

# Evolution of Plio-Pleistocene voles with the special reference to demographic features of fossil assemblages

**N. E. Kazantseva**

Laboratory of Biogeography, Institute of Geography, Russian Academy of Sciences, Staromonetnyi 29, Moscow 109017, Russia

**A. S. Tesakov**

Laboratory of Quaternary Stratigraphy, Geological Institute, Russian Academy of Sciences, Pyzhevskii 7, Moscow 109017, Russia

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## **Abstract**

*Evolution of the numerous rooted vole lineages in the Plio-Pleistocene gives clear examples of rapid dental changes in the direction of hypsodonty. The relationships between the morphological stages of the molar roots development and the demographic features of vole population have been studied on the basis of several samples of fossil voles and the analysis of modern neontological literature. Young individuals from the beginning of the first to the third month are among the most numerous and vulnerable to environmental influences. The remains of voles of this age dominate in fossil assemblages. Based on this conclusion, the formation of the root system in the ontogenesis of several vole species has been investigated. The following 3 major groups were distinguished according to the ontogenic timing of root formation: in Group A roots are formed among voles of juvenile-adolescent age; in Group B roots are formed among subadult voles; in Group C the root formation occurs among adults.*

## Introduction

The rich material of voles, which evolved intensively in the Pliocene-Pleistocene, provides a wide field for investigation of consecutive dental modifications. The transition from rooted to rootless forms in the lineages *Mimomys* (s.l.) - *Aliophaiomys* - *Microtus*, *Mimomys* - *Arvicoia*, *Clethrionomys* - *Phaulomys*, and *Borsodia* - *Prolagurus* - *Lagurus* were investigated by Von Mehely (1914), Zazhigin (1980), Agadjanian (Agadjanian & Erbajeva, 1983), Rabeder (1987), Kawamura (1988), Tesakov (1993) and many others. The dependence on individual age on factors such as variability of molar occlusal surface, time of enamel islet existence, crown height and the root formation, on the individual age is widely known. L. von Mehely (1914) was among the first to describe the ontogenetic succession of morphological stages in the root formation of rooted voles. Many palaeontologists have subsequently returned to this problem (Suchov, 1970; Von Koenigswald, 1982; Motuzko, 1985; Smirnov et al., 1986; Kawamura, 1988 and others). However, until recently the data on the distribution of ontogenetical stages in fossil assemblages was rarely analyzed from the viewpoint of the demography of the source populations.

## Materials and methods

The authors mainly used original collection materials of the following species: *Mimomys polonicus* Kowalski, 1960 - Upper Pliocene, Nagavskaya locality in the Volgograd region (Zastrozhnov & Kazantseva, 1992); *M. pliocenicus* F. Major, 1902 - Tegelen; *M. reidi* Hinton, 1910 - Upper Pliocene, Tegelen Locality; *Mimomys* ex gr. *tornensis* Janossy & Van der Meulen, 1975 - Tegelen; *Mimomys pusillus*: von Mehely, 1914 - Early Pleistocene, M'inka, layers 4 and 2, (Krasnenkov et al., 1992); *Mimomys savini* Hinton, 1910 (=intermedius Newton, 1881) - Early Pleistocene, Yablonovets locality 2 in the Tambov region (Lieberman et al., 1984); *Borsodia praeungarica* Schevtschenko, 1965 - Upper Pliocene, Kryzhanovka locality 3 (Tesakov, 1994); *Clethrionomys kretzoi* Kowalski, 1958 - Tegelen; *Clethrionomys glareolus* Schreber, 1780 - Upper Pleistocene-Holocene, Luchinskoe in the Moscow region (Tesakov et al., 1993). We have also used the data on *Clethrionomys japonicus* Kawamura, 1988 from the Middle Pleistocene, Ube Kozan locality (Kawamura, 1988).

It was long ago established that during ontogenesis the cheek dentition of rooted voles passes through a succession of distinct stages of root formation (Von Mehely, 1914). High correlation of these stages with the individual age led to their broad use in neontological practice, mainly in the studies of age structure of populations (Koshkina, 1955; Tupikova et al., 1968; Viitala 1971, Basheina, 1981, Olenev, 1989). In palaeontology the distribution of root formation stages have been studied mainly to evaluate the comparative degree of evolutionary ad-

vancement of a certain fossil sample because of a marked reduction of the roots in the course of evolution of all lineages of Arvicolines (Von Mehely, 1914; Suchov, 1970; Topachevsky et al., 1979; Rabeder, 1987; Smirnov et al., 1986; Kawamura, 1988). Here we attempt to synthesize both approaches and involve demographic features into the analysis of fossil rooted voles.

In our investigation we deliberately simplified the distinction of root formation stages in order to increase representativeness of materials and avoid highly split data sequences. We classified molars in the following stages: I - pulp cavity is widely open, re-entrants are not closed at the base (unrooted stage); II - re-entrants are closed at the base and form the crown 'neck' (transitional or intermediate stage); III - pulp cavity is closed and root shafts are formed (rooted stage). Rabeder (1987) distinguished similar stages, namely rhizodont, merorhiz and arhiz. The juvenile stage, characterized by thin, poorly differentiated enamel, is also usually distinguished (Rabeder, 1981, Von Koenigswald, 1982), though it is typically very rare in fossil material. In this study we include the juvenile specimens in the first (arhiz) stage.

## Main features of the evolution of the Pliocene-Pleistocene voles with rooted molars

The Late Pliocene is unique time when a number of lineages of rooted voles demonstrate fast parallel evolution in the direction of increasing hypsodonty. This means that the crown height increases and the roots are gradually reduced. The progressive retardation of the root formation and its shift to later individual age subsequently led to origination of rootless forms which never form roots in their dentition (for details see Von Koenigswald, 1982). The processes is believed to be a reflection of the dietary adaptation to more cellulose-enriched grasses and is characteristic for many groups of the herbivorous mammals. The rooted voles of the late Pliocene show this very intensive evolution and it is possible to use the hypsodonty features in a very detailed stratigraphy and establishing of fine inter-regional correlations.

Morphological changes of the arvicoline molars in the course of the progressive hypsodonty are well known and studied (e.g. Hinton, 1926; Michaux, 1971; Rabeder, 1981; Horacek, 1990). It is primarily crown height increase and reduction of roots. One of the most obvious morphological features tightly associated with the process is the increase of the dentine tracts' height. Dentine tracts (also referred to as sinuous line, *linea sinuosa*, enamel free areas etc.) are the areas of the molar surface not coated with the enamel layer. They serve as the places of periodontal ligament attachments anchoring molars in alveolas. With the reduction of roots the progressing development of dentine tracts take place. Thus, dentine tracts gradually take the role of roots. Finally, in rootless arvicolines, which appeared in the fossil record on the large

scale at the Pliocene-Pleistocene boundary (e.g. *Aliophaiomys* and *Prolagurus*), only dentine tracts attach molars to the walls of alveolas. Dentine tracts have been successfully used in the study of the evolutionary lineages of a number of vole groups (e.g. Nelson & Semken, 1970; Rabeder, 1981; Tesakov, 1993). Rabeder (1981) proposed a thorough system of measurements and terminology of dentine tracts.

In many groups of voles, hypsodonty increase is accompanied by growing accumulation of the external cement in the re-entrant angles of the crown. Like most other hypsodonty-related characters, the external dental cement is not unique for voles and is known in many groups of herbivorous mammals (i.e. horses, bovids, elephants, etc.). Strangely enough, some vole groups never developed external dental cement even in fully rootless (hypsodont) evolutionary stage (Lagurini, Dicrostonyxini).

A number of clearly developed characters are typical for a large group of so-called 'Mimomys' voles (sensu Zazhigin, 1980). This group strongly dominated the Arvicoline communities of the Late Pliocene. Most of the characters in question are typical of the most diagnostic, the first lower and third upper molars. These are the so-called *Mimomys* ridge (= *Mimomys* kante), the additional salient ridge on the antero-external surface of the first lower molar; and enamel islets, ring-shaped parts of the enamel band, actually the hollow enamel column, originated through invagination of antero-external re-entrants in first lower molars and postero-internal re-entrants in third upper molars. With the increase of hypsodonty, the 'Mimomys' characters are shifted to the early wear stages and finally completely reduced. Generally, the 'Mimomys' ridge becomes shorter and disappears with wear in still earlier ontogenetic stages. Insulation (origination of enamel islet) takes place earlier and the depth of the enamel column decreases.

Another important set of morphological features closely related to hypsodonty lies in the histology of the enamel band. Long known directional changes of the thickness of enamel band in the course of evolution of many vole lineages is the development of the changes of enamel microstructure, the Schmelzmuster (Von Koenigswald, 1980).

The geological history of voles, Arvicolinae (Cricetidae, Rodentia, Mammalia) is an example of rapid explosive evolution and adaptive radiation which strongly effected the small mammal communities of the Northern Hemisphere. The history is mainly known from the fossil dental remains. There are several different viewpoints on the systematic and taxonomy of the group. Here we review only very generally the development of voles.

After the origination of voles from the hypsodont hamsters in the late Miocene, by the end of early Pliocene (Ruscinian, MN15) the group occupied the dominant position in communities of small mammals of the Palearctic. This time witnessed the first radiation of voles when the primitive *Mimomys*-Wke forms (*Promimomys* s.l./Cseria)

with the compact anteroconid, the anterior part of the first lower molar, gave rise to *Pliomys* and *Dolomys* range of forms with complex structure of anteroconid (Kretzoi, 1956, Fejfar & Heinrich, 1983). However, extensive adaptive radiation of the subfamily took place during the late Pliocene (Villanyian, MN16 -MN 17) and Early Pleistocene (Early Biharian). Several major stems of Arvicolinae are recognized in the Palearctic during the late Pliocene. The arvicoline assemblages of the Pliocene and Early Pleistocene are dominated by the broad group of *Mimomys* voles. This comprises several genera related to *Mimomys*, like *Mimomys* itself (including (sub)genera *Microtomys*, *Kislangia*, *Cromeromys*, etc.), "*Pusillomimus*" and *Borsodia*.

The contemporaneous *Pliomys* group was differentiated into *Pliomys* proper (with several (sub)genera) and *Clethrionomys*, the direct ancestors of the modern wood backed voles. Large *Dolomys* declined by the middle of the late Pliocene. Apart from *Mimomys* and *Pliomys*, several vole groups existed with simplified dental pattern, like *Ellobius*, *Afganomys*, *Ungaromys*, etc. It is likely that these forms were specialized to burrowing.

All these forms formed roots in their molars and are frequently referred to as rooted voles.

It was mainly the 'Mimomys' group that showed the most intensive diversification and development of hypsodonty. By the very end of the late Pliocene (MN 17) the development of two groups of *Mimomys* voles resulted in the almost simultaneous appearance of fully rootless forms. These are the *Mimomys* S.I. - *Allophaiomys* and *Borsodia* - Lagurini transitions. It is interesting that at least one other group of Palearctic Arvicolines, Lemmini and Dicrostonyxini, had already developed full rootlessness at the beginning of Late Pliocene (MN 16), though their rooted ancestors are unknown.

The development of hypsodonty in almost all lineages of voles has long attracted attention. In most studies the conventional set of characters already mentioned was utilized, including crown height, root length, dentine tracts, etc. The other important side of the process of hypsodonty increase is the consistent shift of the root formation stages in ontogenesis and phylogenesis. Moreover the extensive material on demography of modern voles make it possible to analyze the rich fossil record of Arvicolinae from this point of view.

#### Demographic features of fossil material

Most conventional studies of fossil Arvicolines utilize the morphometric and morphotypic approaches mentioned above. Only very rarely has the distribution of the age classes (as a reflection of the demographic characters of the palaeopopulation) in the fossil material been studied. However, it is evident that many morphological features are closely associated with ontogenetic variability. Therefore, insufficient attention towards ratio of age classes in

fossil samples can lead to a considerable misinterpretation of the degree of its comparative evolutionary advancement. Projection of the data on demographic dynamics of modern populations on fossil material is one of the ways to achieve a general understanding of the demographic properties of a fossil community.

In the modern literature many authors consider the frequency of age groups of fossil samples. Age profiles of large mammals have been constructed (Voorhies, 1969; Klein, Cruz-Uribe, 1983), which characterize burials formed both under catastrophic conditions, with the sudden death of the whole population, and as a result of a gradual, or attritional, mortality occurring in a stable environment. In the former case, the material successively decreases from young to old age groups. In the latter, selective mortality occurred, because the most vulnerable groups died and thus remains of middle-aged animals in a burial are substantially rarer than those of young and old individuals. Korth and Evander (1986) presented age profiles constructed on the basis of the study of small mammals. These authors studied the frequency of occurrence of age groups among a laboratory colony of grey voles (*Microtus*). In the mortality profile they obtained, most individuals belong to the three youngest groups, with the number in the youngest being somewhat lower than the two subsequent ones, whereas in the population age profile it is the most numerous. The decline in the middle part of the histogram, which is typical for attritional mortality profiles of large mammals, is not pronounced. Theoretically, this decline corresponds to lower mortality of middle-aged animals.

Numerous studies on the ecology, structure and dynamics of rodent population numbers, for instance in voles, using different methods, are agreed on one point: on the whole, more of the generally more abundant juvenile and adolescent animals die than adult individuals. The mortality of juvenile specimens varies strongly from year to year, but since the fossil material in small mammal localities accumulated over a long time, the averaged data on long-standing cycles are most valuable. Substantial fluctuations in the structure of both modern and ancient populations of voles result from natural conditions, such as temperature, snow cover, food availability and other factors, as well as from the laws of population dynamics. In this connection, general regularities of the age group relationships in population are of special interest.

The mortality of the youngest group of animals up to 15 days old is relatively small and constitutes about 15% (Buchalczyk, 1970; Bashenina, 1975; Malgunajte & Prusajte, 1981). Evidently, most voles, die in the second or the beginning of the third month. It should be mentioned that the maximum life expectancy in voles is generally about 1.5 -2.0 years (Polyakov, 1977). Tupikova and Konovalova (1971) presented data on reproduction and mortality of modern red voles from the Vyatka-Kama interfluvium, which were collected for 5 years (1960-1964) from

May to August - September. Their material demonstrates that during the whole period the maximum mortality of juveniles occurred during the second month ranging from 35 to 96% of the juvenile population. The results of a three-year investigation of an isolated population of *Clethrionomys glareolus* on an island in eastern Lithuania were reported by Malgunajte and Prusajte (1981). In the mortality dynamics the authors distinguished two periods of increased individual death: the first from leaving the burrow to the getting in a trap, which according to the table of the death dynamics of age groups, corresponds to the end of the first-the second month of life and on the average constitutes 53% of that group (maximum 74%, minimum 34%); and the second, which occurs in the autumn - winter season. On the basis of materials collected in the Il'men' Natural Reserve in the Chelyabinsk region, and in the south-eastern Sverdlovsk region, Gashev (1980) reported that the monthly mortality of bank voles which do not reach maturity ranges from 33 to 83% with a mean of 60% of the juvenile population. Polyakov (1977) published the data on common voles. At different localities of the Vinnitsa region, the percentage of individuals, which did not live till maturity (i.e. which died during the first to third months), varied from 50 to 78% and on the average constitutes 60% of the juvenile population. Among *Microtus socialis* of the Crimea the death of juveniles varies from 92 to 22%, constituting on the average 56% of the juvenile population. Thus, as typical r-strategists, voles show high young individual mortality. Calculations of mortality of young individuals leaving the hole show that through long-standing cycles about 50-60% of voles have died from the end of the first to the beginning of the third month. In this period voles respond particularly acutely to unfavourable conditions and experience strong competition from older, experienced individuals. These facts are well known and have often been described in the literature. For instance, investigations by Panteleev and Terekhina (1976) on water voles showed that most young individuals (sometimes up to 90% of the first litters) die during the spring run-off time, whereas the remaining young animals are driven out by adults to less favourable places, where they starve, lose weight and have higher chances of dying.

In order to evaluate the ratio of vole remains from different age groups in fossil assemblages, in addition to establishment of the most vulnerable ones, it is necessary to take into account changes of the animal's numbers during different phases of the population cycle. During phases of maximum population density the relative mortality of young individuals increases (Bashenina, 1962; Koshkina, 1965; Tupikova & Konovalova, 1971). Therefore, during the long accumulation of material in a primary burial-place and then in a final burial-place (corresponding respectively, to a thanatocoenosis and oryctocoenosis, sensu Efremov, 1950), the over-representation of young individuals increases. We suggest that it is most likely

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that approximately 70-80% of the remains of voles in burials are from animals with an age of one to three months. Another important aspect is the accessibility of a certain age group for avian and mammal predators. These predators are among the most important intermediate links in the formation of fossil assemblages. Young voles that do not leave a hole can rarely be prey, unless their refuge is found and ravaged by carnivores such as martens or foxes. Moreover, finds of juvenile molars in alluvial deposits are few, apparently reflecting their fragility and destruction during transport. In cave localities, where the material is better preserved and transport may be minimal, juvenile teeth are more numerous. In general non-worn vole teeth of individuals younger than 15 days old are so rare that they can be disregarded by convention in evaluating the quantity. A different situation arises with juveniles that have left the nest and begun an independent life. This usually occurs on the third or fourth week after birth. If it is granted that first month animals die as commonly as older juveniles, the period when they can be prey for carnivores is two to three times shorter than that of voles of one to two months old. This is supported by the find of voles in their first month constitute approximately 15-30% of the entire vole assemblage in burials. Therefore, in primary and subsequently secondary assemblages (thanato- and oryctocoenoses) the young, 30-90 day voles, substantially dominate.

**Influence of demographic and evolutionary factors on the composition of ontogenetic stages of root formation in fossil material**

During the Pliocene-Pleistocene the dentition of arvicolines evolved in the direction of increasing hypsodonty and related root reduction. The rate of this process varied substantially in different lineages, though its course, controlled by similar biomechanical factors, appears to have been the same. We have tried to analyze the major simi-

larities and differences in the percentage of molars of several fossil forms from different genera (see Table 1). In figure 1 the relation of arhiz to rhizodont stages is plotted on the abscissa. We call it the arhizodonty index (A). It is suggested that the more numerous are unrooted molars in a fossil species, the longer was the time from tooth eruption to the formation of roots in this species. The solid line represents the percentage for the rhizodont stage, and that the merorhiz stage is shown by the dashed line. As the figure shows, the species are grouped in one of three major classes. The first includes forms with predominately rooted molars; the frequency of the arhiz stage within this group ranges from 0 to 10% and that of the second, from 8-10 to 30%. In the interval from 0.5 to 0.8 A the number of rhizodont teeth abruptly decreases to 20-30%, whereas the transitional stage increases to 50-70%. Beginning from 0.8 A, the number of transitional and rooted stages gradually declines, at first approximately in equal proportion to about 20%, and then the rhizodont stage also decreases. Therefore, increasing hypsodonty leads to a decrease of rooted and a rise of unrooted remains in burial. During this process the representation of the intermediate (merorhiz) stage undergoes an irregular change with an initial rise followed by a subsequent drop. Thus it appears that increase in numbers of merorhiz molars results from the mortality pattern of the voles. The point is that during the time interval from the beginning of root formation to the formation of definitive roots (the first to third months of life) voles are most numerous and most vulnerable.

Characterizing the variability of the occlusal surface of arvicolid molars, Von Koenigswald (1982) noted that the transition from unrooted to rooted molars represented increasing lag in formation of the crown base, the phase preceding that of the root formation. At some level the block in root formation continues beyond the animals life span, and in this case the capacity for root formation is not lost, but only has no time to manifest itself. We sug-

Table 1  
Percentage of root development stages and arhizodonty index (mean values).

species	A (arhizodonty index, I / III)	I arhiz stage %	II merorhiz stage %	III rhizodont stage %
<i>Mimomys polonicus</i>	0	0	8	92
<i>Borsodia praeungarica</i>	0.1	3	25	72
<i>Mimomys pliocaenicus</i>	0.1	5	11	84
<i>Clethrionomys kretzoi</i>	0.1	9	13	78
<i>Mimomys reidi</i>	0.1	9	14	76
<i>Mimomys exgr. tornensis</i>	0.4	21	27	52
<i>Mimomys pusillus (lev.4)</i>	0.5	10	69	21
<i>Mimomys pusillus (lev.2)</i>	0.7	12	70	18
<i>C. glareolus (Hoi.)</i>	0.8	22	51	27
<i>C. japonicus (loc. 1)</i>	2.5	57	20	23
<i>Mimomys intermedius</i>	3.0	60	20	20
<i>C. japonicus (loc.3)</i>	8.9	80	11	9

gest that this model does reflect the actual natural process. The shift of the intermediate stage of root formation to later age groups proceeds in parallel with changes in comparative mortality of different age groups in population. This results in a different representation of this stage in fossil accumulations.

Among more brachiodont forms the development of the first and second phases occurs very rapidly. Their roots are apparently formed early among subadult individuals. Among fossil voles of this stage the rooted molars are dominant. Then, with the beginning of the retardation of the merorhiz stage, roots are formed among older individuals. Finally the time of formation of this stage is completely displaced to middle-aged voles, which are less numerous, more tolerant in stress situations and, therefore, better able to survive. In this case the representation of this group in fossil material is abruptly reduced as compared to previous ones. Later, with retarding of root formation, rooted voles gradually decrease and at last completely disappear. We have a somewhat different situation with the development of the transitional stage. At the initial level, when tooth neck is being formed in young voles, i.e. the re-entrants are closed in the lower part of a crown, though the pulp cavity is still widely open, the number of remains of this developmental phase increases. They markedly exceed the unrooted molars that occur only among the youngest voles with an age of one to one and a half months. When roots begin to be formed among animals not younger than the end of the third to the fourth month, apparently the highest percentage of voles of the transitional stage is observed. For example, among modern *Clethrionomys glareolus*, the transitional

stage occurs during the second-third month, whereas roots are formed on the third-fifth month depending on the seasonal cohort (Koshkina, 1965; Tupikova et al., 1968; Olenev, 1989). In the Holocene locality of Luchinskoe in the Moscow region (Tesakov et al., 1993), molars of *Clethrionomys glareolus* of the transitional phase represent 51% of the total number, unrooted ones 22%, respectively. *Mimomys pusillus* from the early Middle Pleistocene Il'inka locality in the Don basin has a still higher percentage of merorhiz molars, namely, 69% of the total number of *M. pusillus* molars in layer 4 and 70% in layer 2. Arhiz molars constitute 10% and 12%, respectively.

In the course of root reduction, further retardation of crown base formation occurs, and at a certain step the transitional stage is formed only among voles of middle-aged groups. In this case the number of voles with molars of the merorhiz phase in the burial sharply decreases, and unrooted individuals reach the highest quantity. Then the process gradually continues, such that molars of the second and third stages decrease, whereas those of the first one correspondingly rise. In Von Koenigswald's (1982) scheme the increase of the II phase (in the present work it corresponds to part of the arhiz stage), figuratively speaking, acts as a piston gradually driving out the time of formation of the III and then IV phases beyond the life span of the vole. Actually this process is complicated by one more circumstance. Apart from the greater retardation of the beginning of the transitional stage, its duration appears to increase. That is, the influence resulting in a decrease of the rhizodont stage leads to rise in duration of both the arhiz and merorhiz stages.

*Mimomys polonicus* from the Late Pliocene (MN 16) Na-

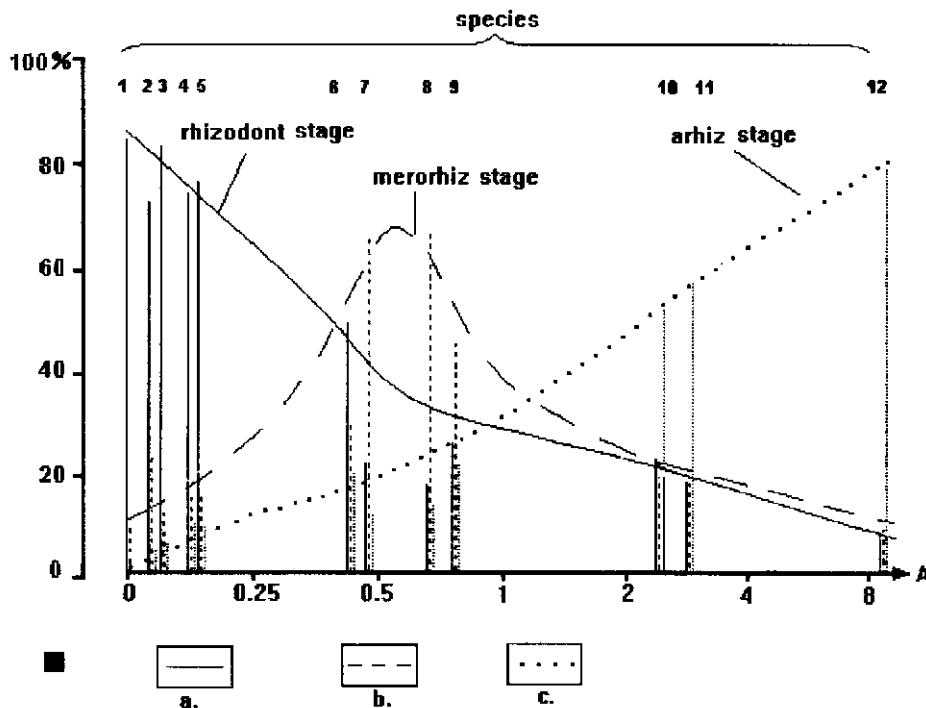


Figure 1  
Percentage of root formation stages in the studied samples.  
a. arhiz stage, b. merorhiz stage, c. rhizodont stage; A- arhizodonty index; species: 1. *Mimomys polonicus*; 2. *Borsodia praehungarica*; 3. *M. pliocaenicus*; 4. *Clethrionomys kretzoi*; 5. *M. reidi*; 6. *M. ex gr. tornensis*; 7. *M. pusillus* (lev.4); 8. *M. pusillus* (lev.2); 9. *C. glareolus* fHoU; 10. *C. japonicus* (loc.1); 11. *M. intermedius*; 12. *C. japonicus* (loc.3).

gavskaya site (Zastrozhnov & Kazantseva, 1992) presents the most primitive sample of material considered in this study. Among its remains there are no unrooted molars, whereas teeth with the formed neck constitute only 8% of the total amount. The arhiz phase of this vole was extremely short, whilst the merorhiz phase, apparently terminated not later than the first month of the voles life and thus is not represented in the fossil material. Among ancient voles *Borsodia praeungarica* (Kryzhanovka 3), *Mimomys pliocaenicus* (Tegelen), *Clethrionomys kretzoi* (Tegelen) and *Mimomys reidi* (Tegelen) the unrooted and transitional stages were most likely formed during the first to the beginning of the second month. The percentage of fossil remains of this ontogenetic level is not yet large, the I and II stages representing together no more than 30% of the molars referred to these species. The duration of the unrooted and transitional stages of recent bank voles is on the average 1-2 months each. The duration of ontogenetic steps and time of root formation vary according to generation. Among spring and early-summer generations roots are formed earlier and the duration of the transitional stage is shorter than among those born at the end of the summer and in the autumn (Olenev, 1989). The more hypsodont grey red-backed vole *Clethrionomys rufocanus* is characterized by a higher ratio of green vegetation in its diet and correspondingly by a greater duration of the unrooted phase. Its merorhiz stage begins in the fourth month, whereas roots are formed in the 8th month, according to Koshkina (1955). Viitala (1971) noted that the majority of wintered grey red-backed voles in the 10th-11th month had already formed roots, except for some individuals. Thus the transitional

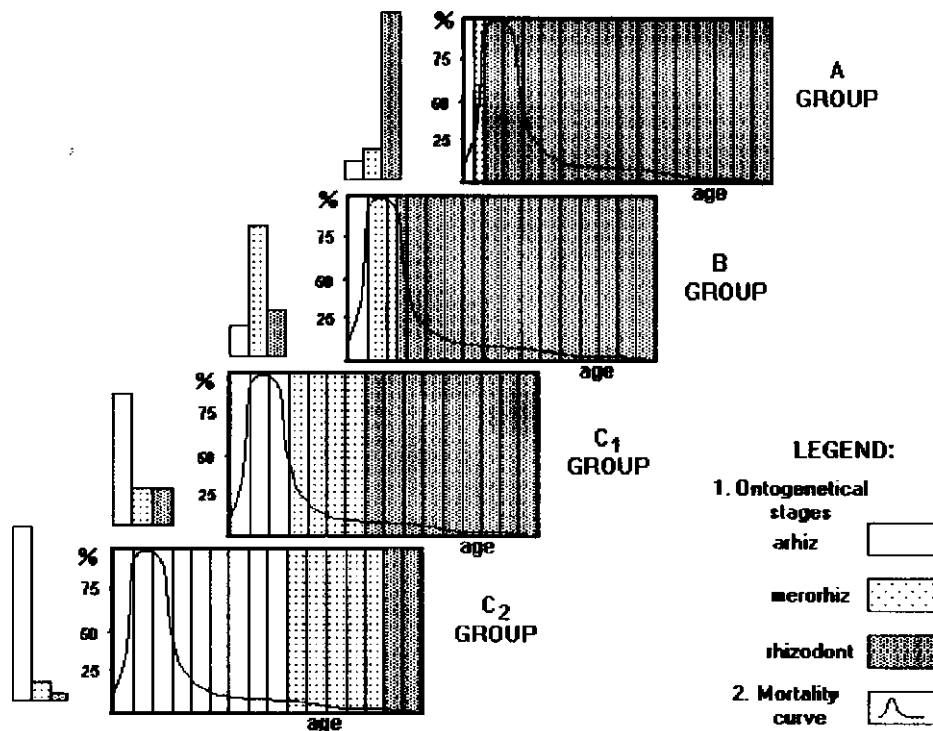
stage, which begins among grey red-backed voles later than among bank voles, lasts for more than 4 months. Figure 2 shows the relationship between reduction of roots and age groups of voles, as well as the possible influence of this process on the percentage of remains of ontogenetic stages in fossil material. Therefore, if molars with the formed roots dominate among fossil remains, we suggest that the rhizodont stage of these species begins at an age of not later than the second month, i.e. in the juvenile, adolescent, and subadult age classes (for details of age groups in voles, see Bashenina, 1981).

We refer to Group A (acquiring roots at juvenile-adolescent age), the Pliocene species *Mimomys polonicus*, *Mimomys pliocaenicus*, *Borsodia praeungarica*, *Clethrionomys kretzoi* and others. The voles *Mimomys intermedius* from the early-late Biharian Port Katon site (Markova collection, Institute of Geography) and *Clethrionomys glareolus* from the somewhat older Sennaya site (Gromov collection, the Zoological Institute, St. Petersburg), are apparently attributable to this group.

When a large proportion of fossils is represented by teeth of the merorhiz stage, the root formation, apparently, occurred no earlier than during the third month of life. These species form Group B. Its members acquire roots at the subadult age. The group includes Late Pleistocene and modern *Clethrionomys glareolus* and modern *C. rutilus*, as well as the Early - Middle Pleistocene *Mimomys pusillus*.

Finally, Group C (root formation among adults) is distinguished. This group includes species with their root formation during (subgroup C1) or after wintering (subgroup C2). The first subgroup includes modern *Clethrionomys rufocanus* as well as Late Biharian *Mimomys intermedius*

Figure 2  
Average mortality (curve)  
and individual time of root  
formation (blocks) in a vole  
species (right), projected to  
the ratio of root stages in its  
fossil assemblage (left).  
Group A, Group B, Group C1,  
Group C2 - groups of species  
(for explanation see text).





and *Clethrionomys japonicus* Uom the Middle Pleistocene deposits of the Ube Kozan quarry (locality 1). The second probably includes the modern Shikotan vole, as well as *Clethrionomys japonicus* from Ube Kozan (locality 3), the possible ancestor of the modern Japanese rootless vole *Phaulomys (Eothenomys) smithii* (Kawamura, 1988). At the next level of evolutionary development roots are not formed during the lifetime or formed so late and rarely that they are almost never represented in fossil material.

#### Application of demographic approach in analysis of Plio-Pleistocene fossil samples

We have studied several collections of Late Pliocene species which belong to the genera *Mimomys*, *Borsodia* and *Clethrionomys*. All these species are attributable to the group A. The most brachyodont form is *Mimomys polonicus* (Nagavskaya, Russia). Its roots were formed very early: by the first or the beginning of the second month of vole life. There were no molars with the open pulp cavity in the collection. A group of other species show equal and a somewhat higher level of development. These are the late Pliocene (MN17) *Borsodia praehungarica* (Kryzhanovka 3, Ukraine), and also *Mimomys pliocaenicus*, *Clethrionomys kretzoi*, and *Mimomys reidi* from the Dutch locality Tegelen. Rooted specimens represent about 70 - 80 % of the total material. Among the samples studied, the highest degree of root reduction is found in *Mimomys* ex gr. *tornensis* (sp. nov; Tesakov, 1998) from Tegelen. The rooted teeth form slightly higher than 50 % of the sample, whereas rootless and intermediate molars do not exceed 21 and 27 %, respectively. Thus, in representatives of the most important vole stems, like *Mimomys-Allophaiomys-Microtus*, *Mimomys-Arvicola*, *Borsodia-Prolagurus-Lagurus* and *Clethrionomys*, by the late Pliocene had molar root formation at the very early ontogenetic stages, most probably in young voles below the reproductive age.

The fastest rate of root reduction was demonstrated by two lineages which gave rise to modern grey voles *Microtus* s.l. (the range of hypsodont *Mimomys-Cromeromys* species) and modern steppe lemmings, *Lagurini* (*Borsodia*).

Large voles of the *Mimomys savini* lineage are the most likely ancestors of the modern water voles of the genus *Arvicola*. These voles retained roots to the early Middle Pleistocene. In the large sample of *Mimomys savini* from the Port Katon locality (Markova, 1982) (late Early Pleistocene, late Biharian, south European Russia) about half of all molars have roots (group A). However, in the terminal Cromerian faunas, at the end of early Middle Pleistocene, this form already belongs to C, group, which means that definitive roots are formed in adults voles of 8-10 months old. For spring generations it is probably late autumn or winter time. The continuation of the process lead to full rootlessness and origination of *Arvicola* in the second part of the Middle Pleistocene.

A still less accelerated rate of root reduction is known in

species of the genus *Clethrionomys*. This is the largest group of modern voles which still have rooted cheek dentition. The modern species predominantly occupy forest habitats and show a considerable 'granivory' in their diet. Among modern *Clethrionomys* of northern Eurasia, *C. rufocanus* has the highest content of the green vegetation in its diet (Vorontzov, 1979). Molar roots in this species are formed much later (group C,) than in more granivorous *C. glareolus* and *C. rutilus* (group B). Bank voles of the *C. glareolus* lineage are a good example of morphological stasis (Chaline, 1987; Tesakov, 1996). The hypsodonty of the modern form (group B) is only slightly higher than in the late Pliocene forms (group A).

On the other hand, it is interesting that the insular conditions in the Far East triggered an accelerated development of hypsodonty in several lineages of *Clethrionomys*. One of the most spectacular examples was studied by Kawamura (1988). He illustrated a transition from the Middle Pleistocene *C. japonicus*, a hypothetical off-spring of the *C. glareolus* stock, to the modern rootless *Phaulomys (Eothenomys) smithii* of Japan Islands. In Middle Pleistocene *C. japonicus* from Ube Kozan locality 1 the rootless (arhiz stage) molars represented over 50 % of the sample (group C,) and 80 % in the Ube Kozan locality 3 (-group C,) (inferred from Kawamura, 1988).

To summarize, at the end of Pliocene the difference in rates of root reduction in different vole lineages become obvious. It was apparently associated with deviant dietary adaptations. Some lineages, like *Mimomys* s.l. - *Microtus* s.l., *Mimomys* s.l. - *Arvicola* and *Borsodia* - *Lagurini* probably proceeded towards the adaptation to more intensive utilisation of green vegetation. They were the first to produce rootless forms. The other direction of development is marked by species of the genus *Clethrionomys*. More mesic habitats and a higher degree of ganivory seemingly enabled the group to retain molar roots. By about 2.0 Ma the considerable differences in the reduction of roots are clear among voles at species and generic levels.

#### Conclusions

The abundant data available on hypsodonty evolution in voles (*Arvicolinae*, *Cricetidae*, *Rodentia*) mainly focus on various dental characters which show transformation in time. The demographic implications of the process are really involved in these studies. In the present work, the ratio of stages of root development in a number of samples have been studied as a function of demographic structure of the vole population considered in its evolutionary aspect.

We have shown that the stages of root development observed in fossil arvicoline assemblages reflect mortality dynamics in populations of voles projected on the hypsodonty evolution in phylogeny. Young individuals of the end of the first to the third month have the highest chances to get fossilized. It is this group that is the most

vulnerable to unfavourable environmental conditions and is characterised by the highest mortality. Remains of the youngest voles not having yet left the burrow (those of the first half of the first month) are rare in fossil material and virtually fail to influence the age composition of a fossil assemblage. The number of molars of adult and old voles, i.e. older than the third month, substantially ranks below that of young individuals and, apparently, does not exceed one third or quarter of the latter. Based on this conclusion we suggest that the group dominating fossil assemblages represents as a rule the ontogenetic phase of a species, which corresponds to the age class of the end of the first to the third month of life. We distinguish three major groups classified by the time of root formation: Group A - roots are formed among juvenile-adolescent voles (1-first half of 2 month of life); Group B - root formation occurs at subadult age (2-3th month of life); Group C - root formation occurs among adults (older than 3th). The latter is divided into two subgroups.

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