

Evolution of bank voles (*Clethrionomys*, Arvicolinae) in the late Pliocene and early Pleistocene of eastern Europe

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Abstract. The morphology and taxonomy of east European *Clethrionomys* is briefly discussed. Special attention is paid to the increase in hypsodonty of the molars. Two major stages of this process have been detected. The initial one, spanning the Pliocene and earliest Pleistocene, is the stage of accelerated hypsodonty increase. The second, Pleistocene, stage is characterized by near stasis in hypsodonty. The beginning of this stage is interpreted as the origination of the modern dietary adaptations of *Clethrionomys*.

Key words: Mammals, voles, *Clethrionomys*, Pliocene, Pleistocene, evolution, hypsodonty.

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I. INTRODUCTION

Voles of the genus *Clethrionomys* have been common members of small mammal communities of the Palearctic since Late Pliocene. The earliest forms, such as *Clethrionomys* sp. from France and *C.* sp. from Lebyazhie in west Siberia, are from faunas of late early Villanyian age, that is late MN16 or early MN17 (CHALINE & MICHAUX 1974; ZAZHIGIN 1980). Since then bank voles have become important components of the small mammal faunas of the Old World. In the modern fauna a few species of *Clethrionomys* are confined to relatively humid forests of moderate latitudes of the Holarctic. Being so closely associated with forests, *Clethrionomys* remains are important indicators of relatively warm and humid conditions during the Pleistocene. *Clethrionomys* is one of few arvicoline genera that retained the roots of the cheek dentition, in contrast to numerous vole lineages that have evolved constantly growing rootless molars.

The fossil record of *Clethrionomys*, the pattern of hypsodonty increase, and its possible interpretation are discussed in this article.

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II. GEOLOGICAL RECORD AND DENTAL MORPHOLOGY OF *CLETHRIONOMYS* IN EAST EUROPE AND WEST SIBERIA

Clethrionomys is a common but relatively sporadic element in Plio-Pleistocene steppe faunas of east Europe and west Siberia (BORODIN 1988, TESAKOV 1993a, TOPACHEVSKY et al. 1987; TOPACHEVSKY & NESIN 1988; ZAZHIGIN 1980).

One of the earliest records of *Clethrionomys* in East Europe is a single first lower molar from the Sablya locality in the north Caucasus (Fig. 3). Advanced *Mimomys polonicus* and *Pusillomimus* cf. *stranzendorfensis* are also known in this fauna. The *Clethrionomys* molar is rather brachyodont and has confluent basic dentine fields and fields of the anteroconid.

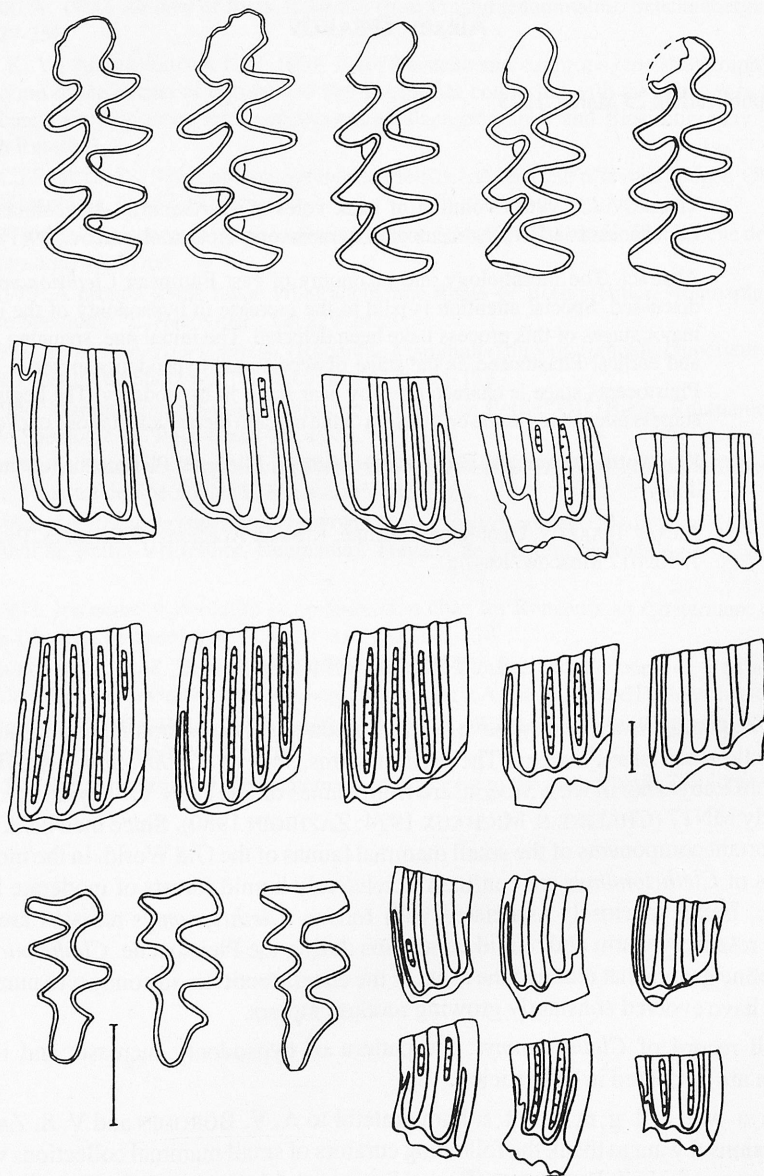


Fig. 1. *Clethrionomys kretzoi* (KOWALSKI), Psekups, north Caucasus. 1 - 5 : M1/1, 6 - 8 : M3/1. Scale 1 mm.

Rare finds of *Clethrionomys* are associated with faunas of the first half of MN17 together with *Mimomys praepliocaenicus* and *Borsodia praeungarica* (Kotlovina 2, Kryzhanovka 3). In west Siberia the earliest find of *Clethrionomys* is associated with the Lebyazhie fauna of the first half of the Late Villanyian, MN 17. Morphologically this form is similar to contemporary east European forms. The HH-index (RABEDER 1981) of the first lower molar ranges from about 1.5 to 2.5 (Figs 4 & 5).

In faunas of the latest Villanyian and earliest Biharian *Clethrionomys* became relatively abundant and widespread. *Clethrionomys* is associated with *Pusillomimus pitymyoides* and progressive *Mimomys* and *Borsodia* species. For the first time *Clethrionomys* had a significant role in the fauna, comprising up to 30% of remains in some forest faunas, like Psekups (VANGENGEM et al. 1990). Other important localities are Kotlovina 3 (upper bed) (TOPACHEVSKY & NESIN 1989), Liventzovka 2 (ALEXANDROVA 1976) and Kryzhanovka 4. In west Siberia these are localities of the Mukkur Suite.

These forms can be classified under the specific name *Clethrionomys kretzoi* (KOWALSKI). They are characterized by broadly confluent dentine fields of the anteroconid (T4 and T5) and anterior cap, and by relatively sparse cement. In M3/ the first buccal reentrant angle (BRA1) is very shallow, being relatively deep only in very young specimens (Fig. 1: 6; Fig. 2: 6). No real anterior enamel islet was encountered. The posterior lobe of M3/ displays features of praehintonianus and clethriosimplex morphotypes (RABEDER 1981; CARLS & RABEDER 1988). The posterior root of M/2 has a semipleurorhize condition, shifted slightly buccally from the incisor. The HH-index of M/1 ranges from 2.5 to 3.5-4.0 (Figs 4 & 5).

There is no sharp distinction between bank voles of the latest Villanyian and early Biharian. However, they have a tendency towards separation of triangles of the anteroconid, a larger amount of cement, and stronger hypsodonty. Third upper molars usually have deep BRA1. The HH-index of *Clethrionomys* from advanced *Allophaiomys* faunas ranges from 3.0 to 4.0 (Fig. 5). These faunas are Akkulaevo (SUCHOV 1970), Chertkov (TOPACHEVSKY 1973), and Tsymbal in East Europe; Razdolie (ZAZHIGIN 1980), Romanovo and Skorodum (SMIRNOV et al. 1986) in west Siberia. The molar morphology implies an assignment of these forms to *Clethrionomys hintonianus* (KRETZOI) (RABEDER 1980; CARLS & RABEDER 1988).

III. TAXONOMY AND PHYLETIC LINEAGES

Late Pliocene and Early Pleistocene *Clethrionomys* of east Europe and west Siberia are morphologically similar. They are rather small, with M/1 varying from 2.0 to 2.5 mm. The general appearance of these forms fits with that of modern *C. glareolus* SCHREBER. The concept of RABEDER (1981) concerning a single phyletic lineage with the stages *C. kretzoi* – *C. hintonianus* – *C. acrorhiza* – *C. glareolus* is followed here.

It is likely that the earliest forms of Euro-Siberian *Clethrionomys* from late MN 16 or early MN 17 deserve a separate species status, *C. burgondiae* (CHALINE).

Insufficiently known or aberrant taxa of west European *Clethrionomys* have been discussed in the literature (GROMOV & POLYAKOV 1977; RABEDER 1981).

An alternative concept of two parallel *Clethrionomys* lineages was suggested by V. TOPACHEVSKY (1965). He described a new subgenus of *Clethrionomys*: *Acrorhizamys* TOPACHEVSKY, 1965 for a new species, *C. (A.) sokolovi* from the early Biharian fauna Nogaïsk. Members of this group differ from other *Clethrionomys* mainly in the acrorhizal position of the posterior root of M/2. According to TOPACHEVSKY (1965), *Acrorhizamys* coexisted with nominal "pleurorhizal" *Clethrionomys* throughout the early Pleistocene. GROMOV (in GROMOV & POLYAKOV 1977) later

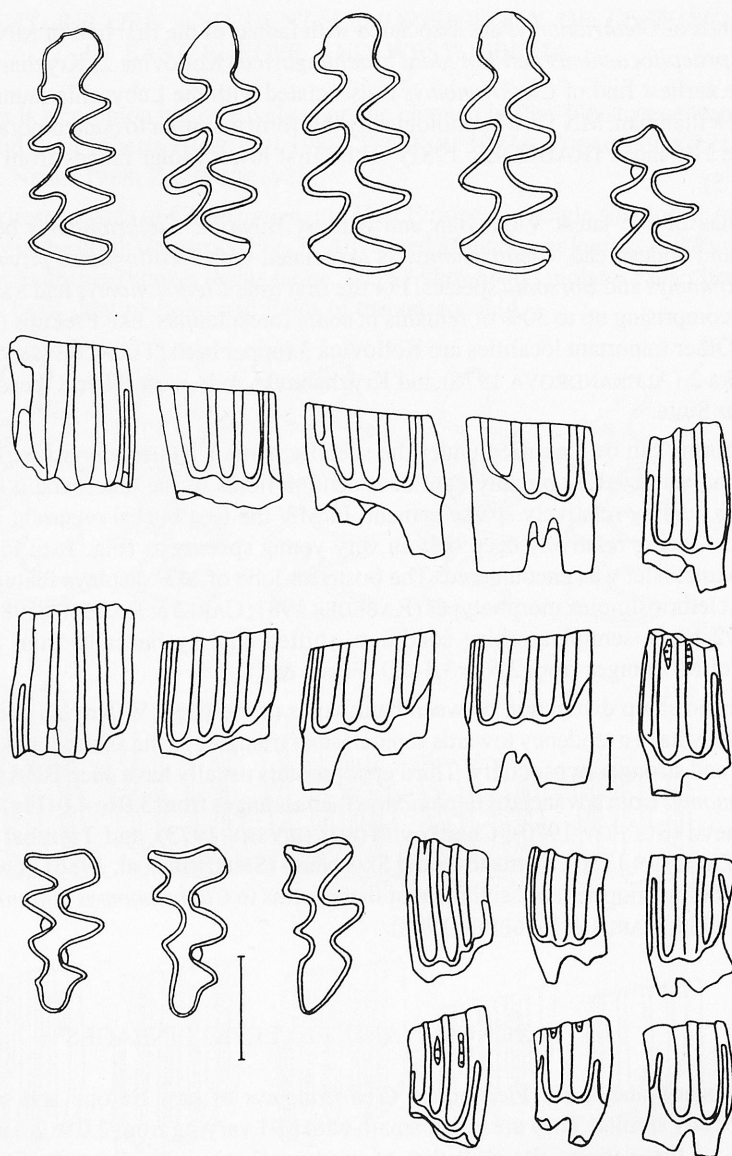


Fig. 2. *Clethrionomys kretzoi* (KOWALSKI), Kryzhanovka 4, Odessa region. 1 - 4 : M/1, 5 : M/2, 6 - 8 : M3/. Scale 1 mm.

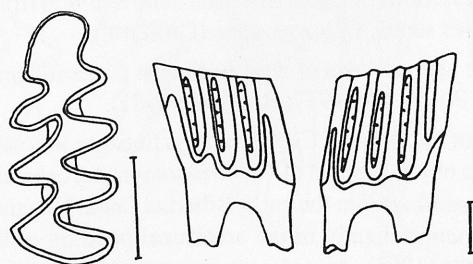


Fig. 3. *Clethrionomys* sp., Sablya, north Caucasus, M/1. Scale 1 mm.

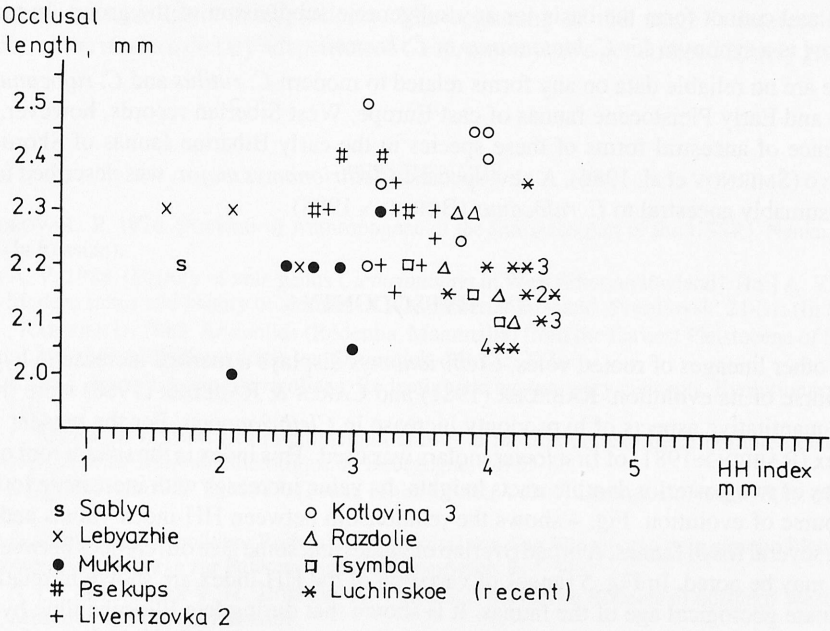


Fig. 4. M₁. Sinugram of *Clethrionomys* from east Europe and west Siberia. HH-index of first lower molar.

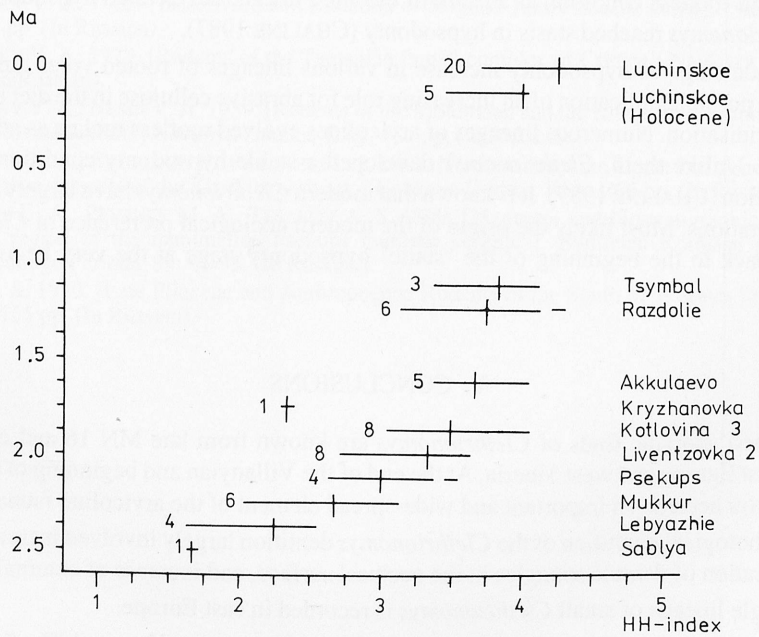


Fig. 5. Range and mean of HH-index of M₁ in various samples of *Clethrionomys* from east Europe and west Siberia. Numbers to the left of ranges indicate the numbers of molars measured.

argued that the position of the posterior root of M/2 is subject to ontogenetic and individual variation and cannot form the basis for any subgeneric subdivision of the group. In most cases *C. sokolovi* is a synonym for *C. hintonianus* or *C. kretzoi*.

There are no reliable data on any forms related to modern *C. rutilus* and *C. rufocanus* in Late Pliocene and Early Pleistocene faunas of east Europe. West Siberian records, however, indicate the presence of ancestral forms of these species in the early Biharian faunas of Skorodum and Romanovo (SMIRNOV et al. 1986). A new species, *Clethrionomys major*, was described for a large form presumably ancestral to *C. rufocanus* (BORODIN 1988).

IV. HYPSONDONTY

Like other lineages of rooted voles, *Clethrionomys* displays a marked increase in hypsodonty in the course of its evolution. RABEDER (1981) and CARLS & RABEDER (1988) were the first to analyze quantitative aspects of hypsodonty increase in *Clethrionomys*. For the present study the HH-index (RABEDER 1981) of first lower molars was used. This index is the square root of the sum of squares of two posterior dentine tracts heights. Its value increases with increasing tooth height in the course of evolution. Fig. 4 shows the relationship between HH-index values and occlusal length in several fossil faunas. A broad overlap of values and some size differences between various samples may be noted. In Fig. 5 ranges of variation of the HH-index are shown in relation to the approximate geological age of the faunas. It is shown that during late Pliocene time hypsodonty increase was much more intensive (twofold) compared to an insignificant increase during all of the Pleistocene. Indeed, even values of early Biharian *Clethrionomys* from Akkulaevo, Razdolie, and Tsymbal broadly overlap those of Holocene and living *C. glareolus* from the Moscow region. The exponential pattern of the curve of HH-index increase is similar to that of the *Borsodia* lineage (TESAKOV 1993b) and to various *Mimomys* lineages. An important difference is that *Borsodia* gained the full rootless condition as a result of the late Pliocene accelerated hypsodonty increase, while *Clethrionomys* reached stasis in hypsodonty (CHALINE 1987).

A common stage of hypsodonty increase in various lineages of rooted voles during the late Pliocene is a possible indication of an increasing role for abrasive cellulose in the diet in the course of general aridisation. Numerous lineages of arvicolines evolved rootless molars as adaptations to grass-eating. Unlike them, *Clethrionomys* developed a stable hypsodonty condition retaining a rooted dentition (CHALINE 1987). It is known that modern *Clethrionomys* have largely granivorous dietary adaptations. Most likely the origin of the modern ecological preference of *Clethrionomys* thus dates back to the beginning of the "static" hypsodonty stage at the very beginning of the Pleistocene.

V. CONCLUSIONS

1. The first sporadic finds of *Clethrionomys* are known from late MN 16 and early MN 17 faunas of east Europe and west Siberia. At the end of the Villanyian and beginning of the Biharian *Clethrionomys* became an important and wide-spread element of the arvicoline fauna.

2. Morphological evolution of the *Clethrionomys* dentition largely involved increase in hypsodonty, separation of dentine triangles in the occlusal surface, and increase of external cement.

3. A single lineage of small *Clethrionomys* is recorded in east Europe.

4. Two major stages of hypsodonty increase in *Clethrionomys* were detected. The first, spanning the Pliocene and earliest Pleistocene, is the stage of accelerated hypsodonty increase related to progressing aridisation of landscapes and growing role of abrasive cellulose in the diet. This stage

is shared by most arvicoline lineages of the Late Pliocene. The second, Pleistocene, stage is characterized by near stasis in hypsodonty. The beginning of this stage is interpreted as the origination of the modern dietary adaptation of *Clethrionomys* as a generalized largely granivorous form.

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