Early evolutionary stages of pitymyoid mimomyine voles  
(*Pitymimomys*, Arvicolinae, Cricetidae) from the Early Villanyian of Eastern Europe

Estadíos evolutivos tempranos de los topillos mimomyinos pitymyoides (*Pitymimomys*, Arvicolinae, Cricetidae) del Villanyense Temprano de Europa Oriental

Alexey S. Tesakov

**Abstract.** Rhizodont voles belonging to the *Mimomys pitymyoides* group are common elements of the European small mammalian faunas from Middle Pliocene to earliest Pleistocene. These voles with characteristic dental morphology are assigned to the genus *Pitymimomys* TESAKOV, 1998. The Early Villanyian evolution of the group is studied on the basis of the sequence: *P. inceptor* sp.nov., *P. altenburgensis* (RABEDER, 1981), and *P. baschkiricus* (SUCHOV, 1970).

**Key words:** Arvicolinae, voles, Pitymimomys, Pliocene, Villanyian, evolution, hypsodonty.


**Palabras clave:** Arvicolinae, topillos, Pitymimomys, Plioceno, Villanyense, evolución, hipsodencia.

**INTRODUCTION**

The spectacular biostratigraphic synthesis of the Spanish continental Neogene presented by Remmert Daams and colleagues serves as a landmark for researchers in other parts of the world. A good example is the plio-pleistocene arvicolid succession in Europe. Despite a dense fossil record, the phyletic history and biostratigraphic applications of many lineages are often far from being established in detail.

After the description of *Mimomys pitymyoides* by D. JÁNOSSY and A. VAN DER MEULEN (1975) it became clear that this phyletic line of mimomyine voles is very widespread and had a long history in the European middle and upper Pliocene (for a review see TESAKOV, 1998). The species name was coined to refer to the similarity of the triangle confluence pattern in the fossil form to modern subterranean voles of the *Microtus* (*Pitymys*) group. The unique structure of wide confluence of some triangular fields in the occlusal pattern of cheek teeth enables easy identification even with a limited amount of fossil remains.

An evolutionary model for the pitymyoid *Mimomys* forms was presented by G. RABEDER (1981). He reconstructed a lineage: *M. altenburgensis* - *M. stranzendorfensis* - *M. stenokorys* - *M. jota* - *M. pitymyoides*, and showed a directional restructuring of dental morphology with increasing confluence of pitymyoid triangles, hypso-

The minimum set of dental characters that defines the genus *Mimomys s.s.* (Zazhin, 1980; Tesakov, 1998) includes crown cement, negative enamel differentiation, and the single (posterior) enamel islet in third upper molar. This combination is believed to mark a closely related group of voles, rather than merely an evolutionary grade of hypodonty. The voles with this morphology appeared by the end of Russian or the beginning of Villanyian throughout the middle latitudes of Palearctic. It is suggested to differentiate from *Mimomys* a variety of mimomyine species of early-middle Pliocene in which the plesiomorphic proto-*Mimomys* morphology camouflage dates of a number of distinct arvicoline groups. One of these lineages is the pitymyoid one. The pitymyoid voles (Tesakov, 1998, Tesakov, in prep.) acquired “Mimomys” characters in parallel with, and somewhat later than true European Pliocene *Mimomys* species.

Moreover, *M. pusillus*, the type species of *Pusillominus* Rabeder, is morphologically successive (Tesakov, 1998) to a well known lineage of middle-late Pliocene smaller true *Mimomys* species (*M. ex gr. hintoni-reidi*). It is obviously unrelated to the pitymyoid group, contrary to the concept of Carls & Rabeder (1988). Therefore, the replacement name *Pitymimomys* Tesakov, 1998 was proposed for the group of pitymyoid species.

Revision of early Middle Pliocene small mammal faunas of Eastern Europe revealed the presence of a new, still more primitive form of the pitymyoid voles described below.


**TERMINOLOGY AND ABBREVIATIONS**


**SYSTEMATIC DESCRIPTION**

Order Rodentia Bowdich, 1821
Family Cricetidae Fischer, 1817
Subfamily Arvicolineae Gray, 1821
Genus *Pitymimomys* Tesakov, 1998

**Diagnosis (emend.):** Medium sized forms. Cement scarce; may be absent in primitive species. Schmelzmuster - pachyknerme. Molars with broadly confluent triangles T2 - T3 (proto- and metaconid) in first lower molars, T1 - T2 (proto- and paracone) in first upper molars, and T2 - T3 (para- and hypocone) in second and third upper molars. In less advanced species the BRA3 in m1, and BRA1 and LRA2 in M3 are reduced with the formation of enamel islet.

**Differentiation diagnosis:** *Pitymimomys* differs from all genera of *Mimomys* group in characteristic confluence pattern.

**Type species:** *Mimomys pitymyoides* Jánossy & van der Meulen, 1975.

COMMENTS

In addition to the main distinctive feature, the specific confluence pattern, *Pitymimomys* differs from *Mimomys* in presence of the anterior enamel islet in M3 in primitive species, by sparse cement, and by less developed *Mimomys* differentiation of enamel; from *Cseria* and *Borsodia* in presence of crown cement; from *Cseria* also in higher hypsodonty; from *Borsodia* also in presence of enamel islet in anteroconid of m1 in primitive species; from *Cromeromys* in persistent reduction of LRA2 in M3 through insulation.

*Pitymimomys inceptor* sp. nov.


Derivatio nominis: Latin *inceptor* - beginner.

Diagnosis: Dentine tracts in m1 less than 1.5 - 2.0 mm. HH-index not higher than 2.0. Enamel islets in m1 and M3 present. Cement absent.

Locality and geological age: Ripa Skortselskaya, upper Levantine deposits of the base of fifth terrace of Prut River, Republic of Moldova. Middle Pliocene, early Villanyian, MN16a.

Material: Detached cheek teeth: 6 m1, 3 m2, 8 M1, 8 M2, 1 M3 (collection GIN EMM-46b).

Holotype: Right side m1 (collection GIN EMM-46b/22). Dimensions of the holotype: L=2.45; W=1.1; A=1.15; H=3.25; Lbas=2.65; EL=0.7; ASD=3.05; HSD=1.45; HSLD=0.7; HH-index=1.61 (Fig.1:1).

Description: Dentine tracts low, interrupted by wear only in very old specimens with full root development. Enamel in medium and strongly worn teeth with negative differentiation. Cement absent. Reentrants straight in younger specimens and vergent in older ones. Elements of occlusal surface connected by wide dentine communications of two or more enamel band thickness.

m1 (Table 1). Anteroconid elements widely confluent. Anteroconid is also widely connected with T3. In the holotype, m1 of a very young individual (Fig.1.1), the anteroconid cap bears short juvenile folds. In younger specimens the long axis of anterior cap (AC) lingually inclined, antero-internal reentrant (LRA4) deep. With wear AC becomes more rounded, LRA4 shallows. Relative length of anteroconid (A/L) regularly decreases from 47% in youngest specimen with crown height 3.25 mm to 39% (0.9 mm). Mimomys ridge deep, situated somewhat posterior relative to islet level. Islet of enamel round. Enamel

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Table 1.- Dimensions and indices of *Pitymimomys inceptor* sp. nov., m1.

Tabla 1.- Dimensiones e índices de *Pitymimomys inceptor* sp. nov., m1.
column deep, spans more than half of the crown height. Islet likely closes at rootless stage of crown development and is present at least till crown height of 1.5 mm. Dentine tracts well developed, form height succession ASD-HSD-HSLD (anterosinuid-hyposinuid-hyposinulid). Among tracts of posterior loop, hyposinuid is almost two times higher than hyposinulid. Tract of mimomys ridge is not developed. Molars narrow, average W/L ratio is 44.7 (n=6).

m2. Posterior root situated at the labial of the incisor. Occlusal length varies from 1.55 to 1.67 (n=3). HH-index values: 0.87, 0.88, 1.28. T1-T2 and T3-T4 confluent.

M1 (Table 2). Molars with three roots (Fig.2).
M2 (Table 3). Dentine fields of occlusal surface are confluent (Fig.3). Anterior loop (AL) is subtriangular. Increasing confluence succession is formed by AL-T2; T3-T4; T2-T3. Specimens with two or three roots are equally represented. In older specimens the anterior root tends to be subdivided into two tightly compressed roots.

M3. The single known specimen (Fig.3: 6) has following dimensions: L=1.60; W=0.85; H=2.3; DS=0.65; AS=0.70; PRS=0.80; Lbas=1.55; PA-index=1.06; PL/L=46.88; PA/L=60.44; AS/L=43.75. Occlusal elements widely confluent. Large posterior and anterior islets present. Posterior loop has well expressed external and internal reentrants (BRA3 and LRA3).

COMPARISON

Mimomys baschkirica from Akkulaev (SUCHOV, 1970) (Fig. 4, 5) and M. aff. baschkirica (SUCHOV, 1977) from Simbugino in south-western fore-Urals. These forms differ from P. inceptor sp.nov in higher hypsodonty, cement accumulations, more shallow enamel islets in m1. HH-index of type sample of P. baschkiricus from Akkulaev (fig. 6) varies from 2.66 to 3.5, with the mean 3.19 (n=17), the sample of Simbugino - 2.28-3.55, mean 3.02 (n=19).
Early evolutionary stages of *Pitymimomys* from the Early Villanyian of Eastern Europe

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Table 2.- Dimensions and indices of *Pitymimomys inceptor* sp. nov., M1.

Tabla 2.- Dimensiones e índices de *Pitymimomys inceptor* sp. nov., M1.

![Figure 2. *Pitymimomys inceptor* sp.nov. M1: 1-5 - occlusal surface, a - labial side, b - lingual side. 1 - 46b/66, 2 - 46b/70, 3 - 46b/69, 4 - 46b/72, 5 - 46b/54. Scale bars equal 1 mm.](image)

Figura 2.- *Pitymimomys inceptor* sp.nov. M1: 1-5 - superficie oclusal, a - lado labial, b - lado lingual. 1 - 46b/66, 2 - 46b/70, 3 - 46b/69, 4 - 46b/72, 5 - 46b/54. Escalas igual a 1 mm.
Tesakov

Early evolutionary stages of *Pitymimomys* from the Early Villanyian of Eastern Europe

Table 3.- Dimensions and indices of *Pitymimomys inceptor* sp. nov., M2.

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Figure 3. - *Pitymimomys inceptor* sp. nov. m2: 1; M2: 2-5; M3: 6; 1-6 - occlusal surface, a - labial side, b - lingual side. 1 - 46b/47, 2 - 46b/90, 3 - 46b/85, 4 - 46b/84, 5 - 46b/91, 6 - 46b/30. 1, 4, 5 - inverse. Scale bars equal 1 mm.

Tabla 3.- Dimensiones e índices de *Pitymimomys inceptor* sp. nov., M2.

Coloquios de Paleontologia
Mimomys aff. gracilis and Mimomys aff. baschkirica from Uryv 1 in the Don River middle drainage basin (Agajanian, 1976). Both forms likely represent a single species of small primitive Pitymimomys. According to illustrations of A. Agajanian (1976), the Don form already has the typical confluence pattern of the genus, lacks cement, and is clearly less hypsodont than P. altenburgensis and P. baschkirica. At this stage, the form is regarded to be conspecific with P. inceptor sp. nov.

Mimomys altenburgensis from Deutsch-Altenburg 21 (Rabeder, 1981). This primitive species of Pitymimomys is more hypsodont (fig.6) compared to P. inceptor sp. nov. Besides, P. altenburgensis differs in the presence of cement, and more shallow enamel islets in m1 and M3, more separated dentine fields in masticatory surfaces, and better developed pitymyoid confluences.

Several Early Pliocene (MN15b) forms represent an array of species that may be ancestral to Pitymimomys:

Cseria gracilis Kretzoi from Csarnota 2 (Kretzoi, 1962, Rabeder, 1981). A small vole with low crowned molars and a compact, antero-posteriorly compressed anteroconid on m1. Dentine tracts much lower than in P. inceptor sp. nov. Confluence pattern is also different: dentine connection of T1-T2 is broad, T2-T3 are clearly separated (Kretzoi, 1962, Rabeder, 1981).

Promimomys gracilis from Biteke (Zazhigin, 1980). This small vole from deposits of the Biteke Suite of late Early Pliocene (Zykin et al., 1987) differs in lower dentine tracts, more separated dentine fields and smaller size.

Mimomys postsilasensis from Deutsch Altenburg 20 (Rabeder, 1981). A small vole with low crowned
molars and very low dentine tracts. The form is more robust, and much less hypsodont compared to P. inceptor sp. nov. and other species of the Pitymimomys group. The concept of this species being an ancestor of P. altenburgensis from Deutsch Altenburg 21 (RABEDER, 1981) is not followed here because both Austrian associations share the primitive M. polonicus of a very similar evolutionary stage. Except for doubtful cement illustrated by G. RABEDER for some molars, M. postsilasensis is not distinguishable from C. gracilis. Therefore, taphonomic contamination of DA 20 assemblage cannot be excluded.

Cseria gracilis from Gundersheim-Findling (FEIFAR & STORCH, 1990) and Wölfersheim (FEIFAR, REPENNING, 1998). Small low crowned vole very similar to the type material from Csarnota 2. The form differs from P. inceptor sp.nov. in much lower dentine tracts, more separated T2-T3 in m1, T2-PL in M3.

DISCUSSION

The newly described form seems to bridge the gap between Late Ruscinian small proto-mimomynine voles and Villanyian Pitymimomys stock. The most obvious morphological predecessor of Pitymimomys inceptor sp. nov. of early middle Pliocene (MN16a) is Cseria gracilis of late Early Pliocene (MN15b). C. gracilis is a good example of a plesiomorphic metaregion of the arvicoline phylogenetic plexus (see MARTIN & TESAKOV, 1998) that could be the source of a number Villanyian lineages of smaller rhizodont voles, like Pitymimomys, Villanyia ex gr. veterior - exilis, Clethrionomys (RABEDER, 1981), etc. However, C. gracilis is too generalized and does not share any advanced characters with P. inceptor sp. nov. Moreover, if there was a phyletic connection between C. gracilis and Pitymimomys spp. a certain character reversal should have taken place. Thus, most pairs of
dentine fields, confluent in pitymyoid condition, are well separated in *C. gracilis*. It is particularly true for the pair of T2-T3 in m1 and T2-PL in M3 (ZAZHIGIN, 1980, p.97: fig.16; FEJFAR & REPENNING, 1998, p.165-166: fig.3:1-3, fig.4: 10-16). The formation of specific confluence pattern begins in *P. inceptor*. The nascent confluent triangular fields are still somewhat subdivided by tips of reentrants. The widest confluences are reached in the upper molars (Fig.2-3).

However, most triangular fields show distinct dentine connections. In this set of characters *P. inceptor* is markedly more primitive compared to more hypsodont *P. altenburgensis*, *P. baschkiricus*, and later species of the lineage.

Cement. The conspicuous feature in the evolution of *Pitymimomys* is the appearance of external cement. Very sparse cement is first recorded at the evolutionary level of *P. altenburgensis* (RABEDER, 1981: Taf. 5, fig.1) and *P. baschkiricus* (Fig.4). The studied material of *P. inceptor* does not show clear evidences of cement accumulations. Acquisition of cement is well known in the course of evolution of some vole genera, as *Ondatra* (MARTIN, 1996) and *Dolomys* (NESIN, 1981).

Enamel differentiation. *P. inceptor* sp.nov. has clear negative or *Mimomys* enamel differentiation with thicker trailing and thinner leading edges of triangle prisms. However, the differentiation is less developed when compared to accompanying *Mimomys* species such as *M. hintoni*, and *M. hajnackensis*.

The schmelzmuster (histological structure of enamel bands) is of the incompletely expressed pachykneme type (RABEDER, 1981), with poorly developed lamellar enamel in the leading edges. The time lag in development of a full pachyknem schmelzmuster, compared to contemporaneous species of true *Mimomys*, is a typical feature in the evolution of *Pitymimomys*. 

Figure 6. - Hypsodonty in m1 of primitive *Pitymimomys* species. Hyposinuid - labial dentine tract of posterior prism. Hyposinulid - lingual dentine tract of posterior prism.

Figura 6.- Hipsodenia en m1 de especies primitivas de Pitymymomys. Hiposinuido - region de la dentina labial del prisma posterior. Hiposinulido - region de dentina lingual del prisma posterior.

![Diagram](image-url)
CONCLUSIONS

Three chronospecies of the Pitymimomys clade of mimomyine voles are recognized in the European Early Villanyian (Fig.6). P. inceptor sp. nov. of MN16a is distinct in low degree of hypsodonty (HH-index of m1 is less than 2.0), deep enamel islets in m1 and M3, and confluent occlusal elements. P. altenburgensis of MN16a/b is distinct in higher hypsodonty (HH-index in m1 varies between 2.0 - 3.0), obvious cement accumulations, and more shallow enamel islets. P. baschkiricus of MN16b is the most hypsodont form (HH-index of m1 is from 3.0 to 3.5), and enamel islets are shallower, with the anterior one in M3 almost reduced.

The origin of the Pitymimomys lineage is tentatively associated with the Late Ruscian Cseria gracilis range of forms.

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REFERENCES


