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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.

Resumen: Los topillos rizodontos pertenecientes al grupo de *Mimomys pitymyoides* son elementos comunes de las faunas europeas de micromamíferos desde el Plioceno Medio hasta el Pleistoceno basal. Estos topillos, con morfología dental característica, son asignados al género *Pitymimomys* TESAKOV, 1998. La Evolucion del grupo duerante el Villanyense Temprano es estudiada sobre la secuencia: *P. inceptor* sp.nov., *P. altenburgensis* (RABEDER, 1981) y *P. baschkiricus* (SUCHOV, 1970).
Palabras clave: Arvicolinae, topillos, *Pitymimomys*, Plioceno, Villanyense, evolución, hipsodoncia.

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, hypsodonty, cement accumula-

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tions, etc. Tesakov (1998) placed *M. baschkirica* (SUCHOV, 1970) in this sequence between *M. altenburgensis* and *M. stranzendorfensis*. G. RABEDER (1981) suggested a phyletic relationship of the pitymyoid forms with the Early Biharian *Mimomys pusillus* (MEHELY, 1914) and assigned them to *Mimomys* (*Pusillomimus*) RABEDER, 1981.

The minimum set of dental characters that defines the genus *Mimomys* s.str. (ZAZHIGIN, 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 hypsodonty. The voles with this morphology appeared by the end of Ruscinian 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 camouflages ancestral forms 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 *Pusillomimus* 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.

One of the earliest Villanyian arvicoline assemblages in the south of Eastern Europe comes from fluviatile deposits of the lower Prut River, Moldova (KONSTANTINOVA, 1967). The rich small mammal assemblage of Ripa Skortselskaya was initially studied by L.P. ALEXANDROVA (1989). The revised vole list contains *Mimomys hajnackensis* FEJFAR, *Mimomys hintoni* FEJFAR, *Pitymimomys inceptor* sp. nov., *Borsodia* cf. *steklovi* ZAZHIGIN, *Dolomys milleri* NEHRING, *Pliomys ucrainicus* TOPACHEVSKY & SCORIK, and *Ungaromys* sp.

TERMINOLOGY AND ABBREVIATIONS

Biostratigraphic assignments follow the scheme of FEJFAR et al. (1998). Elements of the occlusal surface of the arvicoline dentition are after A. VAN DER MEULEN (1973); dentine tracts and hypsodonty indices, after G. RABEDER (1981): HH-index, the square root of the sum of heights of dentine tracts of hypoconid and hypoconulid in lower molars; PA-index, the square root of the sum of heights of dentine tracts of protocone and anterocone in upper molars; ASD - anterosinuid, HSD - hyposinuid, HSLD - hyposinulid, PRS - protosinus, AS - anterosinus, DS - distosinus. Enamel histology and thickness differentiation terms, after W.v. KOENIGSWALD (1980) and R. MARTIN (1989). Lower case m - lower molars, upper case M - upper molars. L - length, W - width, A - length of anteroconid, H - labial crown height, Lbas - basal crown length, EL - elevation of mimomys ridge above crown base of m1, AL - anterior loop; PL - posterior loop. GIN - Geological Institute of Russian Academy of Sciences.

SYSTEMATIC DESCRIPTION

Order Rodentia BOWDICH, 1821
Family Cricetidae FISCHER, 1817
Subfamily Arvicolinae GRAY, 1821
Genus *Pitymimomys* TESAKOV, 1998

Diagnosis (emend.): Medium sized forms. Cement scarce; may be absent in primitive species. Schmelzmuster - pachykneme. 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.

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

Type species: Mimomys pitymyoides JÁNOSSY & VAN DER MEULEN, 1975.

Species content: P. inceptor sp.nov., *P. altenburgensis* (RABEDER, 1981), *P. baschkiricus* (SUCHOV, 1970), *P. stranzendorfensis* (RABEDER, 1981), *P. stenokorys* (RABEDER, 1981), *P. jota* (RABEDER, 1981), *P. 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.
(Fig.1-3. Table 1-3)

1976 *Mimomys* aff. *gracilis* KRETZOI: AGAJANIAN A.K., Polyovki (Microtinae, Rodentia): pp. 79-84, fig.7-8.

1976 *Mimomys* aff. *baschkirica* SUCHOV: AGAJANIAN A.K., Polyovki (Microtinae, Rodentia): pp. 85-89, fig. 9-10.

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

	N	MEAN	SE	MIN	MAX	SD	CV
L	6	2.49	0.0625	2.30	2.72	0.1532	6.16
W	6	1.11	0.0201	1.05	1.20	0.0492	4.44
ASD	4	2.49	0.1951	2.15	3.05	0.3902	15.69
HSD	5	1.31	0.0941	1.00	1.55	0.2104	16.06
HSLD	6	0.59	0.0651	0.35	0.80	0.1594	26.95
Lbas	6	2.58	0.0641	2.30	2.70	0.1571	6.08
EL	6	0.81	0.0539	0.65	1.00	0.1320	16.33
HH-index	5	1.46	0.1030	1.14	1.74	0.2302	15.78
A/L	6	42.71	1.3510	38.60	46.94	3.3093	7.75
HH/L	5	57.82	3.9151	48.56	68.40	8.7544	15.14
HSD/L	5	51.89	3.5744	42.55	60.78	7.9926	15.40
HSLD/L	6	23.68	2.3904	15.22	31.37	5.8553	24.73
Hsl/Hsld	5	2.07	0.1385	1.82	2.60	0.3096	14.96

Table 1.- Dimensions and indices of *Pitymimomys inceptor* sp. nov., m1.
Tabla 1.- Dimensiones e índices de Pitymimomys inceptor *sp. nov., m1.*

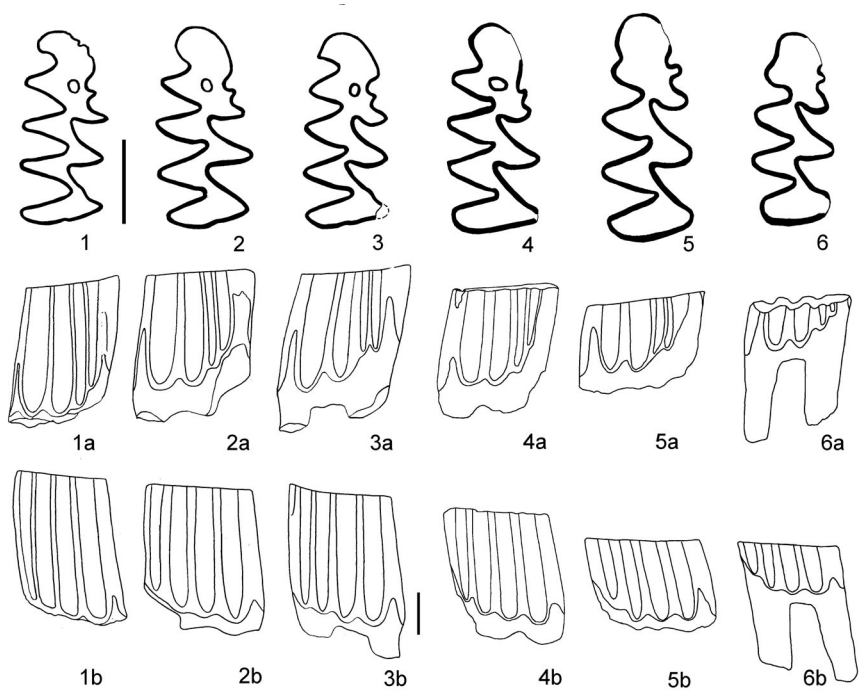

Figure 1.- *Pitymimomys inceptor* sp.nov. m1: 1-6 - occlusal surface, a - labial side, b - lingual side. 1 - 46b/22, 2 - 46b/25, 3 - 46b/23, 4 - 46b/24, 5 - 46b/26, 5 - 46b/29. 1 - holotype. 4-6 - inverse. Scale bars equal 1 mm.
Figura 1.- Pitymimomys inceptor *sp.nov. m1: 1-6 - superficie oclusal, a - lado labial, b - lado lingual. 1 - 46b/22, 2 - 46b/25, 3 - 46b/23, 4 - 46b/24, 5 - 46b/26, 5 - 46b/29. 1 - holotipo. 4-6 - inversos. Escalas igual a 1 mm.*

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=66.44; 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 Akkulaevo (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 Akkulaevo (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).

	N	MEAN	SE	MIN	MAX	SD	CV
L	8	2.20	0.0366	2.05	2.35	0.1035	4.70
W	8	1.18	0.0434	1.00	1.35	0.1227	10.42
DS	6	1.69	0.1332	1.20	2.00	0.3262	19.28
AS	7	0.53	0.0407	0.35	0.67	0.1076	20.25
ASL	8	0.49	0.0448	0.35	0.75	0.1266	25.64
PRS	8	1.23	0.0598	1.00	1.50	0.1690	13.80
Lbas	8	2.21	0.0383	2.05	2.35	0.1084	4.91
PA-index	7	1.37	0.0673	1.15	1.62	0.1780	13.03
PA/L	7	61.98	3.7394	49.12	75.14	9.8935	15.96
AS/L	7	24.16	2.0750	14.89	31.16	5.4900	22.73
PRS/L	8	55.85	3.0668	46.81	69.77	8.6742	15.53

Table 2.- Dimensions and indices of *Pitymimomys inceptor* sp. nov., M1.
Tabla 2.- Dimensiones e índices de Pitymimomys inceptor *sp. nov., M1.*

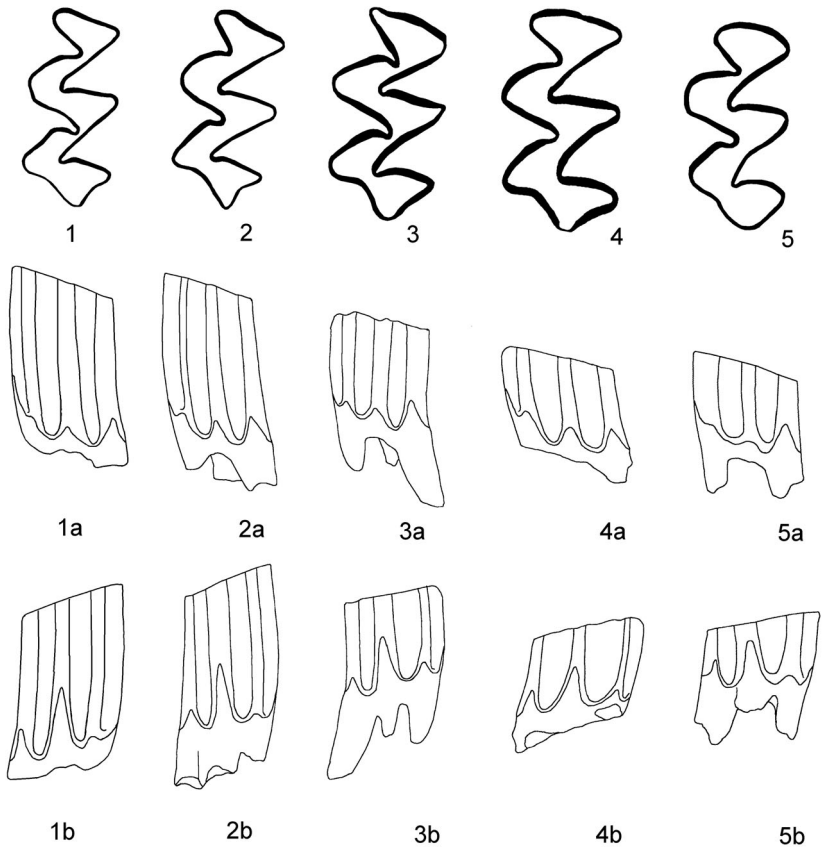

Figure 2.- *Pitymimomys inceptor* sp.nov. M1: 1-5 - occlusal surface, a - labial side, b - lingual side. 1 - 46b/66, 2 - 46b/70, 3 - 46b/69, 4 - 46b/72, 5 - 46b/54. Scale bars equal 1 mm.
Figura 2.- Pitymimomys inceptor *sp.nov. M1: 1-5 - superficie oclusal, a - lado labial, b - lado lingual. 1 - 46b/66,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

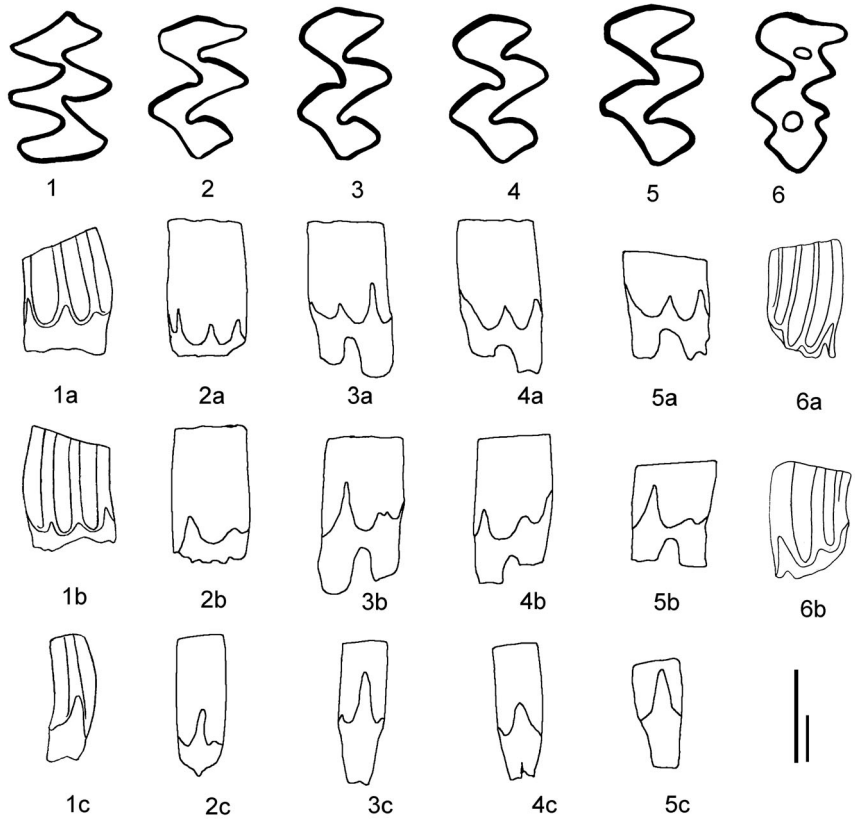

Figure 3.- *Pitymimomys inceptor* sp.nov. m2: 1; M2: 2-5; M3: 6; 1-6 - occlusal surface, a - labial side, b - lingual side. 1 - 46b/47, 2 - 46b/90, 3 - 46b/85, 4 - 46b/84, 5 - 46b/91, 6 - 46b/30. 1,4,5 - inverse. Scale bars equal 1 mm.
Figura 3.- Pitymimomys inceptor *sp.nov. m2: 1; M2: 2-5; M3: 6; 1-6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

	N	MEAN	SE	MIN	MAX	SD	CV
L	7	1.69	0.0333	1.55	1.77	0.0880	5.21
W	8	1.10	0.0162	1.02	1.15	0.0458	4.16
DS	6	1.10	0.0592	0.90	1.30	0.1449	13.17
AS	7	0.60	0.0362	0.50	0.75	0.0957	15.96
PRS	7	0.73	0.1011	0.50	1.30	0.2675	36.71
Lbas	7	1.81	0.0688	1.65	2.20	0.1819	10.03
PA-index	7	0.95	0.1007	0.71	1.50	0.2663	28.09
PA/L	7	56.01	5.5017	44.63	85.76	14.5561	25.99
AS/L	7	35.57	2.1023	28.57	42.86	5.5622	15.64

Table 3.- Dimensions and indices of *Pitymimomys inceptor* sp. nov., M2.
Tabla 3.- Dimensiones e índices de Pitymimomys inceptor *sp. nov., M2.*

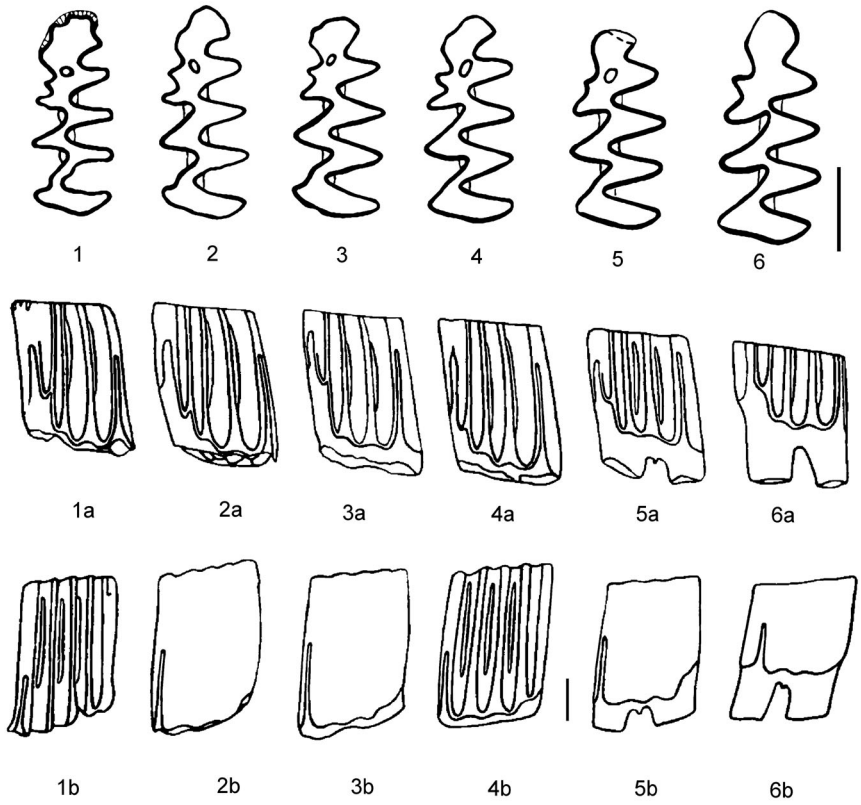

Figure 4.- *Pitymimomys baschkiricus* (Suchov, 1970). m1: 1-6 - occlusal surface, a - labial side, b - lingual side. (coll. of Ufa Institute of Geology). 4 - holotype. Scale bars equal 1 mm.
Figura 4.- Pitymimomys baschkiricus *(Suchov, 1970). m1: 1-5 - superficie oclusal , a - lado labial , b - lado lingual. (coll. del Ufa Institute of Geology). 4 - holotipo. Escalas igual a 1 mm.*

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. baschkirika*. 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

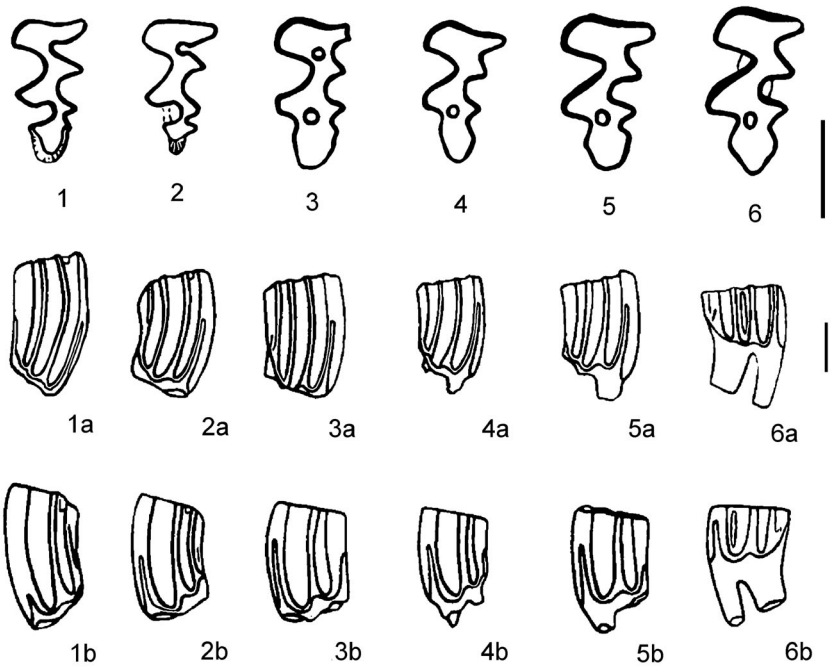

Figure 5.- *Pitymimomys baschkiricus* (Suchov, 1970). **m1:** 1-5 - occlusal surface, a - labial side, b - lingual side. (coll. of Ufa Institute of Geology). Scale bars equal 1 mm.
Figura 5.- Pitymimomys baschkiricus *(Suchov, 1970). m1: 1-5 - superficie oclusal , a - lado labial , b - lado lingual. (coll. del Ufa Institute of Geology). Escalas igual a 1 mm.*

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 (FEJFAR & STORCH, 1990) and Wölfersheim (FEJFAR, 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-mimomyine 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 den-

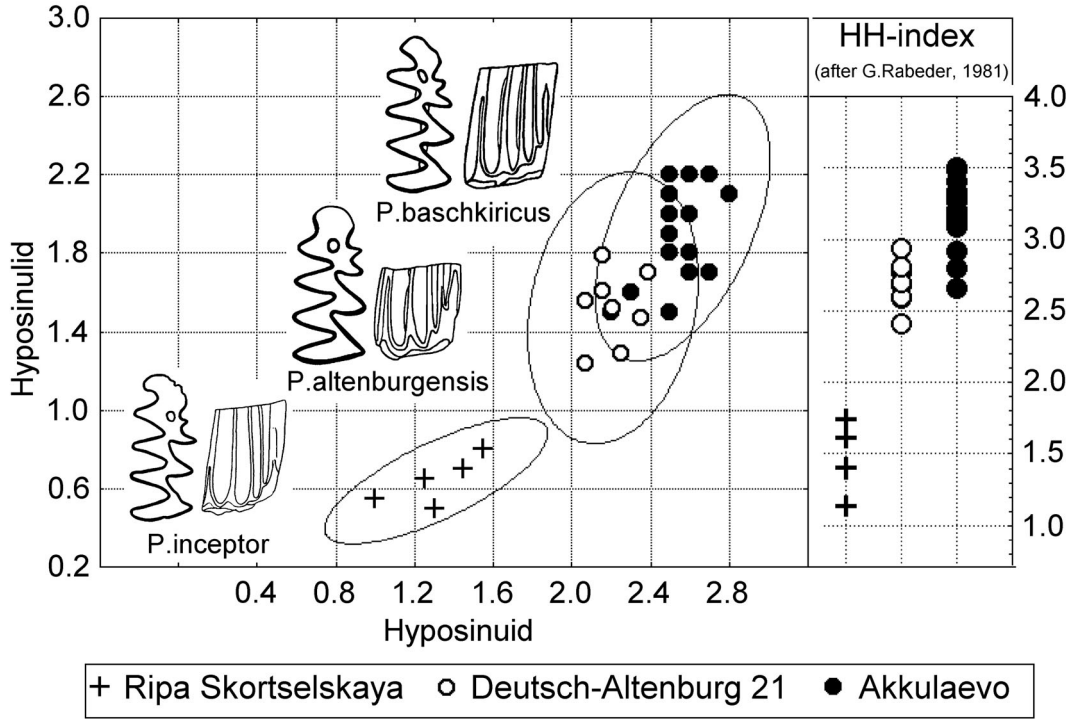

Figure 6.- Hypsodonty in m1 of primitive *Pitymimomys* species. Hyposinuid - labial dentine tract of posterior prism. Hyposinulid - lingual dentine tract of posterior prism.
Figura 6.- Hipsodoncia en m1 de species primitivas de Pitymymomys*. Hiposinuido - region de la dentina labial del prisma posterior. Hiposinulido - region de dentina lingual del prisma posterior.*

tine 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.

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 Ruscinian *Cseria gracilis* range of forms.

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