

The Early Pleistocene *Mimomys hordijki* (Arvicolinae, Rodentia) from Europe and the origin of modern nearctic sagebrush voles (*Lemmiscus*)

Alexey S. Tesakov and Thijs van Kolfschoten

ABSTRACT

Ancient voles with rooted cheek dentitions assigned to the subgenus *Cromeromys* of the genus *Mimomys* are known in the Early Pleistocene (Gelasian and 'Calabrian') fossil record of northeastern Siberia and in the late Early Pleistocene ('Calabrian') record of Canada and United States. The Late Pliocene to Early Pleistocene Holarctic rooted voles of the *Mimomys* (*Cromeromys*) group, including (here redescribed) European *Mimomys* (*C.*) *hordijki*, shows affinities with the modern *Lemmiscus* and provides clues for a robust hypothesis on the origin that genus. The modern Nearctic arvicolini rodents *Lemmiscus* (sagebrush voles) were long thought to represent a closely related sister group of Palearctic steppe lemmings of the tribe Lagurini. However, ample morphological, paleontological, and genetic evidence suggests their attribution to the tribe Arvicolini, as a sister clade of modern *Microtus*. Arvicolini have rootless molars and are assumed to have originated from the Pliocene rhizodont *Mimomys*.

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INTRODUCTION

The Late Pliocene to Early Pleistocene (Piacenzian to Gelasian) adaptive radiation of *Mimomys* is one of the most significant processes in small mammal communities in the middle latitudes of Eurasia. The radiation produced several lineages, one of which is the (sub)genus *Cromero-*

mys. The concept of *Cromeromys* as a separate genus of Pliocene and Pleistocene mimomyoid voles was established by Zazhigin in 1980. According to Zazhigin, *Cromeromys* includes forms with the characteristic features of external cement in the molar reentrants, the anteroconid of the lower m1 always without an enamel islet, and the posterolingual reentrant of the upper M3 always deep, never

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forming an enamel islet. The taxon was based on scarce remains of a small *Mimomys* species (*Mimomys irtyschensis*) from Late Pliocene deposits located in southern Siberia. Zazhigin (1980) also included in the genus a small *Mimomys* species from the Early Pleistocene (Gelasian) crags of East Anglia that was referred to as *Mimomys newtoni* and eventually re-described as *Mimomys tigliensis* (see Mayhew and Stuart 1986; Tesakov 1998). Zazhigin (1980) also included a large species of the *Mimomys savini* group (see discussion by Neraudeau et al. 1995) in the genus. Zazhigin (1980) later listed *Cromeromys irtyschensis* and *C. cf. irtyschensis* from the Early Pleistocene (early Gelasian through 'Calabrian' equivalents) levels of the Arctic Krestovka locality in northeastern Arctic Siberia (Zazhigin 1997). It is these forms that most closely correspond to the original definition of *Cromeromys*, showing an early reduction of the enamel islet in the m1, and with the M3 having a hook-like posterior lobe without an enamel islet. Another stable feature of the m1 is the strong development of the *Mimomys*-ridge (= *Mimomys* Kante), a peculiar indentation of the fourth dental triangle that is persistently present in many Pliocene archaic rhizodont voles. This morphology is also known in several Early Pleistocene (Irvingtonian = 'Calabrian') molars from the United States assigned to three different species: *Mimomys monohani*, *M. virginianus*, and *M. dakotaensis* (L. Martin 1972; Repenning and Grady 1988; R. Martin 1989; Bell and Barnosky 2000). Repenning (Repenning and Grady 1988; Repenning 2003) considered *Cromeromys* to be a subgenus of *Mimomys* that includes all these forms.

The remarkable Zuurland drilling project of Mr. L. Hordijk (Brielle, The Netherlands) in Western Europe produced a rich superposed sequence of arvicoline faunas ranging from Early Pleistocene (Gelasian) to Holocene (Hordijk 1988; Van Kolfschoten 1988). A form morphologically similar to *Cromeromys* was discovered in materials from Early Pleistocene (Gelasian, Late Villanyian, MN17) levels of the Zuurland sequence. Van Kolfschoten and Tesakov (1998) described this vole as *Mimomys hordijki* based on limited material available at that time. Although the general similarity to *Mimomys* (*Cromeromys*) species was obvious to van Kolfschoten and Tesakov (1998), they refrained from attributing the new species to that subgenus because no M3 were known at that time.

C. Repenning (personal commun., 1999) suggested in his comments that the new European vole is conspecific with the late Irvingtonian spe-

cies from Hamilton Cave, USA and stated, ".... but what makes less sense is to say 'we do not have the last upper molar and therefore are not sure that the specimens from Mr. Hordijk's borehole are not *Mimomys virginianus*, so we will give it a new name' How did you two bright men miss seeing the error of this action?"

New material from the Zuurland boreholes fortunately included third upper molars, confirmed the attribution of *M. hordijki* to *Mimomys* (*Cromeromys*), and showed that this European vole is a distinct species probably ancestral to North American forms. It reconciles us with our conscience and, furthermore, we hope that Repenning would have been glad to see this contribution. We describe the new *M. hordijki* material and discuss the possible relation between *Mimomys* (*Cromeromys*) and the modern Nearctic sagebrush vole, genus *Lemmiscus*.

The Subgenus *Cromeromys*

Study of the *Cromeromys* record of Eurasia and North America suggests that *Cromeromys* in its original definition includes different lineages. According to Zazhigin (1980), it is the *Cromeromys* group of *Mimomys*-like or mimomyoid voles that gave rise to the modern *Microtus* and *Arvicola*, and this affinity is marked in the dental morphology by complex third upper molars and absence of enamel islets in all members of *Cromeromys* group. In *Mimomys*, in contrast to the former group, the m1 and M3 have enamel islets. However, a number of the forms included in *Cromeromys* do not comply with the original diagnosis (see also Repenning and Grady 1988). The common occurrence of an enamel islet in the anteroconid of the m1 of juvenile *Mimomys savini* (and even its modern descendant *Arvicola*), and the posterior enamel islet normally occurring on the M3 of *Mimomys tigliensis*, and, possibly (personal observation) even in the type species, indicates that it is likely that all forms originally included in *Cromeromys* represent different lineages of the genus *Mimomys*. The original definition of the (sub)genus is not accurate enough. Nevertheless, we agree with Repenning and Grady (1988) that the name is useful to denote Eurasian and North American mimomyoid voles with a well developed *Mimomys*-ridge and complex third upper molars, and its use considered here as a subgenus of the genus *Mimomys*. The authors also agree with R. Martin (2003) that, apart from *Microtus* s.l., this particular clade of *Mimomys* (*Cromeromys*) represents the only known group of the Palearctic *Mimomys* radiation

to ever reach North America. Multiple arvicolines with rooted dentition of Pliocene Blancan age (e.g., *Ogmodontomys*, *Ophiomys*) represent native North American vole lineages that are distinct from the *Mimomys* lineage sensu stricto. *Mimomys* s.str. includes only post Early Pliocene forms sharing the character syndrome of *Mimomys pliocaenicus* Forsyth Major 1902, with the important role of external cement and pachyknem Schmelzmuster.

TERMINOLOGY AND MATERIAL

An international common standard is used to describe the new material referred to *M. hordijki*. The terminology used to describe the occlusal pattern of the arvicoline molars is after van der Meulen (1973). Terminology of the dentine tracts follows the system proposed by Rabeder (1981) in which HH-index is the square root of the sum of heights of dentine tracts of hypoconid and hypoconulid in lower molars; PA-index is the square root of the sum of heights of dentine tracts of protocone and anterocone in upper molars; ASD is anterosinuid; HSD hyposinuid; HSLD hyposinulid; MSD mimosinuid; PRS protosinus; AS anterosinus; and DS distosinus. Lower case m designates lower molars, and upper case M designates upper molars. L = length, W = width, A/L = index of anteroconid, H = labial crown height, Lbas = basal crown length, EL = elevation of *Mimomys* ridge above crown base of m1, P/L = index of posterior loop of M3 (includes T4), AL = anterior loop, and PL = posterior loop. All measurements are in mm.

The global stratigraphic terminology of the Pliocene-Pleistocene follows the new usage of the International Commission on Stratigraphy (2009) with the Late Pliocene (Piacenzian) ranging from 3.6 to 2.588 Ma, and Early Pleistocene including Gelasian (2.588 to 1.81 Ma) and 'Calabrian' (1.806 to 0.781 Ma). The Zuurland materials are stored in the Local Museum of Brielle (LMB), The Netherlands. The investigated material comes from 11 different parallel boreholes (Z1 – Z11) located very close to each other.

SYSTEMATIC PALEONTOLOGY

Family Cricetidae Fischer, 1817
Subfamily Arvicolinae Gray, 1821
Tribe Arvicolini Gray, 1821

Genus MIMOMYS Forsyth Major, 1902
Subgenus CROMEROMYS Zazhigin, 1980

Mimomys hordijki van Kolfschoten et Tesakov,
1998

Figs. 1–3, 4: 1–2, 5: 1.

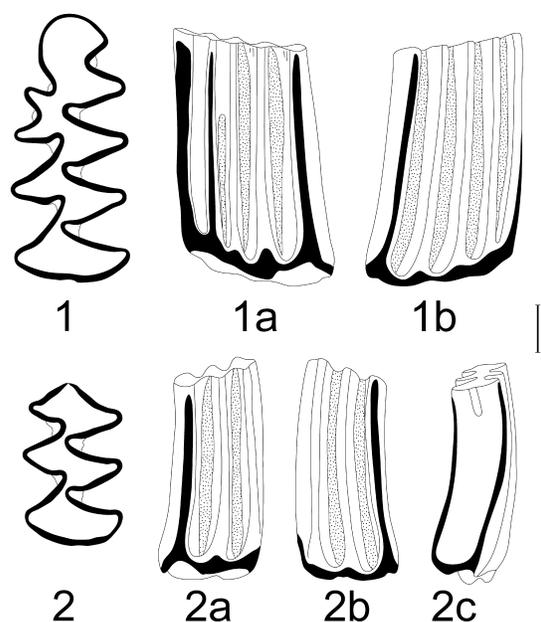


FIGURE 1. *Mimomys hordijki*, holotype, (LMB no. Z3-201). 1. m1, occlusal view; 2. m2, occlusal view; a: labial view; b: lingual view; c: posterior view. Scale bars equal 1 mm: the longer bar stands for occlusal view, the shorter one is for lateral view.

1998 *Mimomys hordijki* sp. nov.; van Kolfschoten and Tesakov, p. 187–192, figs. 1, 2.

Emended diagnosis. Medium-sized hypsodont *Mimomys* with sparse cement in reentrants, thick and mostly undifferentiated enamel, without enamel islets, m1 with a prominent *Mimomys*-ridge running to crown base. Lower m2 in pleurorhizal position. Dentine tracts high, HH-index in m1 more than 6. The tract of the *Mimomys*-ridge well developed.

Type. Lower m1 (2.8 x 1.22 mm) and m2 (1.74 x 1.05) originating from the same mandible, BRM (Brielle Local Museum), no. Z3-201 (Figure 1).

Material. 12 complete lower m1s (Z7-1, Z11-2, Z11-1, Z6-1, Z7-2, Z7-3, Z10-1, Z2-17, Z2-2, Z2-166, Z2-1, Z5-167) except the holotype, and one damaged m1 without PL (Z9-1), 2 M3 (Z6-2, Z9-2). All specimens are in collection of Brielle Local Museum (BRM), The Netherlands: ZU-4 (=Zuurland Unit 4, depth level of 61 to 66 m), Early Pleistocene, Gelasian, Late Villanyian, MN17.

Description. The vole is of medium size (Tables 1 and 2). The enamel band is thick and mostly undifferentiated. However, some triangles show a tendency to a weak thickness differentiation, according the *Mimomys* pattern (negative type), with trailing edges of the triangles being somewhat

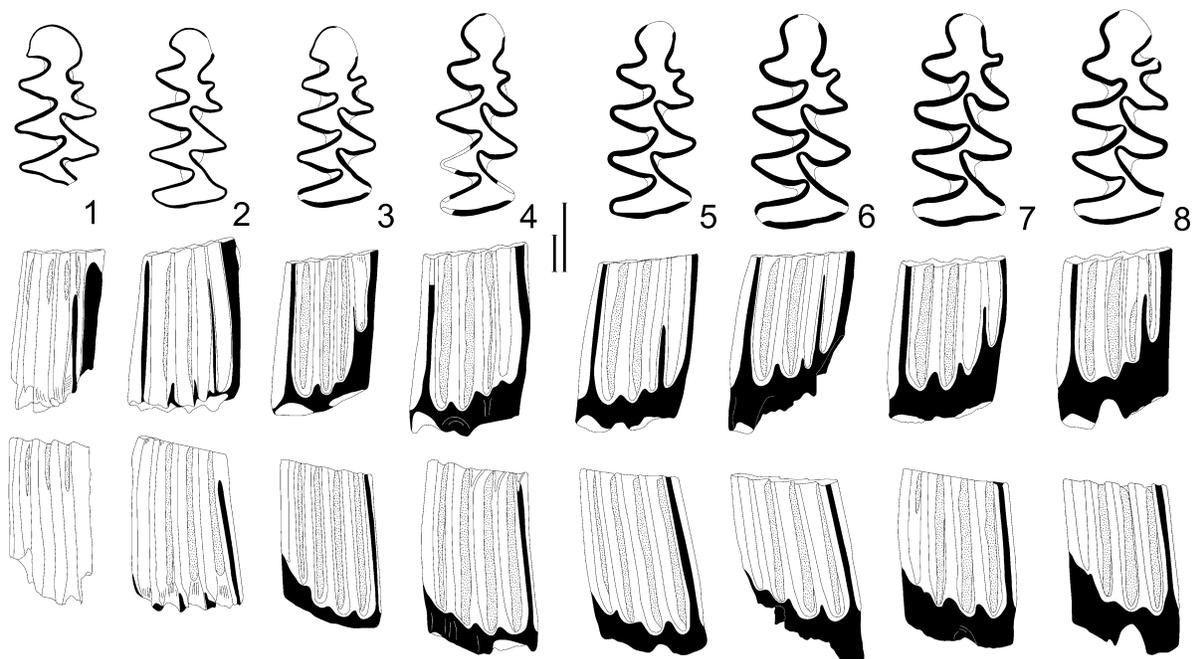


FIGURE 2. *Mimomys hordijki*, lower m1. 1. Z9-1; 2. Z7-1; 3. Z11-2; 4. Z11-1; 5. Z6-1; 6. Z7-2; 7. Z7-3; 8. Z10-1. Upper row: occlusal surface, middle row: labial side, lower row: lingual side. Scale bars equal 1 mm: the longer bar stands for occlusal view, the shorter one is for lateral view.

thicker than the leading edges. The visible lighter zone along the outer margin of the trailing edges corresponds to tangential enamel and suggests a normal *Mimomys* Schmelzmuster. Triangles are well separated and alternate, and reentrant angles are strongly curving (vergent). The amount of cement varies from sparse in younger animals to moderate in older ones; cement never fills more than half of the depth of the re-entrants. The molars are hypsodont, dentine tracts are strongly developed, and their tips are interrupted by wear in younger ontogenetic stages when the molar base is still open. However, some tracts still show their complete height (Figures 1-3). High-crowned molars with early root formation stages are predominant in the studied material.

Lower m1. The anteroconid has a strongly developed *Mimomys*-ridge opposing the posterior part of T5. Reentrants of the anteroconid are deep; T4 tends to be more isolated in advanced stages of wear. The mimosinuid is normally high (e.g., Figure 2: 2) or of medium height (Figure 2: 5); it is only rarely not developed (Figure 2: 4). The posterolingual tract (HSLD) is slightly higher than the labial one. The base of the islet reentrant (BRA3) is deep. No signs of an enamel islet are present, not even in the two juvenile specimens (Figure 2: 1, 2).

Lower m2. The occlusal surface consists of a PL and two pairs of broadly fused triangles, T1–T2 and T3–T4 (Figure 1: 2). The base of the molar is strongly curved lingually indicating the pleurorhizal condition (at the outer side of the incisor). The base of LRA1 is deep, and the height is not reduced by the contact with the incisor. $H = 3.50$, $ASD > 4.14$, $HSD = 3.33$, $HSLD = 4.00$, $Lbas = 2.00$, $HH\text{-index} = 5.20$.

Upper M3. The occlusal surface consists of an AL, two alternating triangles (T2, T3) and a posterior loop (T4 plus posterior cap). All occlusal elements are broadly confluent. The antero-labial re-entrant, BRA1, is more shallow than BRA2. LRA2 and LRA3 are retrovergent. A shallow LRA4 is present (Figure 3).

Comparison. The Hordijk's *Mimomys* differs from *Mimomys monohani* L. Martin, 1972 from Mullen l.f. (of possibly Irvingtonian age) in a somewhat larger size, smaller amount of cement and less divided occlusal elements in the m2. All these characters tentatively indicate a more advanced evolutionary stage of *M. monohani*.

Mimomys virginianus Repenning and Grady, 1988, late Irvingtonian in age from Hamilton Cave, differs from *M. hordijki* in having smaller size, more abundant cement accumulations, a more anterior

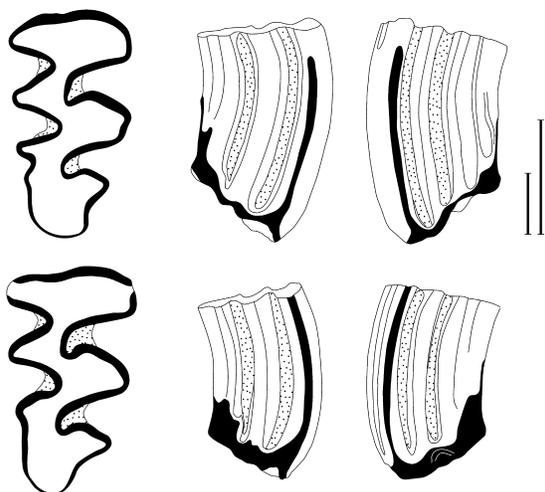


FIGURE 3. *Mimomys hordijki*, upper M3. 1. Z9-2, right M3, occlusal view; 2. Z6-2, right M3, occlusal view; a: lingual side; b: labial side. Scale bars equal 1 mm: the longer bar stands for occlusal view, the shorter one is for lateral view.

position of the *Mimomys*-ridge (opposite the center of T5), and more separated T2 and T3 in the M3. Some molars of *M. virginianus* from Porcupine Cave (Bell and Barnosky 2000, p. 101, figure 4: D) seem to have thicker leading edges of the enamel band (*Microtus*-type or positive differentiation sensu R. Martin 2003).

Mimomys dakotaensis R. Martin, 1989, Java l.f. of Irvingtonian age, is similar to *M. hordijki* in the structure of the only known m1 (R. Martin 1989, p. 443, figure 5: A; figure 4: 3). However, the m2 and the M3 have more separated occlusal fields than in the Dutch *Mimomys hordijki* vole.

Remarks. *Mimomys hordijki* is the second most hypsodont rhizodont vole in the Zuurland Late Villanyian fauna after the *Mimomys tigliensis*. An abrasive, graminivorous diet can be inferred for *M. hordijki*.

Mimomys hordijki and North American Irvingtonian *Mimomys* show close morphological similarities. The most important distinctive features are the structure of the m1 with a strongly developed *Mimomys*-ridge and without enamel islets, and of an M3 with a hook-like posterior part and a deep postero-lingual re-entrant. This group is known from the Early Pleistocene (Gelasian, Villanyian LMA) of Europe, the Early Pleistocene (Gelasian to 'Calabrian', Kutuyakhian through Olyorian) of western Beringia (Kolyma lowland) and eastern Beringia (Repenning 2003), and from Early Pleistocene (Irvingtonian) faunas of conterminous United States. This indicates a high latitude Holarctic distribution of this group during the early Early Pleistocene and a dispersal to more southern regions of North America in the late Early Pleistocene. A proper name for this group of mimomyoid voles has yet to be established.

Potentially the name *Cromeromys* Zazhigin, 1980 can be discredited if the type material represents a mixture of different forms. This possibility should be studied, and at least the type series should be carefully revised. The next available synonym may be *Loupomys* von Koenigswald and L. Martin, 1984. This monotypic taxon is based on *Mimomys monohani* L. Martin, 1972. The illustrated first lower molars of that form have the characteristic "*Cromeromys*" morphology. However, other illustrated teeth (M1, M2) certainly do not

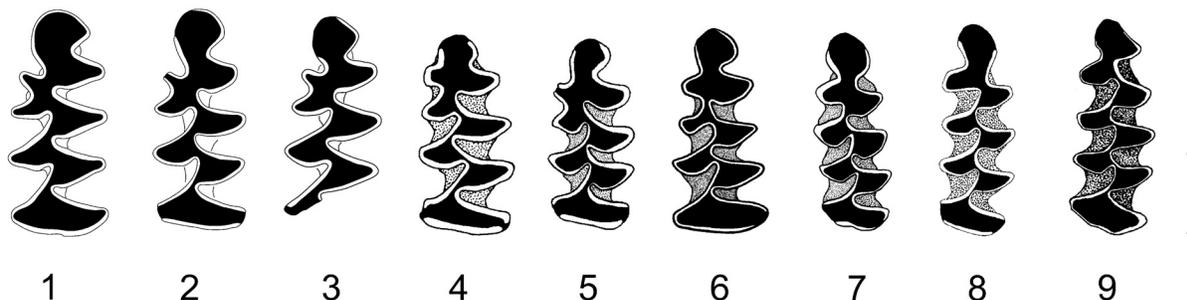


FIGURE 4. Hypothetical transformation series represented by known fossil record of *Mimomys* (*Cromeromys*) and *Lemmiscus* m1s, shown as left side molars. 1–2: *Mimomys hordijki*, Zuurland, early Early Pleistocene, 1: LMB, no. Z3-201, type; 2: LBM, no. Z2-002; 3: *Mimomys dakotaensis*, Java, Early Pleistocene, type; 4–6: *Mimomys virginianus*, Early Pleistocene, 4: Hamilton Cave (after Repenning and Grady 1988, p.6, figure 1 D), 5–6: Porcupine Cave, 5: (after Bell and Barnosky 2000, p. 101, figure 4 D), 6: (after Repenning 2003, p. 506, figure 17.9, reversed); 7–8: *Lemmiscus* sp., Early Pleistocene, 7: Porcupine Cave (after Bell and Barnosky 2000, p. 113, figure 8 D, reversed), 8: SAM Cave (after Repenning 1992, p. 35, figure 6 F); *Lemmiscus curtatus*, Snake Creek Burial Cave, Late Pleistocene-Holocene (after Bell and Mead 1998, p.84, figure 1 B). Scale bar equals 1 mm.

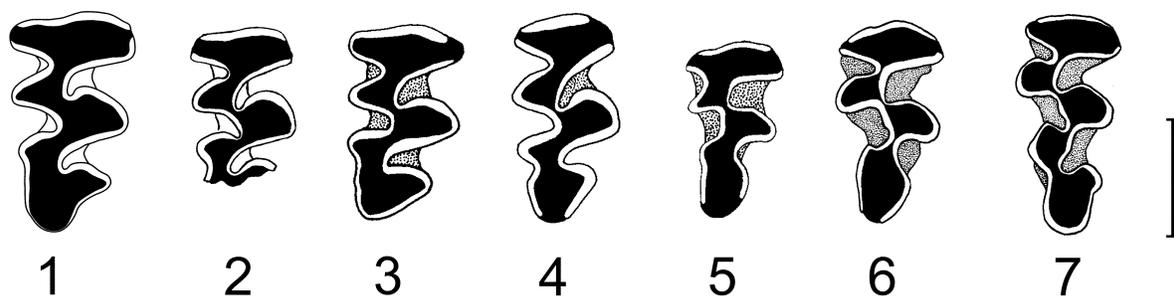


FIGURE 5. Hypothetical transformation series represented by known fossil record of *Mimomys* (“*Cromeromys*”) and *Lemmiscus* M3s, shown as right side molars. 1: *Mimomys hordijki*, Zuurland, Early Pleistocene (LBM, no. Z6-2); 2: *Mimomys dakotaensis*, Java, Early Pleistocene, reversed; 3-4: *Mimomys virginianus*, Hamilton Cave, Early Pleistocene (after Repenning and Grady, 1988, p.6, fig. 1 B, C); 5: *Lemmiscus* sp., SAM Cave, Early Pleistocene (after Repenning, 1992: p.35, fig.6 J); 6-7: Kokoweef Cave, Late Pleistocene-Holocene (after Bell and Jass, 2004, p.7, fig.4 A, B, reversed). Scale bar equals 1 mm.

belong to *Mimomys* but have a clethrionomyine appearance. Moreover, the illustrated M1 has three independent roots with the lingual (protocone) root in quite a posterior position, a character not compatible with the stage of hypsodonty of first lower molars. The possible admixture of *Clethrionomys* in the Mullen material may explain the non-*Mimomys* Schmelzmuster (studied in one M1, erroneously labeled as m2), which was the base for the description of the new genus. In fact, the described enamel microstructure closely fits that known for *Clethrionomys* voles with discrete lamellar and primitive tangential enamel (von Koenigswald 1980). A careful revision of the material is needed in this case too. After a revision, the valid name for Irvingtonian North American forms may turn out to be *Mimomys monohani*, as the senior available name.

Evolutionary polarities of characters evolving in vole dentitions permit reconstruction of the following sequence of species attributable to *Cromeromys*. The most primitive of the forms described so far is Early Pleistocene *M. hordijki* from Europe. The sparse cement and still-measurable complete dentine tracts in younger individuals are the most reliable indicators of its evolutionary level.

A more primitive form from the Kutuyakh beds (early Late Pliocene, ca. 2.5 Ma) of northeastern Siberia is still undescribed and only listed in the literature (Zazhigin 1997). Also undescribed are Early Pleistocene (Irvingtonian) records from eastern Beringia (Repenning 2003). The Irvingtonian forms from the conterminous United States show a number of characters that are more advanced than those of *M. hordijki*, including more abundant cement, smaller size, a more anteriorly shifted T6, and more separated triangles in the m2.

Range and occurrence. The species is known from the type locality, Zuurland, The Netherlands, Zuurland faunal unit 4 (ZU-4), Late Villanian, MN17, Early Pleistocene. Recently, we identified a fragment of an m1 of this species in the broadly synchronous Dutch locality, Tegelen-Maalbeek (so far unnumbered specimen, collection of Faculty of Archaeology, Leiden University, The Netherlands).

The Taxonomic Position of *Lemmiscus*

Studying the material referred to *Mimomys* (“*Cromeromys*”) *hordijki* led to the discovery of a number of similarities between this species and species referred to the genus *Lemmiscus*. Those similarities suggested that it was worth exploring the possibility that the two are related.

The Nearctic sagebrush voles of the genus *Lemmiscus* have long been suspected to be related to Palearctic lagurines or steppe lemmings (genera *Lagurus* and *Eolagurus*) because of obvious similarities in ecology and morphology of these voles (Gromov and Polyakov 1977; Carrol and Genoways 1980), and for a long time both were assigned to the same genus *Lagurus*. However, karyological data support close sister-group relationships of *Lemmiscus* with Arvicolini (Modi 1996) and most recent reviews reestablished the independent generic status for the North American *Lemmiscus* (Carleton and Musser 2005).

A grouping of *Lemmiscus* with Arvicolini is supported by a number of morphological features. One feature includes external molar cement shared by both *Lemmiscus* and *Microtus* s.l. but absent in all lagurines. Views on the taxonomic value of this character range from a total disregard to the understanding of its utmost importance (Zazhigin 1980). Another tribe-specific character of

TABLE 1. Measurements and indexes, *Mimomys hordijki*, Zuurland 4, m1.

	N	MEAN	SE	MIN	MAX	SD	CV
L	13	2.76	0.0488	2.45	3.08	0.1760	6.39
W	14	1.18	0.0266	1.06	1.34	0.0994	8.39
A/L	13	43.7	0.65	38.9	47.1	2.33	5.33
H	14	3.60	0.2130	1.51	4.37	0.7970	22.12
ASD	1	4.4	–	–	–	–	–
HSD	1	4.35	–	–	–	–	–
HSLD	2	4.56	0.1000	4.46	4.66	0.1414	3.10
MSD	12	2.09	0.3532	0.15	3.89	1.2236	58.50
Lbas	12	3.02	0.0322	2.75	3.10	0.1116	3.70
EL	13	0.67	0.1111	0.30	1.7	0.4008	59.61
HH-index	1	6.37	–	–	–	–	–
HH/L	1	228	–	–	–	–	–
HSD/L	1	155	–	–	–	–	–
HSLD/L	2	160	6.31	154	166	8.93	5.58
Hsl/Hslid	1	93	–	–	–	–	–

Lagurini, which is lacking in *Lemmiscus*, is the so-called lagurine foramen (Zazhigin 1980) or *foramen lagurinum*, the small opening for a nerve or blood vessel on the mesiodorsal surface of the mandible, below the antero-internal part of first lower molar. A conspicuous dental character shared by *Lemmiscus* and Lagurini is the so-called *Lagurus* fold in the lingual reentrants of the upper molars (R. Martin 1989). However, *Lemmiscus* has a distinct pattern of these indentations including their presence in posterio-internal reentrant angles of the M1 and M2, a character never observed in lagurines. Moreover, additional enamel folds frequently occur in molars of different groups of rootless voles, including, for example, *Arvicola*, *Microtus*, and *Alticola*. Thus, these characters likely originated in parallel in many lineages as an apparent way to strengthen the molar structure, rather than representing remnants of ancestral cusped elements (Martin 1989) such as a 'protoconule' (Hinton 1926).

Another important dental feature common to both *Lemmiscus* and *Lagurus* is the additional dentine tract in the lower m1. In the evolution of the dentition of voles, the dentine tracts originated in primitive rhizodont forms from undulations of the enamel-dentine boundary. With increasing hypsodonty, dentine tracts also grow, serving as anchoring zones of molars in the alveoli (L. Martin 1979; Rabeder 1981). After the evolutionary acquisition of rootlessness in molars, dentine tracts were transformed into permanent interruptions of the enamel wall present in molars for most of the animal's life. Only in unerupted or hardly worn teeth of juvenile rootless voles can the uninterrupted tips of dentine tracts still be observed. The number and

positions of the dentine tracts are stable in molars; they are regarded as an important taxonomic character. Normally, many arvicoline lineages have only three basic dentine tracts in the first lower molars: two at both sides of the posterior loop and one at the anterolabial side of the anteroconid. The first lower molars of *Lemmiscus* and *Lagurus* both have, apart from the normal arvicoline set of tracts, an additional tract along the BRA4 or T6. This tract topologically and homologically corresponds to the *Mimomys*-ridge, a feature that is particularly well-developed in Eurasian voles of the genera *Mimomys* and *Borsodia*. This ridge often bears an additional dentine tract (*mimosinuid*, according to the terminology of Rabeder); the development of that tract is variable. However, mimomyoid features, including the ridge and the corresponding tract, are usually reduced in most lineages with an increasing hypsodonty of the molars. None of almost 60 extant species of *Microtus* show additional tracts in the T6. The stable presence of this character in *Lemmiscus* and *Lagurus* implies a strong development of the *Mimomys*-ridge and its tract in their rhizodont ancestors. The history and origin of the additional tract in *Lagurus* is relatively well known and can be traced back in time at least to the Early Pleistocene (Biharian LMA) and eventually to early Early Pleistocene (Villanyian) species of the ancestral genus *Borsodia* that had both the ridge and tract (Zazhigin 1970, 1980; Rabeder 1981; Tesakov 1993, 2004). The history of the additional dentine tract in *Lemmiscus* is yet to be traced back in time. In many published accounts, interruptions of the enamel band are frequently not studied and not illustrated. Anyway, though quite rare, this feature

TABLE 2. Measurements and indexes, *Mimomys hordijki*, Zuurland 4, M3

	N	MEAN	MIN	MAX
L	2	1.85	1.85	1.85
W	2	1.01	0.96	1.05
P/L	2	45.95	45.40	46.47
H	2	3.02	3.10	2.94
AS	2	–	2.7	>2.94
PRS	2	–	2.5	>2.7
DS	2	1.36	1.12	1.60
Lbas	2	1.81	1.80	1.82
PA-index	2	–	3.68	>3.99
PA/L	2	–	198.9	>215.7

cannot automatically be considered as a synapomorphy.

Despite of the similarities between *Lemmiscus* and *Lagurus*, taking into account the different arguments mentioned above, it can be stated that a close affinity between *Lemmiscus* and the Palearctic Lagurini should be rejected and most morphological similarities of the two groups may be interpreted as a parallel evolution in conditions of open, steppe-like landscapes.

Looking for Possible Ancestors of *Lemmiscus*

The rejection of an affinity with lagurines and the strong evidence for microtine affinities of *Lemmiscus* provides a clue for the search of an ancestral group for *Lemmiscus*. In fact, Repenning (1992) already assumed that *Lemmiscus* originated from the group of primitive *Allophaiomys* voles, a presumably ancestral group for modern *Microtus*. *Allophaiomys* is hypothesized to have evolved in Eurasia from a group of hypsodont *Mimomys* (*Tcharinomys*) species (*M. gr. tornensis-haplodontatus*) with abundant external cement and a strongly reduced complex of primitive mimomyoid characters such as a *Mimomys*-ridge and enamel islets (Rabeder 1986; Tesakov 1998, 2004).

Lemmiscus is distinct from all the hypsodont *Mimomys* (*Tcharinomys*) species and all descendant *Microtus* species in the stable presence of an additional dentine tract in the m1. On the other hand, a close morphological and genetic similarity to Arvicolini permits the suggestion of a hypothetical *Mimomys* ancestor for the modern sagebrush voles. To fit this hypothesis, the ancestral form should display a strongly developed *mimosinuid* and a dentine tract homological to the additional tract on the sixth dental prism of the m1 of *Lemmiscus*. Although several Eurasian *Mimomys* clades show a developed *mimosinuid* (Rabeder 1981;

Zheng and Li 1986; Tesakov 2004), it is rarely so well-developed as in the Early Pleistocene (Villanyan) *Mimomys hordijki* from The Netherlands and in *Mimomys* (*Cromeromys*) spp. in the Irvingtonian faunas of North America. This fact, combined with the occurrence of the latest *Mimomys* (*Cromeromys*) and earliest *Lemmiscus* in the same Nearctic region, suggests a phyletic link between *Mimomys hordijki* and the genus *Lemmiscus*.

Fossil Record and Morphology of *Lemmiscus*: Testing the *Cromeromys* Origin

The known history of *Lemmiscus* starts in the late Early Pleistocene with the record from the SAM Cave in New Mexico (Repenning 1992; Rogers et al. 2000). The next oldest record is from the sequence of Porcupine Cave in Colorado (Bell and Barnosky 2000; Barnosky and Bell 2003; Bell et al. 2004) ranging in age from latest Early Pleistocene to the Middle Pleistocene. Contrary to the common dental pattern of the m1 with five or more closed triangles in modern *Lemmiscus*, the fossil record shows an increasing number of more primitive four-triangle morphotypes back in time (Barnosky and Bell 2003). A coining of a separate chronotaxon name is recommended for samples with the predominance of this morphology.

The short co-occurrence or time overlap of presumed ancestral (rhizodont) and descendant (rootless) forms in Late Irvingtonian (Bell and Barnosky 2000) do not contradict the hypothesis of a *Mimomys*–*Lemmiscus* phyletic lineage. In fact, it could be the time of a rapid disappearance of molar roots characterized by the occurrence of transitional populations with rooted and rootless morphotypes. The known transitions from rhizodont to arhizodont condition in voles are usually so fast in time that transitional populations are only rarely represented in the fossil record (Tesakov 1993, 2004; Maul et al. 2000).

A hypothetical morphological transition of the m1 morphology from *Mimomys* (*Cromeromys*) to *Lemmiscus* conditions constructed with published examples of dental structure and with regard to geological age is presented in Figure 4. Note the gradual anterior shift of the *Mimomys*-ridge and the successive separation of the dental triangles. If valid, this sequence shows the formation of the sixth dental triangle of the modern *Lemmiscus* from the gradually enlarged *Mimomys*-ridge. The strongly developed *mimosinuid* of *Mimomys* (*Cromeromys*) gave rise to the enamel band interruption at the tip of T6 in *Lemmiscus*.

A similar reconstruction of the transition in morphology of the upper M3 is presented in Figure 5. Note the close morphology of *Mimomys* species (Figure 5: 1–4) and considerable change in the shape of the M3 of the rootless *Lemmiscus* (Figure 5: 5–7). However, such a character as the confluence of AL and T2 can be traced from the *Mimomys* stage to the early *Lemmiscus* (Figure 5: 5). According to Barnosky and Bell (2003), the predominant morphotype of the M3 with a shallow antero-labial re-entrant is characteristic for the Early Pleistocene *Lemmiscus*, and it is completely replaced by a morphotype with deep reentrant in the modern species. Noteworthy is a lack of apparent complication in M3 in rootless *Lemmiscus* parallel to a trend to more complex morphology (addition of dental triangles) in m1s. But given the much smaller amount of material on M3s any straightforward conclusions would be premature at the present state of knowledge.

CONCLUSIONS

New material from the Zuurland borehole (The Netherlands) indicated that *Mimomys hordijki* from Early Pleistocene (Gelasian) level of the Zuurland faunal sequence represents an early stage of the peculiar *Cromeromys* group known from Early Pleistocene (Gelasian to ‘Calabrian’ equivalents) faunas of Beringia and from Irvingtonian faunas of the conterminous United States. *Cromeromys* share characteristic molar morphology of the m1 with a strongly developed *Mimomys*-ridge and without an enamel islet, and of the M3 with a deep LRA3 that is not reduced by insulation (formation of an enamel islet).

This study of the molars of *Mimomys hordijki* indicated a number of similarities between *M. hordijki* and the genus *Lemmiscus*. The general assumption is that the Nearctic sagebrush vole *Lemmiscus* is closely related to the Palearctic lagurines. However, our observations support karyological data that suggest a close relation of this genus to the tribe Arvicolini being a sister taxon of the genus *Microtus*. The morphological similarities between *Lemmiscus* and the lagurines most likely reflect parallel evolution in similar environmental conditions of open landscapes.

During the early Early Pleistocene, *Mimomys* (*Cromeromys*) voles occurred in northern Europe as well as western and eastern Beringia and dispersed to more southern areas of North America in the late Early Pleistocene. Morphological evidence suggests a phyletic transformation of this group of

rhizodont voles into rootless *Lemmiscus* took place at the end of the Early Pleistocene. More studies are required to support or reject the proposed hypothesis.

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