel islet, separating it from most younger species of North American *Mimomys*; but the wall closing off the reentrant is low so that the islet would form only after

the tooth was about half worn, suggesting that the islet was in the processes of being lost. Two similar M3s of *Mimomys davakosi* from Macedonia also have a low wall forming the islet (Fejfar et al., 1990: fig. 12, nos. 29, 30). UCMP 142436, M3 from near South Alturas (locality UCMP V95030) also had an islet, but had the anterior two roots fused. Five other M3s from the Upper Alturas localities have no islet and three roots, as do all known M3s from the type locality.

The Schmelzmuster of a specimen from the Upper Alturas faunas (Barnes Grade) is primitive and consists entirely of radial enamel (W. von Koenigswald, personal commun., 1991). That of the abundant material from Panaca, Nevada, is more complicated (Mou, 1998) and, in fact, more so than that shown by Koenigswald (1980) for *M. (Ogmodontomys) poaphagus*. The Panaca population may be a distinct species, as treated by Mou (1997), but has no known descendants.

The *Mimomys* specimens from the four localities of the Upper Alturas fauna revealed a range in size that includes the sizes formerly believed to separate *Cosomys* and *Ogmodontomys* from *Ophiomys* (of former usage). This size range in the Upper Alturas faunas ($N = 8$) overlaps that of topotypic *Mimomys sawrockensis* and makes it seem that the species at Alturas, California, and at White Bluffs, Washington, cannot be separated by size, as was formerly thought.

Although four localities are included in the Upper Alturas fauna, the sample of measured m1s of *Mimomys* is small. The range of measured lengths (2.41, 2.50, 2.50, 2.53, 2.77, 2.92 mm) includes the size of "*Ophiomys mcknighti*" from White Bluffs, Washington (length of three m1s is 2.67, 2.71, and 2.92 with a mean of 2.7 mm as measured by Yun Mou, personal commun., 1995). The size range from the Alturas localities is broader, and averages somewhat smaller, than that recorded for the type population of *Mimomys sawrockensis* from Kansas (2.9 mm mean for 11 m1s; Zakrzewski, 1967: 138), but is very close to that recorded for the European sororal species, *Mimomys davakosi* (van de Weerd, 1979).

In view of the similarity of the sample from Alturas to the type population of *Mimomys sawrockensis* and the overlapping

size range, and in view of the nearly identical size range of *Mimomys davakosi* from south-eastern Europe, it is felt that only one species is represented in North America, and that it should be called *Mimomys sawrockensis* on the basis of priority. No difference is noted between the species in the WFR and that from Macedonia except geography, but differences between the WFR and EFR populations are noted.

Type *Mimomys sawrockensis* differs from the Alturas population in the following ways: (1) *average size* is larger, although overlapped by the range from Alturas; (2) *ACC* is consistently smaller and more rectangular (best seen in the little worn specimen illustrated by Hibbard, 1964: fig. 3B), its anterior end not extended lingually as in Alturas specimens; (3) *enamel islet* of the ACC is distinctly smaller and shallower and is seen only in individuals with little wear (shown in Hibbard, 1964: fig. 3 and Hibbard, 1949: fig. 2); (4) *M3* never has a posterior islet but always has three roots ($N = 7$ to 10; Zakrzewski, 1967). Of these differences, #1, #3, and #4 seem to be without exception between the type population of *M. sawrockensis* and the sample from Alturas; the character of the ACC cap and the M3 are variable in the Alturas population, and are inferred to be so in the population from the type locality of "*Ophiomys mcknighti*" in Washington. All samples are so small that I am hesitant to say that a larger sample would not demonstrate additional exceptions.

Differences #1, #3, and #4, as well as a lack of further DT development, are those that carry on into the subgenus *Ogmodontomys* from the type population of *M. sawrockensis*; therefore type *M. sawrockensis* is "advanced" in the direction of *M. (Ogmodontomys)*. The "advancements" of retaining three roots on M3 and of not developing significant dentine tracts, not seen in the WFR, are retained plesiomorphs in agreement with ancestry to the subgenus *Ogmodontomys* and occur only in the Great Plains.

The remaining question is whether or not these few differences represent a specific difference from the Alturas population. This cannot be answered as the samples from California, Washington, and Kansas are far too small to evaluate population characteristics.

The undated Kansas sample is widely separated geographically, in a different FR, and reproductive isolation might be suspected. For now, the type and topotypes of *Mimomys sawrockensis*, from Saw Rock Canyon, are considered members of an advanced population having some characters shared by the western populations but others that are precursory to the evolution of the subgenus *M.* (*Ogmodontomys*) of the EFR. This is in agreement with the inferred immigration down the Pacific Coast and with the slightly greater similarity of these western populations to those from Eurasia.

The presence of three roots and an islet on the M3 are primitive but individually variable in WFR localities and there are no samples in North America large enough to judge frequency. Two of the eight M3s from the Alturas fauna have an islet and all have three roots (one with the anterior roots fused). Of 48 M3s from the Panaca, Nevada, fauna assigned to *Mimomys sawrockensis* with hesitation, 32 have three roots (San Bernardino County Museum specimens, B.L. Albright, personal commun., 1995), and 23 of 53 additional M3s from the same localities do also (UALP specimens; Y. Mou, personal commun., 1995). At least one (UALP 17980) has a posterior islet. In addition, the Schmelzmuster is unique; inclusion of the Panaca specimens in this species is for simplicity, not in contradiction to assignment to *Mimomys panacaensis*.

Gustafson (1978: 32) stated that M3 ($N = 6$) of the population from the White Bluffs fauna (ca. 4.25 Ma) of Washington (that he named "*Ophiomys mcknighti*") had only two roots, and makes no mention of the presence of a posterior enamel islet. This suggests a more advanced population than the referred material from Alturas (4.8 Ma) or Panaca (age possibly the same as Alturas). Age constraints (paleomagnetic only) suggest that the White Bluffs population is, in fact, younger (ca. 4.3 Ma; Gustafson, 1985; Repenning, 1987).

The even younger *Mimomys sawrockensis-taylori* sample (about 3.9 Ma, discussed next) from the Blufftop faunas (also in the Ringold Formation and overlying the White Bluffs fauna by about 300 ft) is much larger and occasionally has M3s with three roots

and a posterior enamel islet (fig. 17.6C, D). Possibly a larger sample from the older White Bluffs fauna would include some three-rooted M3s.

There appears to be interregional (WFR and EFR) and regional (WFR) population variation in *Mimomys sawrockensis* in size range, depth of the enamel islet on m1, shape of the cap, and number of roots on M3. *Mimomys sawrockensis* thus appears to represent a species that is variable, including population differences that later polarized into a distinct subgenus in the EFR [*Mimomys* (*Ogmodontomys*)]. As here grouped, the species lived at least half a million years.

Mimomys sawrockensis from Alturas, California, is only slightly more advanced than *Mimomys antiquus* from Western Siberia in having an undulating DT that only slightly rises up the buccal side of the ACC of its m1 (compare fig. 17.1E, F with figs. 17.3 and 17.4A, B). In addition, the primary wings are more developed in *M. sawrockensis* from Alturas than in Asian *M. antiquus*.

BIOGEOGRAPHY AND BIOCHRONOLOGY: As here inferred, *Mimomys sawrockensis* was an immigrant from Eurasia by 4.8 Ma. Its ancestor was *Mimomys antiquus* (Zazhigin), known from Peshniovo along the Ishim River in southernmost Western Siberia, about 60 mi north of Petropavlosk (Kazakhstan) and Novotroitskoe, on the Irtysh River about 20 mi north of Omsk (southern Western Siberia). This is near the northeastern limit of the Paratethyan FR. *Mimomys antiquus*, the most primitive form included in *Mimomys*, is unknown in North America or Europe, but was also ancestral to *Mimomys davakosi* of southern Europe, and possibly *M. (Aratomys)* spp. of the Oriental FR.

The Blancan mammal age of the United States began with the immigration of *Mimomys sawrockensis* to North America (part of original definition). With the beginning development of dentine tracts, and the gradual loss of the MK and islet, with increase in prominence of the primary wings on m1, and with the gradual reduction to two roots and loss of a posterior islet on M3 (each changing at separate rates in all FRs), this first *Mimomys* evolved into more advanced species that differed in the two faunal regions of the United States and from Eurasian lineages.

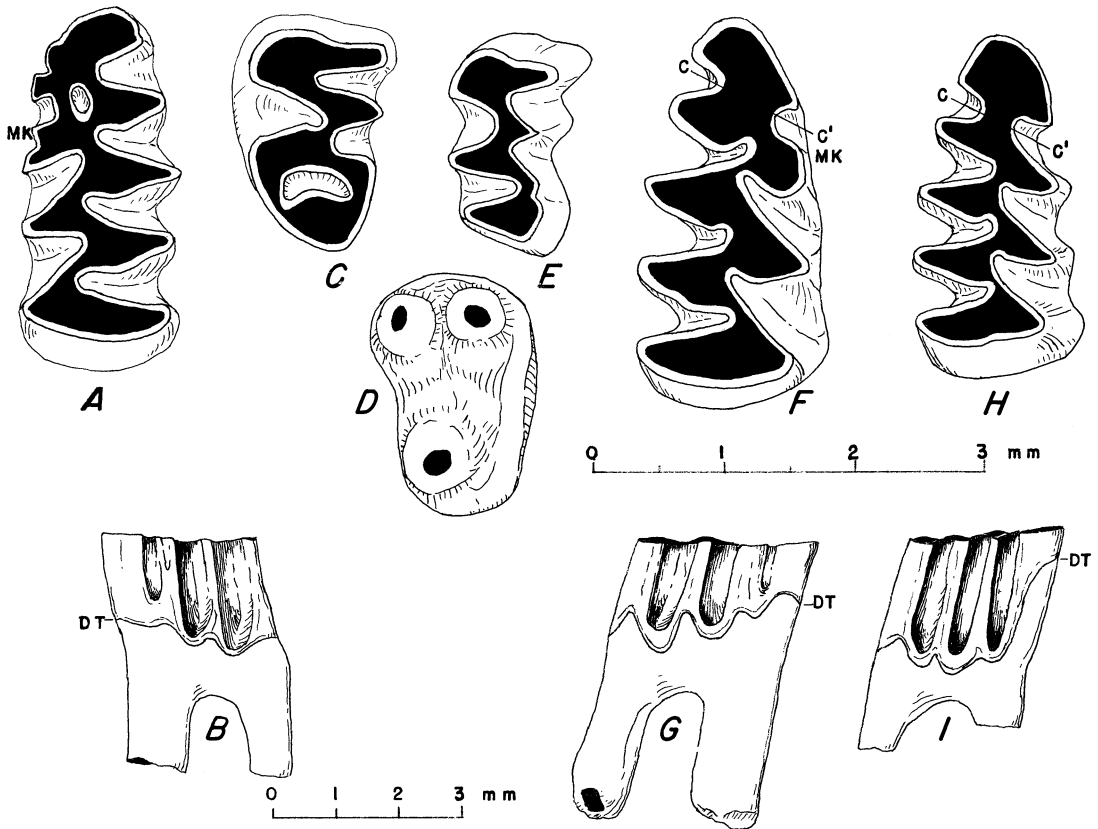


Fig. 17.6. Transitional *Mimomys sawrockensis-taylori*, *Mimomys taylora*, and *Ophiomys parvus*. *M. sawrockensis-taylori* from Ellner locality, Franklin County, Washington (3.9+ Ma). A, B, m1. C, D, M3 with posterior islet and three roots. E, M3 without islet. F, G, *M. taylora* (Hibbard) from Hagerman, Idaho, quite worn (3.6 Ma). H, I, *Ophiomys parvus* (Wilson) from Jackass Butte, Idaho (2.2± Ma).

After dispersal of *Mimomys sawrockensis* to the EFR (not dated but possibly 4.4 Ma), faunal exchange of the genus between the EFR and WFR is not evident for some time, until an estimated 3.0–2.8 Ma ago, although Czaplewski's (1990) record before 4.2 Ma of *M. (Ogmodontomys) poaphagus* from Arizona (see *M. (Ogmodontomys) transitionalis* below) indicates that Great Plains *M. (Ogmodontomys) transitionalis* nearly completed dispersal, back to the WFR, around the south end of the Rocky Mountains.

Mimomys sawrockensis-taylori
[informal designation]
(Western Faunal Region)

Figure 17.6A, B, C, D, E

Ophiomys cf. *mcknighti*, Gustafson, 1985.
Mimomys (Ophiomys) mcknighti-taylori, Repen-

ning, 1987: 254–255; Repenning et al., 1990: 397.

DIAGNOSIS: A population of *Mimomys* of moderate size range (m1 range = 2.60–2.97 mm, average = 2.72 mm, $N = 13$, uncataloged UW specimens; by no means the entire sample, as over 100 lower jaws are known). First lower molar with dentine tract slightly higher than in *M. sawrockensis* but lower than *M. taylora*. MK always present, m1 islet usually present, and cap large and curved lingually. Last upper molar sometimes has posterior islet and three roots. A lower DT and some individuals with islet and three roots on the M3 separate it from *M. taylora*. Slightly higher DT separates it from *M. sawrockensis* from White Bluffs fauna 300 ft lower in section.

DISCUSSION: Fossil microtines were found

very near the top of the section at White Bluffs in 1978, well above the type locality of "*Ophiomys mcknighti*". This locality was named the Haymaker's Orchard locality [USGS M-1439 (VPR); Repenning, 1987: 254–255]. It was considered significant because the form of *Mimomys* present was transitional between "*M. (Ophiomys) mcknighti*" lower in the same section and "*Mimomys (Ophiomys) taylori*" of Hagerman, Idaho (names used in 1987). A few months earlier the Ellner locality (UW CO149) had been found some 12 mi to the north in what proved to be the same stratigraphic horizon referred to under the name "Blufftop faunas" (Gustafson, 1985).

As an informal name, no type species or locality has been designated for this intermediate form from the Blufftop faunas. Most specimens are from the Ellner locality, and are or will be placed in the Burke Museum (UW). This intermediate form is not known from localities other than the Blufftop faunas. Stratigraphically just below the Cochiti event of the Gilbert Chron, it dates to ca. 3.9 Ma, late Blancan II, about 0.8 Ma older than the oldest *Mimomys taylori* from Hagerman, Idaho, and about 0.35 Ma younger than the White Bluffs fauna in the same formation (see discussions in Gustafson, 1985; Neville, 1981).

The enamel pattern of the m1 (fig. 17.6A–E) of *M. sawrockensis-taylori* is essentially identical to that of *M. sawrockensis* from the underlying White Bluffs fauna and can be closely matched by individuals of *M. taylori* from the Hagerman faunas (fig. 17.6F, G; Hibbard and Zakrzewski, 1967: fig. 1).

An anomaly appears in the M3 of *M. sawrockensis-taylori*: about one-third have three roots and a few have a posterior enamel islet on their occlusal surface (fig. 17.6C, D). Hibbard and Zakrzewski (1967) and Zakrzewski (1969) mentioned several times that the M3 of *M. taylori* from Hagerman localities has only two roots; no mention was made of the occlusal pattern of this tooth. Similarly Gustafson (1978: 30, 32) stated that the six M3s of *M. sawrockensis* from the underlying White Bluffs fauna (his "*Ophiomys mcknighti*") had two roots. As mentioned, the White Bluffs (older) sample is small and is contradicted by the condition

of *M. sawrockensis-taylori* from the Blufftop faunas, suggesting that the six M3s with only two roots from the White Bluffs fauna is too small a sample for reliable interpretation.

BIOGEOGRAPHY AND BIOCHRONOLOGY: The stage of evolution represented by *Mimomys sawrockensis-taylori* has not been seen in the EFR or elsewhere in the WFR. Retention of the plesiomorphic islet found in *M. sawrockensis* of the WFR (except at White Bluffs?) but lost in the type *M. sawrockensis* and descendants in the EFR as subgenus *M. (Ogmodontomys)* indicates interregional divergence of evolutionary traits.

M. sawrockensis-taylori is known only from Washington in the Pacific Northwest, not even in Idaho, as the Snake River was not yet connected with the Columbia River; when the Snake became connected *M. taylori* appeared in the Hagerman, Idaho, section (Repenning et al., 1995; ca 3.6 Ma). There are pre-Cochiti deposits (>3.9 Ma; Neville et al., 1979) in the Glenns Ferry Formation near Hagerman, but no mammalian fossils are known from them.

Mimomys taylori (Hibbard)
(Western Faunal Region)

Figure 17.6F, G

Nebraskomys? taylori Hibbard, 1959.

Nebraskomys? taylori Hibbard; Taylor, 1966.

Ophiomys taylori (Hibbard), Hibbard and Zakrzewski, 1967 [in part]; Zakrzewski, 1969; Shotwell, 1970.

Mimomys (Ophiomys) taylori (Hibbard), Repenning, 1987.

NOT: *Ophiomys taylori*, Gustafson, 1985 (Taunton fauna, WA); Tomida, 1987 (Duncan fauna, AZ).

TYPE SPECIMEN: USNM 21832, part of a lower jaw with all teeth, well worn.

TYPE POPULATION: Large; Zakrzewski (1969) cited 165 individuals from the type locality, presumably, only UMMP and USNM specimens; many more collections exist.

TYPE LOCALITY: USGS Cenozoic locality 19216 (TMR), Hagerman bluffs, Twin Falls County, Idaho.

REFERRED LOCALITIES: In addition to the type locality, there are many other localities in the Hagerman faunal succession (Hibbard

and Zakrzewski, 1967; Zakrzewski, 1969), all of Blancan III age.

The specimens from the Sand Point fauna, Owyhee County, Idaho (Blancan IV age), that Hibbard and Zakrzewski (1967) referred to this species are here included in the transitional form *Mimomys meadensis* to be discussed next, as are the specimens from the Taunton fauna, Washington (Blancan IV age). This species change is made for reasons noted by Hibbard and Zakrzewski (1967): (1) dentine tract elongation, (2) reduction or loss of the MK, and (3) constriction of the dentine confluence between the primary wings and the cap of the ACC (toward forming triangles 4 and 5), all of which are leading to the characters of *Ophiomys*.

Mimomys taylori is not known outside of the Pacific Northwest, but similar forms are known from the Old World (fig. 17.2). The position of *M. taylori*, in the graded evolutionary series between *M. sawrockensis-taylori* of Washington and *M. meadensis* of Idaho, is obvious in the Pacific Northwest and similar series occur in different geographic lineages throughout the Old World. Although older and younger faunas containing *Mimomys* are known from southeastern Washington, faunas equal in age to the Hagerman section are unknown there.

DIAGNOSIS: *Mimomys taylori* differs from earlier forms in having a higher DT on the buccal face of the ACC (compare on figs. 17.3, 17.4, 17.6), and this trend continues into younger forms (fig. 17.6H, I). Hibbard and Zakrzewski (1967) noted that the primary wings (their triangles 4 and 5) become more prominent and the MK less common in younger faunas as they approach the condition of the younger genus *Ophiomys parvus*. However, they also include *M. taylori* in this genus. The variation was also discussed by Conrad (1980). Hibbard and Zakrzewski (1967) gave length ranges for the first lower molar of 2.1 to 2.8 mm. At the stage of evolution represented by *Mimomys taylori*, the lineage has only two roots on M3 and no enamel islet is present. Schmelzmuster is unknown for either *Mimomys sawrockensis-taylori* or *M. taylori*.

DISCUSSION: *Mimomys taylori* is derived from *M. sawrockensis*, through the intermediate form here referred to as *M. sawrock-*

ensis-taylori (fig. 17.6). Gustafson (1985) outlined the evidence showing that three forms here called *Mimomys sawrockensis*, *M. sawrockensis-taylori*, and *M. meadensis* are found in stratigraphic succession in the Ringold Formation of south-central Washington.⁷ Hibbard and Zakrzewski (1967: 264), Zakrzewski (1969: 20), and Conrad (1980: 138–142) noted that between the Hagerman localities and the nearby Sand Point locality, *M. taylori* shows some differences that grade toward the later *Ophiomys parvus* of the younger Grand View faunas. Because of these intermediate morphotypes, the Sand Point population was called “*Mimomys (Ophiomys) taylori-parvus*” by Repenning (1987: 257), and “*Pliophenacomys idahoensis*” by Hibbard (1959), but these usages are junior synonyms of *Mimomys meadensis* of Hibbard (1956; see below).

BIOGEOGRAPHY AND BIOCHRONOLOGY: The ages of most Idaho and Washington faunas are constrained by magnetic polarity determinations (Neville et al., 1979) as well as by stratigraphic superposition (Repenning et al., 1995). According to these controls, *Mimomys taylori* ranges in age from about 3.6 to nearly 3.3 Ma (the beginning of the Mammoth event of the Gauss Chron).

Mimomys meadensis (Hibbard)

(Western Faunal Region, and dispersing to Eastern)

Figures 17.5G, H and 17.7A, B, C, D, E, F

Pliophenacomys meadensis Hibbard, 1956: 187–191, fig. 14 except 14J [in part, type and topotypes only].

Pliophenacomys idahoensis Hibbard, 1959: 15–22, fig. 4A–I.

Ophiomys meadensis (Hibbard), Hibbard and Zakrzewski, 1967: 261–262, not figured.

Ophiomys taylori (Hibbard), Hibbard and Zakrzewski, 1967: 262–268 [in part: those specimens from Sand Point, their fig. 1L]; Zakrzewski, 1969, table 5 [in part]; Shotwell, 1970 [in part]; Gustafson, 1985.

⁷ Although Gustafson (1985: 90–91) referred to the Taunton fauna species as “*Ophiomys taylori*” it is here included in the transitional *Mimomys meadensis*, as will be discussed. Morphologically, the population from the Taunton fauna of Washington appears identical to that of Sand Point, Idaho; compare figure 17.7A–F with Hibbard and Zakrzewski (1967) and Hibbard (1959).

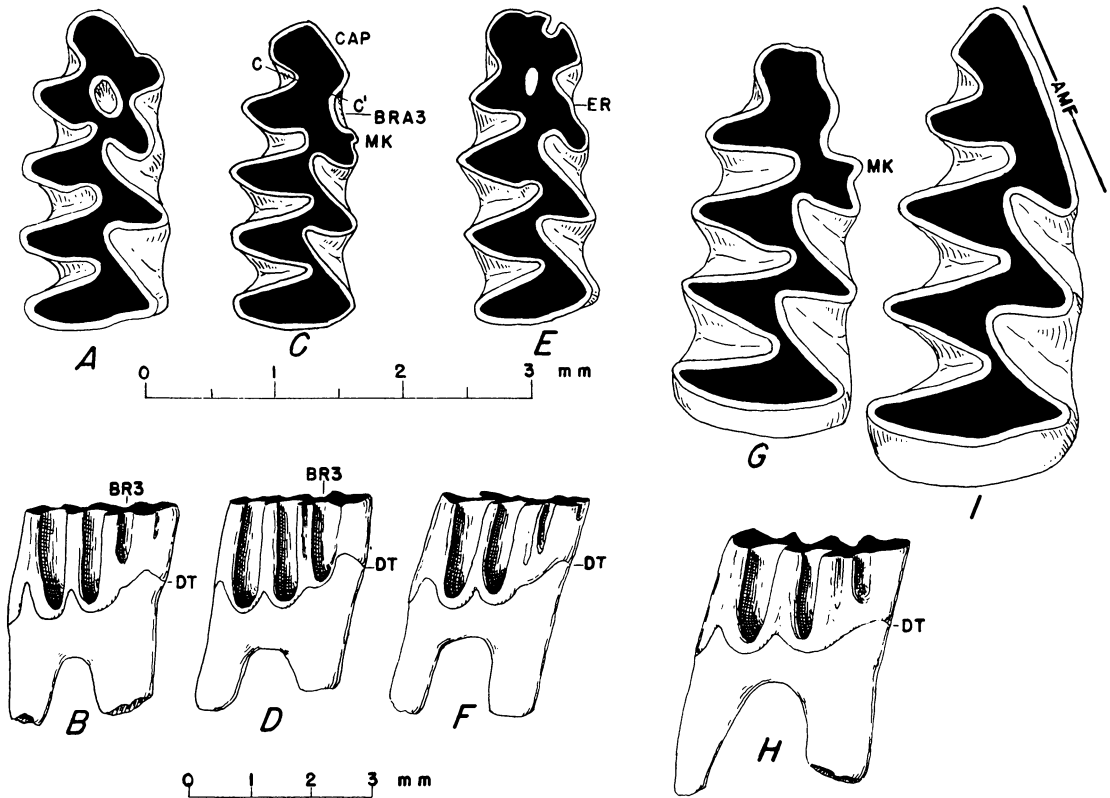


Fig. 17.7. Transitional *Mimomys meadensis* and *Mimomys (Ogmodontomys) poaphagus*. A–F, *Mimomys meadensis* (Hibbard) m1s from Taunton fauna, Franklin County, Washington (UW specimens; 2.9 Ma). C, D, An individual morphotype approaching *Ophiomys parvus* but still retaining a *Mimomys* Kante; note simple cap, no islet, constriction between cap and primary wings, and vertical depth of buccal reentrant 3 (on buccal view). E, Specimen has a slight remnant of the islet, just the base of the depression, and a slight remnant of the *Mimomys* Kante, what Hibbard referred to as an “enamel ridge”. G–I, *Mimomys (Ogmodontomys) poaphagus* (Hibbard) from Rexroad 3, Meade County, Kansas (3.8 Ma). G, H, Moderately worn; note low DT and *Mimomys* Kante. I, Well worn (and larger); note the prominent anteromedial alignment of the buccal face of the anteroconid complex and the wider confluence between basic triangles 1 and 2 than between 2 and 3—these characters are common but not universal. Symbols: MK = *Mimomys* Kante; AMF = anteromedial face of the buccal side of the anteroconid complex; ER = enamel ridge of Hibbard (= *Mimomys* Kante); C–C' = constriction between the cap and primary wings of the anteroconid complex; BRA3 = buccal reentrant 3; DT = dentine tract.

Ophiomys sp. cf. *O. taylori* (Hibbard), Tomida, 1987 (Duncan, AZ).

Ophiomys magilli Hibbard, 1972: 97–99, figs. 40, 41.

Ophiomys fricki Hibbard, 1972: 99–100, fig. 42.

Mimomys (Ophiomys) taylori (Hibbard), Conrad, 1980.

Mimomys (Ophiomys) taylori-parvus [informal designation], Repenning, 1987, to Repenning et al., 1995; Morgan and Morgan, 1995.

NOT: *Mimomys (Ophiomys) magilli* Hibbard, Repenning, 1987: 256 (incorrect identifications at

Panaca, Nevada, and at Buttonwillow and Kettleman Hills, California).

NOT: specimens referred by Hibbard (1956: 164–167, fig. 6) to *Pliophenacomys meadensis* from the Dixon fauna in the original description of the species; these were collected on the Dixon farm, Kingman County, Kansas, approximately 115 mi east of the type Sanders fauna.

TYPE SPECIMEN: UMMP 32019, a nearly complete left lower jaw with M1–2 and having the *Ophiomys parvus* dental morphotype.

TYPE POPULATION: Hibbard (1956: 187) lists only 3 m1s (including that in the type jaw) and 1 M3 but illustrates the occlusal pattern of 9 M3s and the buccal and occlusal view of an m1 not listed. I do not believe that he indicated the size of the type population.

TYPE LOCALITY: UMMP K2–53, Meade Formation, the Sanders fauna on Big Springs Ranch, Meade County, Kansas. Blancan IV age (3.02 to about 2.85 Ma). This is not a large fauna, but resembles the Sand Draw fauna, more strongly than indicated by Skinner and Hibbard (1972: table 21) when adjustments are made for the synonymy of two species from Sand Draw (“*Ophiomys magilli*” and “*O. fricki*”) with *Mimomys meadensis* here made and when the material from Dixon that Hibbard (1956) referred to this species is removed from *M. meadensis*.

REFERRED LOCALITIES: 1.—*Sand Draw fauna* (broad sense), *Brown County, Nebraska*,⁸ UMMP Nebr. 3–67 in Magill Draw, 4 mi NNW of Long Pine, NE, Blancan IV age by faunal interpretation only. This is the type locality of “*Ophiomys magilli*” of Hibbard (1972) and *Hibbardomys skinneri* Zakrzewski (1984). The locality also contained *Pliophenacomys primaevus*. Age is about 2.8 Ma by faunal interpretation (see below).

2.—*Sand Draw fauna* (broad sense), *Brown County, Nebraska*, UMMP Nebr. 2–68 along Plum Creek. This is the type and only locality of “*Ophiomys fricki*” of Hibbard (1972) and is 16 mi NW of Magill Draw. It also contained *Pliopotamys meadensis*, *Pliolemmus antiquus*, and *Pliophenacomys primaevus*.

3.—*Beck Ranch fauna*, *Scurry County, Texas*, MSU locality (no locality number published nor indicated with the specimens), Blancan IV age by faunal interpretation (associated with *Ogmodontomys poaphagus* and

Pliophenacomys sp., both advanced forms; Repenning, 1987: 257).

4.—*Sand Point fauna*, *Owyhee County, Idaho*, USGS 19128 (TMR), earliest Blancan IV and about 3.09 Ma, small exposure near river level on the south side of the Snake River opposite (south) of the village of Hammett. This is the type locality of *Pliophenacomys idahoensis* Hibbard (1959: 19–21).

There are two faunal horizons: in the lower part (normally polarized) and near the top of the exposure (reversely polarized). Neville et al. (1979) indicated that the Sand Point locality contains only reversely polarized deposits, but this was an error (C. Neville, personal commun., 1978). The reversed deposits, high at Sand Point, represent the Kaena event of the Gauss Chron and thus are about 3.09 Ma.

5.—*Taunton fauna*, *Adams County, Washington*. There are no other localities in southwestern Idaho (Glenns Ferry Formation) that appear to be the same age as the Sand Point fauna. However, both faunal and available paleomagnetic control of the Taunton fauna in south-central Washington (Ringold Formation; Morgan and Morgan, 1995; UW specimens) indicate that it is the same age as the Sand Point fauna (early Blancan IV age; ca. 3.09 Ma). Inclusion of the taxon designation “*Mimomys taylori-parvus*” in the Taunton faunal list by Morgan and Morgan (1995) was my error and followed Repenning (1987).

6.—*Flatiron Butte*, *Owyhee County, Idaho*, IMNH locality; younger than the Sand Point fauna (Neville, 1981) and geographically closer to Jackass Butte, this fauna contains a more advanced stage of the intermediate species *Mimomys meadensis*. Specimens from here are much higher crowned and have a higher DT on the buccal face of the ACC. The enamel pattern on the first lower molar more frequently matches that of *Ophiomys parvus*, lacks an islet, and has a much greater constriction of the confluence between the primary wings and the cap of the ACC (Conrad, 1980). Conrad, however, referred to it as *M. (Ophiomys) taylori*, as he followed Hibbard and Zakrzewski (1967), who only suggested that the Sand Point specimens might be referred to the subspecies

⁸ As described by Skinner and Hibbard (1972), the Sand Draw fauna contains at least 19 Blancan mammal localities as much as 17 mi apart within a filled paleo-valley and three named formations all marked by cut-and-fill deposition and having no age control except carefully documented superposition and biochronology; this entire group is called “Sand Draw fauna (broad sense)”. Specific localities are named separately in this report.

idahoensis but included them in *Ophiomys taylori*.

7.—*Other pre-Jackass Butte faunas of the Glens Ferry Formation.* There are four more published localities stratigraphically and geographically between the Flatiron Butte fauna and the faunas of Jackass Butte. Jackass Butte contains *Ophiomys parvus* (the descendant, as will be discussed). These other faunas contain transitional forms of *Mimomys meadensis* and are the Ninefoot Rapids (IMNH), Shoofly Creek (IMNH and UO), Poison Creek (IMNH), and Birch Creek (IMNH) faunas (Repenning et al., 1995: 59–62). Three are associated with an ash fall that is slightly younger than the Gauss Chron (<2.6 Ma) and are earliest Blancan V age, as they contain new immigrants.

8.—*Duncan fauna, Greenlee County, Arizona, UALP 7937, about 3.09 Ma.* Tomida (1987: 121) assigned three upper and three lower teeth from the Duncan fauna of southeastern Arizona to "*Ophiomys* sp. cf. *O. taylori*" but he found no m1. Without this tooth, the specimens cannot be assigned even to a morphotype. Of the two M3s collected, only one is illustrated and it is a good "*M. sawrockensis*" occlusal morphotype but with two roots, and, as such, it could be *M. taylori* or early (Sand Point age) *M. meadensis*.

Tomida's (1987: fig. 8) paleomagnetic control suggested that the position in the polarity stratigraphy is in the lower part of the Mammoth event of the Gauss Chron, but the Kaena event was recognized as a possibility. In view of this, Tomida's assignment, cf. *M. taylori* is just as reasonable as is cf. *M. meadensis* of the present report. My change is based on climatic considerations (discussed below) and the wide geographic distribution of *M. meadensis*, as contrasted with the very limited distribution of *M. taylori*. As such, correlation with the Kaena event is preferred.

Regardless of what species is represented in the Duncan fauna, it is, along with Beck Ranch, the southernmost record of the genus in North America, and it strongly suggests that *M. meadensis* dispersed across the Rocky Mountains to the Great Plains, for it is not known south of Idaho in the WFR but is the first record of a WFR lineage of *Mi-*

momys in the EFR. It is not of the *M. (Ogmodontomys)* lineage.

DIAGNOSIS: Diagnosis of intermediate and morphologically transitional forms, named or otherwise, is difficult because they include a series of morphologic gradations. The oldest forms (in this case those from Sand Point, Idaho, Taunton, Washington, and possibly Duncan, Arizona) are more like the ancestral form (*M. taylori* from Hagerman). The younger forms from later faunas (Flatiron Butte and earliest Blancan V faunas, Ninefoot Rapids, Poison Creek, and Birch Creek, all in the Glens Ferry Formation of Idaho, and "*O. fricki*" with "*O. magilli*" from the Sand Draw faunas of Nebraska and the type *Mimomys meadensis* from the Sanders fauna of Kansas) are much more like the descendant *Ophiomys parvus* from Jackass Butte, Idaho, and Dixon, Kansas. All morphotypes are included in the "transitional" species *M. meadensis* in the northern part of the WFR, but similar forms have been assigned to separate species in the EFR.

The persuading evidence is that both *Mimomys* and *Ophiomys* morphotypes are present in the poorly dated faunas of Kansas and Nebraska, as they are in the dated Idaho faunas from Flatiron Butte and Birch Creek of the Grand View faunal succession in Idaho (Repenning et al., 1995; Hibbard and Zakrzewski, 1967).

The gradational sequence of morphotypes included in the species *Mimomys meadensis* covers a time span of 0.7 Ma; the derived but morphologically stable species *Ophiomys parvus* covers, with almost no morphologic change, a time span of the next 0.8 Ma (the youngest dated record is in the Froman Ferry faunal succession of Idaho and is very close to 1.5 Ma; Repenning et al., 1995). By the time of Jackass Butte deposition, character stability of *Ophiomys parvus* had been reached.

First Lower Molar: Mimomys meadensis differs from earlier forms in having a higher DT on the buccal face of the ACC (compare *M. meadensis* on fig. 17.7B, D, F, with *M. sawrockensis-taylori*, *M. taylori*, and *Ophiomys parvus* on figs. 17.6H, I, 17.8). Hibbard and Zakrzewski (1967) noted that the primary wings (their T4 and T5) become more prominent in *M. meadensis* by constrict-

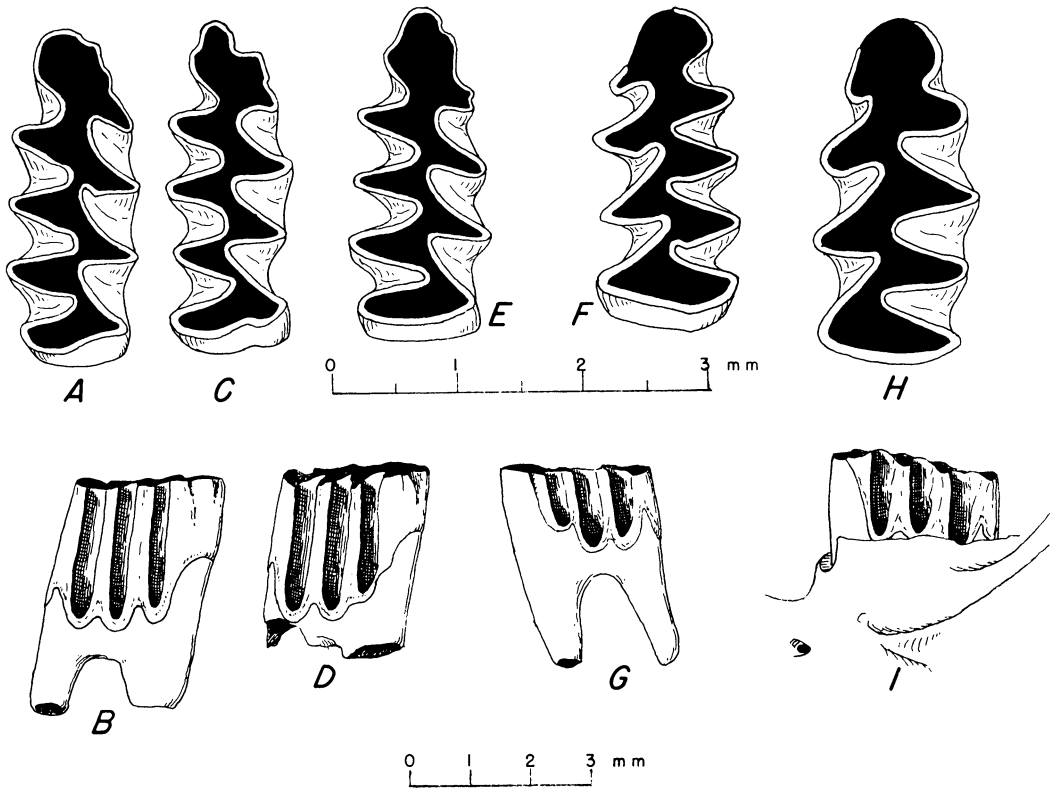


Fig. 17.8. *Ophiomys parvus*. See also figure 17.6H, I, which has the highest complete DT. A–G, All are from one locality near the base of Jackass Butte, Grand View, Idaho (about 2.3 Ma). H, I, UMMP 32053, drawn from cast and figured by Hibbard (1956: fig. 6–G) and referred to “*Pliophenacomys meadensis*” from the Dixon fauna, Kingman County, Kansas.

tion of their confluence with the cap of the ACC, and the MK is either reduced to what they call the “enamel ridge” or missing (compare fig. 17.7A, C, E with fig. 17.8). Some individuals nearly match the occlusal pattern of *Ophiomys parvus*, but retain a lower DT (fig. 17.7C, D and fig. 17.8). Hibbard and Zakrzewski (1967) gave a range of the length of the first lower molar at Sand Point of 2.4 to 2.7 mm. The available material from Taunton, Washington, is 2.39 to 2.81 mm.

Last Upper Molar: Only two roots are present (one known exception from Sand Point, Idaho: Hibbard, 1959: fig. 4I, a specimen with two anterior roots that are fused). Earlier forms retain an M3 occlusal pattern closer to that of *M. taylori* and the posterior loop, although shaped like an “inverted bell” [V] (for illustration, see Repenning et al., 1995:

fig. 8E and Hibbard, 1956: figs. A–K). Earlier forms also have a less prominent posterior extension than *O. parvus*. The M3 of “*Pliophenacomys meadensis*” (original designation by Hibbard, 1959) from the type locality (Sanders) shows a relatively strong similarity to the “inverted bell” that forms the posterior loop on the M3 of *Ophiomys parvus* (Hibbard, 1956: fig. 14B–E); the single M3 shown of “*Ophiomys magilli*” from Sand Draw (Hibbard, 1972: fig. 40L) is rather close, but has a smaller posterior extension.

The Schmelzmuster of specimens from the type locality (Sanders) is unknown, but is presumed to be similar to that of *Ophiomys parvus*, which is rather primitive (Koenigswald and Martin, 1984).

DISCUSSION: Hibbard and Zakrzewski (1967: 264, 267–268) discussed variation in

Mimomys from Sand Point, Idaho, where it varies in the direction of *Ophiomys parvus* (Wilson) from the 0.8 m.y. younger type locality on Jackass Butte. They mentioned the possible recognition of a separate taxon, the subspecies *O. taylori idahoensis*, because of this variation (which would preserve Hibbard's (1959) species name *Pliophenacomys idahoensis* for the same specimens). As younger faunas, closer in age and geography to Jackass Butte, were found, the gradation of *M. taylori* from Hagerman into Wilson's species from Jackass Butte became more obvious (Conrad, 1980: 139–142).

Later collecting in the Glenns Ferry Formation of Idaho by Conrad (1980) and by others (Repenning et al., 1995: 47–62) between Sand Point and Jackass Butte, coupled with paleomagnetic controls by Colleen Neville (Neville et al., 1979; Neville, 1981) and increased stratigraphic understanding, clearly show that the species gradation into *Ophiomys parvus* of Jackass Butte, suggested by Hibbard and Zakrzewski (1967), was real and continuous. Individual variations in single populations become increasingly similar to *O. parvus* in increasingly younger parts of the depositional sequence, closer to the stratigraphic zone of Jackass Butte. The actuality of a gradational "*M. (O.) taylori-parvus*" (or "*Ophiomys taylori idahoensis*") became indisputable as its progression of morphological gradation was documented.

Although Conrad (1980) called the Flatiron Butte material "*Mimomys (Ophiomys) taylori*" (in partial recognition of my declared affinity of the form from Hagerman to *Mimomys*), he noted that the DT on the buccal side of the ACC was quite high (it is approaching *Ophiomys parvus* in his figs. 12Q, R, and his fig. 13C shows the extreme development of that species from Jackass Butte). He also noted that the traces of the MK are totally missing as in *Ophiomys parvus*.

DISPERSAL TO THE EFR: When I called this transitional form "*Mimomys (Ophiomys) taylori-parvus*" (Repenning, 1987: 257), I did not realize that Hibbard (1957) had named it "*Pliophenacomys idahoensis*". The distinction between two-sided wings and three-sided triangles was never clear in Hibbard's reports, but I did not think that he would name

a form with only three triangles *Pliophenacomys*.

Pliophenacomys meadensis Hibbard (1956) from Kansas has three to five triangles, the same variation as *Pliophenacomys idahoensis* Hibbard (1959) in the WFR. That the gradation from Sand Point to Jackass Butte was the same as that which Hibbard (1956) had described from the Sanders fauna of Meade County, Kansas, revealed an unrecognized history of faunal dispersal between the WFR and the EFR, and that "*Mimomys (Ophiomys) taylori-parvus*" of Repenning (1987) had not only been named before, but four times before by Hibbard (1956, 1959, and as two species in Skinner and Hibbard, 1972). Its increasing height of the DT is a "foreign" character to the EFR, not present in the *Mimomys (Ogmodontomys)* character trends. *M. meadensis* brought the WFR evolutionary pattern to the EFR, a further reason for applying the same name to this transitional species in both regions.

The type material of *Mimomys meadensis* from the Sanders fauna of Kansas is older than the referred specimens from the Dixon fauna of Kansas. The topotypic hypodigm of *M. meadensis* (from Sanders) has a morphologic variability identical to that of the Idaho populations just discussed and here assigned to it, whereas the species from Dixon and later faunas of the Great Plains appears to be fixed in its dental morphology, as is *Ophiomys parvus* from Jackass Butte and younger Idaho faunas.

The topotypic *Mimomys meadensis* also resembles the contemporaneous "*Ophiomys magilli*" and "*Ophiomys fricki*" from Sand Draw faunas of Nebraska (found in separate localities at Sand Draw). The samples are too small to evaluate population characteristics, but the similarity with Idaho and Sanders specimens is strong. Hibbard specifically named the Sanders fauna (not Dixon) as the type locality, but he illustrated the occlusal pattern of the first lower molar of seven specimens from Dixon, and only two from Sanders. One illustrated tooth from Dixon (Hibbard, 1956: fig. 6F) was specifically excluded from the species at a later date (Hibbard and Zakrzewski, 1967: 262) and is apparently the species *Hibbardomys fayae* Zakrzewski

(1984), although the specimen is identified by a different catalog number.

The six remaining m1s from Dixon that were illustrated by Hibbard strongly resemble Wilson's *Ophiomys parvus* from Jackass Butte and lack the individual variability of the older Idaho faunas as well as of Sanders. Martin and Schultz (1985) noted the difficulty in evaluating Hibbard's species and called their Great Plains specimens from the Seneca fauna, Nebraska, *O. parvus* because it looked like that species. Others seized the single character of Hibbard and Zakrzewski (1967: 261) who said that *O. parvus* was apparently more advanced than *O. meadensis* in having higher DTs. Thus Barnosky (1985) concluded that his specimens from Boyle Ditch, Wyoming, at the crest of Yellowstone Pass, were *O. meadensis* because they had relatively lower DTs, but he was relying entirely on the written statement of Hibbard and Zakrzewski (1967). Barnosky (1985) did not mention DTs of *M. meadensis* described by Hibbard nearly 30 years earlier (1956) from Dixon and Sanders.

Of the type material from Sanders illustrated by Hibbard (1956) there were *two* m1, only *one* of which (the type specimen, UMMP 32019) had a *narrow* confluence between the primary wings and the cap of the ACC (dimension A-A' on fig. 17.6 herein), resembling the referred material from Dixon, but the *other* specimen from Sanders (UMMP 32016) had a *broad* confluence and greatly resembled the tooth from Sand Draw, Nebraska, (UMMP V59819) that Hibbard (1972: fig. 40) named "*Ophiomys magilli*" and also resembled the tooth from Sand Point, Idaho, that Hibbard (1959) named "*Pliophenacomys idahoensis*".

As no dentine tracts were shown, or mentioned, in Hibbard (1956), it is difficult to judge whether the tooth is closer in this character to Hagerman *Mimomys taylori* or Sand Point early *Mimomys meadensis*, but his figure of UMMP 32016 from Sanders shows that a black line indicating *either* the enamel margin of the occlusal surface, and its thickness, or the edge of the dentine where the enamel is missing, is *intentionally* drawn *thin* in the area of the anterobuccal side of the cap of the ACC. At this position on the occlusal surface of the illustrated teeth of

"*Ophiomys magilli*" from Sand Draw (UMMP V59819 and V57187), Skinner and Hibbard (1972) *illustrated* the DT cut by the occlusal surface, exactly where the enamel was drawn thin in the 1956 illustration. Thus the 1956 drawing of the topotype of "*Pliophenacomys*" *meadensis* (UMMP 32016) *suggests* that the DT of *Mimomys meadensis* is about as well developed as that on "*Ophiomys magilli*" from Sand Draw but does not approach the tract height of *Ophiomys parvus* from the WFR or from the Dixon fauna of Kansas.

Additionally, "*Ophiomys fricki*" from Sand Draw (UMMP V57288) shows that this species (*O. magilli* and *O. fricki*) varies in the confluence between the primary wings (triangles 4, 5) and the cap of the ACC; only *some* of the type population of *Mimomys meadensis* could be said to have five alternating triangles as does Sand Draw *Ophiomys fricki*, Jackass Butte *Ophiomys parvus*, and all Dixon specimens referred to *Pliophenacomys meadensis* in 1956. The very few others have a broad connection with the ACC cap and primary wings as in the Sand Point to Flatiron Butte specimens.

Hibbard (1956: fig. 6) shows that *all* of the six figured m1s from the Dixon fauna have five alternating salient angles, but gives little clue about DT height. Figure 17.8H, I of the present report shows a cast of UMMP 32053 from Dixon (drawn without its DT in Hibbard, 1956: fig. 6G); it has a rather low DT, but is in the range of *Ophiomys parvus*. It also is small.

A further problem when considering similarity of the species from the Sanders and Dixon faunas arises with age considerations. Both Sanders and Dixon faunas are rather small faunas, and they have only two taxa in common; one of them was "*Ophiomys*" *meadensis* (here rejected) and the other is the rather long-lived *Pliolemmus antiquus*. Dixon has the immigrant *Pliotomys rinker* (type locality), which first arrived from Beringia and Asia during the latest part of the Gauss Chron (Cita Canyon, Texas, about 15 ft below the end of the Gauss and inferred to be ca. 2.65 Ma); it has a younger record from Alaskan Beringia (ca. 2.4 Ma; Repenning et al., 1987). This genus spent most of its existence in the United States (ca. 0.54 m.y.)

during the reversed magnetic polarity of the early Matuyama Chron.

The Sanders fauna is older and does not have immigrant *Pliotomys*. From the paleomagnetic evidence shown by Lindsay et al. (1975: fig. 6), the entire section containing the Sanders fauna has normal polarity. The end of the Gauss is not recorded in even the 10 m of the paleomagnetic section above the fauna, nor is the Kaena reversed event of the Gauss.⁹

The presence in the Sanders fauna of both an *Ophiomys parvus* morphotype (UMMP 32019, the type, fig. 14M) and a *Mimomys taylori* (or "*Ophiomys magilli*") morphotype (UMMP 32016, the paratype, fig. 14L, both of Hibbard, 1956) indicates an intermediate population, transitional between *Mimomys* and *Ophiomys*. Although the Sanders sample is small, it is comparable in transitional morphology to that of Flatiron Butte, Idaho, and possibly approximates a midpoint age for the transitional species, about 2.8 Ma and during late Gauss Chron. This age agrees with the normal section at Sanders (Lindsay et al., 1975) and with the lack of similarity between the Sanders and the Dixon faunas.

The Sanders fauna and its approximately coeval faunas, Sand Draw and Broadwater (Nebraska), Bender and Deer Park (Kansas), Red Corral and Beck Ranch (Texas), and Duncan (Arizona), are older than the Dixon fauna and than the immigration of primitive bog lemmings *Pliotomys rinker* (to EFR) and *Mictomys vetus* (to WFR; Repenning, 1987; Repenning et al., 1995). Shortly before their arrival, the southern part of the WFR became very warm, and South American faunal elements invaded southeastern Arizona; however, they did not spread westward into the hot and dry areas of the WFR at this time. This was near the time of the Flat Tire faunas, 111 Ranch near Safford, Arizona (Galusha et al., 1984) and about 23 mi west of the Duncan record of *Mimomys*, which ap-

parently had crossed the Rocky Mountains (via Yellowstone Pass?) and spread southward to Texas under a wet and cool summer climate. It did not spread southward from Idaho into the heat of the southern WFR (Repenning, 2001).

The climate allowing cool-summer, wet-temperate *Mimomys* at Beck Ranch, Texas, and Duncan, Arizona, constricted as indicated by wet-tropical capybara (and other South American immigrants) 20 mi farther west near Safford, Arizona, and hot, arid southern WFR farther west in California. This may explain the inability of *M. meadensis* to disperse to the EFR through the southern WFR and around the southern end of the Rocky Mountains. The early muskrat, *Pliopotamys*, with its great indifference to climate, did, however, and is present with capybara near Safford, Arizona (Galusha et al., 1984), and appears slightly later on the Great Plains in the Sand Draw and Broadwater faunas of Nebraska. As near as can be judged, *Pliopotamys* appears at the same time and with capybara in the Elizabethtown 1 fauna of North Carolina (unpublished, Univ. North Carolina; Gerry Britt, personal commun., 1982).

Although clearly younger than the Sanders fauna, the age of the Dixon fauna, Kingman County, Kansas is not certain. The Dixon fauna has no paleomagnetic section, but the presence of *Pliotomys rinker* and *Ophiomys parvus* indicate that it is younger than 2.6 Ma.

Mimomys meadensis is emphatically excluded from the Dixon fauna, and those specimens are now identified as *Ophiomys parvus* (see below). *M. meadensis* includes "*Ophiomys magilli*" of Sand Draw, Nebraska, and Beck Ranch, Texas, "*O. fricki*" of Sand Draw, and the gradational forms between *M. taylori* and *O. parvus* of Idaho and Washington. The species *M. meadensis* has clear priority for the name of this transitional immigrant. It originated in the WFR and shortly dispersed down the Snake River to Washington and up the Snake River to Yellowstone Pass and the Great Plains between 3.0 and 2.8 Ma. This was in the initial stages of climate imbalance that produced the first extensive continental glaciation of North America that peaked around 2.3 Ma and collapsed before 2.2 Ma (Repenning, 2001).

⁹ Lindsay et al. (1975) show a brief reversed event above the Sanders fauna in their polarity section, but no reversed sample to defend it. Possibly this expresses their thought that the fauna lies beneath the Mammoth or Kaena reversed events of the Gauss Chron, but the Texas, Idaho, and Arizona records of immigrants argue against the fauna being this old, and no argument for the reversal shown at Sanders is made in their text.

BIOGEOGRAPHY AND BIOCHRONOLOGY: In the WFR, the Blancan III mammal age ends, and the Blancan IV age begins about 3 Ma with the extinction of the subgenus *Mimomys* (*Cosomys*) not yet discussed, and with the evolution of the transitional species *M. meadensis* out of *M. taylori* in the Snake River Plain of Idaho. Earlier (by 3.6 Ma, based on earliest record at Hagerman, Idaho) *M. taylori* dispersed southward from the Columbia River basin with diversion of the Snake River to that basin (ca. 4 Ma; bringing the muskrat *Pliopotamys* with it), and the muskrat dispersed northward from the Snake River Plain to the Columbia River basin (Taunton fauna, Washington, ca. 3.1 Ma; Morgan and Morgan, 1995; Repenning et al., 1995). *M. meadensis* dispersed to the Great Plains up the Snake River and through Yellowstone Pass as well at this time.

As well as dispersing up the Sacramento River and the old Snake River, to be diverted with it to the modern Snake River Plain and the Columbia River, the muskrat, *Pliopotamys*, also dispersed from the inland sea in central California around the southern end of the Rocky Mountains to southeast Arizona and the Great Plains. At about the same time, *Mimomys meadensis* dispersed through Yellowstone Pass to the Great Plains, and the two microtines met again in the Sand Draw faunas of Nebraska. Later (~2.4 Ma), *Pliopotamys meadensis* moved westward again, but through Yellowstone Pass and (as *Ondatra idahoensis*) down the Snake River to replace the native *P. minor* in the Snake River Plains; it passed *Ophiomys parvus* headed in the opposite direction in the pass (Barnosky, 1995; Repenning et al., 1995).

The most reasonable faunal change to define the beginning of Blancan III in the EFR thus is marked by the appearance of *Mimomys meadensis* and *Pliopotamys meadensis*, contemporaneous with the faunal transition in the WFR, about 3 Ma. There were no intercontinental immigrants at this time.

The prolonged time of buildup (~3.0 to 2.3 Ma) for the first (late Neogene) continental glaciation of the Northern Hemisphere thus involved at least three dispersal events between the WFR and the EFR and covers Blancan IV and part of Blancan V: (1) The extinction of *Mimomys* (*Cosomys*) *primus*

(discussed next) was coincident with or slightly before WFR *Mimomys meadensis* and *Pliopotamys meadensis* dispersed to the EFR (3.0 to 2.8 Ma, by different routes); this marks Blancan IV. (2) EFR *Pliophenacomys dixonensis*? dispersed to WFR (by Yellowstone Pass) and Eurasian *Mictomys vetus* dispersed to the WFR (by Pacific Coast route) and Eurasian *Pliotomys rinker* dispersed (by the East of Rockies Route—the first to do so) to the EFR from Beringia (~2.65 Ma); this marks Blancan V. (3) EFR *Pliopotamys meadensis* dispersed to the WFR and WFR *Ophiomys parvus* to the EFR (~2.4 Ma) early in Blancan V. By 2.3 Ma, glacial deposits were deposited in Iowa (Boellstorff, 1978), and no more dispersals are known until after this first major but very brief glaciation. However, at this same time, the lake level in the Snake River Plain rose as a result of greater precipitation and mountain glaciation in Yellowstone Park, headwaters of the Snake River.

SUBGENUS *MIMOMYS* (*COSOMYS*) WILSON (Western Faunal Region)

TYPE SPECIES: *Cosomys primus* Wilson, 1932, only species included.

DIAGNOSIS: *First Lower Molar:* Dentine tract on the buccal surface of the ACC is moderately high (fig. 17.4H); MK missing on about 10% of individuals; islet in the ACC missing in about 25% of individuals; length of first lower molar averages about 3.0 mm with very little variation (range for different sample localities at Hagerman about 2.8 to 3.1 mm). Cement is lacking in the reentrants, as in all North American forms derived from the first immigrant *Mimomys*. Unique Schmelzmuster (Koenigswald, 1980).

Last Upper Molar: Two roots only on more than 92%; posterior islet lacking (data based upon observation of over 400 M1s and 183 M3s by Zakrzewski, 1969: fig. 9, table 6).

DISCUSSION: A larger differentiate of the size-variable *Mimomys sawrockensis* in the WFR is known (by its single species) from about 3.7 to 3.0 Ma (at Hagerman, Idaho), after which it appears to have become extinct. Although its similarity to ancestral *Mi-*

momys sawrockensis is fairly obvious (see fig. 17.4A, B, G, H), there are no known intermediate populations.

As only one species is included, the subgenus *Cosomys* may not be needed, but it can be recognized as a separate lineage by the above diagnosis. I prefer to change existing nomenclature as little as possible; it does not affect the history of the other taxa included in *Mimomys*, and its recognition indicates that the included species are a North American evolutionary product and not a species of any Eurasian subgenus of *Mimomys*.

At least toward the end of its history (3 Ma) it ranged from the Mojave Desert of California to southern Idaho (see below). As has been noted, shortly after this time, climate became quite warm in the southern part of the WFR, and possibly its extinction was related to climate change. The sororal subgenus *Ogmodontomys*, which evolved from the EFR population of *Mimomys sawrockensis*, is not known to have dispersed westward toward WFR farther than the Verde (House Mountain) fauna of north-central Arizona (Czaplewski, 1990) and does not seem to have been a significant competitor; the smaller and more successful northern *M. taylori* may have competed. *Mimomys (Cosomys)* became extinct about 3 Ma, at the time when *Mimomys taylori* was changing, through *M. meadensis*, in the direction of the later widespread *Ophiomys parvus*, which survived at least until 1.5 Ma.

Mimomys (Cosomys) primus (Wilson)

Figure 17.4G, H

Cosomys primus Wilson, 1932; Hibbard, 1949, 1964; Zakrzewski, 1967, 1969; Repenning, 1980; Koenigswald, 1980; Koenigswald and Martin, 1984.

Mimomys primus (Wilson), Hinton, 1932; Hesse, 1934.

Mimomys (Cosomys) primus (Wilson), Wilson, 1934; Hibbard, 1957, 1959; Repenning, 1987; Repenning et al., 1990.

TYPE SPECIMEN: LACM(CIT) 500, a crushed skull with lower jaw.

TYPE POPULATION: Wilson (1932) mentioned only two other lower jaws. In the late 1970s the Natural History Museum of Los Angeles County (LACM) recollected the

type locality and obtained many more specimens. I have not seen these.

TYPE LOCALITY: CIT 131, Coso Mountains, 9.5 mi east of Olancha, Inyo County, California. Latest Blancan III age (3.0 Ma).

REFERRED LOCALITIES: 1.—*Buttonwillow locality, Kern County, California*, Blancan III age well core (Hesse, 1934).

2.—*Pecten Bed, Kettleman Hills, Kings County, California* (Repenning, 1987: 256, as "*M. (Ophiomys) magilli*", an error).¹⁰

3.—*Hagerman, Twin Falls County, Idaho* (Wilson, 1934; Zakrzewski, 1969), many localities, all Blancan III age.

DIAGNOSIS: As for the subgenus.

DISCUSSION: The Schmelzmuster of *Mimomys (Cosomys) primus* was described by Koenigswald (1980: 46) and found to differ from European *Mimomys polonicus*, a species in which cementum had developed. This difference led Koenigswald and Martin (1984) to believe that *Mimomys* had never been present in North America, as mentioned above under "North American Record of *Mimomys*".

Because they were unaware that the genus arrived here earlier and with simple, entirely radial Schmelzmuster, Koenigswald and Martin (1984) assumed that the European Schmelzmuster should be seen in North America. As it happened, North American species originated at a stage that had primitive Schmelzmuster, and then the enamel evolved independently, as it did in the two faunal regions of the United States, as discussed under the subgenus *M. (Ogmodontomys)*.

Although known from southern California to southwestern Idaho, it is only the Hagerman and Coso Mountain faunas in which the species is found in abundance. These localities are widely separated in the WFR and the species must be considered as having been well established, but apparently only in the former Sacramento River drainage basin, and around and southeast of the inland sea then

¹⁰ The *Pecten* bed in the upper part of the San Joaquin Formation of Kettleman Hills, California, has never been thoroughly collected for fossil rodents, except by hobbyists whose results are seldom disclosed. We owe our knowledge of this species from the Kettleman Hills to Mr. A.C. Hall and Mr. B. Williams, who collected and donated the single specimen in 1935 (UCMP 32952).

present in the Central Valley of California. It is not known from the Columbia River basin.

At Hagerman, *M. (Cosomys) primus* has a stratigraphic range that extends from the lower part of the section (late Gilbert Chron, a short stratigraphic distance above the Cochiti event) into the lower part of the Gauss Normal-polarity Chron, slightly higher than shown by Neville et al. (1979: fig. 10; it was found in the USNM Horse Quarry at Hagerman). But there are few opportunities at Hagerman for finding a fossil fauna above this horizon because depositional facies become more fluvial as the delta of the Snake River advanced northwest down the basin and because there are few exposures in this highest part of the Hagerman bluffs.

Mimomys (Cosomys) primus is present with, and lower in the Hagerman section than, the oldest record of *Mimomys taylori*—part of the reason for believing that *M. taylori* may have evolved in the Columbia River basin. It is present in the Hagerman section at least as high as the “Horse Quarry”, which is very near the top of the section.

The date of the Coso Mountain fauna appears to be 3.0 Ma (Bacon et al., 1979, and C.R. Bacon, personal commun., 1980). Despite repeated collection in younger, post-Hagerman parts of the Glens Ferry Formation in southwestern Idaho (the Sand Point locality and younger), no younger record of the species has been found. The species and subgenus likely became extinct around 3 Ma, and its absence is considered a characteristic of the Blancan IV microtine age (a slight revision of Repenning, 1987: 246). The species appears never to have dispersed to the EFR.

BIOGEOGRAPHY AND BIOCHRONOLOGY: By definition, *Mimomys (Cosomys) primus* is thus confined to the Blancan III mammal age in the WFR, the beginning of which is at the end of the Cochiti event (3.8 Ma) of the Gilbert Chron and the end of which is in the early part of the Gauss Chron, during the reversed Mammoth event, with the presumed extinction of *Mimomys (Cosomys) primus* in the WFR.

In the EFR (where *M. (Cosomys) primus* is not present), the end of Blancan III age is marked by Blancan IV immigration of *Mimomys meadensis* (3.0–2.8 Ma, to judge by

the Duncan fauna or the Sanders fauna) and the muskrat *Pliopotamys meadensis* (about the same time but possibly earlier because of its greater climate tolerance); both are found in several faunas of the Great Plains (discussed above).

The earliest species of *Hibbardomys* and/or the last of *M. (Ogmodontomys)* also occur near the end of Blancan III (Sand Draw faunas). The beginning of Blancan III in the EFR is placed at the end of the Cochiti event (3.8 Ma, just after the Rexroad 3 fauna of Kansas). Blancan III faunas of the EFR are marked by the co-occurrence of *Mimomys (Ogmodontomys) poaphagus* and *Pliophenacomys primaevus*, with no immigrants from the WFR.

SUBGENUS *MIMOMYS*
(*OGMODONTOMYS*) (HIBBARD)
(Eastern Faunal Region)

TYPE SPECIES: *Ogmodontomys poaphagus* Hibbard, 1941, KUMVP 4594.

INCLUDED SPECIES: Zakrzewski's (1967) subspecies are here elevated to species: *Mimomys (Ogmodontomys) transitionalis* (Zakrzewski) and *Mimomys (Ogmodontomys) poaphagus* (Hibbard).

DIAGNOSIS: *First Lower Molar:* Large, averaging about 3.0 mm in length (Zakrzewski, 1967: fig. 3), with only *slightly* more prominent DT on the buccal face of the ACC than in *M. sawrockensis* and not as prominent as in WFR lineages; lacks *Hibbardomys*-like conspicuous, narrow DT running far up the salient angle of a rudimentary buccal secondary wing (T6); rudimentary lingual secondary wing (T7) sometimes developed, but ACC usually a simple trefoil with small cap that is somewhat rectangular and lacks the conspicuous lingual curvature present in *M. (Cosomys) primus*; MK present in only some individuals; islet very shallow and worn off in most specimens; third lingual reentrant (behind the lingual primary wing) usually elongate transversely, passing buccally and anterior to the apex of the second buccal reentrant (approaching the normal condition of lingual reentrant 2 and never butting directly against it as in more primitive forms); dentine confluence between triangles 1 and 2 wider than that between 2 and 3, sometimes

conspicuously so and reminiscent of the lemming genus *Mictomys*.

Last Upper Molar: Persistently retains three roots (the anterior two fusing in latest forms, cf. Sand Draw), but no islet is ever present; occlusal pattern otherwise about as in *Mimomys sawrockensis*.

DISCUSSION: One or more of these features separate subgenus *Ogmodontomys* from previously discussed species and from *Ophiomys* and *Hibbardomys*. With moderate to great wear, there is a strong tendency for the anterobuccal face of the ACC to assume the form of a straight line directed anteromedially (fig. 17.7I: "AMF"); this feature appears, with less wear, in the younger *M. (Ogmodontomys) poaphagus*, but is a prominent character of both species. It is lost with the evolution of *Hibbardomys* because of the development of a (usually) short buccal secondary wing that breaks up the lineament and that has a remarkably high DT on its side.

Zakrzewski (1967) clearly pointed out the morphologic and temporal differences between the two taxa (my two species) from Fox Canyon and Rexroad 3, Kansas. The two species are clearly of successive age and have an ancestor-descendant relationship.

Mimomys (Ogmodontomys) is a large-sized derivative of *M. sawrockensis*, in the Great Plains of the EFR. There appears to have been little time represented between the Rexroad 3 record of *M. sawrockensis* and the oldest species of the subgenus *Ogmodontomys*, *M. (O.) transitionalis*, and possibly no more between the latter and the first *M. (O.) poaphagus*; evolution was rapid in the Great Plains, but distinct from that in the WFR in little development of the DT and retention of three roots on M3. The subgenus is known as far west as north-central Arizona; only rarely is the genus found south of the latitude of the Rocky Mountains. Thus Beck Ranch (Texas), Duncan and Verde (Arizona) must represent faunas of cooler and more humid summers.

As a subgenus, *Ogmodontomys* persisted throughout much of the Great Plains from at least 4.2 Ma (Verde fauna, Arizona, and probably Fox Canyon fauna, Kansas) until at least 3 Ma (Sand Draw and Broadwater, Nebraska, and possibly the Deer Park fauna,

Kansas). The lineage appears to have outlived the subgenus, and Zakrzewski (1984) put the younger forms in the new genus *Hibbardomys*, which survived at least until the end of Blancan time (ca. 1.9 Ma in the EFR), but evolved beyond the diagnostic limits of *Mimomys*.

Mimomys (Ogmodontomys) transitionalis
Zakrzewski

Figure 17.4E, F

Ogmodontomys poaphagus Hibbard, 1950.

Ogmodontomys poaphagus transitionalis Zakrzewski, 1967.

Mimomys (Ogmodontomys) poaphagus Repenning, 1987; Czaplewski, 1990.

TYPE SPECIMEN: UMMP 28234; palate with right tooth row.

TYPE POPULATION: Large, including 104 isolated teeth, 90 lower jaws, and 75 isolated M3s; listed by Zakrzewski (1967: 140).

TYPE LOCALITY: UMMP U-K1-47, Fox Canyon, Meade County, Kansas. Earliest Blancan II age, more than 4.2 Ma.

REFERRED LOCALITIES: 1.—*Lisco fauna, Garden County, Nebraska*. Although often listed as being essentially the same, the Broadwater and Lisco faunas are about 14 mi apart in different counties, have a different lithology, and appear to be different in age—the Broadwater fauna being, possibly, both Blancan III and IV and the Lisco fauna being Blancan II. To my recollection, the rodents of both localities are largely undescribed and I am not even aware of a list of forms from Lisco, although several lists have been published for Broadwater (see Repenning, 1987: 258).

In the mid-1980s the National Museum of Natural History (USNM) sent a crew to Lisco to excavate a camel for exhibition and in the process they collected a number of specimens that I called *Ogmodontomys poaphagus* at that time, but that have all the characters of Zakrzewski's species *Mimomys (Ogmodontomys) transitionalis*, to which they are here assigned. There may be other records in the Great Plains assigned to *M. (O.) poaphagus* that might be recognized as this species on closer examination.

2.—*Verde fauna, Yavapai County, Arizona*, earliest Blancan II (4.2+ Ma) by paleo-

magnetic stratigraphy (just below the Nuni-vak event of the Gilbert Chron). Czaplowski's (1990) specimens from the Verde fauna (MNA locality 319) were assigned to *Mimomys* (*Ogmodontomys*) *poaphagus* (which is correct following Zakrzewski, 1967). The morphology of these specimens indicates that the fossils belong to *O. transitionalis*.

The Verde specimens are too few and too incomplete to evaluate population variability, but three characters that they show suggest that Czaplowski's specimens are *M. (O.) transitionalis* in the usage of this report. Comparison of Fox Canyon occlusal patterns of Hibbard (1950: fig. 17M; also fig. 17.4E, F of this report) with those of Rexroad 3 of Hibbard (1941: pl. 3:7 or 12; also fig. 17.7G–I of this report) suggests that although Verde specimen V4871 is badly worn, it shows lingual reentrant 3 extending farther buccal relative to the apex of buccal reentrant 2 and little difference in dentine confluence between triangle 1 and 2 and between triangle 2 and 3. Fragmentary V4872, less worn, shows a strong MK, and this structure also seems more common in the Fox Canyon species than the one at Rexroad 3.

DIAGNOSIS: *First Lower Molar* (fig. 17.4E, F): DT on the buccal face of the ACC very low and hardly different from the condition in *Mimomys sawrockensis*; enamel islet present only in specimens with very little wear (islet very shallow); MK present (usually with a prism fold distal to it) in most specimens; cap rounded with very little lingual curvature and no sign of developing secondary wings (T6 and T7); lingual reentrant 3 usually extending buccally beyond apex of buccal reentrant 2 and usually hooked anteriorly, even in some well-worn teeth; dentine confluence between triangles 1 and 2 occasionally slightly wider than between 2 and 3.

Last Upper Molar: Three roots persistent, but posterior enamel islet lacking.

Schmelzmuster for *Mimomys* (*Ogmodontomys*) *transitionalis* is unknown. *M. sawrockensis* has only simple radial enamel (specimen from Alturas, California; W. von Koenigswald, personal commun., 1991) but is complex in specimens from Panaca, Nevada (Mou, 1998). As discussed before, the Schmelzmuster of the Panaca material suggests that the history is more complicated

than here understood. *Mimomys* (*Ogmodontomys*) *poaphagus* (from the younger Rexroad 3 fauna) has a surprisingly simple pattern as well, with only primitive (poorly formed) tangential enamel on the outer edge of the posterior face of the lower triangles, strangely doubled into two layers on the buccal side (Koenigswald, 1980: 48–49).

DISCUSSION: The evolution of *Mimomys* (*Ogmodontomys*) *transitionalis* of the Fox Canyon fauna (4.2+ Ma) from *Mimomys sawrockensis* of the Saw Rock Canyon fauna¹¹ and into *M. (O.) poaphagus* of younger faunas of the Rexroad Formation of Kansas (3.8–3.9 Ma, as will be discussed) and the Sand Draw fauna of Nebraska (ca. 2.8–3.0 Ma), and the association of *M. (O.) poaphagus* in the Sand Draw fauna with the derived genus *Hibbardomys* (discussed below) is a record of progressive evolution that nearly equals in detail that in the WFR of *Mimomys sawrockensis* to *Ophiomys parvus*. The records from the EFR are not in stratigraphically successive faunas, however.

BIOGEOGRAPHY AND BIOCHRONOLOGY: *Mimomys* (*Ogmodontomys*) *transitionalis*, from central Arizona, Kansas, and Nebraska, is a derivative of *Mimomys sawrockensis* in the EFR and the obvious source of *Mimomys* (*Ogmodontomys*) *poaphagus* from the younger Rexroad 3 fauna of the Rexroad Formation in Kansas (Zakrzewski, 1967). To judge from the Verde record in Arizona, closely controlled by a paleomagnetic section and permissively in agreement with the polarity reported from Fox Canyon, Kansas (the type locality; Lindsay et al., 1975), the species *Mimomys* (*Ogmodontomys*) *transitionalis* had evolved before the beginning of the Nuni-vak event of the Gilbert Chron (>4.2 Ma). This is not much younger than the supposed age of the Saw Rock Canyon fauna containing the ancestral form, and speaks for rapid evolution in the Great Plains with advancement of characters seen in *Mimomys sawrockensis* at its type locality; these are different characters than those that evolved in

¹¹ There is no age control for the Saw Rock Canyon fauna, but it is assumed to be near that of the dated records in WFR (4.8–4.3+ Ma), which is in agreement with the history of the fossil moles given by Voorhies (1977) and with the age of the Verde fauna of Arizona containing *M. (O.) transitionalis*.

the WFR. *Mimomys (O.) transitionalis* thus marks the beginning of Blancan II mammal age and *Mimomys (O.) poaphagus*, from Rexroad 3, Kansas, marks the end of the same mammal age, as will be discussed.

There is no prominent evolutionary change in *Mimomys* in the WFR to mark the beginning of Blancan II, and it is there marked by a meager record of the first immigration of the ondatrine *Pliopotamys* from Eurasia (Repenning et al., 1995: 67, as *Dolomys*). The earliest appearance of *Pliopotamys* coincides, paleomagnetically, with the Verde record of *M. (O.) transitionalis*. As discussed, the end of Blancan II in the WFR is marked by the dispersal of both *M. (Cosomys) primus* and *Pliopotamys* to southwestern Idaho with the redirection of the Snake River to the Columbia River system.

Mimomys (Ogmodontomys) poaphagus
(Hibbard)

Figure 17.7G, H, I

Ogmodontomys poaphagus Hibbard, 1941 to 1972.

Ogmodontomys poaphagus poaphagus Zakrzewski, 1967.

Mimomys (Ogmodontomys) poaphagus Repenning, 1987.

NOT: *Ogmodontomys* sp. Eshelman, 1975.

TYPE SPECIMEN: KUMVP no. 4594; upper dentition of one individual.

TYPE POPULATION: Large; Hibbard listed 24 cataloged specimens in the type description (University of Kansas collection) and Zakrzewski (1967) listed 318 m1s and more than 149 M3s (University of Michigan specimens).

TYPE LOCALITY: Kansas University (KU) locality 3, Rexroad Formation, Rexroad Ranch, Meade County, Kansas (often called "Rexroad 3"). Late Blancan II age (but see following discussion).

REFERRED LOCALITIES: 1.—*Rexroad Formation, Meade County Kansas*. Zakrzewski (1967) listed nine more localities in the Rexroad Formation of Meade County, Kansas.

2.—*Sand Draw faunas, Brown County, Nebraska* (Zakrzewski, 1967; Skinner and Hibbard, 1972). These localities cluster around the area of the Sand Draw quarry, and are likely close to the same age. If so,

they appear to be younger than 3.0 Ma, probably around 2.8 Ma on the basis of the stage of evolution of associated *Mimomys meadensis*, as has been discussed. However, little published information has been directed toward establishing a faunal sequence out of the several localities included in Sand Draw faunas. However, great detail has been published regarding the stratigraphic relationships of the units (Skinner and Hibbard, 1972).

3.—*Broadwater, Morrill County, Nebraska*. The species was questionably reported from here (Schultz and Stout, 1948; Skinner and Hibbard, 1972), but the presence of *Mimomys meadensis* and *Pliopotamys meadensis* (already discussed) indicates a younger age than Rexroad 3; the material could be a species of *Hibbardomys* and I have not examined it. This is significantly younger than the nearby Lisco Fauna, as has been noted.

4.—*Deer Park, Meade County State Park, Kansas*, an ancient spring deposit, probably with mixed fauna (Hibbard, 1956; Zakrzewski, 1967).

DIAGNOSIS: *First Lower Molar*: The DT on the buccal face of the ACC is slightly higher than in *M. (O.) transitionalis*. Due to a postero-lateral projection of the buccal primary wing and an anterolingual enlargement of the rather narrow cap of the ACC, the buccal face of the ACC has, in occlusal view, a decided anteromedial alignment and elongation that is very evident on worn teeth (fig. 17.7I, "AMF") and can be seen on little-worn teeth despite the irregularities of its outline created by the MK (fig. 17.7G). The MK is present (but not evident in well-worn specimens); the islet is present only in extremely little-worn individuals; there is a suggestion on several little-worn teeth of an incipient buccal secondary wing; triangles 1 and 2 are usually broadly confluent but 2 and 3 are separated; and the tendency for lingual reentrant 3 to extend buccally beyond the apex of buccal reentrant 2 and to hook forward, noted in *M. (O.) transitionalis* (fig. 17.4E) is much less obvious in *M. (O.) poaphagus*. Zakrzewski (1967: 144) noted that *M. (O.) poaphagus* is slightly larger than the older species.

Last Upper Molar: Retains three roots and a simple occlusal pattern without islet except

in latest forms (Sand Draw fauna, Nebraska) in which Hibbard (1972: 97) noted that the two anterior roots are well fused, an advanced trend that began 2 Ma earlier in the WFR.

Schmelzmuster from Rexroad 3, described by Koenigswald (1980), was discussed above under *M. (O.) transitionalis*. It is not complicated, but has a rather unusual double layer of tangential enamel on the posterior faces of buccal triangles.

DISCUSSION: The two species *Mimomys (Ogmodontomys) transitionalis* and *M. (O.) poaphagus* are quite similar, and possibly the anterolabial and elongate face of the ACC is the quickest way to distinguish the two, but I have not seen a large sample from Fox Canyon or Rexroad 3.

An incipient angle on the buccal side of the cap of the ACC (fig. 17.7G, weak and unlabeled), evident in little-worn m1s and suggesting a rudimentary buccal secondary wing, seems possibly significant in consideration of the ancestry of *Hibbardomys* (discussed below). The presence of a buccal secondary wing that has a very elongate DT, in all illustrated cases extending to the occlusal surface (Zakrzewski, 1984), is characteristic of *Hibbardomys*. The earliest species, *Hibbardomys skinneri*, occurs in the Sand Draw fauna with *M. (O.) poaphagus* (although not at the same locality), but does occur at the same locality as the "magilli" morphotype of *M. meadensis*.

BIOGEOGRAPHY AND BIOCHRONOLOGY: Lindsay et al. (1975) showed four paleomagnetic sites in the $65 \pm$ foot stratigraphic span from the Bender fauna to "Rexroad 3" and "Rexroad 2A" localities on Rexroad Ranch, Kansas, but there are about 30 ft of unexposed strata between Bender and Rexroad 3 with no polarity control, which they assumed is all normally polarized and in stratigraphic continuity. Because they inferred continuous normal polarity over this unknown half of the section, they suggested that the section probably represents part of the Gauss Normal-polarity Chron, but biochronologic considerations suggest that the Cochiti event is more likely represented in the lower part of their section containing the Rexroad 3 fauna; the Gauss may well be represented in the upper part of their paleomagnetic section con-

taining the Bender fauna (which would make the Bender fauna Blancan III or younger).¹²

Mimomys (O.) poaphagus is undoubtedly the descendant of *M. (O.) transitionalis*, as Zakrzewski (1967) has pointed out. It also seems likely, as indicated in the Sand Draw fauna of Nebraska, that *M. (O.) poaphagus* is the ancestor of the genus *Hibbardomys* in later faunas, developing about 2.8 to 3.0 Ma just before *M. (O.) poaphagus* became extinct. Hibbard (1972) notes that in the Sand Draw fauna, *M. (O.) poaphagus* at last fuses the two anterior roots of M3 perhaps 700,000 years later than was done in the WFR. Rexroad 3 likely represents the latest Blancan II fauna of the Great Plains and is, possibly, only 300,000 years younger than the Fox Canyon fauna, again indicating rapid evolution of this subgenus in the Great Plains.

NORTH AMERICAN DERIVATIVES OF *MIMOMYS*

With the development of additional characters exceeding the diagnosis of *Mimomys*, forms that must be considered new genera developed in both the EFR and the WFR. Additional characters include having more than the three basic triangles and increasing DT development; in the WFR, loss of the MK is also included; in the EFR, DT breaks the low development characteristic of *Mimomys (Ogmodontomys)*. The new forms have been named *Ophiomys* Hibbard and Zakrzewski (1967), and *Hibbardomys* Zakrzewski (1984).

Hibbardomys appeared earlier and was confined to the EFR. Its oldest record is in the Sand Draw faunas, at the Magill Draw locality (UMMP Nebr. 3-67; ca. 2.8 Ma). None are known to be younger than about 2 Ma and all are of Blancan IV or V age. The principal characters of *Hibbardomys* are more than three triangles and a prominent

¹² Lindsay et al. (1975) inferred that the reversed deposits of Fox Canyon represent the last part of the Gilbert Chron (near the Cochiti event, forcing the correlation of the normal polarity of Rexroad 3 with lower Gauss Chron), but other evidence (Verde fauna) suggests that Fox Canyon was below the Nunivak event of the Gilbert (4.2+ Ma). The slight change between Fox Canyon *M. (O.) transitionalis* and Rexroad 3 *M. (O.) poaphagus* argues strongly against nearly a million years difference in age.

and narrow DT running well up the buccal secondary wing. This new and extended dentine tract ended the prolonged trend of little DT elongation in *Mimomys* (*Ogmodontomys*).

Zakrzewski (1984) named four species that are confined to localities in Kansas and Nebraska (one m1, MSU 9444, may represent the genus in Beck Ranch, Texas) and show no recognizable evolutionary trends but extreme morphologic differences. One species has been named from the Irvingtonian age Java fauna, South Dakota (R. Martin, 1989), but seems abraded and likely represents a species of *Phenacomys*.

The transition from *Mimomys taylori* into *Ophiomys parvus* (figs. 17.8, 17.6H, I) in the WFR has been discussed at length under *Mimomys meadensis*; this transition took about 400,000 years, and, near the beginning of the transition (~2.8 Ma), *M. meadensis* dispersed to the Great Plains, where it is known from Arizona, Texas, Kansas, and Nebraska. After the transition was completed (~2.4 Ma), *Ophiomys parvus* dispersed to the Great Plains. Because climate became more favorable, *O. parvus* was much more widely distributed in the WFR and has been found from southern Idaho, central Utah (Repenning, 1987: 264 as *Mimomys* (*Ophiomys*) *meadensis*), and southernmost California (Repenning et al., 1995: 30), but is not known so far south on the Great Plains. It has been recognized by only the single species, which survived in post-Blancan faunas at least until about 1.5 Ma (Repenning et al., 1995).

Following the development of *Ophiomys parvus* and the four species of *Hibbardomys*, the second invasion of the genus *Mimomys* from Eurasia took place. This was a dispersal down the eastern side of the Rocky Mountains to the Great Plains, as the route down the Pacific Coast became restricted, and often closed, at least by 2.65 Ma. It seems to have become permanently closed after about 1.6 Ma. Much later this new immigrant crossed the Rocky Mountains and occurs in the WFR, as well as eastward in the Appalachian Mountains.

The new immigrant *Mimomys* had two outstanding features that had evolved in Eurasia but not in North America: cement on the

cheek teeth and a "European"-type Schmelzmuster.

SUBGENUS *MIMOMYS* (*CROMEROMYS*) (ZAZHIGIN)

(EFR, but dispersed to WFR)

?*Mimomys* (*Pusillomimus*) Rabeder, 1981 [in part].

TYPE SPECIES: *Cromeromys irtyshevskensis* Zazhigin, 1980: 108; Geological Institute, Russian Academy of Sciences (then "Soviet") No. 950/5, a little-worn right m1.

INCLUDED SPECIES: In North America only *M. (C.) virginianus* Repenning and Grady and *M. (C.) dakotaensis* R. Martin.

DIAGNOSIS: *First Lower Molar*: Subgenus of *Mimomys* with cement present in the reentrant valleys, enamel islet lost and MK usually present but sometimes shifting forward to a point in the middle of buccal reentrant 3 (anterior to its usual position on the anterior face of the buccal primary wing) or farther anterior. Well-developed DTs present on the buccal and lingual angles of the posterior loop, as in the subgenus *Phenacomys* (*Phenacomys*), and on the buccal-anterior face of the cap of the ACC. These break the continuity of the enamel pattern of the occlusal surface at almost all stages of wear. A low tract is sometimes present on the MK.

Last Upper Molar: M3 of *Mimomys* (*Cromeromys*) is like that of *M. sawrockensis* except that it has cement, a DT on the posterior surface of the posterior loop, and only two roots (although the anterior one may be seen as two fused roots on some specimens).

DISCUSSION: The most striking hallmark of *Mimomys* (*Cromeromys*) in the microtine fauna of the United States is its possession of cement in the reentrant angles. Until this time (about 1.3 Ma) there was no cement in any species of North American *Mimomys* or its two derived genera just mentioned. Equally striking is the appearance of a European "Mimomys type" Schmelzmuster, as reported by R. Martin (1989: 443); all prior North American species (except earliest *M. sawrockensis*) had "non-*Mimomys* type" Schmelzmuster, as far as has been determined.

Also striking, when one considers these new occurrences, is the abrupt return of a

“typical” *Mimomys* occlusal enamel pattern on m1, including a strong MK and only the three basic triangles, this at about the time of the last record of *Ophiomys parvus* (with five alternating triangles) in the WFR and perhaps 600,000 years after the last record of *Hibbardomys voorhiesi* (with as many as seven alternating triangles) in the EFR. These species had completely lost the MK in the evolution of their ACC.

This departure from the 3.5 Ma North American history of *Mimomys*, coupled with west Beringian records of an older species (*M. (C.) irtyshensis*) similar to these new species of the United States (Sher et al., 1979) and records of *M. (Cromeromys)* cf. *M. (C.) virginianus* from younger deposits in east Beringia (Old Crow basin, Yukon Territory, Morlan, personal commun., 1991; Cape Deceit, Alaska, see below) requires the interpretation of a second invasion of North America by the genus *Mimomys* at a stage of evolution reflecting that of this genus in Eurasia.

Cromeromys is a subgenus of *Mimomys* derived from the subgenus *M. (Mimomys)* in Eurasia by the relatively early loss of some dental characters (the islet on m1 and lack of cement). In addition, the subgenus appears to have acquired a tolerance for higher-latitude climate, and its known records in the United States are from mountain areas with the exception of the Java fauna and north of there (Beringian FR). In Eurasia, the subgenus is most common from England to Poland and from the Siberian Beringian FR (Kolyma drainage basin; Sher et al., 1979). Its earliest record in the United States (Java fauna) is Irvingtonian.

Zazhigin (1980: 109) divided *Cromeromys* into two groups based upon size: the *intermedius* group has an m1 from 2.7 to 3.5 mm long and the *newtoni* group has an m1 from 2.3 to 2.9 mm long. Based on this, the U.S. species seem to belong in the “*newtoni*” group (m1 about 2.2 mm to 2.76 mm long), but the scanty record so far published in the United States suggests a progressive reduction in size.

Mimomys (Cromeromys) dakotaensis

R. Martin

Mimomys dakotaensis R. Martin, 1989.

TYPE SPECIMEN: SDSM 12920, little worn

left m1 with posterior part of the posterior loop broken off.

TYPE POPULATION: The not-quite-complete type, a second m1 listed (SDSM 12925), and possibly one M3, although the illustration (Martin’s fig. 5B) does not quite look like this tooth (it is incomplete).

TYPE LOCALITY: Java fauna, Walworth County, South Dakota. The fauna has no external evidence of age, but on weak biochronologic reasoning it was estimated at about 1.3 Ma (Repenning et al., 1995: 15, 32, revised). It is now suspected that the fauna is probably about as old as Sappa fauna, Nebraska, but has reworked older fossils in it. The Sappa fauna is 6 ft below a 1.2 Ma ash. The species is known with certainty only from the type material and locality, which is conceivably in glacial outwash.

DIAGNOSIS: *First Lower Molar*: A species of *Mimomys (Cromeromys)* with about the same amount of cement deposited in the re-entrant angles of the cheek teeth as *M. (C.) irtyshensis* from the Siberian part of the Beringian FR, but somewhat smaller. The species has less cement deposition and appears ($N = 1$) larger than *M. (C.) virginianus*. R. Martin (1989) indicated that an additional narrow DT runs up the MK to the occlusal surface, and shows it in his buccal view, but not in the occlusal view (his fig. 5A); the tooth is broken and the possibility that the “tract” on this single specimen might have resulted from postmortem abrasion cannot be evaluated.

The very limited sample from the Java fauna suggests that it is intermediate in size and possibly in amount of cement deposition between *M. (C.) irtyshensis* of the late Pliocene (ca. 2.6 Ma) of Siberian Russia (Zazhigin, 1980: fig. 23) and *M. (C.) virginianus* of the early Irvingtonian II (estimated ca. 0.84 Ma) of West Virginia (Repenning and Grady, 1988: fig. 1). The length of the holotype m1 is 2.76 mm. The Schmelzmuster was indicated by Martin (1989: 444) as typical of European species of *Mimomys*.

DISCUSSION: Although Martin (1989) was aware of *Mimomys (Cromeromys) irtyshensis* from Yakutia and of *M. (C.) virginianus* from West Virginia, and discussed them in describing *M. (C.) dakotaensis*, he did not note that his species was not only intermediate in

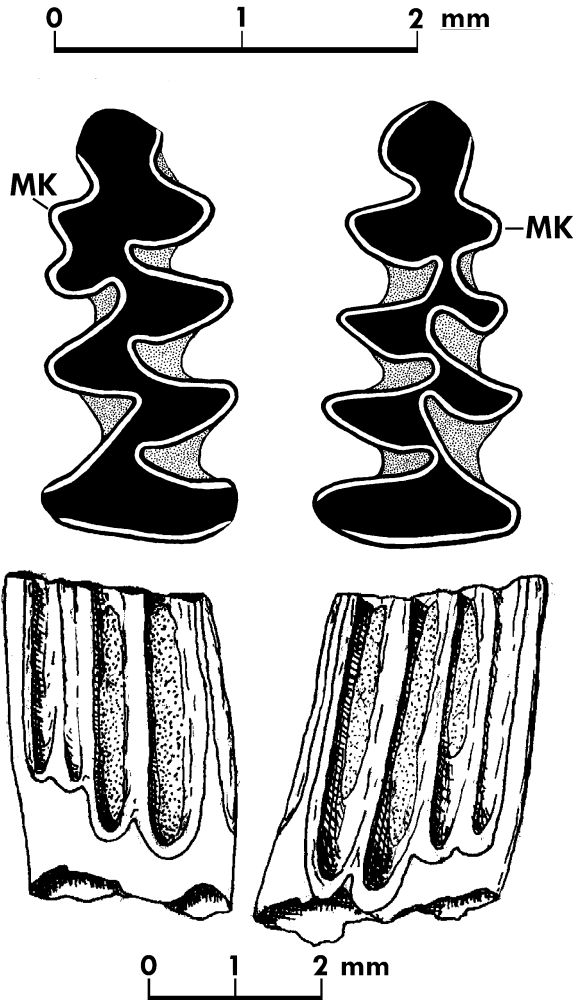


Fig. 17.9. *Mimomys (Cromeromys) virginianus*. Left and right first lower molars from Mark's Sink, Velvet Room, Porcupine Cave, Park County, Colorado; DMNH specimens. This rather abundant material is from talus filling a depression in the floor of the Velvet Room and has no stratigraphic context, but incorporates material of different ages (see text). The specimen on the right is aberrant in that the buccal primary wing is closed, forming a strange fourth "triangle" and the MK is enlarged so that it appears to be a buccal secondary wing.

time, but also in some characters. A North American trend in increasing cement deposition and decreasing size is possible.

Mimomys (Cromeromys) virginianus
Repenning and Grady

Repenning and Grady, 1988: fig. 1;

Figure 17.9 of this report

Mimomys (Cromeromys) virginianus Repenning and Grady, 1988.

Mimomys (Cromeromys) sp., Morlan (personal commun., 1991).

Clethrionomys sp., Guilday, 1971 (cited by several authors).

TYPE SPECIMEN: USNM 264308, a little-worn right m1.

TYPE POPULATION: 3 m1s, 2 M3s. More specimens from the type locality exist in the USNM, of which I was not aware in 1988, and I have not seen them.

TYPE LOCALITY: Cheetah Room of Hamilton Cave, Pendleton County, West Virginia (elevation 2,000 ft), EFR. Earliest Irvingtonian II age estimated ca. 0.84 Ma on biochronologic grounds (Repenning, 1992: table 1).

REFERRED LOCALITIES: Although not yet studied and of uncertain age, specimens of *M. (Cromeromys) virginianus* are being discovered rapidly. Mostly unpublished records are:

1.—*Localities CRH47 and CRH44 from the Old Crow basin, Yukon Territory, Canada*, 68°16' north latitude (ca. 160 mi north of the Arctic Circle) in easternmost Beringian FR. These records are described in a manuscript by Richard E. Morlan that was sent to me in essentially final form in 1991 but has not yet been published. Probably 0.95–1.0 Ma on fauna and paleomagnetic evidence (Repenning and Brouwers, 1992, updated); the history of the species in eastern Beringia is not well known.

2.—*Porcupine Cave, Park County, Colorado*, elevation 9,514 ft, at the western edge of the EFR. Records in several rooms of the cave are of different ages. Figure 17.9 illustrates two specimens from “Mark’s Sink” in the Velvet Room of the cave, one of very unusual form. This locality, a talus deposit, produced a mixed fauna that appears to represent at least two distinct ages. The older material appears, on biochronologic grounds, to be between 1.3 and 1.2 Ma and has *Ondatra idahoensis-annectens*, *Mictomys vetus*, *Mictomys vetus-kansasensis*, *Pliolemmus antiquus*, and *Phenacomys gryci*. The younger material appears to be less than 0.85 Ma and has *Mimomys (Cromeromys) virginianus*, *Terricola meadensis*, and *Lemmiscus curtatus* of the modern morphotype; these are not discrete faunas but are mixed. The *M. (C.) virginianus* specimens are more hypsodont (and so seem to be somewhat younger) than the type material from the Cheetah Room fauna, and *Terricola meadensis* appears to have immigrated to the USA about 850,000 years ago. Also present, presumably in the younger specimens but not yet assignable to the younger or older groups, are *Phenacomys intermedius*, *Microtus* cf. *M. californicus*, and *Allophaiomys* cf. *A. pliocenicus*, all DMNH specimens.

3.—*Little Dell Dam, Salt Lake County, Utah*, 12 mi east of Salt Lake City, elevation 5,800 ft. Probably less than 1 Ma on associated fauna, WFR. Collected by the Utah Geological Survey and to be placed in the University of Utah Museum of Natural History (Gillette et al., 1999).

4.—*Cathedral Cave, White Pine County, Nevada*, elevation 6,400 ft. Less than 0.85 Ma on associated fauna. Still under study at this time but discussed by Bell (1993, 1995) and Bell and Barnosky (2000). Collected by the NAU Quaternary Studies Program and in their collection.

5.—*Cape Deceit, Alaska*, University of Alaska State Museum specimen. A single undescribed m1 was found in the Cape Deceit section, but is not published. The section at Cape Deceit is fairly long and there appears to be no record of where in the section the specimen was found. The section is of normal polarity (Brigham-Grette and Hopkins, 1991) and considering the fauna, the best guess at present is that it represents the Jaramillo event of the Matuyama Chron.

DIAGNOSIS: *Mimomys (Cromeromys) virginianus* apparently differs from *M. (C.) dakotaensis* in being smaller. It has been said that the reentrants of *M. (C.) virginianus* are more completely filled with cement than is the case with the older species. The Schmelzmuster is unknown in those populations assigned to *M. (C.) virginianus*.

DISCUSSION: *Mimomys (Cromeromys) irtyshensis* of Siberia (Zazhigin, 1980: 109–111) is larger than the size given for *M. (C.) dakotaensis*, but this is a questionable character in view of the very small sample available for *M. (C.) dakotaensis*, and the inadequate size of the type population of *M. (C.) virginianus* available to me at the time of its description. The Porcupine Cave specimens (fig. 17.9) are somewhat smaller and more hypsodont than the Cheetah Room specimens. The length of the first lower molar is about 2.5 mm from the Cheetah Room fauna (see Repenning and Grady, 1988, for more details).

The recognition of *Mimomys (C.) virginianus* in the early Irvingtonian II Cheetah Room fauna of West Virginia was a surprise, as there had been no idea that this subgenus had entered North America or that the genus

Mimomys was present in the Pleistocene of North America. Within a year, however, Martin (1989) published the record from the Java fauna of South Dakota, and in succeeding years other records have become known, from Yukon Territory (Canada), Alaska, Colorado, Utah, and Nevada (the last three are cave faunas like the Cheetah Room fauna). These new records have not yet been dated well, but they suggest that the record of *Mimomys* in North America may be nearly as late as in Eurasia, although much less varied during the Pleistocene.

BIOGEOGRAPHY AND BIOCHRONOLOGY: To the extent that the small sample from Java, South Dakota, can be considered as representative of its population, *Mimomys* (*Cromeromys*) *virginianus* appears to represent a derivative of the older *M. (C.) dakotaensis*. There appears to be an uncomfortably large gap of time (about 1.5 Ma) between the Siberian and North American records. The species *M. virginianus* probably lived into the Brunhes Chron (somewhat less than 0.78 Ma), and appears to have had colder climate adaptations from its records in Beringia and from mountain areas of the USA. In the past, and in the Appalachian Mountains in eastern USA, it had previously been called an unusual species of *Clethrionomys*.

SUMMARY

The microtine genus *Mimomys* twice dispersed from Eurasia to North America, first at 4.8 Ma as a temperate lineage and second between 1.5 and 1.3 Ma as a cool temperate to subarctic form. Its history of evolution in North America was different than in Eurasia, and even in Eurasia there are lineages that evolved differently in different FRs. These few contacts with Eurasian populations provide little help in correlating North American *Mimomys* with that of Eurasian populations, yet similar character trends throughout Holarctica are seen in varying combinations.

Within North America, there were variations of changing group characters between the EFR and the WFR and the frequent exchange of species between the two faunal regions of the United States allows temporal correlation between them, a helpful tool in correlation where availability of time control

varies between the regions. The principal barrier between the EFR and the WFR was the Rocky Mountains and two routes appear to be documented across this barrier: through Yellowstone Pass and around its southern end and through southern California and Nevada and Arizona, and to the Great Plains. These avenues were opened to dispersal by *Mimomys* as a result of climate changes and correlate well with glacial history when known.

Dispersal was made possible by the greater precipitation and seasonal equability that accompanied the development of glacial maxima. Prior to known continental glaciation, climate change appears to have occurred, to judge by the distinct periodicity of faunal exchange, both east and west, between the faunal regions.

The record of these movements of populations between faunal regions provides no evidence of time lapse during dispersals that cannot be explained by local climatic variation and the dispersal barriers they created.

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