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The status of *Mimomys* in North America revisited

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Dental characters of the type species of *Mimomys*, *M. pliocaenicus* FORSYTH MAJOR, 1902, are compared with those from the earliest North American arvicolids. *Mimomys* on this continent is limited to the early Pleistocene (early Irvingtonian) *M. virginianus* REPENNING & GRADY 1988 and *M. dakotaensis* MARTIN 1989. The crucial characters for *Mimomys* are well-developed negative enamel differentiation and a *Mimomys*-type schmelzmuster (microscopic enamel banding pattern), in concert with rooted molars (to separate *Mimomys* from early *Microtus* and *Arvicola*). Because mosaic character evolution often dominates in the early expression of character states in a highly speciose clade, it seems appropriate to use unique character combinations to define higher level taxa, even if the characters are individually homoplasic or symplesiomorphic within the clade.

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INTRODUCTION

The presence of *Mimomys* (FORSYTH MAJOR, 1902) in North America has been debated for many years. For example, although initially described as *Cosomys primus* (Wilson 1932), this species has also been considered as a member of *Mimomys* by Hinton (1926) and more recently by Repenning (1987) and Bell (2000). Originally described as *Mimomys monohani* (Martin 1972), an arvicolid from the Irvingtonian Mullen Assemblage of Nebraska was later referred to the new genus *Loupomys* by von Koenigswald & Martin (1984). At that time, von Koenigswald & Martin concluded that *Mimomys* had not dispersed to North America. However, Repenning (1987) included *Ogmodontomys*, *Ophiomys*, and *Cosomys* as subgenera of *Mimomys*, and Mou (1997) recently described a new species of *Mimomys*, *M. panacaensis*, from an early Blancan locality in Nevada.

It is not surprising that many early arvicolids from North America with rooted molars are considered members of the genus *Mimomys*; the occlusal m1 (first lower molar) patterns of a number of taxa (particularly *Cosomys primus*; Figs. 1D-G) are very similar to those of a variety of European *Mimomys*. Mou (1997, p. 381) lists the following as the distinguishing synapomorphies for *Mimomys*: "… presence of a *Mimomys*-kante and development of dentine tract on m1." Repenning & Grady (1988) also included: three triangles, the presence of an enamel atoll (=islet) in the anteroconid of m1, and a simple M3 with a posterior atoll. The

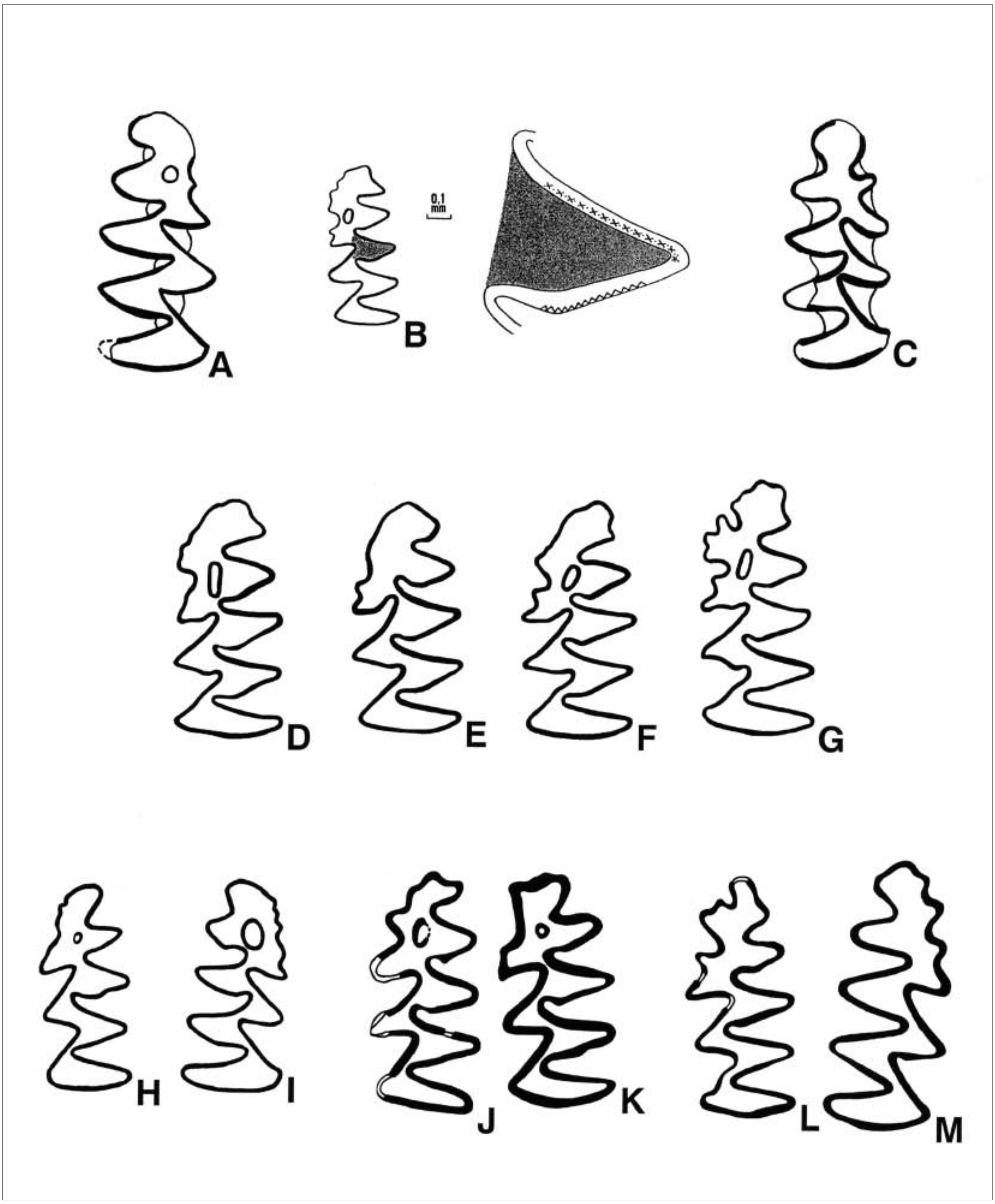

Figure 1 First lower molars of select arvicolid species. **A** = *Mimomys pliocaenicus*, Tegelen (Egypte quarry), the Netherlands, redrawn from Tesakov (1998); **B** =*Mimomys schmelzmuster* (from von Koenigswald & Martin 1984). Expanded diagram of triangle 3 shows thinner leading edge with L-R pattern, and thicker trailing edge with R-T bands; **C** = *Mimomys* (*Cromeromys*) *virginianus*, Cheetah Room l.f. of Hamilton Cave, West Virginia (early Irvingtonian), redrawn from Repenning & Grady (1988); **D-G** = variation in *Cosomys primus* from the Hagerman l.f., Idaho (middle Blancan) (from Zakrzewski 1969) **J-K** = *Ogmodontomys sawrockensis*, Saw rock Canyon l.f., Kansas (early Blancan) (original illustrations); **H-I** = *Ophiomys panacaensis*, Panaca, Nevada (early Blancan) (from Mou 1997). **L-M** = *Ogmodontomys poaphagus*, Wendell Fox Pasture, Kansas (middle Blancan) (original illustrations). Early, middle, and late Blancan refer to roughly even segments of the Blancan, with an approximate range of 5.0 - 1.8 Ma. Illustrations not to same scale.

Mimomys-kante (Fig. 1A) is an enamel ridge developed from triangle 4 (T4) in some arvicolid dentitions. It is most commonly present in unworn or lightly worn dentitions, and often disappears with wear. Dentine tracts are extensions of the dentine from the undulating dentine-enamel border called the linea sinuosa (Rabeder 1981) towards the occlusal tooth surface. The problem with the features used by these authors is that they are, individually or in aggregate, symplesiomorphic for most early arvicolids, and are therefore inadequate to define the taxon *Mimomys*. For example, we now know that a *Mimomys*-kante was present in early species of at least the following groups: *Phenacomys* (Repenning *et al.* 1987), the synaptomyinine lemmings (Fejfar & Repenning 1998), *Protopliophenacomys* (L. Martin 1994; von Koenigswald & Martin 1984; = *Propliophenacomys* L. MARTIN, 1975), the Lagurini (von Koenigswald & Tesakov 1997), *Dolomys* (Maul 1996; Radalescu & Samson 1996), *Ungaromys* (Tesakov 1998), *Ogmodontomys* (Zakrzewski 1967), *Ophiomys* (Hibbard & Zakrzewski 1967), *Pliopotamys* (Zakrzewski 1969), *Hibbardomys* (Zakrzewski 1984; Martin 1989), as well as *Mimomys* from Europe (e.g., Hinton 1926; Michaux 1971; Janossy & van der Meulen 1975; Chaline & Laurin 1986). In many of these arvicolid groups there is also a trend towards increase of dentine tract height over geological time, accompanied by an increase in hypsodonty. Enamel atolls are present and common on the anteroconid of m1 in the earliest synaptomyinine lemmings (Fejfar & Repenning 1998), *Promimomys* (= *Prosomys*), *Dolomys*, *Ungaromys*, *Mimomys* (sensu stricto), *Ophiomys*, and *Cosomys*; they are also present, though infrequently, in *Ondatra* (= *Pliopotamys*) (Zakrzewski 1969). A posterior enamel atoll on M3 is seen in *Promimomys*, *Propliomys*, *Borsodia*, and *Dolomys* in the Old World and *Cosomys* and *Ophiomys* (tentatively including "*Mimomys*" *panacaensis* MOU, 1997) in North America. If the presence of these characters cannot be used to define *Mimomys* (except by construction of an all-inclusive genus that would obscure phylogenetic relationships among them), are there more suitable features? In this brief study, I evaluate the character suite of the type species of *Mimomys*, *M. pliocaenicus* (FORSYTH MAJOR, 1902), and suggest that the presence of *Mimomys* in North America is limited to two species, *M. virginianus* REPENNING & GRADY, 1988 and *M. dakotaensis* MARTIN, 1989.

METHODS AND ABBREVIATIONS

Macroscopic dental characters of *Mimomys pliocaenicus* were taken from illustrations and descriptions in Forsyth Major (1902), Hinton (1926), Michaux (1971), and Tesakov (1998). The microscopic enamel banding pattern, or schmelzmuster information for *Mimomys* and other arvicolid taxa is based on work by von Koenigswald (1980), von Koenigswald & Martin (1984), and unpublished research at Murray State University by R. Martin, L. Duobinis-Gray, C. Crockett, and A. Tesakov.

Dental terminology for arvicolid molars follows van der Meulen (1973, 1978) and Martin (1987). Schmelzmusters are defined from the enamel-dentine junction outwards, so L-R implies an inner lamellar and an outer radial layer; R-T = an inner radial and an outer tangential layer. Leading edges of molar triangles are anterior on the lowers and posterior on the uppers; trailing edges are posterior on lower and anterior on uppers. Leading edges tend to have the same schmelzmuster, as do trailing edges. Negative enamel differentiation = trailing edges thicker than leading edges (e.g., *Mimomys*); undifferentiated enamel = leading and trailing edges same thickness; positive differentiation = trailing edges thinner than leading edges (e.g., most *Microtus*).

RESULTS AND DISCUSSION

Molars of *Mimomys pliocaenicus* collectively display the following characters: (1) relatively high-crowned cheek teeth with roots, (2) relatively high dentine tracts, (3) m1 with three triangles plus a simple anterior cap (Fig. 1A), (4) m1 with a *Mimomys*-kante and enamel atoll in lightly worn dentitions, (5) provergent lingual re-entrant angles on lower molars that are deeper than labial ones, but not excessively so, (6) M3 with posterior enamel atoll, (7) negatively differentiated enamel, (8) cement in re-entrant angles, and (9) a schmelzmuster composed of L-R on leading and R-T on trailing edges of triangles (Fig. 1B). All of these features can be found individually in other arvicolid genera, and many change through time within *Mimomys*, but this combination is unique to advanced *Mimomys*. (It should not be surprising that the character distribution in a rapidly evolving, highly speciose clade should be expressed in a mosaic fashion, leading to the result of defining taxa not necessarily on unique attributes, or synapomorphies, but rather on unique combinations of characters distributed among them). Some of the characters of *Mimomys pliocaenicus*, such as high dentine tracts and cementum, are lacking in ancient species referred to *Mimomys* (e.g., *M. cappetai*) and others may be lacking in more specialized, younger species (e.g., enamel atolls absent from the m1 and M3 in advanced populations of *M. tornensis*, *M. pitymyoides*, and *M. pusillus*). It is axiomatic that at some point, moving both backwards and forwards in time and morphospace, it will no longer be possible to recognize some species within the genus *Mimomys*. The question is, where do we draw the lines? We could limit the genus *Mimomys* only to taxa combining the features of *M. pliocaenicus* (Tesakov 1998), and perhaps ultimately this would be the best solution. However, for now I prefer a broader concept for *Mimomys*, and choose to focus on the most stable features that are likely to help in extending *Mimomys* as a monophyletic group back to its origins among early arvicolids.

Almost all Old World species currently recognized as *Mimomys*, with the exception of *Mimomys vandermeuleni* and *M. davakosi*, have negative enamel differentiation that is clearly obvious under the light microscope. The trailing edges are distinctly bulbous with respect to the leading edges. Taxa derived from ancestral *Mimomys* species (e.g., *Microtus*, *Arvicola*) have presumed ancestors with negative enamel differentiation (van der Meulen 1974; Heinrich 1990). Also, all but the most primitive *Mimomys* species that have been examined, display a typical L-R (leading edges), R-T (trailing edges) schmelzmuster (von Koenigswald 1980; von Koenigswald & Martin 1984), and taxa that are descended from *Mimomys* have a schmelzmuster that is best understood as being derived from this type (e.g., *Microtus*, with reduced trailing edges but essentially the same pattern). Restricting the definition of *Mimomys* to these core characters, highly developed negative enamel differentiation and a *Mimomys* schmelzmuster, plus the presence of rooted molars, allows a new concept that recognizes the earliest species that can be combined in Old World *Mimomys*, and just as clearly distinguishes it from (a) its New World relatives that are not *Mimomys* and (b) its more specialized, derived taxa in the Old World, such as *Arvicola* and *Microtus*. Incidentally, this definition allows certain other characters to be added or lost (e.g., dentine tracts, cementum, enamel atolls) within *Mimomys*.

Some of the early North American arvicolid species with m1s that superficially resemble those of Old World *Mimomys* include *Ogmodontomys sawrockensis* (Figs. 1J-K), from the early Blancan Saw Rock l.f. of Kansas (Hibbard 1957; Martin *et al.* 2000), *O. poaphagus* (Figs. 1L-M) from early through late Blancan localities in Kansas (Hibbard 1941; Martin *et al.* 2000), *Ophiomys panacaensis* (Figs. 1H-I) from early Blancan deposits in Nevada (Mou 1997, 1998), *O. mcknighti*, from the early Blancan Ringold Fm. of Washington state (Gustafson 1978), *O. taylori* from the Haymaker's Orchard l.f. of Washington and the Hagerman l.f. of Idaho (Hibbard 1959; Hibbard &

Zakrzewski 1967; Repenning 1987), and *Cosomys primus* from Coso Mt. in California and Hagerman, Idaho (Wilson 1932; Zakrzewski 1969). However, none of these taxa have well developed negatively differentiated enamel or a *Mimomys*-type schmelzmuster (von Koenigswald 1980). For example, *Ogmodontomys poaphagus* has only radial enamel on the leading edges of its molars, coupled with an R-T pattern on the trailing edges (von Koenigswald 1980). This is a consistent pattern in *O. poaphagus* that seems to be present throughout its Blancan lifespan (R. Martin & Crockett, unpublished). *Cosomys primus* has both lamellar and tangential bands, but also has an extra layer of radial enamel on both the leading and trailing edges (R-L-R, R-T-R). According to von Koenigswald & L. Martin (1984), this implies that *Cosomys* is distinct from *Mimomys*. A few of these taxa, particularly *Ogmodontomys sawrockensis* and the *Ophiomys* species noted above, may have a primitive (plesiomorphic) schmelzmuster composed primarily of radial enamel, in combination with primitive lamellar and/or tangential patches. Nevertheless, in none, including the more advanced *O. parvus* and *O. meadensis*, has a typical *Mimomys* schmelzmuster been observed (von Koenigswald 1980; Mou 1998; R. Martin, personal observation). By the time that the most advanced *Ophiomys*, *O. parvus* and *O. meadensis*, occur in North America, *Mimomys* in Europe already has its typical schmelzmuster (von Koenigswald & Martin 1984). Because these North American species do not share the composite characters that define *Mimomys*, they should not be included in that genus, and appear instead to represent part of a series of distinct North American arvicolid radiations.

This concept creates a problem for the systematics of Eurasian species such as *Mimomys vandermeuleni* (Fejfar *et al.* 1990), *M. davakosi* (van de Weerd 1979), and *Promimomys antiquus* (Zazhigin 1980; referred to *Mimomys* by Repenning 1998). Although these species are slightly more advanced than *Promimomys* because they have a fourth lingual reentrant (LRA4) on m1, whereas *Promimomys* have only three lingual reentrants, this morphology is shared by most vole lineages during the early Pliocene and therefore is not a distinguishing feature for *Mimomys* or any other early arvicolid genus. In addition, the molars of *M. vandermeuleni*, *M. davakosi*, and *P. antiquus* have undifferentiated enamel. The schmelzmuster has not been examined in these species. Although it is probably premature to discuss the relationships of these species before detailed morphological investigations have been accomplished, we can speculate on relationships depending on various outcomes. For example, if the schmelzmuster of these species is mostly radial enamel, and if the triangle edges are undifferentiated, then it will not be possible to allocate them to *Mimomys*. Perhaps they should be referred to *Promimomys*. Zazhigin's (1980) original determination of the species *antiquus* as *Promimomys antiquus* seems reasonable, and is followed here. On the other hand, if the schmelzmuster demonstrates primitive lamellar enamel as a distinct band on the leading edges and a tangential band on the trailing edges, it would be suggestive of, and reasonable evidence for, inclusion in Old World *Mimomys*. Of course, one could also construct a new genus, perhaps called "*Protomimomys*," representing an intermediate step in the cloud of species comprising the *Mimomys* metaregion (see Martin & Tesakov 1998), but this seems like an unnecessary proliferation of names for a set of species we all recognize as being in a potentially ancestral position, but for which we have no distinct symapomorphies linking them to later clades. My preference, in the absence of such information, is to view them as slightly advanced species of *Promimomys*.

Mimomys in North America?

Given these considerations, are there any *Mimomys* in North America? Two species, the late Blancan or early Irvingtonian *M. dakota-*

ensis Martin, 1989 from the Java l.f. of South Dakota, and *M. virginianus* Repenning & Grady, 1988 (Fig. 1C), from the Irvingtonian Cheetah Room l.f. of Hamilton Cave and deposits in Porcupine Cave of Colorado (Bell & Barnosky 2000) appear to be the only arvicolid species in North America that can be identified as *Mimomys*. Although the schmelzmuster for *M. virginianus* has not been evaluated, that of *M. dakotaensis* has been reported to show a *Mimomys* pattern (Martin 1989). Both species have negative enamel differentiation. They are advanced species, with high dentine tracts at various points, loss of enamel atolls on m1 and M3, and cementum in the re-entrant angles. Based on our current knowledge, they probably should be classified in the subgenus *Cromeromys* (Zazhigin, 1980). *Mimomys* appears to have entered North America across Beringia during the earliest Pleistocene, perhaps about the same time that *Microtus* first dispersed to this continent. Based on published information, it became extinct in North America prior to the late Pleistocene. A more extensive review of North American arvicolids will be published in Martin (2002).

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