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Morphology and evolutionary position of the Early Pliocene vole *Propliomys jalpugensis* from Eastern Europe

Albina A. Yakimova, Alexey S. Tesakov* & Natalya V. Pogodina

ABSTRACT. *Propliomys jalpugensis*, a fossil rhizodont vole (late Early Pliocene, late Ruscinian, MN15), is revised based on materials from the type locality Kotlovina (southwestern Ukraine). This form is interpreted as a phyletic stage, marked by dental complication of first lower molar and hypsodonty, intermediate between the preceding late Early Pliocene *Propliomys kowalskii* and *P. destinatus*, and successive Late Pliocene *Propliomys ucrainicus*. Molar enamel of *P. jalpugensis* shows a pattern with the radial enamel in leading edges, occasionally with the incipient lamellar enamel, and the inner radial and outer primitive tangental enamel in trailing and closing edges.

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KEY WORDS: Arvicolinae, enamel microstructure, stratigraphy, Pliocene, Pleistocene, Eastern Europe.

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Морфология и эволюционная позиция раннеплиоценовой полёвки *Propliomys jalpugensis* из Восточной Европы

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РЕЗЮМЕ. Проведена ревизия *Propliomys jalpugensis*, ископаемой корнезубой полёвки (конец раннего плиоцена, поздний русциний, MN15), по материалу из типового местонахождения Котловина (юго-запад Украины). Эта форма представляет собой промежуточную филетическую стадию, диагностируемую по степени усложнения первого нижнего моляра и гипсодонтии, между предшествующими ей *Propliomys kowalskii* и *P. destinatus* конца раннего плиоцена и последующей позднеплиоценовой *Propliomys ucrainicus*. Микроструктура эмали *P. jalpugensis* состоит из радиальной эмали на ведущих краях (иногда с зонами зачаточной пластинчатой эмали) и внутренней радиальной и внешней примитивной тангенциальной эмали на замыкающих и завершающем краях.

КЛЮЧЕВЫЕ СЛОВА: Arvicolinae, микроструктура эмали, стратиграфия, плиоцен, плейстоцен, Восточная Европа.

Introduction

Fossil rhizodont voles of the genus *Pliomys* Mehely, 1914 are indicative elements of arvicolid assemblages in Early Pliocene and earliest Late Pliocene of Eastern Europe. Several successive chronospecies show a rapid morphological evolution. *Pliomys jalpugensis* Nesin, 1983 is a relatively primitive species known so far from the single locality Kotlovina in SW Ukraine. Nesin (1983) and Topachevsky & Nesin (1989) described two co-occurring species of *Pliomys* from the middle bed of this locality, *P. jalpugensis* and *P. ucrainicus topachevskii* Nesin, 1983. Recently we began a revision of Kotlovina arvicoline materials (Yakimova *et al*., 2019; Yakimova, 2020). The main goal of the present contribution is the detailed description of dental morphology and the first study of enamel microstructure of the primitive pliomyine vole *P. jalpugensis.*

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The Kotlovina locality (Odessa region, Ukraine) is known for its rich and diverse fauna of small mammals of the Plio-Pleistocene age (Alexandrova, 1965; Konstantinova, 1965, 1967). The fauna is dominated by voles (Arvicolinae, Rodentia). Ukrainian researchers divided the lithological sequence into three fluviatile members corresponding to separate cycles of sedimentation and collected a large material on small mammals from each unit. Erosional unconformities are well expressed at the base of the lower and middle members. Each member contains bone-bearing layers that differ in the species composition of mammalian fauna (Topachevsky & Nesin, 1989). It was shown that the lower member was formed in the Early Pliocene (Moldavian faunal complex), and the middle and upper members, in the Late Pliocene (Khapry faunal complex) (Topachevsky & Nesin, 1989). According to the modern chronostratigraphic terminology, the two upper levels characterise the beginning of the Early Pleistocene (Gelasian, Khaprovian faunal unit). A subsequent analysis has shown that the middle and upper members of the locality, in addition to the Late Khaprovian (MN17) association proper, apparently contain several generations of redeposited remains of small mammals of the Early and Late Pliocene. These faunal associations are attributable to late Early Pliocene, Zanclean (Moldavian faunal unit), to Late Pliocene, Piacenzian (Uryvian faunal unit), and earliest Early Pleistocene, Gelasian (Khapry faunal unit) (Tesakov, 2004). Judging from the faunal composition, the materials collected by Konstantinova in the 60-s of the last century are correlated to the middle bed/member of the Kotlovina sequence of Topachevsky & Nesin (1989). The primitive pliomyine vole *P. jalpugensis* is tentatively dated to late Early Pliocene (Yakimova *et al*., 2019).

Material and methods

The study is based on materials stored in the Geological Institute of the Russian Academy of Sciences in Moscow (GIN) and Zoological Institute of the Russian Academy of Sciences in Saint Petersburg (ZIN). These materials were collected by field teams of the Geological and Zoological Institutes of the USSR Academy of Sciences in early 1960-s (Konstantinova, 1965, 1967; Alexandrova, 1965). Currently *Pliomys* collections from Kotlovina are stored in GIN under collection number 689, and in ZIN, under collection numbers ZIN 105447 and ZIN 105448. Additional materials, important for the stratification of small mammal associations of the locality, were studied by the second author (AT) in in the National Natural History Museum of the National Academy of Sciences of Ukraine, Kiev (Tesakov, 2004).

The terminology of occlusal elements of vole molars follows van der Meulen (1973). Terms for enamel-dentine boundary (linea sinuosa) in dentition of rhizodont voles are after 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, DS, distosinus, AS, anterosinus, ASL, anterosinulus, PRS, protosinus. Terminology of the enamel types (radial, lamellar, tangental) and patterns (schmelzmuster) follows von Koenigswald (1980) and Rabeder (1981): eopachyknem, the enamel type combining inner radial and outer primitive tangental enamel in the trailing edges and radial enamel in trailing and closing edges; protopachyknem type, combining radial and primitive tangental to tangental enamel in trailing and closing edges and leading edges with inner incipient (discreet) lamellar and outer radial enamel; leptoknem type, combining lamellar-radial enamel in leading edges and radial enamel in closing edges. Lower case m, lower molars (e.g., m1), upper case, upper molars (e.g., M1). L, length; W, width; A, length of anteroconid; A/L, index of anteroconid length.

Systematic paleontology

Order Rodentia Bowdich, 1821
Family Cricetidae G.Fischer, 1817
Subfamily Arvicolidae Gray, 1821
Genus *Propliomys* Kretzoi, 1959
Propliomys jalpugensis (Nesin, 1983)
Figs 1–7, Tabs 1–6.

Original diagnosis. (Nesin, 1983): *Medium size. Molar enamel is not differentiated. Anterior loop of m1 without evident folds of the second complication of paraconid [=anteroconid]. External reentrant of paraconid is blunt or has traces of early disappearing (worn) Mimomys ridge. M3 with two enamel islets.*

Emended diagnosis. Small pliomyine vole with undifferentiated enamel width, eopachyknem to incipient protopachyknem schmelzmuster, low hypsodonty level with HH-index of m1 between 0.5 and 0.9, simple rounded to rounded-triangular anteroconid cap in m1, and M3 with shallow anterior and deeper posterior enamel islets.

Studied material. 15 m1; 6 m2; 4 m3; 8 M1; 8 M2; 11 M3.

Measurements are tabulated in Tables 1-6. The length and width of the type are 2.55 × 0.95 mm (Nesin, 1983).

Locality and geological age. Kotlovina, Odessa Region, Ukraine. Taphonomically mixed association including material of late Early Pliocene (MN15), Late Pliocene (MN16), and Early Pleistocene (MN17) age.

m1 (Figs 1, 6, 7, Tab. 1). Two roots. A third small labial rootlet presents on three out of 15 teeth. In the lateral aspect, some crowns show a characteristic bulge of the anterior side outline (Fig. 1: 3). T1 and T2 are confluent. T4 is well separated, T5 demonstrates a wide connection with the anterior loop (wider than that of T4–T5). The anterior loop is of the rounded or triangular shape. The anterior cap of juvenile specimens can bear a poorly developed reentrant angle (LRA5) on the lingual side (Fig. 1: 1). The tips of T4 and T5 are more blunt,

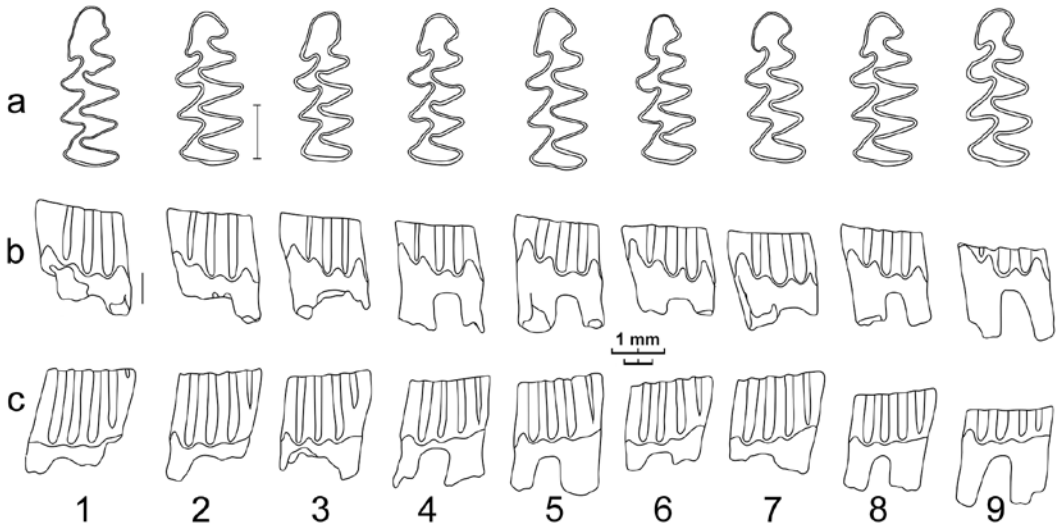


Fig. 1. First lower molars, m1, of *Pliomys jalpugensis*. a — occlusal view, b — labial view, c — lingual view; 1 — GIN-689/003, 2 — GIN-689/004, 3 — GIN-689/005, 4 — GIN-689/006, 5 — GIN-689/007, 6 — GIN-689/008, 7 — GIN-689/009, 8 — GIN GIN-689/010, 9 — GIN-689/011. 2, 4, 6, 7 — reversed. Occlusal and lateral scales, 1 mm.

Table 1. Measurements and indexes of m1, *Propliomys jalpugensis*.

	n	Mean	Min	Max	SE	SD	CV
L	15	2.76	2.33	3.02	0.049	0.191	6.91
W	15	1.10	0.99	1.30	0.024	0.094	8.54
ASD	12	0.90	0.47	1.21	0.062	0.213	23.59
HSD	15	0.54	0.42	0.69	0.023	0.090	16.79
HSLD	15	0.30	0.20	0.48	0.025	0.099	32.49
LBAS	15	2.84	2.69	3.15	0.034	0.132	4.66
HH-index	15	0.62	0.48	0.84	0.028	0.109	17.44
A/L	15	0.48	0.40	0.55	0.010	0.039	8.14
Sum of tracts	12	63.63	44.03	77.97	3.073	10.645	16.73

in contrast to the acute tips of the main triangles. BSA3 (tip of T4) is consistently blunt but never shows a well-expressed *Mimomys* ridge.

Two morphotypes of m1 can be defined in the sample of *Propliomys jalpugensis* from Kotlovina. Both morphotypes do not differ in size and height of the dentine tracts and are partly wear dependent. The first, typical morphotype, *jalpugensis,* has a characteristic wide confluence of rounded-triangular anterior loop and T5, reentrant angles curved anteriorly (Fig. 1: 4). About 75% of the sample belongs to this morphotype. The second morphotype, *ucrainicus*, shows features that bring it closer to *Propliomys ucrainicus topachevskii*: an almost complete separation of T5, a triangular anterior loop, a weak tendency of the reentrant angles to bend anteriorly, dentine elements appear as isosceles triangles, with the very weak curving of the walls (Fig. 1: 6).

m2 (Fig. 2, Tab. 2). Two roots. The posterior root is acrorhizal. Pairs of occlusal triangles, T1 and T2, and T3 and T4 are broadly confluent. Lingual reentrants are deeper than labial ones. The antero-lingual reentrant (LRA3) represents a right angle in the high-crown molar (Fig. 2: 1), and modifies into a blunt reentrant with wear (Fig. 2: 2). The anterosinuid is sometimes complicated by a variably expressed tract of the adjacent BSA3 thus acquiring a doubled tip (Fig. 2: 1b).

m3 (Fig. 2, Tab. 3). Two roots. Pairs of occlusal triangles, T1 and T2, and especially T3 and T4 are broadly confluent. The antero-lingual reentrant (LRA3) represents a right angle in juvenile teeth, and becomes obtuse with wear (Fig. 2: 4a, 6a).

M1 (Fig. 3, Tab. 4). Three roots. Tips of reentrant angles of the labial and lingual sides have a tendency to bend posteriorly. The postero-lingual reentrant (LRA3) shows a wear-dependent transformation from right to obtuse angles (Fig. 3: 2, 3).

M2 (Figs 3, 5, Tab. 5). All studied molars have three roots. The pulpar cavities of the anterior roots are divided, although there is a tendency for subsequent fusion of these roots. The anterior prism has a triangular shape. Tips of reentrant angles bend posteriorly. The postero-lingual reentrant (LRA3) is close to right angle (Fig. 3: 4, 6).

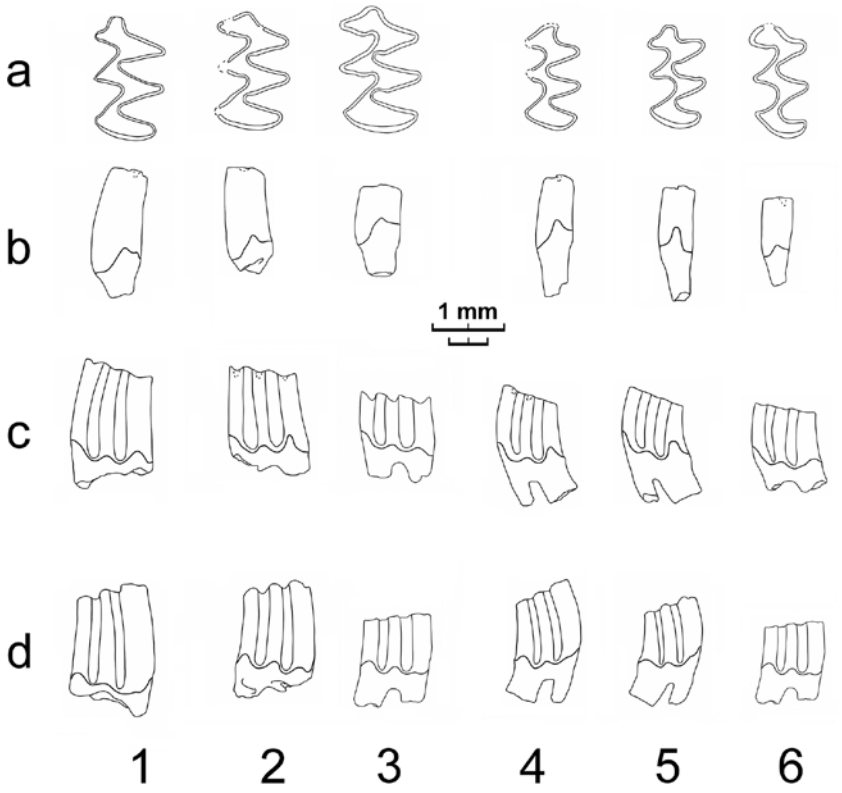


Fig. 2. Second (1–3), m2, and third (4–6), m3, lower molars, of *Pliomys jalpugensis*. a — occlusal view, b — dorsal view, c — labial view, d — lingual view; 1 — GIN-689/050, 2 — GIN-689/054, 3 — GIN-689/056), 4 — GIN-689/059, 5 — GIN-689/062, 6 — GIN-689/064. 1, 4, 5 — reversed. Occlusal and lateral scales, 1 mm.

Table 2. Measurements and indexes of m2, *Propliomys jalpugensis*.

	n	Mean	Min	Max	SE	SD	CV
L	6	1.66	1.58	1.75	0.031	0.076	4.57
W	6	0.99	0.9	1.12	0.03	0.073	7.43
ASD	6	0.58	0.38	0.75	0.05	0.122	20.93
HSD	6	0.32	0.28	0.36	0.012	0.031	9.4
HSLD	6	0.28	0.24	0.31	0.011	0.027	9.58
HH-index	6	0.43	0.37	0.48	0.016	0.04	9.27

M3 (Fig. 4, Tab. 6). Two roots. The anterior root is somewhat flattened in the transverse direction. Elements of occlusal surface are broadly confluent; the narrowest isthmus is between T2 and T3. The confluence of anterior lobe and T2 widens with wears. The posterior loop has a shape of a rounded rhombus. LRA3 is deep (Fig. 4: 4). Enamel islets are present in 3 out of 11 teeth: one molar has both anterior and posterior islets (Fig. 4: 1), others have only posterior islet (Fig. 4: 2, 3). The posterior islet disappears at the crown height near 1.83 mm.

Comparison. *Pliomys kowalskii* Schevtschenko, 1965 from Kotlovina, Ukraine (Topachevsky & Nesin, 1989) and Moskovei, Moldova (Schevtschenko, 1965). Molars are smaller with lower height of dentine tracts. First lower molar has a well developed groove on the BSA3.

Pliomys destinatus Tesakov, 2005 from Odessa Catacombs, Ukraine (Tesakov, 2005, and recent additional enamel study). Odessa form differs in a smaller occlusal length of m1, less advanced hypsodonty stage (HH-index is between 0.4 and 0.7), some m1 have a shallow groove along the BSA3 indicating a relic of the *Mimomys* ridge. Radial enamel is located almost along the entire enamel band both in leading and trailing edges. Small irregular zones of discreet lamellar enamel occur in outer parts of the leading edges. Tangential enamel is present in the closing edge.

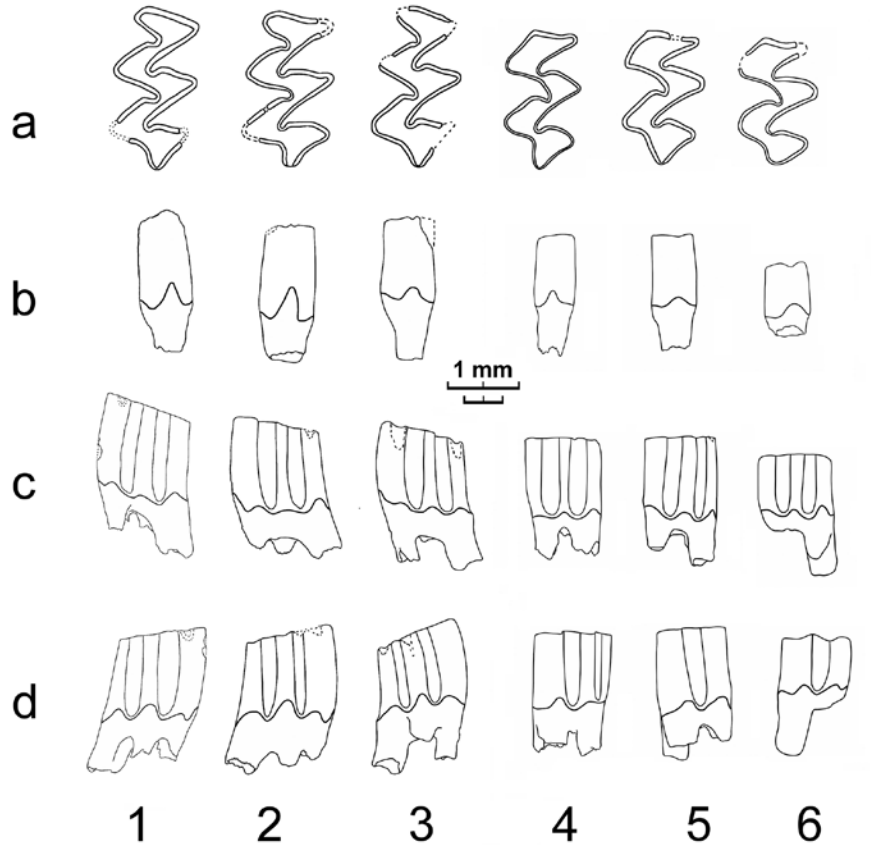
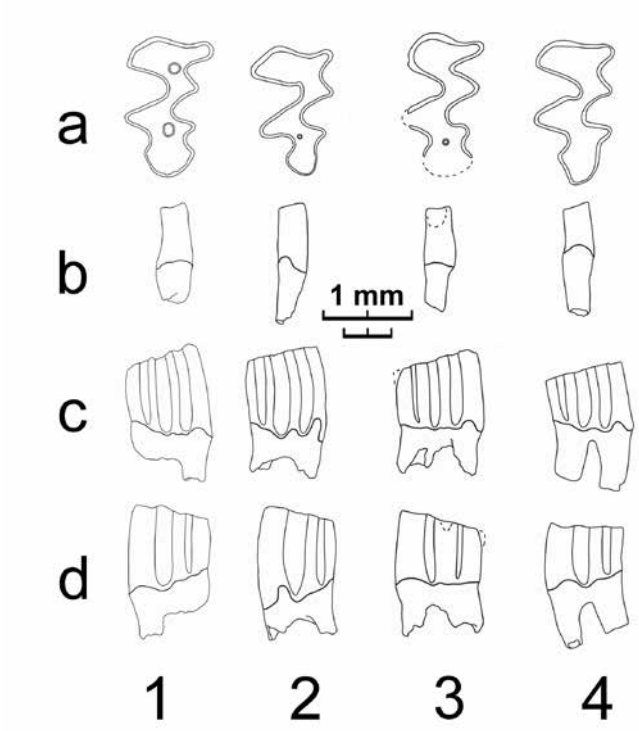


Fig. 3. First (1–3), M1, and second (4–6), M2, upper molars of *Pliomys jalpugensis* (a — occlusal view, b — posterior view, c — labial view, d — lingual view; 1 — GIN-689/013, 2 — GIN-689/017, 3 — GIN-689/020, 4 — GIN-689/025, 5 — GIN-689/026, 6 — GIN-689/031). Occlusal and lateral scales, 1 mm.



Pliomys cf. *destinatus* from Zverinogolovskoye, Russia (Pogodina & Strukova, 2016). This form differs in smaller size, lower dentine tracts and some m1 have a small groove on the BSA3.

Pliomys ucrainicus topachevskii from Kotlovina, Ukraine (Topachevsky & Nesin, 1989). It distinctly differs from *P. jalpugensis* in higher dentine tracts, longer occlusal surface, more complex anterior loop of m1. M3 is somewhat narrower and has a more elongated posterior loop. The discreet lamellar enamel runs along almost the entire leading edge including the tips of salient angles of the tooth, except for the depth of the reentrant angles.

Propliomys hungaricus Kormos, 1934 from Csarnóta 2, Hungary (Kormos, 1934; Kretzoi, 1959). It differs in a longer lower teeth row. Anteroconid of m1 is more complex and shows sharper tips of T4 and T5. *Mimomys* ridge is

Fig. 4. Third upper molars, M3, of *Pliomys jalpugensis* (a — occlusal view, b — posterior view, c — labial view, d — lingual view; 1 — GIN-689/036, 2 — GIN-689/038, 3 — GIN-689/044, 4 — GIN-689/047). Occlusal and lateral scales, 1 mm.

Table 3. Measurements and indexes of m3, *Propliomys jalpugensis*.

	n	Mean	Min	Max	SE	SD	CV
L	4	1.47	1.4	1.54	0.029	0.059	4.01
W	4	0.76	0.67	0.79	0.028	0.057	7.53
ASD	4	0.65	0.54	0.77	0.046	0.092	14.05
HSD	4	0.35	0.26	0.41	0.034	0.068	19.25
HSLD	4	0.25	0.2	0.29	0.022	0.043	17.57
HH-index	4	0.43	0.37	0.46	0.02	0.041	9.42

Table 4. Measurements and indexes of M1, *Propliomys jalpugensis*.

	n	Mean	Min	Max	SE	SD	CV
L	8	2.32	2.15	2.55	0.054	0.152	6.55
W	8	1.20	1.08	1.43	0.045	0.128	10.66
AS	8	0.32	0.16	0.53	0.045	0.127	39.44
DS	8	0.59	0.34	1.02	0.078	0.219	36.86
PRS	8	0.40	0.26	0.53	0.032	0.089	22.05
PA-index	8	0.53	0.36	0.63	0.038	0.106	20.13

Table 5. Measurements and indexes of M2, *Propliomys jalpugensis*.

	n	Mean	Min	Max	SE	SD	CV
L	8	1.89	1.79	2.02	0.033	0.093	4.95
W	8	1.11	1.02	1.25	0.023	0.065	5.86
AS	8	0.29	0.23	0.45	0.024	0.069	23.40
DS	8	0.36	0.22	0.67	0.052	0.148	41.65
PRS	8	0.25	0.13	0.35	0.024	0.069	28.14
PA-index	8	0.39	0.26	0.57	0.031	0.087	22.60

Table 6. Measurements and indexes of M3, *Propliomys jalpugensis*.

	n	Mean	Min	Max	SE	SD	CV
L	11	1.66	1.42	1.86	0.036	0.12	7.23
W	11	0.89	0.81	1.01	0.022	0.073	8.17
AS	11	0.38	0.19	0.51	0.029	0.097	25.67
DS	11	0.35	0.15	0.5	0.035	0.117	41.34
PRS	11	0.26	0.17	0.4	0.022	0.073	28.06
PA-index	11	0.46	0.28	0.6	0.033	0.111	23.85

frequently observed in BSA3. Dentine tracts are somewhat higher than in *P. jalpugensis*.

Dolomys cf. *hungaricus* from Węże, Poland (Sulimski, 1964). Molars are larger, they have less advanced hypsodonty stage. The anterior loop of m1 is wider and simpler. The schmelzmuster shows lamellar enamel along the leading edges both in younger and older ontogenetic stages (von Koenigswald, 1980).

Pliomys episcopalis Méhely, 1914, *P. simplicior* Kretzoi, 1956 and *P. hollitzeri* Rabeder, 1981 from Deutsch-Altenburg 2 C1 and 4 B, Germany (Rabeder, 1981), and *Pliomys schernfeldensis* Carls & Rabeder, 1988 from Schernfeld, Germany (Carls & Rabeder, 1988). Listed species distinctly differ from *P. jalpugensis* in more advanced hypsodonty stage, explicit *Pliomys*-knick, a specific enamel thickening at the trailing

side of triangle tips, and differentiated enamel bend with a thicker leading edge. The anteroconid of m1 is complicated by forming an additional dentine triangle. Crowns of m1 do not show a bulge of the anterior side. Posterior loop of M3 is narrower and longer. M3 has no enamel islets. Enamel shows a leptoknem pattern with radial and lamellar types in leading and only radial in trailing edges.

Schmelzmuster of *Propliomys jalpugensis*. Seven molars were selected for the study of enamel microstructure: 3 m1, 2 M1, and 2 M2. The enamel structure of all upper teeth is similar (Fig. 5). The enamel band of a uniform thickness with a slight thinning in depth of reentrant angles. The leading edges are completely formed by the radial enamel. The trailing edges are two-layered with the inner thick part consisting of the

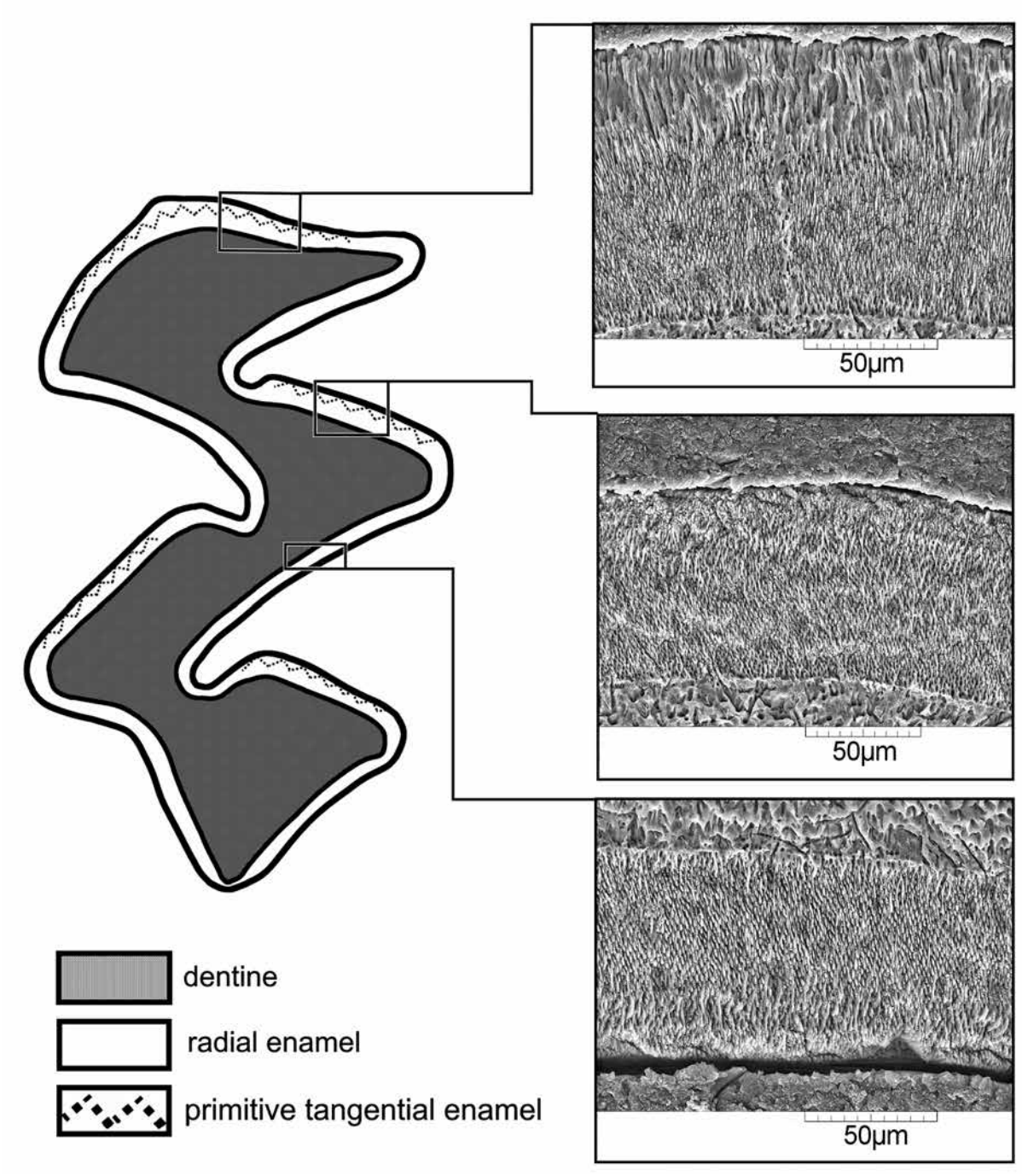


Fig. 5. Schmelzmuster of *Pliomys jalpugensis* (M2, GIN-689/026).

radial enamel, and the outer thin one, of the primitive tangential enamel. The ratio of layers: 50/50% for M1 and 90/10% for M2. The tangental enamel of closing edge is notably more well expressed (with flatter prisms) than in the trailing edges. The enamel of the closing edges is similar in structure to the trailing edge, but the ratio of layers is 60/40%. This schmelzmuster is close to the eopachyknem type of Rabeder (1981).

The enamel of two out of three studied m1 (*jalpugensis* morphotype, Fig. 1: 4, Fig. 6) are similar to the enamel of the upper molars (the ratio of the radial and tangential enamel layers is close to 60/40%,

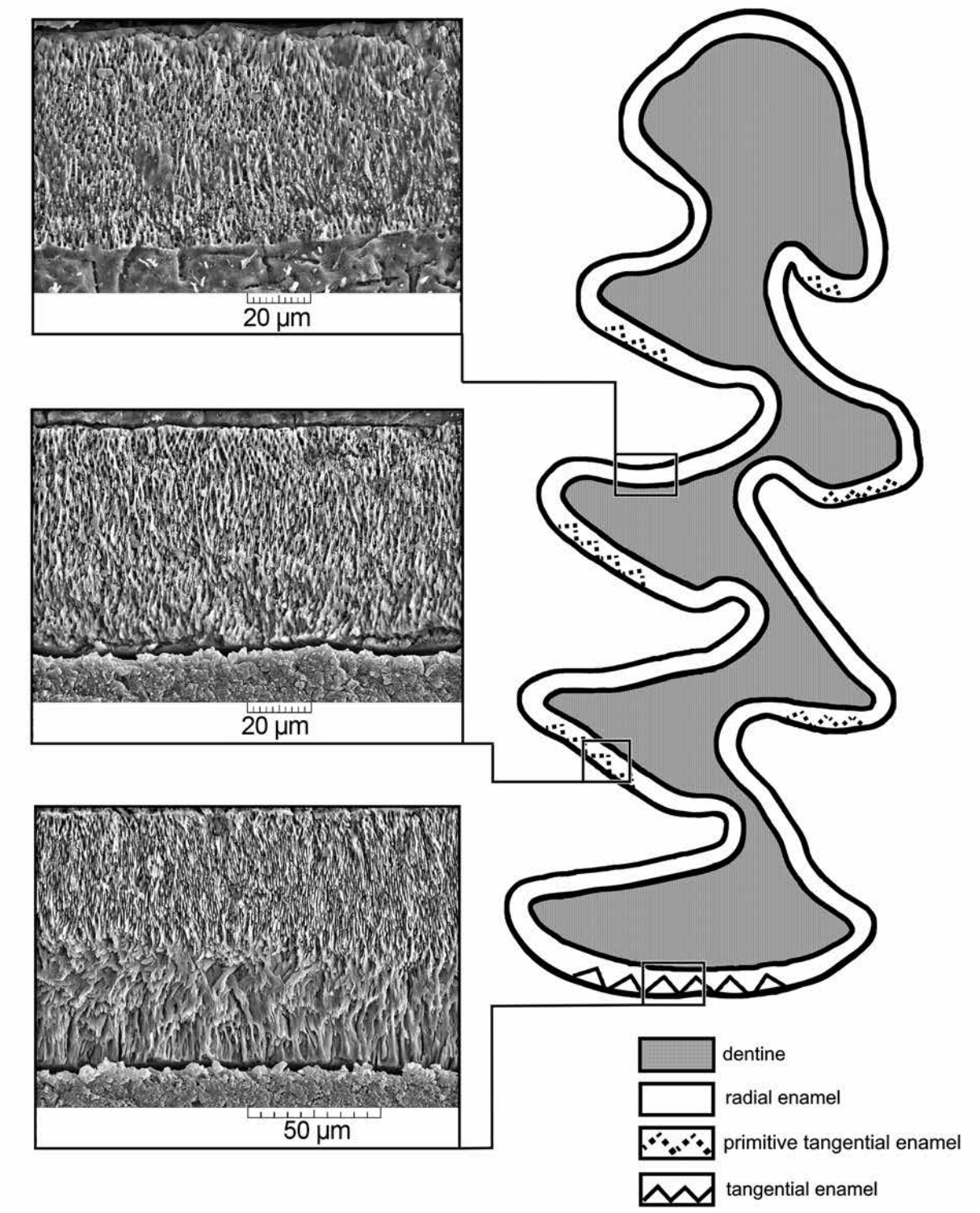


Fig. 6. Schmelzmuster of *Pliomys jalpugensis* (m1, morphotype jalpugensis, GIN-689/006).

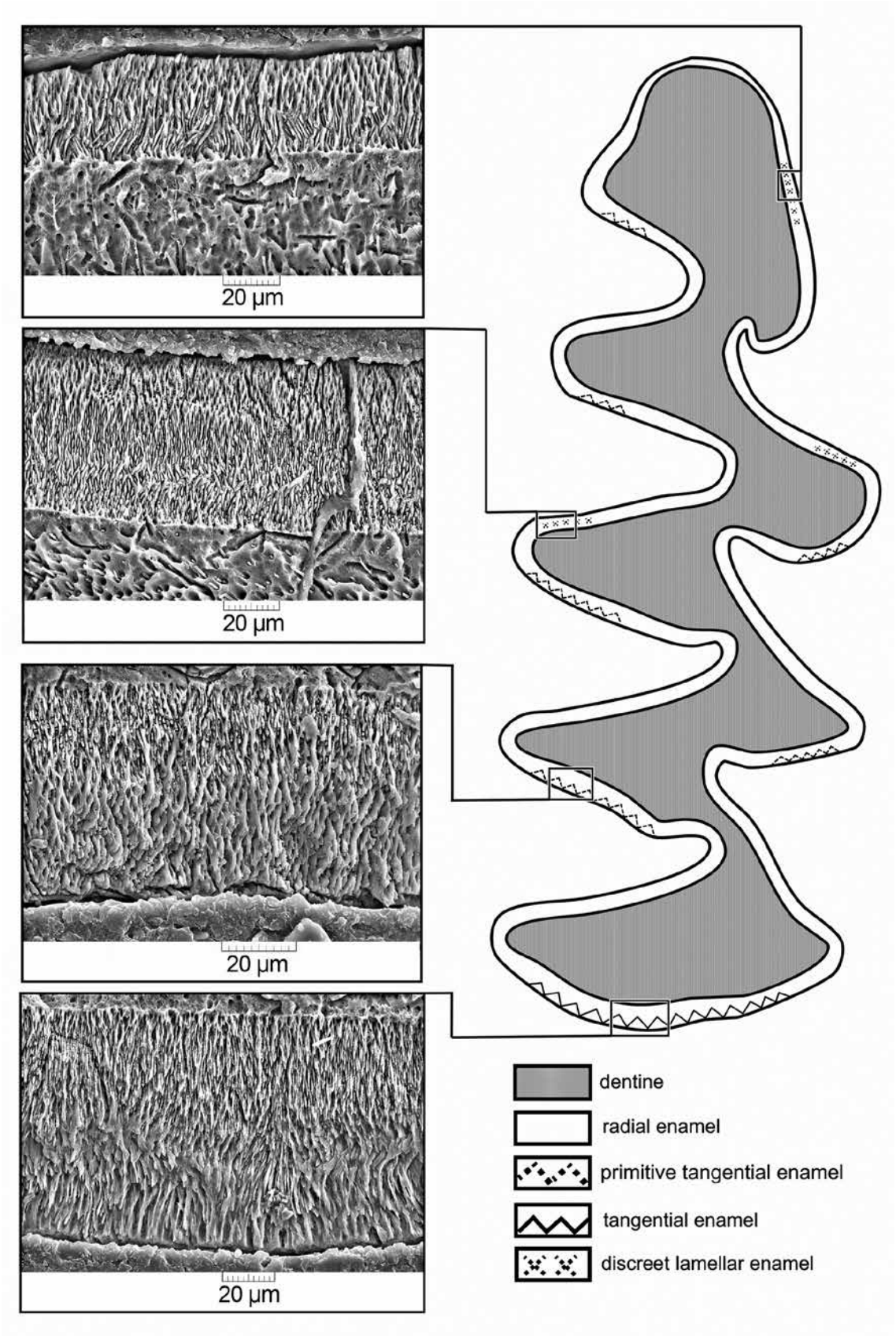


Fig. 7. Schmelzmuster of *Pliomys jalpugensis* (m1, morphotype ucrainicus, GIN-689/008).

eopachyknem type). The third m1 (*ucrainicus*-like morphotype, Fig. 1: 8, Fig. 7) presents a very primitive (discreet) lamellar enamel in the outer part of leading edges near tips of salient angles (protopachyknem type of Rabeder, 1981). The trailing and closing edges are similar according to the structure and ratio of layers: radial and primitive tangential enamel are approximately equal in thickness. Tangental enamel of the closing edge is better expressed (showing flatter prisms) than in trailing edges.

Discussion

Pliomyine voles of the European Pliocene were among the first emerging lineages deviating from the general promimomyoid morphology in course of the adaptive radiation of Arvicolinae. Progressive retention of the deep labial reentrant in the anteroconid area of m1 ("islet fold", BRA3) produced first anteroconid complication and 5-triangle pliomyine structure of this molar as compared to compact anteroconid with early insulation of BRA3 and three-triangle m1 in mimomyiod voles (Rabeder, 1981). This "pliomysation" occurred in Eastern and Central Europe in the late Early Pliocene and continued into the Pleistocene. Several phyletic lineages of pliomyine voles are known in Europe. One of the earliest lineages represented by *Propliomys hungaricus* (MN15) could likely be an ancestral stem of the extant Balkan vole *Dinaromys* (Kretzoi, 1955). The early Pliocene sequence of primitive stages possibly related to this lineage is described in the Dacic Basin in Romania (Radulesco, Samson, 1996). The similar sequence of promimomyoid-pliomyoid forms is know in Moldova and SW Ukraine (Alexandrova, 1989; Nesin, 1983). The pliomyine forms elaborated in this region by late Early Pliocene (MN15) were described as *Pliomys ucrainicus* (Topachevsky & Scorik, 1967). This form shows obvious distinctions from *Propliomys hungaricus* in more angular dental morphology. Summing up the available information of Pliocene pliomyines of Eastern Europe, the concept of a phyletic lineage including *Pliomys kowalskii, P. destinatus, P. jalpugensis, P. topachevskii*, and *P. ucrainicus* was proposed (Tesakov, 2005). We currently consider this lineage within the genus *Propliomys* Kretzoi, 1959. We do not support a phyletic scheme of pliomyine voles proposed by Nesin (1983) that considered forms from Kotlovina as synchronous due to an unrecognized taphonomic mixing of the material. Phyletic connections of this group to Middle–Late Pleistocene *Pliomys* lineages of Europe (*P. lenki-episcopalis*) seem to be highly unlikely. More comparative data from Early Pliocene of Eastern and Central Europe and Asia Minor is needed to elucidate the Ruscinian radiation of pliomyine voles.

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