Russian J. Theriol. 25 (2): 145–178 © RUSSIAN JOURNAL OF THERIOLOGY, 2026

Pliocene voles (Rodentia: Cricetidae) from Kabakova Balka (Western Ciscaucasia): morphology, enamel microstructure, and biostratigraphic significance

Albina A. Yakimova & Alexey S. Tesakov*

ABSTRACT. Kabakova Balka is the oldest mammalian locality of Early Pliocene age in the Western Ciscaucasia. It documents previously unknown stage of small mammal evolution in the region. Remains of voles (Arvicolinae, Cricetidae, Rodentia) are predominant in the fossil material. Association of Arvicolinae includes *Promimomys* (*Cseria*) *gracilis* Kretzoi, 1959*, Mimomys* cf. *hajnackensis* Fejfar, 1961, *Mimomys* cf. *stehlini* Kormos, 1931, *Dolomys nehringi* Kretzoi, 1959, and *Propliomys jalpugensis* (Nesin, 1983). The vole *Mimomys* cf. *hajnackensis* is considered as a basal phyletic predecessor of the widespread Late Pliocene larger vole *Mimomys hajnackensis* of the early Late Pliocene. Based on biostratigraphic and paleomagnetic data, this transitional fauna is dated to late Early Pliocene, MN15b unit of the European biochronological scale, and to the regional zone MNR7 of Eastern Europe. This new fauna elucidates the important stage of arvicoline radiation near the Early–Late Pliocene transition in southern Eastern Europe.

How to cite this article: Yakimova A.A., Tesakov A.S. 2026. Pliocene voles (Rodentia: Cricetidae) from Kabakova Balka (Western Ciscaucasia): morphology, enamel microstructure, and biostratigraphic significance // Russian J. Theriol. Vol.25. No.2. P.145–178. doi: 10.15298/rusjtheriol.25.2.04

KEY WORDS: voles, fossil dental remains, schmelzmuster, systematics, biostratigraphy, Pliocene, Western Ciscaucasia, Russia.

Albina A. Yakimova [albina.yakimova@ginras.ru], Alexey S. Tesakov [tesak@ginras.ru], Geological Institute of the Russian Academy of Sciences, Pyzhevskii per. 7, Moscow 119017, Russia.

Плиоценовые полевки (Rodentia: Cricetidae) Кабаковой Балки (Западное Предкавказье): морфология, микроструктура эмали и биостратиграфическое значение

А.А. Якимова, А.С. Тесаков*

РЕЗЮМЕ. Кабакова Балка — древнейшее местонахождение млекопитающих раннего плиоцена в Западном Предкавказье. Оно документирует ранее неизвестный этап эволюции мелких млекопитающих в регионе. В ископаемом материале преобладают остатки полёвок (Arvicolinae, Cricetidae, Rodentia). Ассоциация Arvicolinae включает *Promimomys* (*Cseria*) *gracilis* Kretzoi, 1959, *Mimomys* cf. *hajnackensis* Fejfar, 1961, *Mimomys* cf. *stehlini* Kormos, 1931, *Dolomys nehringi* Kretzoi, 1959 и *Propliomys jalpugensis* (Nesin, 1983). Полёвка *Mimomys* cf. *hajnackensis* рассматривается как базальный филетический предшественник широко распространённой в начале позднего плиоцена крупной полёвки *Mimomys hajnackensis*. На основании биостратиграфических и палеомагнитных данных, эта переходная фауна относится к концу раннего плиоцена, зоне MN15b европейской биохронологической шкалы, и к региональной зоне MNR7 Восточной Европы. Эта новая фауна проливает свет на важный этап радиации полёвок в период перехода от раннего к позднему плиоцену на юге Восточной Европы.

КЛЮЧЕВЫЕ СЛОВА: полёвки, ископаемые остатки зубов, микроструктура эмали, систематика, биостратиграфия, плиоцен, Западное Предкавказье, Россия.

Introduction

The Pliocene history of arvicoline rodents in the Northern Caucasus is poorly known, due to scarcity of non-marine deposits of this age in the region. Until recently the geographically closest to the Caucasus faunal localities of Early Pliocene age were known from northwestern peri-Black Sea areas in Ukraine and

* Corresponding author

Moldova (Konstantinova, 1965; Schevchenko, 1965; Topachevsky & Nesin, 1989), Romania (Radulescu & Samson, 1987, 1996), Bulgaria (Popov, 2004), and Greece (van de Weerd, 1979; van de Weerd *et al.*, 1982). Pliocene fossil record of Asia Minor and in the southern Caucasus provides information on the succession of arvicoline faunas in Early and Late Pliocene (Şen, 1977; Ünay & de Bruijn, 1998; van den Hoek Ostende *et al.*, 2015; Lazarev *et al*., 2023; Skandalos *et al.*, 2023; Tesakov *et al.*, 2024). In Russia, the transitional Early–Late Pliocene faunas are known in the middle (Agadjanian, 1976, 2009) and lower (Tesakov, 2004) reaches of the Don River. In Taman Peninsula, recent discovery brought first information on the Late Pliocene small mammals (Frolov *et al.*, 2024). Thus, the discovery of a new Early Pliocene locality in the Ciscaucasia is an important event for the paleontology of not only the Caucasus, but also the entire south of Eastern Europe and surrounding areas.

Pliocene small mammal faunas of southern Eastern Europe and western Asia well conform to the European biochrons, European Land Mammal Ages (ELMA): Ruscinian, MN14–15 (Early Pliocene, 5.333–3.6 Ma) and Early Villanyian, MN16 (Late Pliocene, 3.6–2.58 Ma). Notwithstanding regional differences, all Pliocene faunas share general features known in the development of Arvicolinae with growing hypsodonty and diversification of phyletic lineages. Earliest Pliocene, Ruscinian faunas are characterized by low arvicoline diversity of very brachyodont smaller archaic voles similar to *Promimomys insuliferus* Kowalski, 1958. These forms have simple oval or rounded triangular anteroconid. Still in the first half of Early Pliocene (MN14) mimomyoid voles with more complex, trifoliate *Mimomys*-like anteroconid, similar to *Promimomys moldavicus* (Kormos, 1932) and *P. davakosi* (van de Weerd, 1979), appeared. The later part of the Ruscinian (MN15) documents the first extensive radiation of voles when several genus-level taxa of different size classes appeared. The general feature of MN15 faunas of the Euxinian-Aegean region is the first appearance, along with mimomyoid voles, of primitive pliomyine and dolomyine voles of the groups *Propliomys ucrainicus* (Topachevsky et Scorik, 1967), *P. hungaricus* Kretzoi, 1959, and *Dolomys nehringi* Kretzoi, 1959, with a more complex m1 and reduction of enamel islets in m1/M3. The Late Pliocene, early Villanyian vole assemblages include growing numbers of parallel lineages with the first true *Mimomys* species with external cement, and more evolved pliomyines and dolomyines. The transition from Ruscinian to Villanyian stages of vole evolution is not very well documented in Europe. The faunas of Csarnóta 2 in Hungary and Węże in Poland are among the most well-known. The recently discovered fauna of Kabakova Balka elucidates the latest Ruscinian stage of vole evolution in the Northern Caucasus.

The goal of this study is a detailed morphological description of the vole remains from Kabakova Balka to give a clear comparative reference for future studies. The diverse mammalian fauna that accompanies the arvicolines (see the list in the Results) will be described elsewhere.

Geological setting

The fossiliferous site Kabakova Balka (Fig. 1) is located in the Western Ciscaucasia, 4 km to the west from the town of Krymsk (Krasnodar Territory, Russia) and in 2.5 km to NE from the settlement Sauk-Dere, in an abandoned sand pit (44.9217° N, 37.9196° E). Geological maps show the easternmost outcrops of the brackish water deposits of the Early Pliocene Kimmerian regional stage in this area. The sand pit exploited the thick accumulations of quartz sands of the Sennoi Formation (bed 1), regionally widespread in the NW Ciscaucasus. The Sennoi Fm is correlated to the Upper Kimmerian and Lower Kujalnik regional stages of the Black Sea stratigraphy (Beluzhenko & Pis'mennaya, 2016). This geological stratum represents sediments of a large lagoon-like bay of the Kimmerian Sea that deeply penetrated into land at the NW margin of emerging periclinal of the Caucasus Mountains along the western part of the Caucasian Foredeep. The fluviatile deposits on top of the lagoonal sands (bed 2, Fig. 1D) mark a regressive stage of the Kimmerian Sea when smaller regional rivers transported sand and gravel towards the near-by brackish water basin forming a nearshore deltaic sequence. As supported by the brackish-water ostracods of the Kimmerian-Kujalnikian appearance (Nikolaeva *et al.*, 2025), reversed paleomagnetic record correlated to the late Gilbert Epoch, and the biochronology of the mammalian fauna, the fluviatile member corresponds to a short period between the regression of the Kimmerian and the transgression of the Kujalnikian Sea near the Early to Late Pliocene transition (Yakimova *et al.*, 2026). The overlying member of fine-grained sands and clays (bed 3) represents the transgressive deposits of lower Kujalnikian, based on characteristic ostracod association (data of A.D. Nikolaeva). The covering reddish-brown loams (bed 4) correspond to Early Pleistocene soil formation ("Scythian clays") widespread in the region.

The northwestern wall of the quarry exposed (from bottom to top) the following composite section (Fig. 1E):

bed 1, white and yellow sands (> 4 m)
bed 2, sands, silts, and gravelstones (2–3 m)
bed 3, fine-grained sands and gray clays (3–4 m)
bed 4, red-brown loam (0.5 m),
bed 5, modern soil (0.3 m)

Bed 2 yielded operculi and shells of molluscs, and remains of vertebrates (fishes, herpetofauna, birds, and mammals) reviewed below.

Material and methods

All fossil remains were obtained by screen-washing the sediments using a set of sieves with mesh size of 0.5–1.0 mm in the field and subsequent manual sorting of bone-bearing concentrate in the laboratory. Altogether ca. 800 kg of sediments were processed. The

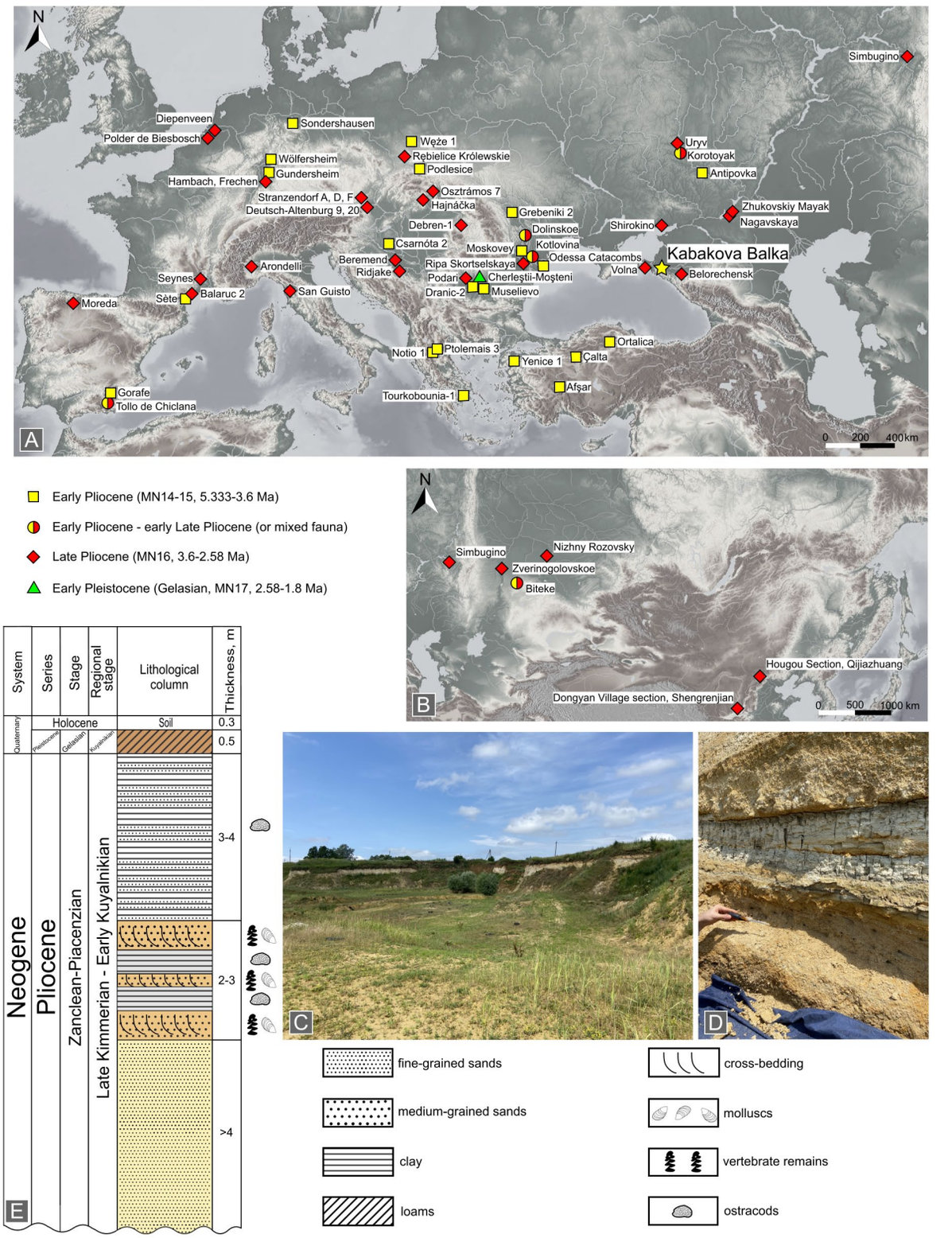

Fig. 1. Geographic position of Kabakova Balka locality and other relative localities in European (A) and Asian (B) parts of Eurasia. C — view of the sandpit Kabakova Balka (photo by A.D. Nikolaeva). D — fossiliferous layers (photo by A.D. Nikolaeva); E — section log, modified after Nikolaeva *et al.*, 2025. Map data from OpenStreetMap.

field work at the site proceeded in 2017–2023, 2025. The studied material is represented by isolated molars of the fossil rhizodont (rooted) voles. The described fossil material is preserved as a part of the paleontological collections 1203 (GIN 1203/001–335, Kabakova Balka locality) and 1180 (GIN 1180/001, Zhukovskiy Mayak locality) of the Geological Institute of the Russian Academy of Sciences in the Laboratory of Quaternary stratigraphy.

We use lower case letters for lower molars (m1, m2, m3) and upper case letters for upper molars (M1, M2, M3). Left and right side molars are correspondently denoted in the figures as sin and dex. The terminology of arvicoline occlusal elements follows van der Meulen (1973). A series of standard measurements were taken in all available molars: the length (L) and width (W) of the occlusal surface, the basal length (Lbas) of the crown, the length of the anteroconid of m1 (A) and the posterior loop of M3 (P), heights of the main dentine tracts: ASD, anterosinuid, HSD, hyposinuid, HSLD, hyposinulid (for lower teeth), and AS, anterosinus, ASL, anterosinulus, DS, distosinus, PRS, protosinus (for upper teeth). Designations of dentine tracts and hypsodonty indices (HH-index for lower molars, PA-index for upper molars) follow Rabeder, 1981. The index of the sum of tracts to the occlusal length of molars (Σ_tracts, Nesin, 1988) was calculated for comparison with some samples from Ukranian localities. For all measured values we calculated standard error of mean (SE), standard deviation (SD), coefficient of variation (CV) based on the measuring system used by Tesakov (2004). The enamel differentiation quotient (SDQ) (Heinrich, 1990) was calculated for T1–T3 in lower molars and M1, and for T2–T4 in upper molars. Statistical data processing was carried out using the software PAST (Hammer *et al.*, 2001).

The drawings of vole molars were produced by tracing the photographs of occlusal, and lateral sides of the teeth.

Studies of enamel microstructure (schmelzmuster) were carried out using scanning electron microscopy according to the method described by von Koenigswald (1980). The terminology of the enamel structures follows von Koenigswald (1980) and Rabeder (1981). The studied molars were embedded in an epoxy resin block, the occlusal surface was polished on a grinding wheel using fine-grained grinding pastes. The polished surfaces were cleaned in the ultrasonic bath. The polished enamel was then etched with a 10% HCl solution, and sputter-coated with gold to produce an electrically conductive layer needed for the use of SEM. Photographs of the enamel microstructure were obtained using scanning electron microscopes of Paleontological Institute and Geological Institute of the Russian Academy of Sciences (PIN RAS and GIN RAS). For patterns of enamel thickness we follow the terminology of Martin (1987) where the negative differentiation describes the condition with trailing edges thicker than the leading ones, and the positive differentiation corresponds to a reverse situation.

The biochronologic standards used in this work follow Fejfar *et al.* (1998), Fejfar (2001), Tesakov (2004, 2021). Time intervals for Early and Late Pliocene Stages follow the latest version of the International Chronostratigraphic Chart (Cohen *et al.*, 2025). The geographic position of the mammalian localities mentioned in the text is shown in Fig. 1A, B.

Results

Biotic record of the Kabakova Balka

Fossil remains of molluscs and vertebrates were obtained from gravels and sands of the bed 2. The association of molluscs includes shells and operculi of gastropods: *Pomatias* sp., *Limax* spp., *Parmacella* sp., *Parafossarulus* sp., *Bithynia* sp., Bithyniidae indet. Smaller vertebrates are represented by remains of fish: *Rutilus rutilus*, *R.* aff. *frisii*, *Tinca* cf. *tinca*; amphibians and reptiles preliminary identified to order or family level: Anura, Colubrinae 1, Colubrinae 2, ?Viperidae, and Testudinata (Tesakov *et al.*, 2018). Birds are represented by an egg shell fragment of *Struthiolithus chersonensis* (Mikhailov & Zelenkov, 2020). Mammals are the most abundant in the material with numerous bones and teeth unearthed. Large mammals include Hyaenidae gen. et sp. indet. (1), *Nyctereutes donnezani* (1), Proboscidea gen. (1), *Procapreolus* sp. (5), Bovidae gen et sp. indet. (1). Small mammals are represented by remains of *Talpa* sp. (5), Desmaninae gen. et sp. indet. (2), *Beremendia fissidens* (2), *Blarinoides* cf. *mariae* (3)*, Hypolagus brachygnathus* (17)*, Pliopetauista* cf. *pliocaenica* (3), *Hylopetes* sp. (2), *Blackia* sp. (1), *Miopetaurista* sp. (1), *Sciurus* sp. (6), *Glis minor* (3), *Trogontherium* sp. (1), *Nannospalax* sp. (16), *Apodemus* cf. *dominans* (12)*, Apodemus* sp. (1), *Allocricetus* sp. (10), *Neocricetodon* sp. (1), *Promimomys gracilis* (72), *Mimomys* cf. *stehlini* (125), *Mimomys* cf. *hajnackensis* (43), *Propliomys jalpugensis* (89), *Dolomys* cf. *nehringi* (6) (Tesakov *et al.*, 2018, 2026; Yakimova & Tesakov, 2026).

Systematic paleontology

Order RODENTIA Bodwich, 1821
Family CRICETIDAE G. Fischer, 1817
Subfamily ARVICOLINAE Gray, 1821

Comments on genus level taxonomy of Pliocene voles

We accept the following genus-level system for archaic rhizodont Arvicolinae and related cricetines:

1. Most primitive transitional cricetine-arvicoline forms of the *Microtodon* grade still having numerous cricetine characters evolve in faunas of Latest Miocene, MN13: *Microtodon atavus* from Ertemte (Fahlbusch & Moser, 2004), more advanced *Microtodon* reported from northern Mongolia and southern Siberia in deposits of terminal Miocene (Devyatkin, 1981; Zazhigin, 1989; Sizov *et al.*, 2024). The large form of this grade, *Microtodon admirabilis* (Nesin, 1996), is also known

from Late Miocene, MN13, of southern Ukraine. The same grade of evolution is known in North American *Prosomys mimus* from McKay Reservoir (Shotwell, 1956).

2. Archaic true voles with simple oval anteroconid (the grade of *Promimomys insuliferus* Kowalski, 1959) are assigned to the genus *Promimomys*, subgenus *Polonomys* Kretzoi, 1959.

3. Archaic cementless voles that developed a trifoliate anteroconid are considered within the formal genus *Promimomys* (*Promimomys*) Kretzoi, 1955. The common practice to assign these forms to *Mimomys* barely based on the shape of anteroconid with no regard to stage of hypsodonty and schmelzmuster (e.g. Hordijk & de Bruijn, 2009) is not followed here (Tesakov *et al.*, 2024). In our study we use all three character features for to distinguish between *Promimomys* and *Mimomys*. *Promimomys* is a taxonomical metaregion (for definition of a metaregion see Martin & Tesakov, 1998) that represents the Early Pliocene radiation of Arvicolinae. One of the lineages of this radiation, the true *Mimomys* voles, evolved within *Promimomys* by acquiring pachyknem schmelzmuster, and external cement at the Ruscinian–Villanyian (Early to Late Pliocene) transition. A shorter lineage of small size forms with low hypsodonty and primitive enamel microstructure, *Cseria,* represents another descendant of *Promimomys*. The problem of a possible paraphyly of *Mimomys,* with several lineages independently reaching the *Mimomys* grade, is acknowledged but not discussed here.

Genus *PROMIMOMYS* Kretzoi, 1955
Subgenus *Cseria* Kretzoi, 1959
Promimomys (*Cseria*) *gracilis* Kretzoi, 1959
Figs 2–3, Tables 1–6.

Studied material. 17 m1, 16 m2, 18 m3, 7 M1, 8 M2, 6 M3 (GIN 1203/001–072).

Type locality. Csarnóta 2, Hungary, Early Pliocene, MN15.

Description. Smaller cementless rhizodont vole. There is a rounded or oval enamel islet on the anterior loop of m1, and anterior and posterior enamel islets in M3. The enamel shows no conspicuous thickness differentiation in most specimens, with a trend from slightly positive (juveniles) to slightly negative (older wear stages). Lower molars have two roots and the upper ones are three-rooted.

Measurements of molars are presented in Tables 1–6.

m1. The anterior loop of anteroconid in m1 bears a deep labial *Mimomys*-ridge and a deep LRA4. *Mimomys*-ridge runs down to lower part of the crown. The elevation of the base of islet fold (BRA3) above the crown base measured at BRA1 varies from 0.8 to 1.4 mm. Juvenile specimens with crown height more than 2.3

Table 1. Measurements (in mm) of m1 *Promimomys* (*Cseria*) *gracilis* from Kabakova Balka locality.

m1	N	Mean	SE	Min	Max	SD	CV
L	10	2.34	0.0719	2.29	2.4	0.2273	9.72
W	16	1.04	0.031	0.85	1.15	0.1241	11.9
Asd	11	0.94	0.0597	0.6	1.3	0.1979	20.99
Hsd	14	0.55	0.0178	0.44	0.65	0.0668	12.1
Hsld	13	0.25	0.0157	0.14	0.35	0.0565	22.59
Lbas	9	2.43	0.0295	2.25	2.53	0.0884	3.64
HH-index	13	0.61	0.0168	0.5	0.7	0.0606	9.93
Σ_tracts	8	72.16	3.3822	52.74	85.15	9.5664	13.26
L/W	6	2.24	0.0642	2.07	2.52	0.1571	7.02
A/L	9	44.95	1.3967	39.13	53.11	4.19	9.32
SDQ	11	111.92	3.7705	90.04	130.60	12.5053	11.17

Table 2. Measurements (in mm) of m2 *Promimomys* (*Cseria*) *gracilis* from Kabakova Balka locality.

m2	N	Mean	SE	Min	Max	SD	CV
L	13	1.46	0.0226	1.37	1.65	0.0816	5.61
W	16	0.99	0.0229	0.83	1.15	0.0916	9.27
Asd	13	0.52	0.0224	0.4	0.67	0.0809	15.43
Hsd	15	0.31	0.0176	0.13	0.39	0.0681	22.28
Hsld	15	0.21	0.0093	0.15	0.27	0.0359	17.1
Lbas	16	1.59	0.0226	1.48	1.8	0.0903	5.66
HH-index	14	0.38	0.0136	0.27	0.45	0.0509	13.38
Σ_tracts	11	64.74	2.6311	52.85	75.47	8.7265	13.48
L/W	13	1.49	0.0322	1.29	1.71	0.116	7.8
SDQ	15	106.71	2.2509	87.6	122.3	8.7176	8.17

Table 3. Measurements (in mm) of m3 *Promimomys* (*Cseria*) *gracilis* from Kabakova Balka locality.

m3	N	Mean	SE	Min	Max	SD	CV
L	18	1.29	0.0236	1.14	1.5	0.1002	7.74
W	18	0.75	0.016	0.65	0.87	0.0681	9.02
Asd	17	0.43	0.022	0.24	0.61	0.0907	21.15
Hsd	18	0.15	0.0102	0.1	0.23	0.0432	28.59
Hsld	17	0.11	0.0054	0.07	0.15	0.0221	20.48
Lbas	18	1.48	0.0207	1.25	1.63	0.0878	5.93
HH-index	17	0.19	0.0104	0.12	0.26	0.043	23.03
Σ_tracts	16	46.01	1.8271	35.4	60.68	7.3085	15.88
L/W	18	1.72	0.0309	1.4	1.89	0.1309	7.60
SDQ	18	116.49	4.2012	86.6	150.9	17.8243	15.30

Table 4. Measurements (in mm) of M1 *Promimomys* (*Cseria*) *gracilis* from Kabakova Balka locality.

M1	N	Mean	SE	Min	Max	SD	CV
L	5	1.88	0.0372	1.77	2	0.0832	4.43
W	7	1.11	0.0229	1.01	1.2	0.0606	5.45
Ds	3	0.52	0.0545	0.43	0.61	0.0943	18.13
As	7	0.22	0.025	0.13	0.32	0.0662	30.06
Asl	7	0.18	0.0185	0.13	0.28	0.0489	26.64
Prs	7	0.46	0.0353	0.29	0.55	0.0934	20.49
Lbas	6	1.94	0.0342	1.8	2.03	0.0838	4.32
PA-index	7	0.51	0.0341	0.36	0.63	0.0902	17.68
AA-index	7	0.29	0.0225	0.2	0.37	0.0596	20.44
Σ_tracts	3	57.37	5.4603	47.2	65.91	9.4576	16.49
L/W	5	1.7	0.0269	1.66	1.78	0.0601	3.52
SDQ	4	119.78	7.7069	104.3	135.8	15.4137	12.87

Table 5. Measurements (in mm) of M2 *Promimomys* (*Cseria*) *gracilis* from Kabakova Balka locality.

M2	N	Mean	SE	Min	Max	SD	CV
L	3	1.42	0.0368	1.38	1.5	0.0637	4.47
W	8	1.01	0.0311	0.87	1.14	0.088	8.7
Ds	3	0.42	0.0569	0.35	0.53	0.0985	23.64
As	8	0.28	0.0191	0.21	0.33	0.054	19.58
Prs	8	0.28	0.0167	0.21	0.33	0.0471	17.07
PA-index	8	0.39	0.0185	0.32	0.46	0.0523	13.25
Lbas	7	1.46	0.0468	1.21	1.57	0.1238	8.46
Σ_tracts	3	66.37	4.5269	57.49	72.33	7.8407	11.81
L/W	3	1.53	0.0276	1.5	1.59	0.0477	3.12
SDQ	4	113.49	6.6186	94.05	123.3	13.2372	11.66

Table 6. Measurements (in mm) of M3 *Promimomys* (*Cseria*) *gracilis* from Kabakova Balka locality.

M3	N	Mean	SE	Min	Max	SD	CV
L	4	1.36	0.0514	1.29	1.51	0.1029	7.58
W	6	0.89	0.0351	0.8	1.02	0.086	9.71
Ds	4	0.27	0.0742	0.12	0.47	0.1483	54.43
As	6	0.18	0.0261	0.12	0.3	0.064	36.19
Prs	6	0.15	0.0183	0.08	0.2	0.0448	30
PA-index	6	0.23	0.0289	0.16	0.36	0.0707	30.27
Lbas	6	1.4	0.0491	1.28	1.54	0.1204	8.6
Σ_tracts	4	40.75	4.7677	26.81	48.28	9.5354	23.4
L/W	4	1.63	0.0666	1.47	1.79	0.1332	8.19
SDQ	4	120.5	8.025	105.58	135.6	16.0499	13.32

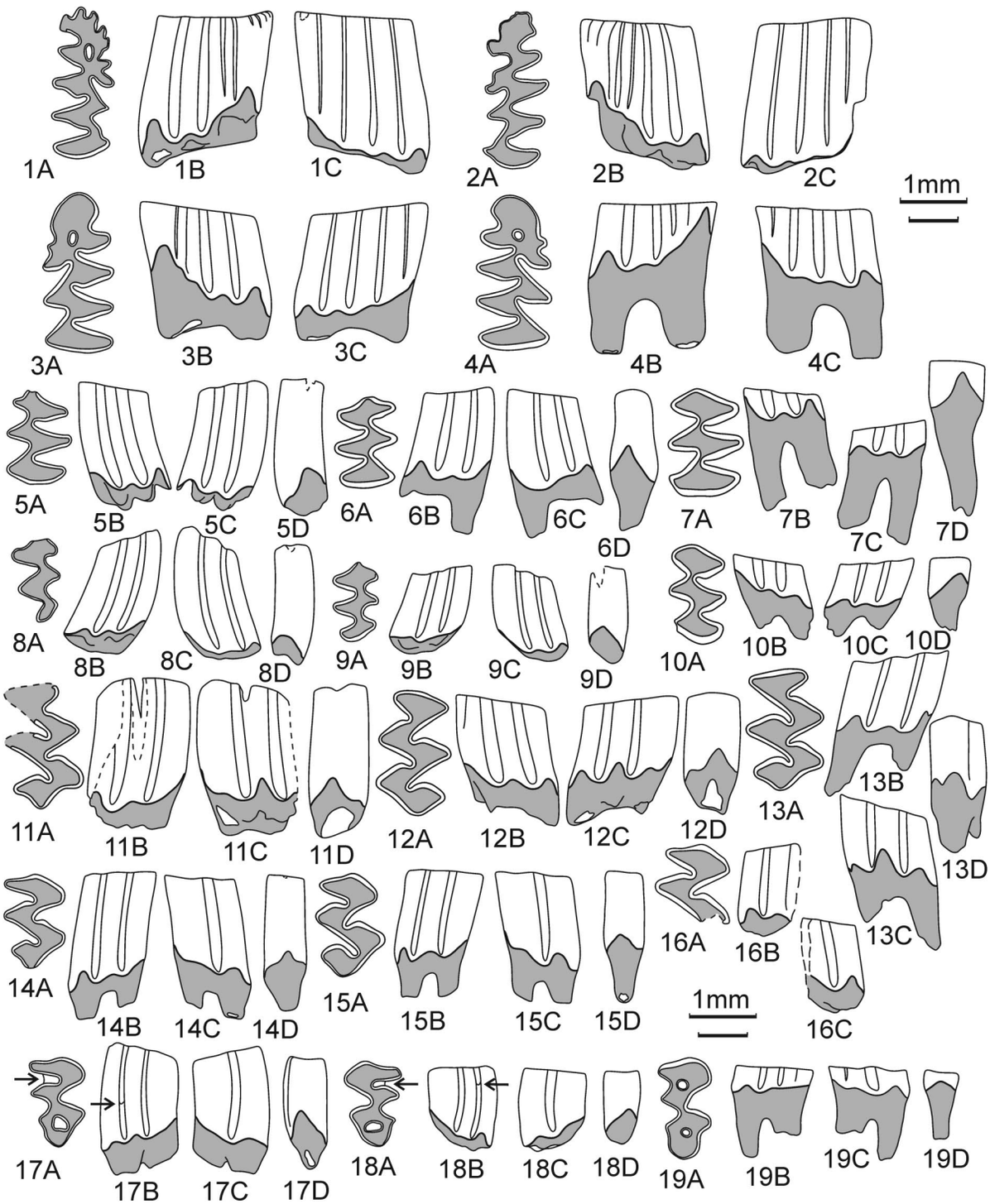

Fig. 2. Molars of *Promimomys* (*Cseria*) *gracilis* from Kabakova Balka. A–D — m1 (GIN 1203/001, 002, 006, 012); E–G — m2 (GIN 1203/018, 025, 033); H–J — m3 (GIN 1203/034, 042, 021)); K–M — M1 (GIN 1203/052, 057, 058); N–P — M2 (GIN 1203/061, 060, 059); R–T — M3 (GIN 1203/067, 069, 072). 1 — occlusal surface; 2 — buccal side; 3 — lingual side; 4 — anterior (lower teeth) or posterior (upper teeth) side. Scale bar, 1 mm for occlusal view (upper line) and lateral views (lower line). Arrow points to closing enamel islet.

mm show crenulated anterior cap and the enamel islet closure (n = 1, Fig. 2B) at the height of 2.25 mm. T1 and T2 are typically widely confluent.

m2 and m3. The molars have a posterior lobe and two pairs of widely confluent triangles. The posterior root of m2 has an acrorhizal structure.

M1. The molar is composed of an anterior lobe and four alternating triangles.

M2. The molar is composed of an anterior lobe and three alternating triangles.

M3. The molar is built of the anterior lobe, one triangle (T2) and a subtriangular posterior lobe. Rarely it can bear a narrow ridge-like BSA4. The anterior islet closes in BRA1 near the mid-crown height, at 0.8 and 1.08 mm (Fig. 2: 17B, 18B). All specimens show closed posterior enamel islet. The shape of the islet grades from angular or oval to circular with wear. It insulates very early, at crown height more than 2 mm.

Schmelzmuster. The enamel microstructure was studied in the M2 (Fig. 3). Enamel thickness differentiation is slightly negative (SDQ = 119.91). The schmelzmuster type is protopachyknem. The leading edge of the dentine triangle is almost entirely composed of radial enamel, but there is also a thin layer of nascent lamellar enamel running along the entire edge, not extending into the reentrant angle, and somewhat better developed at apices of triangles (Fig. 3A, C). The trailing edge consists of radial and primitive tangential enamel that occupies one third of the thickness of the enamel wall (Fig. 3A). The closing edge of the anterior lobe likewise consists of radial and primitive tangential enamel. In contrast to leading edges, its medial part shows enamel thickening with the tangential enamel building from one third to nearly half of the total wall thickness (Fig. 3C).

Comparison. Here we provide comparison with selected, well documented records of smaller *Promimomys* from late Early Ruscinian faunas with supposed close affinities with *Cseria gracilis* Kretzoi, 1959. Unrelated Pliocene forms assigned in the literature to this species (larger promimomyid voles, villanyines, and primitive pliomyines) are only briefly discussed.

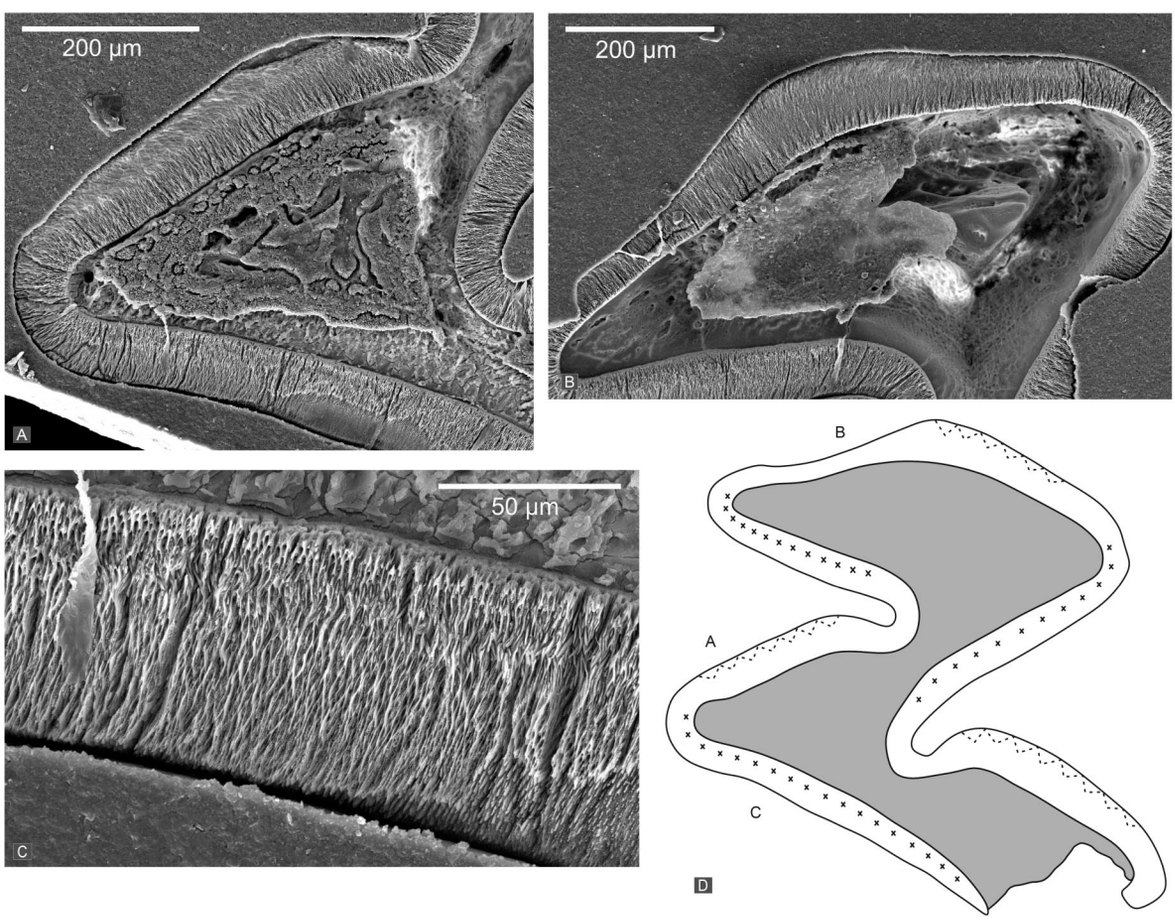

Fig. 3. Enamel microstructure of *Promimomys* (*Cseria*) *gracilis* from Kabakova Balka, M2 dex (GIN 1203/059). A — triangle T2; B — anterior lobe; C — leading enamel edge of T2; D — overview image with the studied enamel fragments and enamel types shown. Crosses denote primitive lamellar enamel; dotted zigzag line stands for primitive tangential enamel; white space shows radial enamel.

Cseria gracilis, Csarnóta 2, Hungary (Kretzoi, 1959). *P. gracilis* from Kabakova Balka closely fits the type form from Hungary, as illustrated by Kretzoi (1959) and Rabeder (1981), in size, proportions of m1, and in the hypsodonty.

Mimomys gracilis, Węże 1, Poland (Kowalski, 1960b; Sulimski, 1964). The smaller vole from Kabakova Balka is morphologically close to the vole from Węże 1, but on average has slightly smaller molar dimensions and higher hypsodonty. Unlike the vole from Kabakova Balka, the vole from Węże 1 does not have tangential enamel on the closing edges of the triangles (von Koenigswald, 1980). Noting a later insulation of BRA3 in m1 of this vole as compared to the type form from Csarnóta 2, Kretzoi (1969) proposed a name *Cseria praegracilis* without designating a type. Rabeder (1981) referred to the description of Sulimski (1964, fig.22, left m1) as a lectotype thus validating the taxon. The senior synonym for this chronospecies can be *C. proseki* (Fejfar, 1961) from the late Ruscinian of Ivanovce B in Slovakia (Radulesco & Samson, 1984).

Mimomys gracilis transylvanicus, Debren-1, Romania (Radulesco & Samson, 1984). This insufficiently known small vole shows m1 with higher hypsodonty than *P. gracilis* from Kabakova Balka and the type fauna of Csarnóta 2. It may represent an advanced chronoform of *P. gracilis* indeed (Radulesco & Samson, 1984), or *Mimomys stehlini*.

Mimomys (*Cseria*) *gracilis,* Wölfersheim and Gundersheim-Findling, Germany (Storch & Fejfar, 1990; Fejfar & Repenning, 1998). The samples from Kabakova Balka and Wölfersheim are similar in morphology and height of the dentine tracts in m1 and M3. The Ciscaucasian record appears to be slightly smaller in size.

Promimomys gracilis, Biteke, Kazakhstan (Zazhigin, 1980). The arvicoline sample from Biteke, assigned by V.S. Zazhigin to *Promimomys gracilis*, apparently represents a mixed group, with some of specimens similar to *Cseria gracilis*. The other part of the sample is morphologically close to the Pliomyini lineage. Later, the research team that studied the Biteke sequence reported the presence of several superposed formations of different age (Zykin *et al.*, 1987). The Biteke materials require revision. There is evidence in the literature about the microstructure of *Cseria gracilis* enamel from Biteke (von Koenigswald, 1980). The enamel is similar to that of the Kabakova Balka vole and more advanced than *C. proseki* from Węże in presence of tangential enamel in trailing edges. In recent contributions Zazhigin reports "*Mimomys gracilis*" from several late Ruscinian localities in the south of West Siberia (Vasilyan *et al.*, 2017).

Promimomys gracilis, Korotoyak-1, Korotoyak-2, Uryv-1, Uryv-2, Voronezh Region, Russia (Agadjanian, 2009). A sequence of Pliocene faunas from the middle course of the Don River yielded abundant remains of smaller promimomyoid voles. Zazhigin (1980) originally noted an affinity of these voles to *P. baschkiricus* (Suchov, 1970) from Early Villanyian fauna of Akkulaevo in the southern Urals. The subsequent revision supports that most of the Late Pliocene material in the Don faunas belongs to archaic stages of *Pitymimomys* voles related to *P. baschkiricus*: *P. inceptor* Tesakov, 2003 and *P. altenburgensis* Rabeder, 1981 (Tesakov, 2003, 2004, 2021). Contrary to *C. gracilis* from Csarnóta 2 and Kabakova Balka, these voles are more hypsodont, show more slender m1 and M3, and display characteristic wide confluences of occlusal triangles.

Cseria cf. *gracilis*, Sondershausen, Germany (Hellmund & Ziegler, 2012). A very small sample of Late Ruscinian age documents a promimomyine vole larger than *C. gracilis* and showing much more advanced negative enamel differentiation. The sample possibly represents a mixture of different species.

Mimomys gracilis, Çalta, Turkey (Şen, 1977). The vole was later reassigned (Sen, 1998) to *Mimomys davakosi* van der Weerd, 1979. Most likely it represents an early stage of pliomyine vole judging by retarded insulation of BRA3 (Tesakov *et al.*, 2024).

Mimomys cf. *gracilis*, Zverinogolovskoe, Russia (Pogodina & Strukova, 2016). A scarce poorly preserved material broadly resembles *C. gracilis* from Kabakova Balka in hypsodonty and size apart from reported external cement in some specimens that likely signals the presence of a smaller species of *Mimomys*.

Mimomys gracilis, Afşar 2 and *Mimomys* cf. *gracilis*, Afşar 1, Turkey (Skandalos *et al.*, 2023). The very limited material and notable larger size of m1 and M3 from the Turkish localities may indicate a smaller *Promimomys* distinct from *Cseria gracilis* but close to it in a stage of hypsodonty.

Mimomys davakosi, Ptolemais 3, Greece (van de Weerd, 1979). The vole from Kabakova Balka is significantly smaller, more hypsodont, and has deeper insular, prismatic, and LRA4 folds on m1 in comparison to the early Ruscinian vole from Greece. Early Pliocene, early Ruscinian brachyodont voles showing uniform *Promimomys* morphology, including *P. moldavicus* (Kormos, 1932), *P. davakosi* (van de Weerd, 1979), *P. antiquus* Zazhigin, 1980*, P. teilhardi* (Qiu et Li, 2016), etc., represent early stages of protomimomyoid radiation in different regions of Eurasia.

Cseria carnuntina Rabeder, 1981, Deutsch-Altenburg 9; *Cseria proopsia* Rabeder, 1981, Stranzendorf A; *Cseria opsia* Rabeder, 1981, Stranzendorf D and F, Austria (Rabeder, 1981).This sequence of forms shows a set of characters (slender outlines, undifferentiated enamel, higher dentine tracts, reduction of *Mimomys*-ridge, etc.) that indicates their belonging to the genus *Villanyia* (sensu Mayhew, 2009).

Comments. The phyletic assignment of late Ruscinian–earliest Villanyian *Cseria proseki-gracilis* lineage is not clear. Basic morphology and hypsodonty stage may indicate affinities to Early Villanyian smaller voles of the genera *Villanyia* and especially *Pitymimomys,* with assumed transitional forms documented (Tesakov, 2003). The vole from Kabakova Balka closely fits the type form from late Ruscinian of Csarnóta 2 and coeval faunas.

Genus *MIMOMYS* F. Major, 1902

Comments. We accept a strict definition of the genus based on its type species, *Mimomys pliocaenicus* Forsyth Major, 1902, combining specific morphology with enamel islets in m1 and M3 at least in juvenile stages, external cement, and pachyknem schmelzmuster. This diagnosis leaves outside the scope of the genus a stem group of morphologically archaic Early Pliocene mimomyine voles not directly related to the *Mimomys* radiation of Late Pliocene–Early Pliestocene. Several long lineages of *Mimomys* radiation deserve subgeneric status: *Mimomys* (*Mimomys*) based on *M. pliocaenicus; Mimomys* (*Pusillomimus*) typified by *M. pusillus* Mehely, 1914; *Mimomys* (*Microtomys*) Mehely, 1914 based on *Arvicola intermedius* Newton, 1881; *Mimomys* (*Tcharinomys*) based on *M. haplodentatus* Savinov et Tutkova, 1987; *Mimomys* (*Heteromimomys*) based on *H. zhengi* Zhang, Jin & Kawamura, 2010. Several additional subgeneric lineages need more detailed descriptions and phylogenetic tracing.

Subgenus *MIMOMYS* F. Major, 1902
Mimomys cf. *hajnackensis* Fejfar, 1961
Figs 4–6, Tables 7–10.

1961 *Mimomys hajnackensis* nov. sp.: Fejfar, 50-51, Abb. 2: a,c, Taf. 15: 1-2.

1961 *Mimomys kretzoii* nov. sp.: Fejfar, 52-54, Abb.3: a,d, Taf. 16: 1-2.

1998 *Mimomys hassiacus* Heller, 1936: Fejfar, Repenning, p.163-164, text-fig.3: 4,6,21-23; text-fig.4:1-3,17-19.

2009 *Mimomys* cf. *hajnackensis* Fejfar, 1961 (partim): Agadjanian, p. 409, fig. 77 (4, 4a).

2009 *Mimomys hajnackensis* Fejfar, 1961 (partim): Agadjanian, p. 411 (table Korotoyak-2).

Studied material. 4 m1, 3 m2, 1 m3, 15 M1, 19 M2, 1 M3 (GIN 1203/073–115).

Type locality. Hajnáčka, Slovakia, Late Pliocene, MN16a (Fejfar, 1961).

Description. A vole with large molars. Measurements are shown in Tables 7–10. Cement fills no more than half of the reentrants depth. The enamel is conspicuously negatively differentiated (the leading edges of the triangles are thinner than the trailing ones) in most specimens. Enamel thickness ranges from a weak positive differentiation in juvenile specimens rapidly grading into negative one with a slight wear. The anteroconid of m1 is triangular with a pronounced *Mimomys*-ridge, which runs almost to the base of the crown, a deep LRA4, and a circular enamel islet which disappears nearly at the base of the crown (Fig. 4 A–D). The posterior root of m2 has the acrorhiz condition. The measurements of a single m3 are: L = 1.65, W = 1.05, Lbas = 1.77, Asd = 0.78, Hsd = 0.2, Hsld = 0.15, HH-index = 0.25, L/W = 1.56, Σ_tracts = 63.94, SDQ = 128.9.

M3 (Fig. 4) with a triangular posterior lobe with BRA3 and LRA3 folds and a flat oval posterior island. The anterior islet closes at a mid-height of the crown (Fig. 4: H1, H2). M3 measurements are as follows: L = 2.06, W = 1.08, P = 0.99, Lbas = 2.03, Ds = 0.46, As = 0.38, Prs = 0.66, PA-index = 0.76, L/W = 1.91, Σ_tracts = 73.89, SDQ = 149.22.

Schmelzmuster. The microstructure of enamel was studied in ontogenetically younger M1 (GIN 1203/095) and older M2 (GIN 1203/096). Thickness differentiation is from weakly positive to negative (SDQ (M1) = 91.4; SDQ (M2) = 126.73. Enamel is of pachyknem type. In M1, the leading edges consist of radial and primitive lamellar enamel, which occupies about a third of the wall thickness (Fig. 6B, C). The trailing edges are mainly built of radial enamel. There is a very primitive tangential enamel, which occurs in no more than a third of the wall thickness. The closing edge of the anterior loop consists of radial and normally developed tangential enamel in a ratio of 1:1 (Fig. 6A). The enamel of M2 is more advanced: the lamellar enamel is normally developed, and occupies up to half the wall thickness (Fig. 6E), also extends to the tips of the dentine triangles, the tangential enamel of the trailing edges is well developed, occupies half of the wall thickness (Fig. 6D). The closing enamel of the ante-

Table 7. Measurements (in mm) of m1 *Mimomys* cf. *hajnackensis* from Kabakova Balka locality.

m1	N	Mean	SE	Min	Max	SD	CV
L	4	2.95	0.0292	2.9	3.02	0.0584	1.98
W	4	1.44	0.018	1.39	1.46	0.036	2.5
Asd	1	1.59		1.59	1.59		
Hsd	4	0.89	0.0625	0.76	1.01	0.125	14.09
Hsld	4	0.32	0.0139	0.3	0.36	0.0278	8.66
Lbas	4	3.04	0.0758	2.88	3.22	0.1517	4.99
HH-index	3	0.98	0.0645	0.86	1.07	0.1118	11.36
Σ_tracts	1	102.72		102.72	102.72		
L/W	4	2.05	0.0254	1.99	2.09	0.0508	2.48
A/L	4	40.32	1.6562	35.38	42.26	3.3124	8.22
SDQ	4	122.7	3.9828	113.66	132.78	7.9655	6.49

Table 8. Measurements (in mm) of m2 *Mimomys* cf. *hajnackensis* from Kabakova Balka locality.

m2	N	Mean	SE	Min	Max	SD	CV
L	3	1.82	0.0143	1.8	1.85	0.0247	1.35
W	3	1.3	0.0291	1.25	1.34	0.0505	3.87
Asd	3	0.78	0.0627	0.67	0.89	0.1086	13.91
Hsd	3	0.43	0.0313	0.39	0.49	0.0542	12.54
Hsld	2	0.37	0.0575	0.31	0.43	0.0812	22.01
Lbas	3	2.05	0.0433	1.98	2.13	0.075	3.66
HH-index	2	0.58	0.0015	0.58	0.58	0.0021	0.37
Σ_tracts	2	76.6	2.1307	74.47	78.73	3.0132	3.93
L/W	3	1.4	0.0357	1.35	1.47	0.0619	4.42
SDQ	3	132.07	9.3852	118.3	150	16.2556	12.31

Table 9. Measurements (in mm) of M1 *Mimomys* cf. *hajnackensis* from Kabakova Balka locality.

M1	N	Mean	SE	Min	Max	SD	CV
L	12	2.41	0.0233	2.3	2.6	0.0808	3.35
W	15	1.43	0.0216	1.31	1.61	0.0836	5.85
Ds	13	0.85	0.0377	0.65	1.04	0.1358	16
As	13	0.35	0.0281	0.2	0.55	0.1012	28.57
Asl	13	0.3	0.0182	0.17	0.41	0.0656	21.88
Prs	15	0.69	0.029	0.39	0.89	0.1124	16.24
Lbas	14	2.48	0.0327	2.23	2.61	0.1225	4.94
PA-index	13	0.77	0.0326	0.47	0.91	0.1175	15.29
PAA-index	12	0.46	0.028	0.3	0.63	0.0971	21.03
Σ_tracts	10	73.23	2.5253	54.31	84.13	7.9856	10.91
L/W	12	1.71	0.0256	1.57	1.86	0.0888	5.18
SDQ	10	120.12	6.2443	91.4	159.3	19.7463	16.44

Table 10. Measurements (in mm) of M2 *Mimomys* cf. *hajnackensis* from Kabakova Balka locality.

M2	N	Mean	SE	Min	Max	SD	CV
L	14	1.94	0.023	1.8	2.15	0.086	4.44
W	19	1.33	0.0212	1.18	1.5	0.0923	6.96
Ds	16	0.62	0.0232	0.4	0.76	0.0929	15.02
As	15	0.31	0.0261	0.15	0.5	0.1011	32.16
Prs	15	0.41	0.0196	0.27	0.53	0.0758	18.36
PA-index	15	0.52	0.0268	0.35	0.71	0.1038	19.83
Lbas	13	1.96	0.03	1.75	2.2	0.1082	5.53
Σ_tracts	10	66.87	3.6545	45.45	81.86	11.5565	17.28
L/W	14	1.47	0.0306	1.33	1.67	0.1144	7.79
SDQ	13	132.19	3.5946	111.9	162.8	12.9606	9.8

rior lobe is similar to the M1. The difference in the enamel structure between M1 and M2 is explained by the different ontogenetic age of the teeth with M1 representing a younger individual.

Comparison. *Mimomys hajnackensis* Fejfar, 1961, Hajnáčka, Slovakia (Fejfar, 1961, 1964; Sabol *et al.*, 2006). First lower molars from Kabakova Balka are generally similar to the material from Hajnáčka, but they are somewhat smaller and less hypsodont. The size of the holotype of *M. hajnackensis* is 3.2×1.5 mm, estimated HH-index in m1 of the holotype is 0.9–1.1 (Fejfar, 1964, fig. 20; Mayhew *et al.*, 2008). The second m1 specimen of the original material, initially described as *Mimomys kretzoii* Fejfar, 1961, fits the concept of a large *Mimomys* species and shows a notably higher hypsodonty (Fejfar, 1964, fig. 23). Its estimated HH-index is 2.3. Additional teeth, attributable to *M. hajnackensis* in the type material is M1 (as *M. pliocaenicus minor* in Fejfar, 1964, fig. 28a–c) with reported L = 2.4 mm, and estimated W = 1.50; PA-index = 1.86. Teeth from Hajnáčka in materials of Sabol *et al.*, 2006 (m2, m3, M2, M3) also show hypsodonty higher than

in the Kabakova Balka sample. The estimated size and hypsodonty in m2, L = 2.14, W = 1.29, HH-index = 1.77; m3, L = 2.01, W = 1.14, HH-index = 1.01; M2, L = 1.93, W = 1.23, PA-index = 1.78; M3, L = 1.9, W = 1.15, PA-index = 0.91.

Mimomys hassiacus Heller, 1936, Gundersheim, Germany. Revision of the original material of Heller and a new material from Gundersheim-Findling provided a clear picture of morphology and hypsodonty of *M. hassiacus*. The teeth from Kabakova Balka are smaller in size than teeth from Gundersheim sites and have lower dentine tracts. The deep islet fold (BRA3) and somewhat eccentric enamel islets in original material of Heller (1936), and in the additional mandible with m1–m2 illustrated by Storch & Fejfar (1990) are peculiar characters not common in several samples of early *Mimomys* (*Mimomys*). This may be an indicator of a distinct taxon. The estimated HH-index of m1 in the type series ranges from 1.4 to 1.7 (Fejfar, Storch, 1990, figs. 21, 24, 25), with one specimen (Fejfar & Storch, 1990, fig. 19) showing more typical *Mimomys* morphology and substantially higher hypsodonty with HH-index near 2.95. This value fits the range of the younger Late Pliocene species of the same group, *Mimomys polonicus* Kowalski, 1960, and clearly indicates a mixed composition of the type Gundersheim material. Additional material on the *M. hassiacus* from Gundersheim-Findling (Fejfar & Storch, 1990, figs.100, 101, 109, 110) show the hypsodonty level comparable to the main material from Gundersheim. A peculiar M3 with a deep, not insulated LRA3 filled with cement may indicate a distinct taxon too.

Mimomys hassiacus, from German MN16a localities Hambach, Germany (Mörs *et al*., 1998) and Frechen (as *M.* cf. *polonicus*, van Kolfschoten *et al*., 1998). The vole from Kabakova Balka is less hypsodont, and

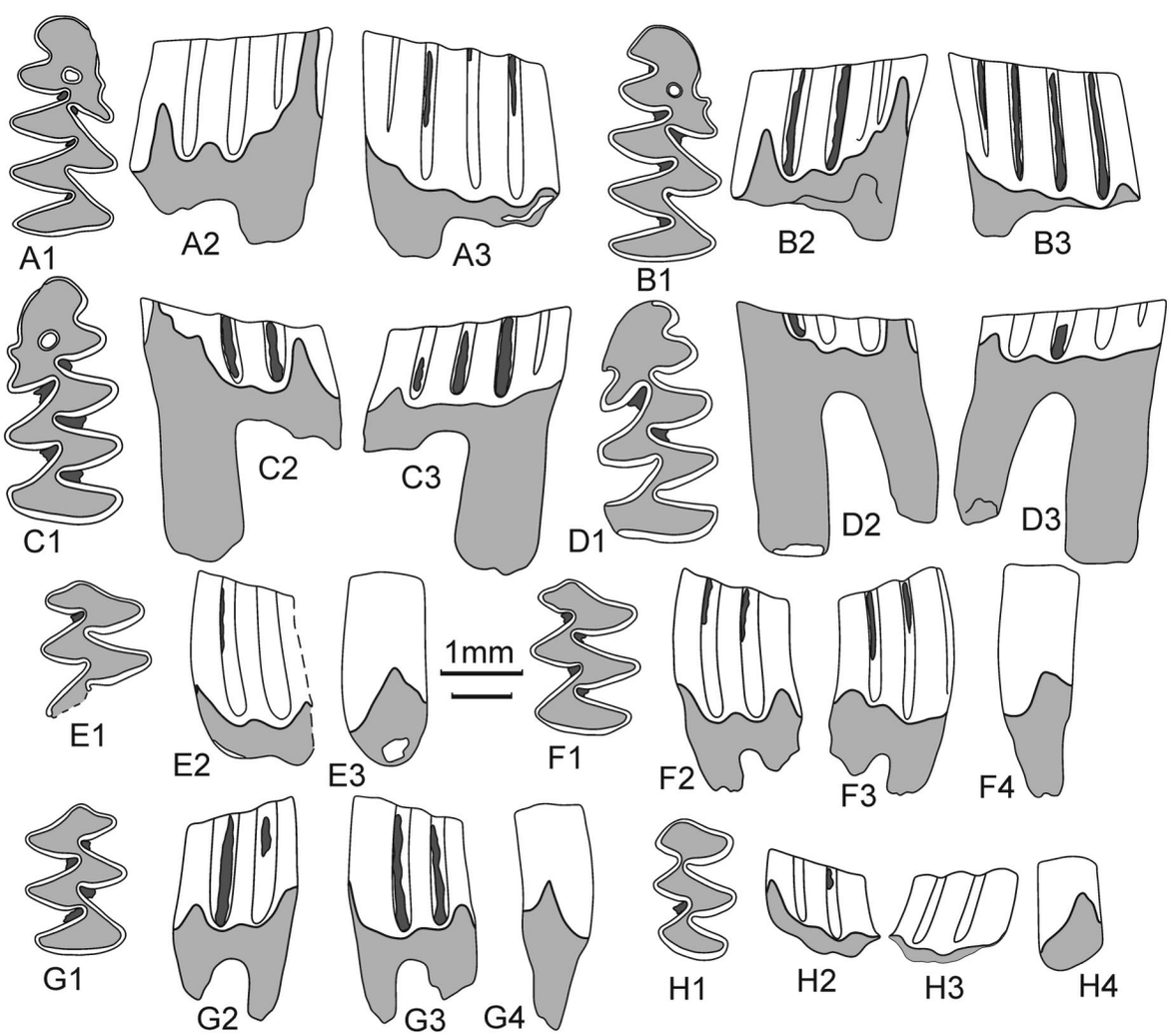

Fig. 4. Lower molars of *Mimomys* cf. *hajnackensis* (Kabakova Balka). A–D — m1 (GIN 1203/073–076); E–G — m2 (GIN 1203/077–079); H — m3 (GIN 1203/080). 1 — occlusal surface; 2 — buccal side; 3 — lingual side; 4 — Asd. Scale bar 1 mm for occlusal view (upper line) and lateral views (lower line).

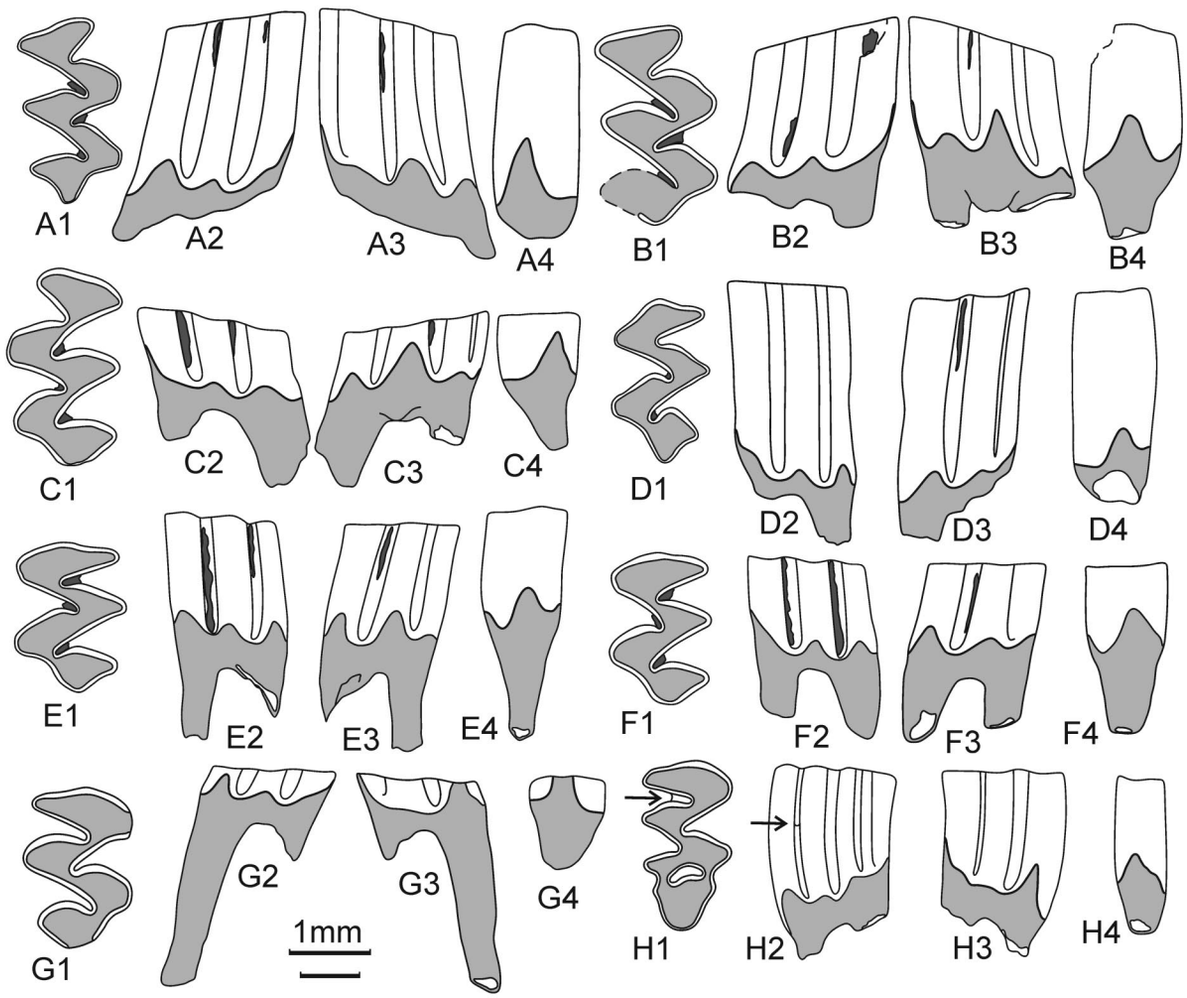

Fig. 5. Upper molars of *Mimomys* cf. *hajnackensis* (Kabakova Balka). A–C — M1 (GIN 1203/082, 087, 093); D–G — M2 (GIN 1203/097, 106, 096, 114); H — M3 (GIN 1203/115). 1 — occlusal surface; 2 — buccal side; 3 — lingual side; 4 — Ds. Scale bar 1 mm for occlusal view (upper line) and lateral views (lower line). Arrow points to closing enamel islet.

in size approaches lower values of the Hambach sample. Both voles have similar enamel microstructure.

Mimomys hassiacus, Wölfersheim, Germany (Fejfar & Repenning, 1998). Morphologically and in terms of the level of hypsodonty, it is similar to the sample from Kabakova Balka, but the latter has a slightly shorter occusal surface of m1. In hypsodonty level the only M3 from KB has a PA-index of 0.76 as compared to estimated values of 0.51–0.55–0.61 in Wölfersheim. This find from southern Germany is among the oldest records of large cemented *Mimomys* in Europe.

Mimomys hassiacus, Arondelli, Italy (Fejfar, 2001). The m1 vole from the Kabakova Balka is similar in size to vole from Arondelli, but it is markedly smaller and less hypsodont.

Mimomys hajnackensis, boreholes Polder de Biesbosch, Deventer and Diepenveen, the Netherlands (Mayhew *et al.*, 2008). The m1 of the vole from Kabakova Balka are smaller in size and show lower dentine tracts (Hsld) than the Dutch records. Likewise, the M2 from Kabakova Balka are significantly smaller and less hypsodont than the tooth from Diepenveen.

Mimomys ex gr. *hajnackensis*, Ripa Skortselskaya (Râpa Scortsescu), Moldova (Tesakov, 2004). Compared to the vole from Ripa Skortselskaya, the specimens from Kabakova Balka are slightly smaller, show less incurving reentrants, and has slightly lower hypsodonty. The vole from Ripa Skortselskaya may represent a different phyletic lineage related to *Kislangia*.

Mimomys hajnackensis, Shirokino (Donetsk Region), Volna (Krasnodar Territory, Russia), and Nagavskaya (Volgograd Region, Russia) (Tesakov, 2004). In terms of size, the sample from Kabakova Balka is near the lower variability limits of the sample from Nagavskaya, and smaller than the sample from Shirokino (HH-index 1.82–2.24–2.57, $n = 4$). In terms of the heights of

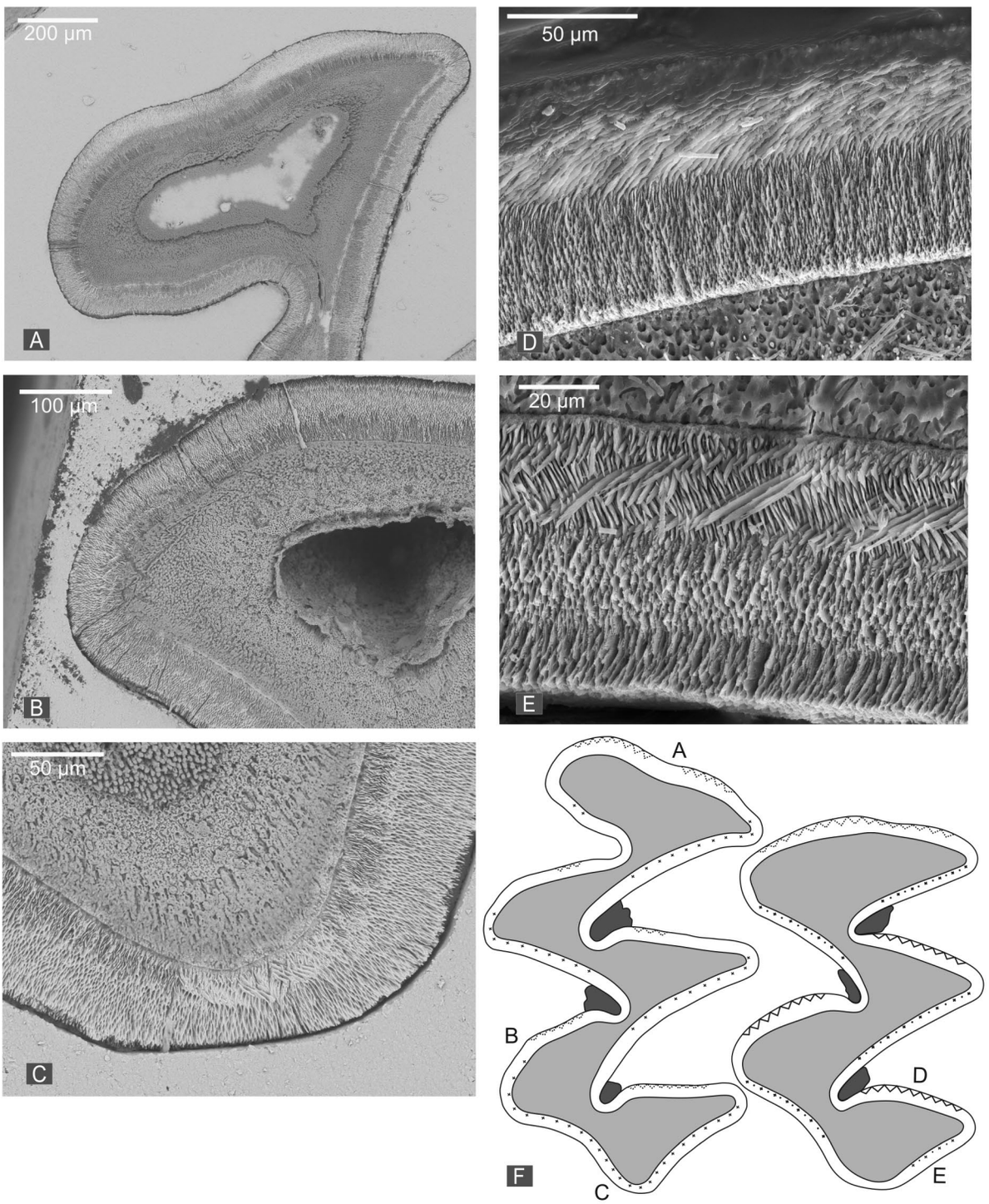

Fig. 6. Enamel microstructure of *Mimomys* cf. *hajnackensis* from Kabakova Balka. A–C — M1 sin (GIN 1203/095); D–E — M2 sin (GIN 1203/096); A — anterior lobe; B — triangle T3; C — posterior part of triangle T4; D— trailing edge, triangle T4; E — leading edge, triangle T4; F — overview images with the studied enamel parts and enamel types shown. Crosses are primitive lamellar enamel; crosses and dots are lamellar enamel; dotted zigzag line is primitive tangential enamel; zigzag line is tangential enamel; white space shows radial enamel.

the dentine tracts, the Kabakova Balka form is much less hypsodont.

Mimomys cf. *hajnackensis*, Korotoyak-1, Voronezh Region, Russia (Agadjanian, 2009). Regarding the very small material from this oldest of the Don Pliocene sites, the two voles seem to be generally comparable in size, hypsodonty, and sparse cement deposits. First lower molars from Kabakova Balka may have slightly higher labial dentine tracts, whereas m2 are nearly identical in size and height of dentine tracts.

Mimomys hajnackensis, Korotoyak-2, Uryv-1, *Mimomys* cf. *polonicus,* Uryv-2, Voronezh Region, Russia (Agadjanian, 2009). The three samples of large *Mimomys* display directed increase of dentine tracts. Based on the published variation limits of labial dentine tracts in these samples (Agadjanian, 2009), their HH-indexes are roughly estimated as 0.5–1.1–1.9 (Korotoyak 2), 0.9–1.3–1.8 (Uryv-1), and 1.05–1.6–1.9 (Korotoyak-2). Thus the oldest samples from Korotoyak-2 and Uryv-1 represent voles less hypsodont than the type *M. hajnackensis* and close to *M.* cf. *hajnackensis* from Kabakova Balka. A slightly more evolved form from Uryv-2 fits the hypsodonty of the type *M. hajnackensis* and should be assigned to this species. All forms from the Don River area and the vole from Kabakova Balka show much lower hypsodonty than the type *Mimomys polonicus* from Rębielice Królewskie with a mean HH-index near 3 (Tesakov, 2004).

Mimomys hassiacus, Tollo de Chiclana 1B, Spain (Minwer-Barakat *et al.*, 2008). The vole from Spain has, on average, a longer m1, estimated HH-index of 0.9–1.5. The large size typical for many endemic Iberian vole lineages can be an indication of a nascent regional lineage. Its hypsodonty level is below typical continental European *M. hajnackesis* and in general close to the vole from Kabakova Balka.

Mimomys hassiacus, Afşar 2, Turkey (Skandalos *et al.*, 2023). The vole from Afşar 2 has relatively wider m1 and m2, as well as higher dentine tracts (HH-index of m1 0.73–1.07–1.29) in the entire dentition.

Mimomys polonicus, Rębielice Królewskie 1, Poland (Kowalski, 1960a). The sample from Kabakova Balka has smaller dimensions and hypsodonty compared to the Polish vole with HH-index 2.43–3.06–3.48, $n = 10$ (Tesakov, 2004).

Mimomys polonicus, Biteke, Kazakhstan (Zazhigin, 1980). The molars from Biteke are larger and more hypsodont than the teeth from the Kabakova Balka.

Mimomys hajnackensis, Nizhny Rozovsky, Russia (Tesakov & Bondarev, 2024). The extensive material of a large *Mimomys* from Early to Late Pliocene transition in Western Siberia documents a brachyodont vole with HH-index 0.6–0.8–1.19 ($n = 13$). As regards hypsodonty it is close the vole from Kabakova Balka.

Mimomys occitanus Thaler, 1955, Sète, France (Chaline, 1974). The described vole from North Caucasus is more hypsodont and notably smaller than type *M. occitanus*. It also indicates better developed schmelzmuster of the pachyknem type versus eopachyknem in the vole from France (von Koenigswald, 1981). *M. occitanus* is regarded a late Early Pliocene (late Ruscinian) phyletic predecessor of larger *Mimomys* of Late Pliocene in Europe (Chaline & Laurin, 1986) or belonging to an independent lineage related to *Dolomys* (Maul, 1996; Fejfar & Repenning, 1998; Popov, 2004). Morphologically this vole is still at *Promimomys* evolutionary level.

Comments. The given comparison shows that the large *Mimomys* from Kabakova Balka represents a hypsodonty stage of *Mimomys* (*Mimomys*) lineage that precedes the type level of *Mimomys hajnackensis.* This stage is diagnosed by HH-index below ca. 1.5. This vole is considered as a phyletic ancestor of *Mimomys hajnackensis* Fejfar, 1961. It represents the least hypsodont (HH-index of m1) form in the lineage of the nominal subgenus of *Mimomys: M.* cf. *hajnackensis* (HH-index < 1.5, MN15b) — *M. hajnackensis* (1.5–2.5, MN16a) — *M. polonicus* (2.5–3.5, MN16b) — *M. praepliocaenicus* (3.5–4.5, MN17) — *M. pliocaenicus* (4.5–5.5, MN17) — *M. ostramosensis* (>5.5, MN17/Q1). Among the reviewed records of Pliocene larger voles this early stage is documented in Wölfersheim (Fejfar & Repenning, 1998) and in Korotoyak-1, Korotoyak-2, and Uryv-1 (Agadjanian, 2009). Some of these localities, like Kabakova Balka, Wölfersheim and Korotoyak-1, may date to the terminal Early Pliocene as indicated by very archaic mammalian fauna and paleomagnetic signals. We refrain from a description of a new taxon here before the study of larger material.

The usage of *Mimomys hassiacus* Heller, 1936 as a senior synonym for *Mimomys hajnackensis* Fejfar, 1961 is discouraged here based on peculiar morphological variability of the vole from Gundersheim samples, and before a revision of their possible mixed origin.

Subgenus *PUSILLOMIMUS* Rabeder, 1981
Mimomys cf. *stehlini* Kormos, 1931
Figs 7–9, Tables 11–16.

Studied material. 25 m1, 18 m2, 10 m3, 24 M1, 31 M2, 17 M3 (GIN 1203/116–240)

Type locality. San Guisto, Italy, Late Pliocene, MN16.

Description. Medium-sized rhizodont vole (Figs 7–9; Tables 11–16), molars with small cement accumulations. Dentine triangles are from sub-triangular in younger individuals to rounded with more wear. Occlusal triangles communicate by notable dentine confluences. The enamel thickness ranges from poorly differentiated of positive type in young individuals to negatively differentiated in older ones and has a protopachyknem microstructure (Fig. 9). Lower molars have two roots, and the upper ones have three roots. Dentine tracts are very low, HH-index of m1 ranges as 0.81–0.65–0.95, $n = 16$.

m1. The m1 anteroconid complex has a deep *Mimomys*-ridge and a prismatic fold that obliterate with strong wear. The LRA4 is deep and U-shaped. AC is diagonally elongated. A circular enamel island disappears when the crown is worn below ca. 1 mm.

Table 11. Measurements (in mm) of m1 *Mimomys* cf. *stehlini* from Kabakova Balka locality.

m1	N	Mean	SE	Min	Max	SD	CV
L	10	2.58	0.0393	2.45	2.76	0.1243	4.82
W	25	1.17	0.0178	1.04	1.35	0.0888	7.57
Asd	11	1.11	0.0815	0.6	1.4	0.2703	24.28
Hsd	16	0.71	0.0251	0.55	0.86	0.1004	14.19
Hsld	17	0.37	0.0175	0.24	0.48	0.0723	19.39
Lbas	14	2.61	0.0409	2.26	2.82	0.1529	5.86
HH-index	16	0.81	0.0211	0.65	0.95	0.0843	10.44
Σ_tracts	7	83.58	5.2735	53.57	94.6	13.9523	16.69
L/W	8	2.19	0.0506	1.92	2.37	0.1432	6.53
A/L	10	42.14	1.979	27.34	48.74	6.2581	14.85
SDQ	14	112.76	3.6524	87.75	135.78	13.6659	12.12

Table 12. Measurements (in mm) of m2 *Mimomys* cf. *stehlini* from Kabakova Balka locality.

m2	N	Mean	SE	Min	Max	SD	CV
L	14	1.65	0.0252	1.5	1.79	0.0942	5.72
W	18	1.05	0.0242	0.83	1.22	0.1025	9.78
Asd	15	0.72	0.04	0.5	1.06	0.1547	21.54
Hsd	17	0.44	0.0243	0.25	0.62	0.1004	22.56
Hsld	17	0.33	0.0246	0.14	0.49	0.1015	30.56
Lbas	18	1.82	0.0295	1.57	2.03	0.1252	6.88
HH-index	17	0.56	0.0299	0.3	0.7	0.1233	22.03
Σ_tracts	14	81.73	4.0963	54.04	102.02	15.3269	18.75
L/W	14	1.58	0.0245	1.45	1.76	0.0918	5.82
SDQ	17	119.76	3.262	86.3	139.1	13.4498	11.23

Table 13. Measurements (in mm) of m3 *Mimomys* cf. *stehlini* from Kabakova Balka locality.

m3	N	Mean	SE	Min	Max	SD	CV
L	10	1.5	0.0192	1.42	1.63	0.0607	4.04
W	10	0.85	0.0157	0.77	0.91	0.0495	5.83
Asd	10	0.6	0.0345	0.47	0.81	0.1091	18.11
Hsd	10	0.2	0.0142	0.15	0.26	0.045	22.75
Hsld	10	0.15	0.0123	0.1	0.23	0.0389	26.16
Lbas	10	1.69	0.0322	1.54	1.86	0.1017	6.01
HH-index	10	0.25	0.0161	0.19	0.34	0.0509	20.43
Σ_tracts	10	56.24	2.2348	45.07	69.74	7.067	12.57
L/W	10	1.77	0.027	1.62	1.88	0.0854	4.83
SDQ	10	118.95	3.8842	105.9	138.9	12.2829	10.33

Table 14. Measurements (in mm) of M1 *Mimomys* cf. *stehlini* from Kabakova Balka locality.

M1	N	Mean	SE	Min	Max	SD	CV
L	21	2.01	0.0297	1.65	2.21	0.1362	6.79
W	24	1.19	0.0191	0.95	1.34	0.0938	7.86
Ds	18	0.54	0.0383	0.3	0.9	0.1624	29.86
As	21	0.25	0.0142	0.14	0.38	0.065	25.63
Asl	23	0.25	0.0189	0.13	0.42	0.0908	36.67
Prs	21	0.56	0.0214	0.36	0.74	0.0983	17.54
Lbas	23	2.11	0.038	1.82	2.56	0.1822	8.65
PA-index	18	0.63	0.0219	0.48	0.82	0.0929	14.64
AA-index	21	0.36	0.0223	0.22	0.55	0.1024	28.35
Σ_tracts	15	66.83	3.594	49.09	98.24	13.9195	20.83
L/W	21	1.71	0.022	1.56	1.9	0.1009	5.92
SDQ	18	115.53	3.6188	94	155.3	15.3533	13.29

Table 15. Measurements (in mm) of M2 *Mimomys* cf. *stehlini* from Kabakova Balka locality.

M2	N	Mean	SE	Min	Max	SD	CV
L	30	1.72	0.018	1.55	1.93	0.0988	5.74
W	31	1.14	0.0133	1	1.25	0.0738	6.46
Ds	28	0.49	0.0327	0.28	1	0.173	35.33
As	30	0.28	0.0161	0.16	0.5	0.0884	31.48
Prs	29	0.33	0.0195	0.17	0.57	0.1048	31.78
PA-index	29	0.44	0.0226	0.3	0.7	0.1215	27.66
Lbas	31	1.75	0.0195	1.58	2.04	0.1085	6.22
Σ_tracts	28	62.52	2.8686	42.01	105.56	15.1793	24.28
L/W	30	1.52	0.0173	1.35	1.75	0.0947	6.25
SDQ	26	125.86	3.0204	97.9	159.7	15.4012	12.24

Table 16. Measurements (in mm) of M3 *Mimomys* cf. *stehlini* from Kabakova Balka locality.

M3	N	Mean	SE	Min	Max	SD	CV
L	13	1.56	0.0347	1.4	1.77	0.125	8
W	17	0.97	0.024	0.84	1.21	0.0989	10.19
Ds	13	0.38	0.0303	0.24	0.65	0.1094	28.45
As	15	0.27	0.0217	0.14	0.4	0.0841	31.27
Prs	15	0.24	0.0186	0.12	0.33	0.072	29.62
PA-index	15	0.37	0.0252	0.18	0.5	0.0975	26.63
Lbas	15	1.6	0.0298	1.43	1.8	0.1153	7.21
Σ_tracts	11	50.61	2.8161	34.71	61.11	9.34	18.46
L/W	13	1.62	0.0352	1.41	1.91	0.1269	7.82
SDQ	12	111.6	4.0132	89.88	133.1	13.902	12.46

m2. The molar has a posterior lobe and two pairs of poorly alternating, widely confluent triangles. BRA1 incompletely separates T1 and T2. The posterior root of m2 has an acrorhiz structure.

m3. The molar has a posterior lobe and two pairs of widely confluent triangles.

M1. The molar has an anterior lobe and four alternating triangles.

M2. The molar has an anterior lobe and three alternating triangles.

M3. The molar has an anterior lobe, one triangle and a widely confluent posterior lobe. The anterior lobe is triangular with barely noticeable LRA3 and BRA3, and there is an oval or bean-shaped posterior enamel island. In some M3, the anterior enamel island may insulate the LRA1 with strong crown wear (Fig. 8G).

Schmelzmuster. The enamel microstructure was studied for M1 (GIN 1203/169). The enamel is negatively differentiated in thickness (SDQ = 121.4). It belongs to the protopachyknem type. The leading edge consists of radial enamel with a very thin layer of primitive lamellar enamel stretched along the enamel-dentine junction (Fig. 9B). The lamellar enamel does not enter into the reentrant angle, it is slightly better developed at the tip of the triangle than along the rest of the edge (Fig. 9D). The trailing edges consist of radial and primitive tangential enamel. They take up about half of the wall thickness each (Fig. 9C). The closing edge of the anterior loop is similar to trailing ones. In its medial part the tangential enamel is interrupted by the radial one (Fig. 9A).

Comparison. *Mimomys stehlini* Kormos, 1931, San Guisto, Italy (Kormos, 1931; Masini & Torre, 1987). Compared with the type material, the Kabakova Balka sample is characterized by lower dentine tracts and small cement accumulations in reentrant angles. The estimated height of HSD in San Guisto type m1 is 1.53 that is notably higher than the mean value 0.65 of this tract in Kabakova Balka.

Smaller brachyodont *Mimomys* from China, *M. nihewanensis* Zheng, Zhang et Cui, 2019 and *M. orientalis* Young, 1935 (Qiu & Li, 2016; Zheng *et al.*, 2019, 2024). These voles from several Late Pliocene sites of North China demonstrate early stages of smaller *Mimomys* radiation in the eastern part of Eurasia. Sparse cement and hypsodonty level of these forms (HH-index between 0.8 and 1.3) overlaps the conditions of *M.* cf. *stehlini* from Kabakova Balka and other Late Pliocene records from Europe. Larger size of the Chinese forms and the missing anterior enamel islet in M3 may indicate lineage(s) distinct from the one of smaller *Mimomys* from Western Eurasia.

Mimomys sp., Tourkobounia-1, Greece (de Brujin & van der Meulen, 1975). The described vole is similar to the Greek record in size and in insulation of anterolabial reentrant in M3 near the mid-height of the crown. The vole from Greece differs in slightly higher hypsodonty, more shallow anterior enamel islet in m1, and

in two-rooted M3. Tesakov (2024) supposed that it belongs to a different lineage of early radiation of smaller *Mimomys* in Europe.

Mimomys postsilasensis, Deutsch Altenburg 20, Austria (Rabeder, 1981). The vole from Kabakova Balka is very similar to this vole in size, hypsodonty, and schmelzmuster. The same Austrian site yielded a sufficient material of another smaller *Mimomys*, assigned by Rabeder to *M. kretzoii* Fejfar, 1961. The original *M. kretzoii* from Hajnáčka is obviously synonymic to *M. hajnackensis* (large size, broad occlusal surface, page posteriority). The smaller vole from Deutsch Altenburg 20 and 9 fits *Mimomys stehlini* concept. The co-occurring "*Mimomys polonicus*" in Deutsch Altenburg 20 is obviously less hypsodont than type *M. polonicus* and actually represents *M. hajnackensis*. The biochronological context of both Austrian faunas well fits MN16a and postdate the level of the Kabakova Balka fauna. At the same time the co-occurrence of two smaller voles broadly similar in size and morphology but different in hypsodonty (more brachyodont *M. postsilasensis* and more hypsodont *M. stehlini*) looks like a co-occurrence of ancestral and descending stages of the same lineage. Whether this is a taphonomic mixing or evidence of early radiation we cannot judge now. Before this issue clarified the use of *M. postsilasensis* is discouraged.

Mimomys stehlini stehlini, Osztrámos 7, Hungary (Fejfar & Heinrich, 1982). The vole from Hungary surpasses the Kabakova Balka vole in the height of the dentine tracts, e.g. its estimated HSD are higher than 2 mm.

Mimomys stehlini, Gundersheim, Germany (Storch & Fejfar, 1990). The sample from Kabakova Balka has a slightly lower dentine tract height than the vole from Germany.

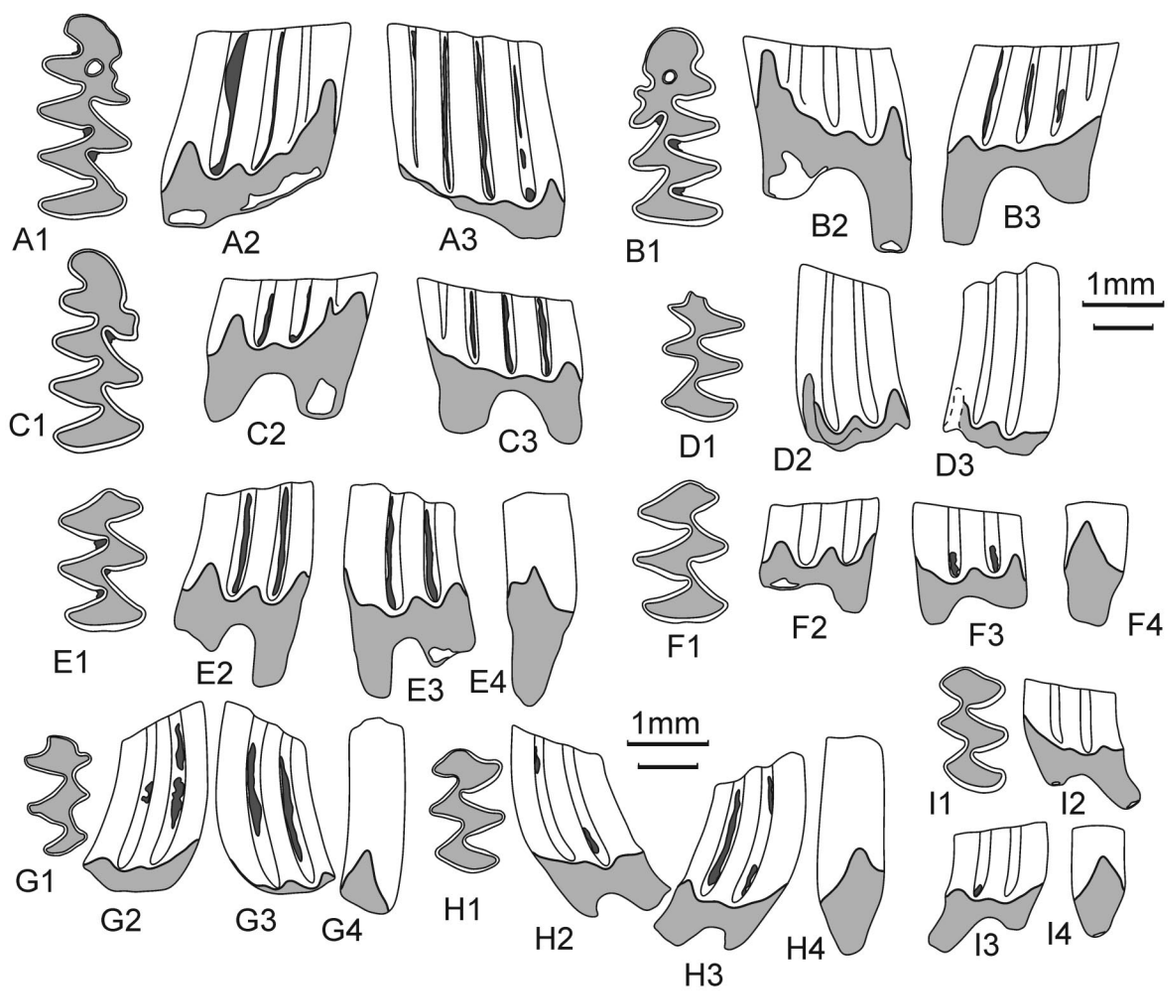

Fig. 7. Lower molars of *Mimomys* cf. *stehlini* (Kabakova Balka). A–C — m1 (GIN 1203/119, 126, 134); D–F — m2 (GIN 1203/141, 148, 158); G–I — m3 (GIN 1203/159, 162, 168). 1 — occlusal surface; 2 — buccal side; 3 — lingual side; 4 — Asd. Scale bar 1 mm for occlusal view (upper line) and lateral views (lower line).

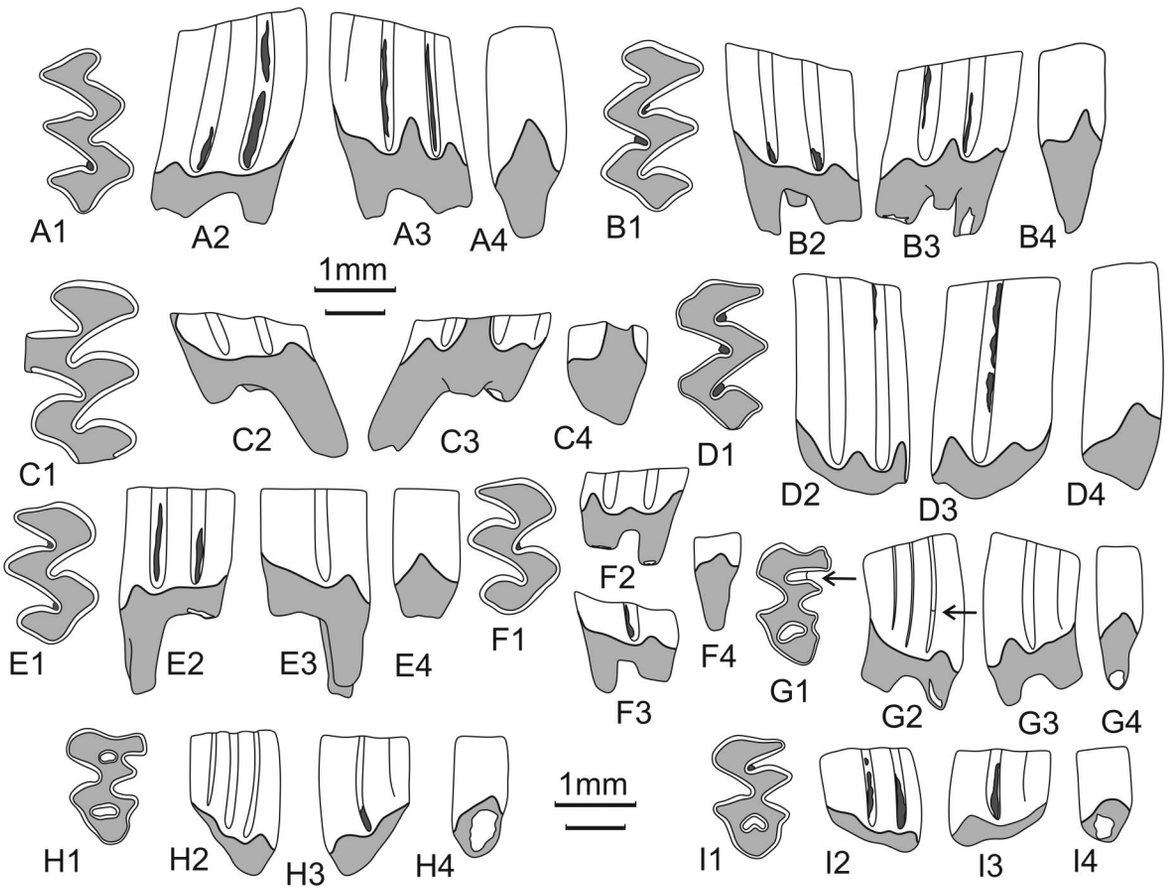

Fig. 8. Upper molars of *Mimomys* cf. *stehlini* (Kabakova Balka). A–C — M1 (GIN 1203/170, 184, 191); D–F — M2 (GIN 1203/196, 212, 221); G–I — M3 (GIN 1203/224, 233, 237). 1 — occlusal surface; 2 — buccal side; 3 — lingual side; 4 — Ds. Scale bar 1 mm for occlusal view (upper line) and lateral views (lower line). Arrow points to closing enamel islet.

Mimomys stehlini Kormos, 1931, Balaruc 2, Seynes (France), Moreda (Spain) (Bachelet *et al.*, 1991). The sample from Kabakova Balka is characterized by a lower height of the dentine tracts than the voles from the listed locations, as well as the presence of cement.

Mimomys stehlini, Arondelli-Triversa, Italy (Fejfar, 2001). The Kabakova Balka vole corresponds to *M. stehlini* from Arondelli in occlusal size and morphology but shows lower hypsodonty (ASD 0.6–1.1–1.4, $n = 11$ contrary to estimated 1.8 and 2.35 in Italian form).

Mimomys stehlini, Tollo de Chiclana 13, Spain (Minwer-Barakat *et al.*, 2008). The Kabakova Balka vole is located in the lower limits of the variability of the Tollo de Chiclana 13 vole, and has a slightly lower height of the dentine tracts.

Mimomys cf. *stehlini*, Węże 1, Poland (Sulimski, 1964). Generally more archaic hypsodonty and occlusal characters of all voles from Węże are seemingly supported by a less hypsodont smaller vole illustrated by Sulimski (1964, fig. 21). Specimens illustrated as *M.* cf. *stehlini* by Kowalski (1960b, fig. 8) may represent a mixture of a large and smaller forms. The single specimen of m1 measured (AT) from this assemblage has HH-index of 0.6, which is at the lower value of the range in Kabakova Balka.

Mimomys cf. *stehlini*, Rębielice Królewskie, Poland (Kowalski, 1960). The sample described under this name represents a mixture of *M. stehlini* (Kowalski, 1960a, fig.3 A–F) and *Pitymimomys* cf. *altenburgensis* Rabeder, 1981 (ibid., fig. 3 C–D). Two specimens of smaller *Mimomys* measured from this fauna (AT) have HH-index of 2.3. This surpasses the maximal value of hypsodonty index (0.98) in Kabakova Balka.

Mimomys hintoni Fejfar, 1961, Kotlovina (middle and upper layers), Ukraine (Topachevsky & Nesin, 1989). The Kabakova Balka vole is distinctly different from the Kotlovina vole by the lower dentine tracts.

Mimomys sp., Dolinskoe, Ukraine (Tesakov, 2004). According to the morphology and height of the m1 dentine tracts, voles from Kabakova Balka and Dolinskoe are similar, but the latter form is somewhat larger.

Mimomys hintoni hintoni, Ripa Skortselskaya, Moldova (Tesakov, 2004). The sample from Kabakova Balka is less hypsodont compared to a vole from Moldova.

Mimomys cf. *hintoni*, Korotoyak-1, Voronezh Region, Russia (Agadjanian, 2009). In morphology, size, and height of dentine tracts, the vole from Kabakova Balka is identical to the vole from Korotoyak-1.

Mimomys hintoni, Uryv-1, Uryv-2, Voronezh Region, Russia (Agadjanian, 2009). The vole from Kabakova Balka vole shows significantly lower dentine tracts.

Comments. The smaller *Mimomys* species co-occurs with large *Mimomys* in numerous Pliocene faunas of Europe. They represent a subgeneric phyletic lineage of *Pusillomimus* Rabeder, 1981 based on *M. pusillus* Mehely, 1914 (see the discussion in Tesakov, 2004). The lineage includes *Mimomys* ex gr. *stehlini* (<1.5) — *M. stehlini* (HH-index 1.5–2.5) — *Mi-*

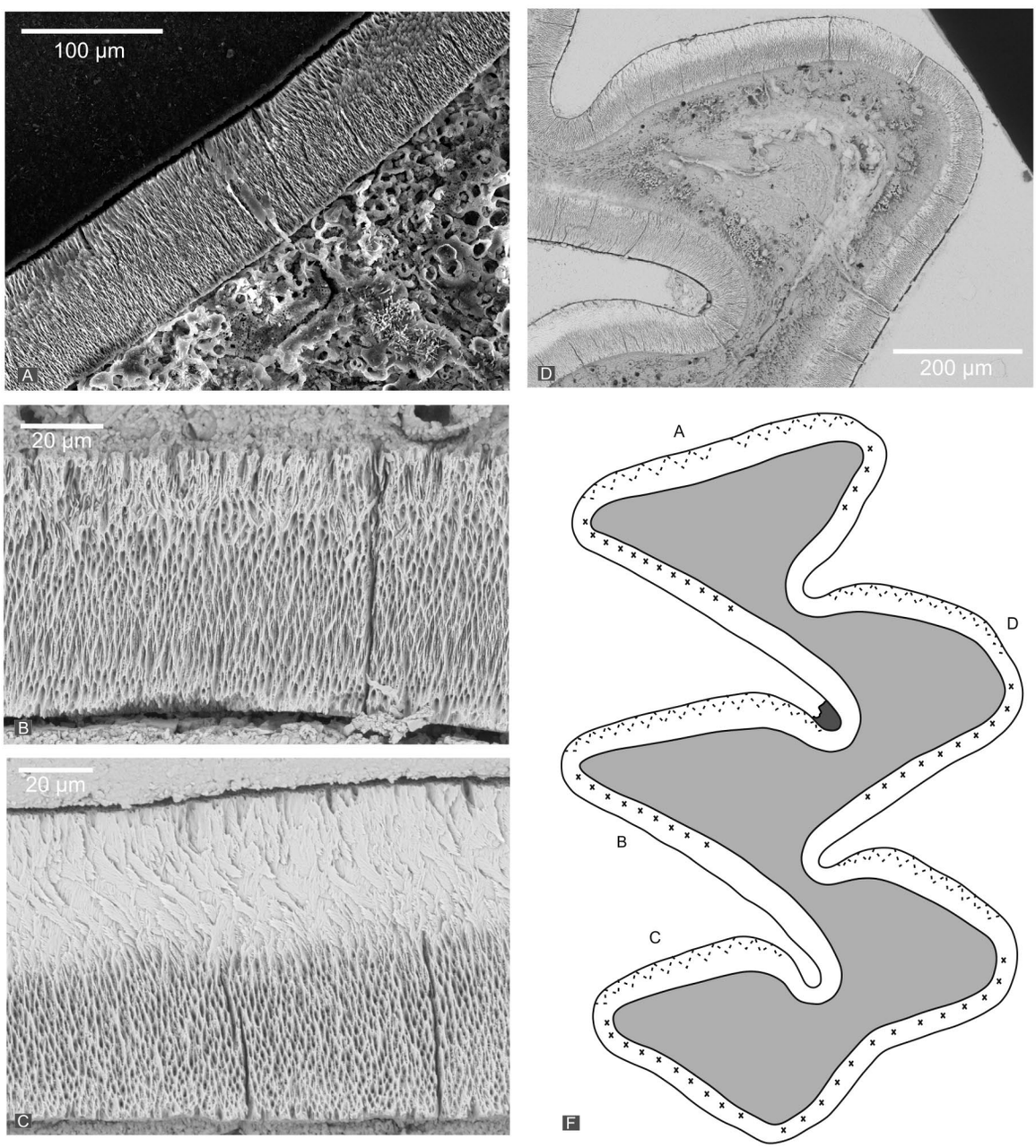

Fig. 9. Enamel microstructure of *Mimomys* cf. *stehlini* from Kabakova Balka, M1 dex (GIN 1203/169). A — closing enamel of anterior lobe; B — leading edge of triangle T2; C — trailing edge of triangle T4; D — triangle T1; E — overview image with the studied enamel parts and enamel types shown. Crosses are primitive lamellar enamel; dotted zigzag line is primitive tangential enamel; white space shows radial enamel.

momys liventsovicus (2.5–3.0) — *M. reidi* (3.0–4.5) — *M. pusillus* (>5). In hypsodonty the Ciscaucasian smaller *Mimomys* ex gr. *stehlini* is less hypsodont and shows more archaic promimomyan characters, e.g. a persistent anterior islet in M3, as compared to most early Villanyian, MN16, smaller *Mimomys* from Europe. On the contrary, similar to the case of *M.* ex gr. *hajnackensis*, it resembles forms from latest Ruscinian, MN15 sites (Węże) and sites close to Ruscinian–Villanyian transition (Korotoyak-1, Dolinskoe, etc.). This phyletic stage deserves a "*praestehlini*" chronospecies status of its own. Whether some of the already described smaller brachyodont species (as *M. silasensis* Janossy, 1974, *M. postsilasensis* Rabeder, 1981, etc.) could be used in this sense is currently not clear.

Genus *DOLOMYS* Nehring, 1898
Dolomys nehringi Kretzoi, 1959
Figs 10–11.

Studied material. 1 M1, 2 M2, 3 M3.

Type locality. Csarnóta 2, Hungary (Kretzoi, 1959).

Description. Large brachyodont vole lacking cement in reentrant angles. The enamel has a distinct negative (*Mimomys*-type) thickness differentiation (SDQ = 150.59). Dentine tracts are very low.

Upper molars large and broad with deep posteriorly curving reentrants, three roots, occlusal triangles connected by relatively wide confluences. M1 consists of AL and four alternating triangles. M2 consists of AL and three alternating triangles. M3 has AL, three alternating triangles and rounded triangular PL separated by three well developed buccal and two lingual reentrants. PL is slightly elongated antero-posteriorly. The postero-lingual reentrant (LRA4) is shallow. A prism of protocone (LSA3) with a shallow fold extending almost to the bottom of the crown.

Measurements. M1: L = 2.42, W = 1.53, Lbas = 2.51, Ds = 0.78, As = 0.2, Asl = 0.18, Prs = 0 .55, PA-index = 0.59, AA-index = 0.27, L/W = 1.58, Σ_tracts = 60.9, SDQ=98.63. M2: L=2.11, W=1.65, Lbas=2.06, Ds=0.47, As = 0.25, Prs = 0.41, PA-index = 0.48, L/W = 1.28, Σ_tracts = 54.93, SDQ = 130.58; W = 1.55. M3: L = 2.07, W = 1.23, P = 0.93, Lbas = 2.14, Ds = 0.49, As = 0.26, Prs = 0.44, PA-index = 0.51, L/W = 1.69, Σ_tracts = 55.71, SDQ = 150.59; L = 2.25, W = 1.36, P = 1.04, Lbas = 2.23, Ds = 0.46, As = 0.22, Prs = 0.29, PA-index = 0.36, L/W = 1.65, Σ_tracts = 43.57, SDQ = 127.5; L = 1.82, W = 1.29, P = 0.89, Lbas = 1.96, Ds = 0.42, As = 0.32, Prs = 0.26, PA-index = 0.41, L/W = 1.42, Σ_tracts = 50.87, SDQ = 115.9.

Schmelzmuster. The microstructure of enamel was studied in M2 (GIN 1203/243). The enamel has a distinctly negative differentiation in thickness (SDQ = 130.58). The leading edge consists of radial and well-developed lamellar enamel (Fig. 11B), lamellar enamel occupies about half the thickness of the enamel wall, on lingual triangles it wraps around the apex of the triangle and can slightly extend into the trailing edge. The trailing edge consists of radial and tangential enamel, each occupying half of the wall thickness (Fig. 11C). The closing edge of anterior loop is arranged similar to the trailing one, with slightly thinner tangential enamel (Fig. 11A).

Comparison. *Dolomys nehringi,* Csarnóta 2, Hungary (Kretzoi, 1959). Judging by the figures from the original (Kretzoi, 1962: Abb. 4) and subsequently published illustrations (Rabeder, 1981), the occlusal morphology and the overall dimensions of the type material and teeth from Kabakova Balka are similar.

Dolomys nehringi, Kotlovina (middle bed), Ukraine (Topachevsky & Nesin, 1989). In size, occlusal morphology, and height of the dentine tracts, the vole from Kabakova Balka corresponds to the sample of smaller

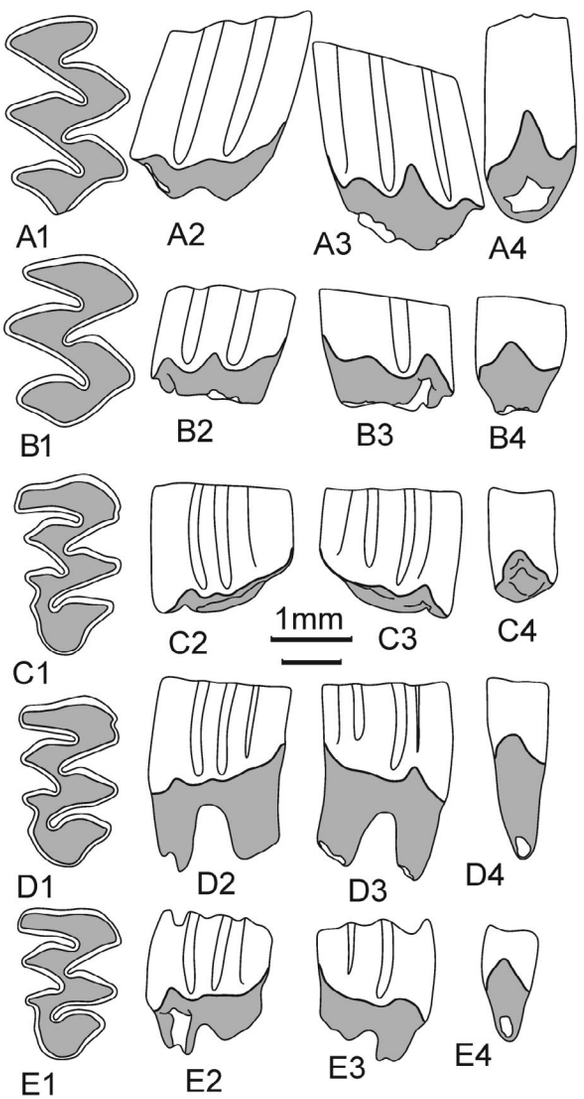

Fig. 10. Molars of *Dolomys nehringi* (Kabakova Balka). A — M1 (GIN 1203/241); B — M2 (GIN 1203/242); C–E — M3 (GIN 1203/244–246). 1 — occlusal surface; 2 — buccal side; 3 — lingual side; 4 — Ds. Scale bar 1 mm for occlusal view (upper line) and lateral views (lower line).

Dolomys attributed to the middle layer of the Kotlovina sequence.

Dolomys nehringi, Podari, Romania (Radulescu & Samson, 1997). This vole from a site correlated to mid-Piacenzian (Andreescu *et al.*, 2013) is much larger than *Dolomys* from Kabakova Balka: length of M3 is 2.7 mm versus 1.82–2.25 in our vole.

Dolomys cf. *nehringi*, Muselievo, Bulgaria (Popov, 2004). The M3 molar from Bulgaria (2.02×1.27 mm) fits the size range of M3 from Kabakova Balka. The Bulgarian specimen shows a less developed PL without LRA4. Very low dentine tracts also fit the low hypsodonty of the Ciscaucasian record.

Dolomys cf. *nehringi*, Notio 1, Greece (Hordijk & de Bruijn, 2009). The illustrated molar fragments from Greece can represent a mixture of forms (*Dolomys* and a large primitive *Mimomys*), and they are larger than the molars from Kabakova Balka.

Dolomys milleri Nehring, 1898, Beremend, Hungary (Mehely, 1914; Kretzoi, 1959; Rabeder, 1981). *Dolomys* form from the Hungarian type locality is significantly larger than the vole from Kabakova Balka.

Dolomys gromovorum Aleksandrova, 1966, Kotlovina (lower layer), Ukraine (Aleksandrova, 1966; Topachevsky & Nesin, 1989). The Kabakova Balka vole is characterized by more developed dentine tracts and a well-developed thickness differentiation of enamel.

Dolomys odessanus Nesin, 1987, Kotlovina (lower layer), Ukraine (Nesin, 1987; Topachevsky & Nesin, 1989). There is no data on the upper teeth of this species, so an adequate comparison is not possible. However, judging by the size of m1 (smaller than m1 *Dolomys nehringi*), it can be expected that M3 of this species will be slightly smaller than those of the Kabakova Balka vole. In addition, *D. odessanus* appears to be less hypsodont than the compared form.

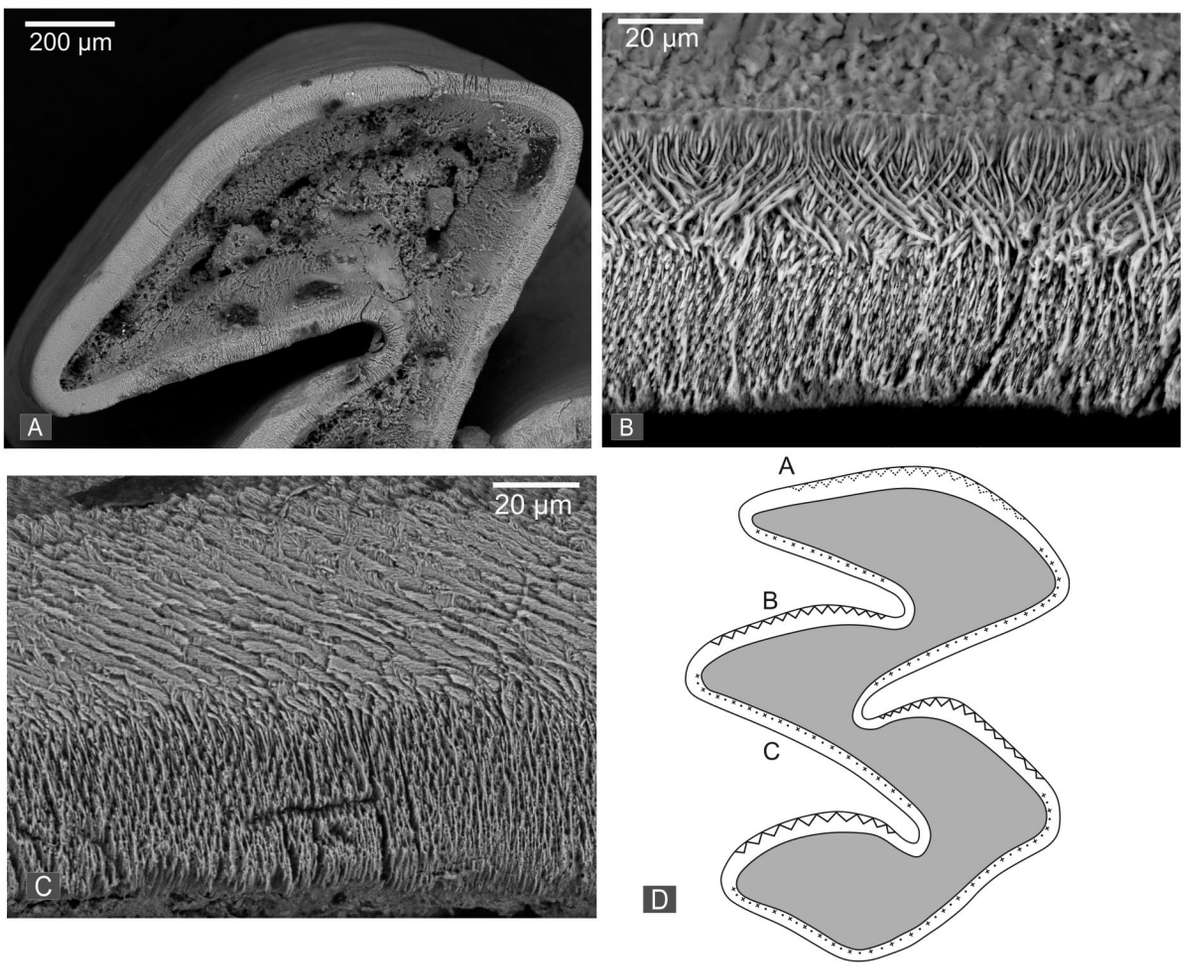

Fig. 11. Enamel microstructure of *Dolomys nehringi* from Kabakova Balka, M2 dex (GIN 1203/243). A — anterior lobe; B — trailing edge of triangle T2; C — leading edge of triangle T2; D — overview image with the studied enamel parts and enamel types shown. Crosses and dots are lamellar enamel; dotted zigzag line is primitive tangential enamel; zigzag line is tangential enamel; white space shows radial enamel.

Dolomys ondatroides Nesin, 1981, Kotlovina (middle layer), Ukraine (Nesin, 1981; Topachevsky & Nesin, 1989). Compared to the record, M3 Kabakova Balka voles are characterized by smaller dimensions and lack of cement in the reentrant angles.

Mimomys konstantinovae Aleksandrova, 1966, Kotlovina, Ukraine (Aleksandrova, 1966; Topachevsky & Nesin, 1989 (as *Promimomys konstantinovae*)). The Kabakova Balka vole differs from this species in higher dentine tracts, more differentiated enamel, and the absence of enamel islets in M3.

Dolomys adroveri, Gorafe, Spain (Fejfar *et al.*, 1990). This southern European dolomyine vole of late Early Pliocene, one of the first arvicolines appearing in the semi-isolated Iberian biogeographic region (Piñero *et al.*, 2017), differs from the vole of Kabakova Balka in lower hypsodonty and occasional insulation of antero-external reentrant (LRA1) in M3.

Dolomys ferui Radulesco et Samson, 1987*,* Cherleştii-Moşteni, Romania (Radulesco & Samson, 1987). This vole originating from fluviatile deposits correlated to Gelasian (Andreescu *et al.*, 2013) is diagnosed to be larger and more hypsodont than *Dolomys milleri* of Late Pliocene. The vole from Kabakova Balka is indeed notably smaller than the *D. ferui,* e.g. the total length of M3 is 1.82–2.25 versus almost 2 mm for broken posterior loop only.

Comments. Dolomyine voles emerged in late Early Pliocene of southern Europe. Currently it is hard to conclude which of an array of brachyodont promimomyid voles with dolomyine variability ("*Mimomys*" *rhabonensis* Radulescu, Samson et Stiuca, 1989, *Promimomys konstantinovae*, *Dolomys gromovorum*, *D. odessanus*, *D. adroveri*, etc.) were closer to the ancestry of Late Pliocene and Early Pleistocene forms. Of the Plio-Pleistocene forms, the Ciscaucasian *Dolomys* closely fits the morphology of the type *D. nehringi* from Csarnóta 2 (MN15b) and shows lower hypsodonty and smaller dimensions compared to a group of large forms similar to *Dolomys milleri* from Beremend (MN16a), including forms that survived into Early Pleistocene, Gelasian, known as *D. ferui* (MN17).

Genus *PROPLIOMYS* Kretzoi, 1959

Comments. The endemic radiation of Pliomyini in Europe and western Asia is clearly divided into two evolutionary grades with still insufficiently resolved phyletic links. The archaic grade of late Early to Late Pliocene is considered within the genus *Propliomys* Kretzoi, 1959 and includes brachyodont voles like the type species *Propliomys hungaricus* (Kormos, 1934), *P. ucrainicus* (Topachevsky & Scorik, 1967), and *P. graecus* (de Bruijn & van der Meulen, 1975). *P. hungaricus* through the chain of intermediate chronotaxa could possibly be an ascendant of the extant Balkan vole *Dinaromys* Kretzoi, 1955. Two extinct lineages of Pleistocene pliomyines are grouped around *Pliomys episcopalis* Mehely, 1914, and *Pl. coronensis* Mehely, 1914 and *Pl. lenki* (Heller, 1930). The recent paleo-DNA data on *Pliomys lenki* from the Late Pleistocene of Spain (Alfaro-Ibáñez *et al.*, 2021) supported the close affinity of *Dinaromys* and *Pliomys* and biological reality of the tribe Pliomyini.

Propliomys jalpugensis (Nesin, 1983)
Figs 12–14, Tables 17–22.

Studied material. 16 m1, 15 m2, 5 m3, 18 M1, 22 M2, 13 M3 (GIN 1202/247–335).

Type locality. Kotlovina, Ukraine, Pliocene

Description. A medium-sized rhizodont vole with low dentine tracts. The measurements are shown in Tables 17–22. Enamel thickness is close to undifferentiated condition. The mean SDQ value are 99.5 (m1), 105.8 (m2), and 97.9 (M2). Most molars show two roots, the M1 and M2 have three roots. Lower molars show slightly broader lingual triangles, upper molars are more symmetrical.

m1 This molar consists of the PL, five alternating triangles and rounded-triangular (*jalpugensis* morphotype) to triangular (*ucrainicus* morphotype) anterior loop. The *ucrainicus*-type morphology (n = 6 out of total 9 specimens) is common in younger specimens transforming into *jalpugensis* type (n = 3) with wear obliterating BRA4 and LRA5. In addition to basic arvicoline dentine tracts, a tract of BSA3 ("mimosinuid") is well defined though always lower than anterosinuid. One specimen (Fig. 12A1) shows a relic of the *Mimomys*-ridge at BSA3. The molar has characteristic pliomyine convex outline of its anterior side in lateral view (Fig. 12A2, A3).

m2 consists of PL and four alternating triangles. The posterior root of m2 has fork-like (acrorhyz) structure and contacts the upper surface of the incisor.

m3 is similar in occlusal structure to m2.

M1 consists of AL and four alternating triangles. Postero-lingual reentrant (LRA3) is deep and in younger specimens may present an acute angle (Fig. 13A1).

M2 consists of AL and three alternating triangles.

M3 consists of AL and two broadly fused triangular elements and a posterior loop (Fig. 13H–K). In juvenile specimens, the lingual and labial triangles are asymmetrical; as the tooth is worn, the asymmetry decreases, and the posterior loop becomes sub-triangular. T2 shows wide connection with AL. Shallow LRA1 and deep LRA3 never insulate.

Schmelzmuster. The enamel microstructure of the lower teeth of the protopachyknem type. The leading edges combine radial and nascent lamellar enamel (Fig. 14B), the trailing edges show radial and primitive tangential enamel (Fig. 14A). The closing enamel of the posterior loop is thicker than the other walls and consists of equally thick radial and tangential enamel. As the crown wears down, the quality of the lamellar enamel slightly improves and it spreads along the entire leading edge. In addition, the enamel on labial triangles has a slightly more advanced appearance than on lingual ones with the lamellar and tangential enamel emerging earlier, albeit in a primitive state. In upper

molars the leading edges are made of radial enamel with nascent lamellar enamel that extends only to the middle of the edge (Fig. 14E). The trailing edges consist entirely of radial enamel, or of radial and a very poorly developed primitive tangential enamel (Fig. 14E). The closing enamel of the anterior lobe consists of radial and primitive tangential enamel, which is thinner than in lower teeth (Fig. 14C). The slightly less perfect enamel types in the upper molars may account for the well-known morphological conservativeness of the upper dentition in voles, e.g. thicker anterior edges inherited from brachyodont hamsters (Gromov & Polyakov, 1977; Markova *et al.*, 2024).

Comparison. Below we provide a comparison only with well characterized Early and Late Pliocene *Propliomys* from southern Europe and Eastern Asia and exclude Pleistocene forms.

Propliomys kowalskii (Shevchenko, 1965), Moskovey, Moldova (Shevchenko, 1965) and Kotlovina, Ukraine (Topachevsky & Nesin, 1989), *Mimomys moldavicus*/*Propliomys,* Dranic-2, Romania (Radulescu & Samson, 1996), *Propliomys destinatus* (Tesakov, 2005), Odessa Catacombs, Ukraine (Tesakov, 2005). In comparison with these transitional forms from *Promimomys* to *Propliomys* grade, the specimens from Kabakova Balka are more hypsodont, have more complex occlusal structure in m1 with a shallow LRA5 present, and does not show insulation of BRA3 in m1, in neither BRA1 and LRA3 in M3. The schmelzmuster of the *P. jalpugensis* from Kabakova Balka differs in incipient development of lamellar enamel, virtually absent in *P. kowalskii* and occasional in *P. destinatus.*

Propliomys jalpugensis, Kotlovina, Ukraine (Nesin, 1983; Topachevsky & Nesin, 1989; Yakimova *et al.*, 2022). In size and hypsodonty of m1 (HH-index) the samples from the Kotlovina and Kabakova Balka are quite similar. However, the share of advanced, "*ucrainicus*" morphotypes in Kabakova Balka is higher than in Kotlovina. The enamel microstructure of *Propliomys* from Kabakova Balka fits the most advanced version of *jalpugensis* morphotypes from the Kotlovina with well discernible incipient lamellar enamel.

Propliomys ucrainicus topacewskii (Nesin, 1983), Kotlovina, Ukraine (Nesin, 1983; Topachevsky & Nesin, 1989). The occlusal morphology of most *Propliomys* first lower molars from Kabakova Balka is similar to that of *P. ucrainicus topacewskii*. The comparison of hypsodonty (Σ_tracts), however, shows definitely higher level in *P. ucrainicus topacewskii*. The quality of lamellar and tangential enamel in *P. u. topacewskii,* as illustrated by the specimen from Late Pliocene (MN16a) site Zhukovskiy Mayak from the lower Don River reaches, is higher too (Fig. 15).

Propliomys ucrainicus topacewskii, Korotoyak-1, Voronezh Region, Russia (Agadjanian, 2009). The sample from Kabakova Balka is very similar to the

Table 17. Measurements (in mm) of m1 *Propliomys jalpugensis* from Kabakova Balka locality.

m1	N	Mean	SE	Min	Max	SD	CV
L	5	2.84	0.0934	2.57	3.04	0.2089	7.35
W	16	1.07	0.027	0.9	1.25	0.1079	10.1
Asd	8	0.88	0.0735	0.69	1.25	0.208	23.76
Hsd	11	0.65	0.025	0.49	0.78	0.0828	12.67
Hsld	11	0.32	0.0246	0.15	0.41	0.0815	25.79
Lbas	6	2.85	0.0422	2.7	2.97	0.1035	3.63
HH-index	11	0.73	0.0278	0.57	0.88	0.0923	12.65
Σ_tracts	4	67.14	3.4236	58.52	75.15	6.8472	10.2
L/W	5	2.59	0.0571	2.38	2.7	0.1277	4.93
A/L	5	50.03	2.3414	43	55.79	5.2356	10.46
SDQ	13	101.12	2.6729	83.5	117.28	9.6373	9.53

Table 18. Measurements (in mm) of m2 *Propliomys jalpugensis* from Kabakova Balka locality.

m2	N	Mean	SE	Min	Max	SD	CV
L	13	1.66	0.0351	1.5	1.85	0.1264	7.59
W	15	1.02	0.0246	0.84	1.13	0.0952	9.34
Asd	12	0.67	0.0546	0.4	0.94	0.1893	28.12
Hsd	13	0.46	0.0203	0.33	0.54	0.0732	16
Hsld	13	0.33	0.023	0.15	0.46	0.083	25.31
Lbas	14	1.82	0.0399	1.57	1.99	0.1494	8.19
HH-index	13	0.57	0.0247	0.43	0.68	0.0892	15.75
Σ_tracts	10	80.97	4.8061	56.12	101.09	15.1982	18.77
L/W	13	1.66	0.0264	1.51	1.78	0.0954	5.76
SDQ	12	105.16	3.863	81.7	132.1	13.3819	12.73

Table 19. Measurements (in mm) of m3 *Propliomys jalpugensis* from Kabakova Balka locality.

m3	N	Mean	SE	Min	Max	SD	CV
L	5	1.53	0.0234	1.45	1.59	0.0524	3.44
W	5	0.92	0.0244	0.85	1	0.0546	5.95
Asd	4	0.69	0.063	0.6	0.87	0.126	18.23
Hsd	5	0.38	0.0342	0.31	0.5	0.0765	19.99
Hsld	5	0.24	0.0063	0.22	0.25	0.0141	5.8
Lbas	4	1.71	0.0102	1.7	1.74	0.0205	1.2
HH-index	5	0.45	0.0286	0.4	0.56	0.064	14.08
Σ_tracts	3	76.55	4.203	69.41	83.96	7.2798	9.51
L/W	5	1.67	0.0453	1.5	1.77	0.1013	6.08
SDQ	3	101.94	11.3694	90.31	124.68	19.6923	19.32

Table 20. Measurements (in mm) of M1 *Propliomys jalpugensis* from Kabakova Balka locality.

M1	N	Mean	SE	Min	Max	SD	CV
L	16	2.31	0.0273	2.13	2.45	0.1092	4.72
W	18	1.31	0.0263	1.13	1.56	0.1116	8.53
Ds	16	0.8	0.0311	0.61	1.15	0.1244	15.5
As	16	0.32	0.0206	0.18	0.41	0.0825	26.14
Asl	15	0.32	0.0158	0.2	0.41	0.0613	18.99
Prs	18	0.64	0.0219	0.52	0.85	0.0931	14.48
Lbas	18	2.47	0.0266	2.3	2.61	0.1128	4.56
PA-index	16	0.71	0.0231	0.6	0.95	0.0925	12.94
AA-index	15	0.47	0.0201	0.3	0.64	0.0777	16.43
Σ_tracts	14	72.25	2.0883	58.77	87.84	7.8136	10.81
L/W	16	1.77	0.0261	1.56	1.91	0.1043	5.88
SDQ	12	98.55	4.332	77	123	15.0064	15.23

Table 21. Measurements (in mm) of M2 *Propliomys jalpugensis* from Kabakova Balka locality.

M2	N	Mean	SE	Min	Max	SD	CV
L	16	1.97	0.0238	1.75	2.12	0.0951	4.82
W	22	1.16	0.0206	0.94	1.29	0.0964	8.32
Ds	20	0.65	0.0299	0.37	0.9	0.1336	20.55
As	19	0.44	0.0249	0.22	0.59	0.1084	24.45
Prs	21	0.38	0.0179	0.25	0.56	0.0821	21.67
PA-index	19	0.59	0.0278	0.39	0.82	0.1211	20.52
Lbas	21	1.97	0.0292	1.64	2.2	0.1338	6.79
Σ_tracts	17	72.65	2.9273	46.14	92.55	12.0696	16.61
L/W	16	1.71	0.0287	1.52	1.9	0.1148	6.72
SDQ	17	101.6	3.1654	82.49	130.3	13.0515	12.85

Table 22. Measurements (in mm) of M3 *Propliomys jalpugensis* from Kabakova Balka locality.

M3	N	Mean	SE	Min	Max	SD	CV
L	8	1.62	0.0426	1.37	1.75	0.1206	7.44
W	13	0.95	0.0181	0.81	1.04	0.0653	6.86
Ds	8	0.3	0.0408	0.13	0.51	0.1153	37.98
As	13	0.34	0.0268	0.18	0.48	0.0966	28.67
Prs	12	0.23	0.0155	0.13	0.35	0.0538	23.17
PA-index	12	0.42	0.0267	0.26	0.56	0.0925	21.91
Lbas	12	1.63	0.0295	1.49	1.83	0.1022	6.27
Σ_tracts	7	49.24	4.8559	26.61	67.91	12.8475	26.09
L/W	8	1.72	0.0258	1.61	1.82	0.0729	4.25
SDQ	10	105.54	3.1312	95.42	124.1	9.9018	9.38

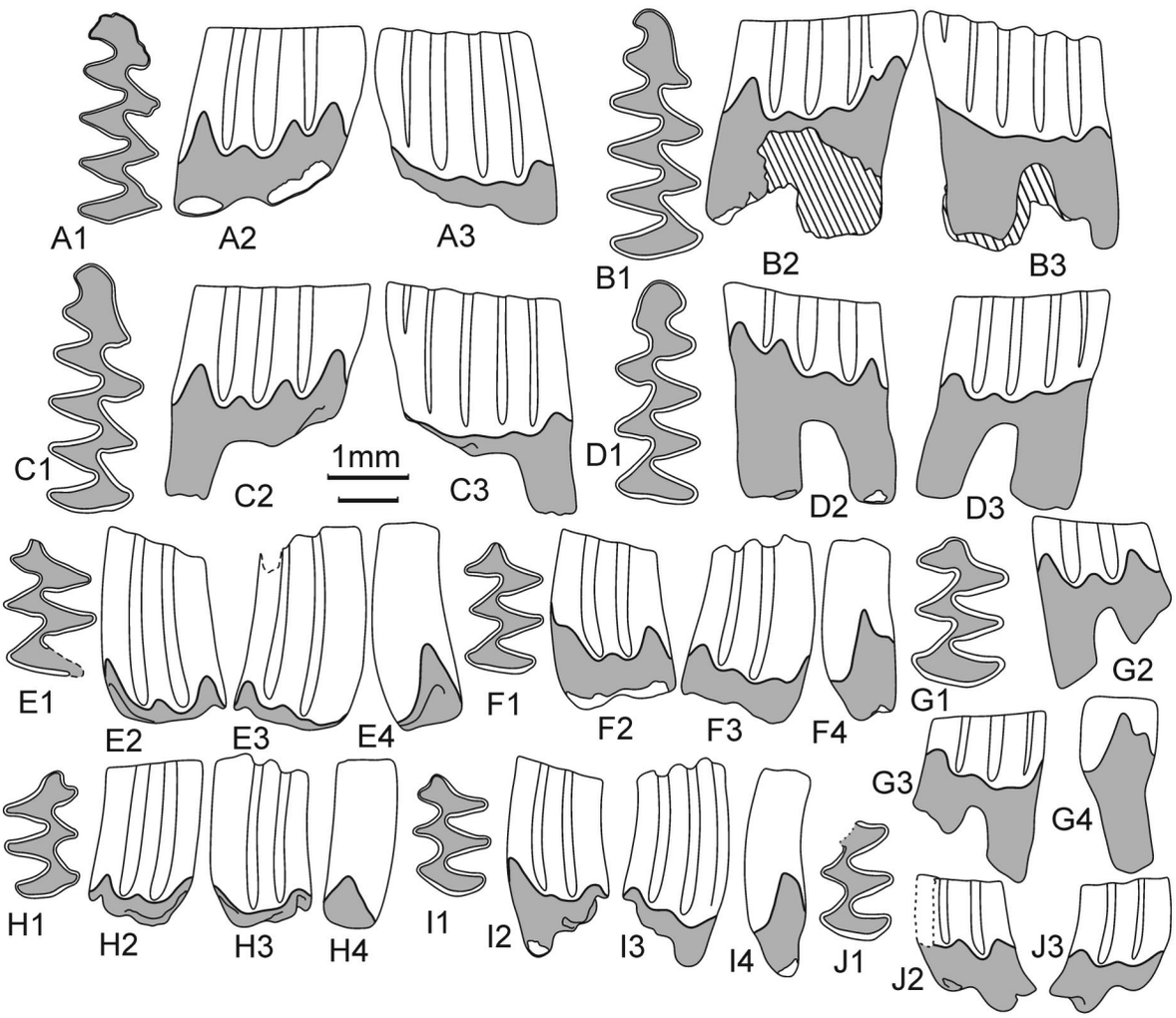

Fig. 12. Lower molars of *Propliomys jalpugensis* (Kabakova Balka). A–D — m1 (GIN 1203/251, 257, 253, 259); E–G — m2 (GIN 1203/264, 263, 275); H–J — m3 (GIN 1203/278, 279, 282). 1 — occlusal surface; 2 — buccal side; 3 — lingual side; 4 — Asd. Scale bar 1 mm for occlusal view (upper line) and lateral views (lower line).

well-described material from Korotoyak-1. The vole from Ciscaucasus, however, has a trend to slightly smaller size and lower dentine tracts.

Pliomys cf. *ucrainicus* Topachevsky et Scorik, 1967, Uryv-1, and *Pliomys ucrainicus*, Korotoyak-2, Voronezh Region, Russia (Agadjanian, 2009). The very small material on *Propliomys* from these two sites from Don River area resemble the vole from Kabakova Balka, though their size and hypsodonty values correspond to the highest values in the latter sample.

Propliomys hungaricus (Kormos, 1934), Csarnóta 2, Hungary (Kretzoi, 1962; de Bruijn & van der Meulen, 1975; Fejfar *et al.*, 1998), *P. hungaricus,* Gundersheim-4, Germany (Fejfar & Storch, 1990) and Podari, Romania (Radulesco & Samson, 1996). This form differs from the described vole in more variably angular anteroconid cap, more blunt BSA3, deeper relic of *Mimomys*-ridge along this prism, and more robust M3 with persistent posterior enamel islet.

Propliomys hungaricus Kormos, 1934, Notio 1, Greece (Hordijk & de Bruijn, 2009). In addition to differences from the type *P. hungaricus*, the from Greece has, on average, a lower degree of hypsodonty, and more archaic structure of m1 with well expressed *Mimomys*-ridge, occasional insulation of BRA3, and M3 with anterior and posterior enamel islands present.

Propliomys ex gr. *hungaricus* from late Early Pliocene sites from Europe, Węże 1, Poland (as *Dolomys hungaricus*), Wölfersheim, Germany (as *Dolomys occitanus*), and Musilevo, Bulgaria (as *D. occitanus*). These arrays of primitive forms express a morphological trend to a more complex m1 at the expense of retarding the insulation of LRA3. In comparison with *Propliomys* from Kabakova Balka, these forms are less hypsodont and retain numerous archaic characters of

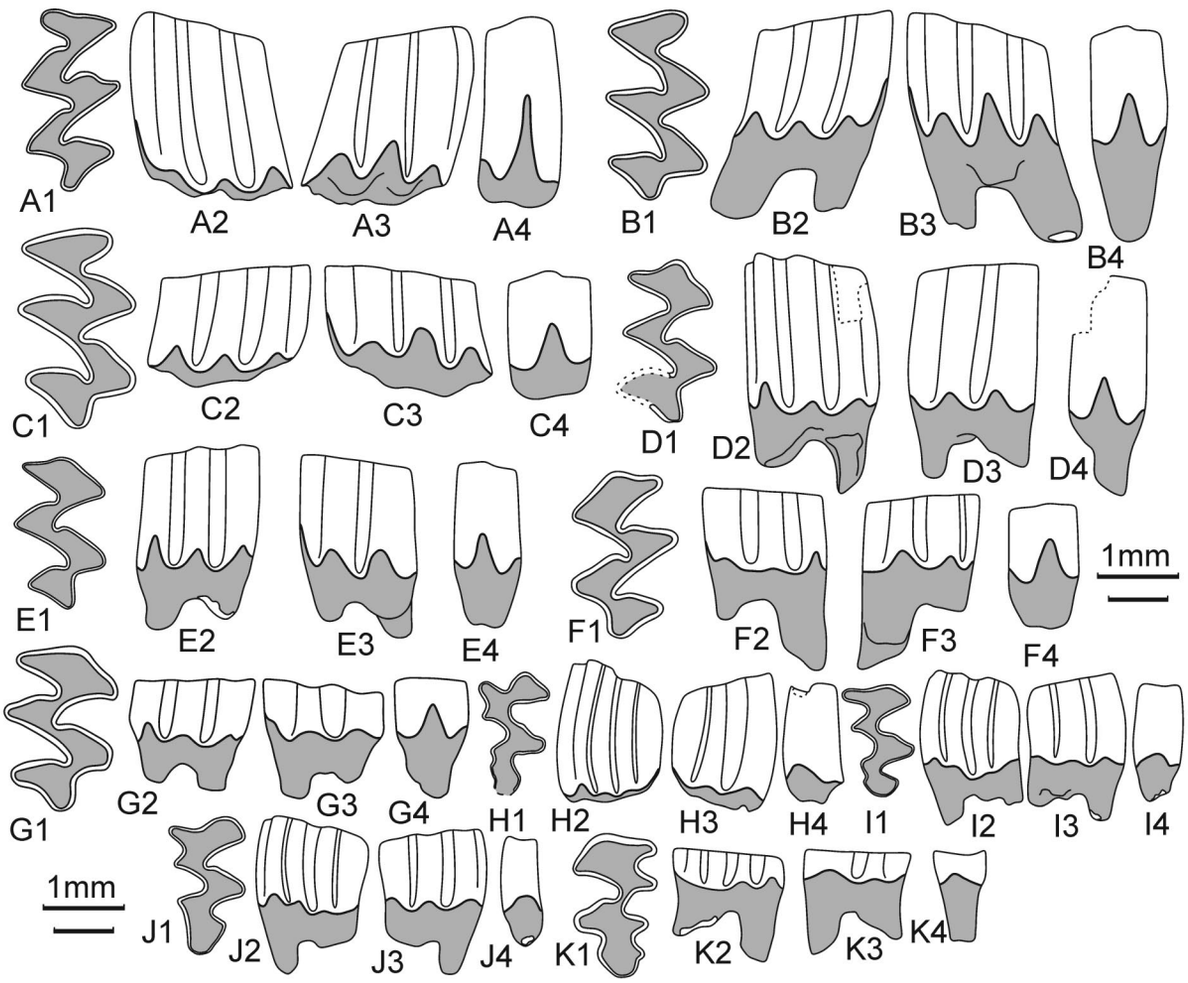

Fig. 13. Upper molars of *Propliomys jalpugensis* (Kabakova Balka). A–C — M1 (GIN 1203/284, 294, 298); D–G — M2 (GIN 1203/301, 316, 302, 322); H–K — M3 (323, 328, 331, 335). 1 — occlusal surface; 2 — buccal side; 3 — lingual side; 4 — Ds. Scale bar 1 mm for occlusal view (upper line) and lateral views (lower line).

the *Promimomys* grade, as *Mimomys*-ridge and enamel islets in m1 and M3.

Propliomys graecus (de Bruijn & van der Meulen, 1975), Tourkobounia-1, Greece (de Bruijn & van der Meulen, 1975), Yenice 1, Ortalica (Ünay & de Bruijn, 1998), Afşar 2, Turkey (Skandalos *et al.*, 2023). The *Propliomys* from the Aegean-Anatolian region differs in somewhat higher hypsodonty, more variable shape of anteroconid cap in m1, a trend to formation of LRA1 in the AL of M2, and in broader M3 with anterior enamel islet in juvenile specimens and very deep BRA2. This group of forms possibly also includes *Propliomys* cf. *hungaricus* from Muselievo, Bulgaria (Popov, 2004) sharing with them size/hypsodonty, and the structure of M3 with deep BRA2.

Comments. In summary, the *Propliomys* from Kabakova Balka mostly resembles forms of the *P. jalpugensis-ucrainicus* group from the northern Black Sea areas. The sample from Kabakova Balka may represent an evolutionarily advanced stage of Euxinian *Propliomys* that documents the transitioning from *P. jalpugensis* to *P. ucrainicus topacewskii*.

Discussion

Arvicoline association of Kabakova Balka

Most voles of the studied fauna are represented by sufficient material that makes it possible to characterize their evolutionary position. The smallest vole, *Promimomys* (*Cseria*) *gracilis*, is for the first time reliably identified outside its type region in Central Europe. Indeed, the lack of conspicuous morphological characters apart from smaller size, lead to the use of this taxon as a place-holder for an array of somewhat smaller brachyodont mimomyine voles throughout Eurasian Pliocene. Medium-size vole *Mimomys* cf.

stehlini, a possible phyletic ancestor of smaller *Mimomys* (*Pusillomimus*) species of Plio-Pleistocene, shows only nascent lamellar enamel, very sparse cement, and still has plesiomorphic anterior enamel islet in BRA1 in M3. Of the three mimomyoid voles in the fauna, the most advanced in acquisition of the true *Mimomys* grade (pachyknem enamel, external cement, reduction of anterior enamel islets in M3) is the larger

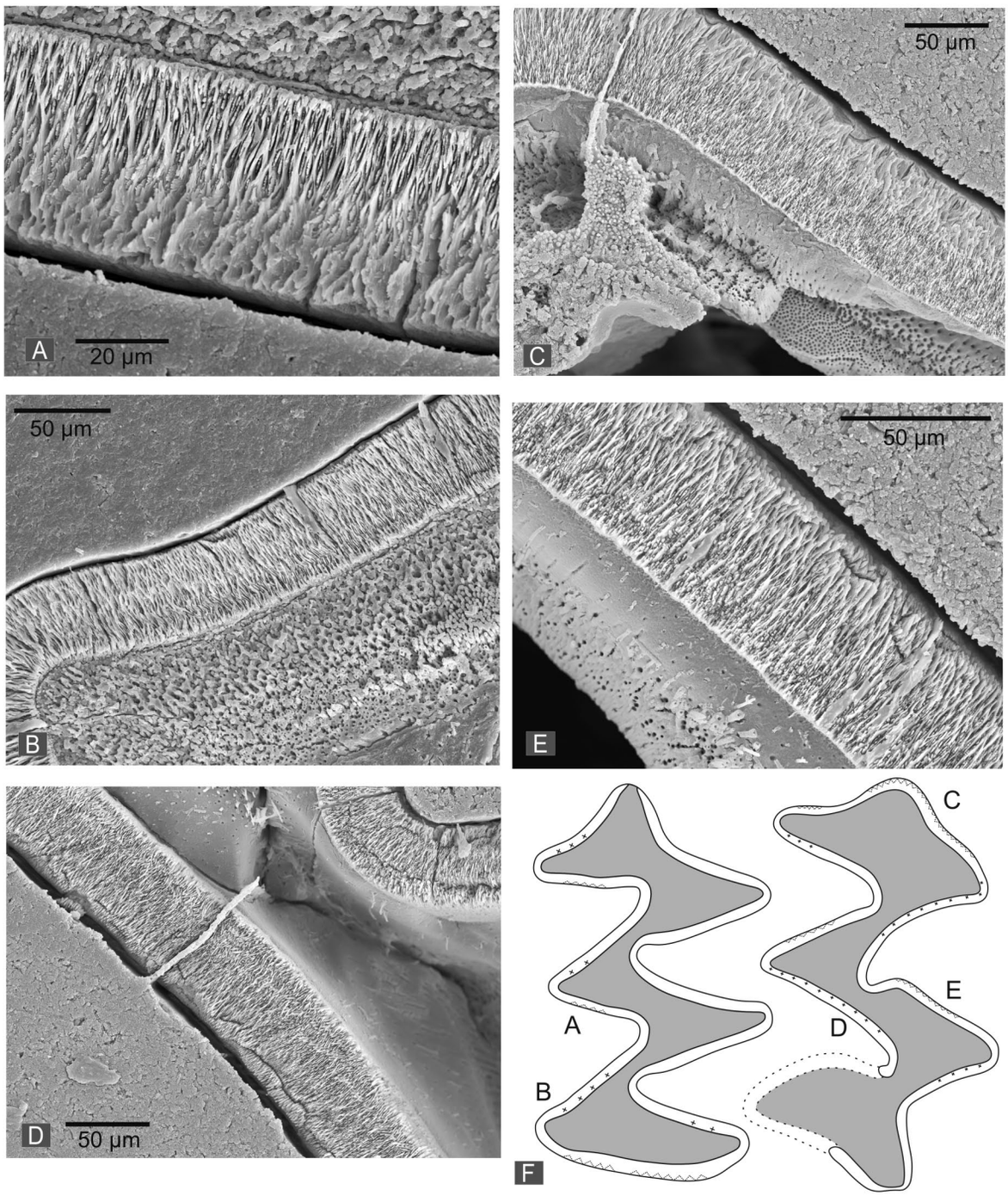

Fig. 14. Enamel microstructure of *Propliomys jalpugensis* from Kabakova Balka. A–B — m2 sin (GIN 1203/263); C–E — M2 dex (GIN 1203/301). A — trailing edge of triangle T2; B — buccal leading edge of posterior lobe; C — closing enamel of anterior lobe; D — leading edge of triangle T2; E — trailing edge of triangle T3; F — overview images with the studied enamel parts and enamel types shown. Crosses are primitive lamellar enamel; dotted zigzag line is primitive tangential enamel; white space shows radial enamel.

M. cf. *hajnackensis*, followed by *M.* cf. *stehlini*, and the less evolved *P.* (*C.*) *gracilis*. Scarcely represented *Dolomys* fits the type and other early samples of *D. nehringi* in size and morphology. Its schmelzmuster is well developed, with a notably advanced lamellar enamel of the leading edges, at this early stratigraphic level. *Propliomys jalpugensis* is only second record of this phyletic chronotaxon in the synchronous faunal context rather than in taxonomically mixed type samples (see also Agajanian, 2009). Schmelzmuster of this form is still very primitive with just emerging discrete lamellar enamel in the leading edges. It is indicative that larger voles of the fauna (*Mimomys* cf. *hajnackensis* and *Dolomys nehringi*) show the most evolved pachyknem schmelzmuster, whereas medium size *M.* cf. *stehlini* and *Propliomys jalpugensis*, and smaller *Promimomys gracilis* are notably less advanced. The hypsodonty level of all voles in the fauna is still very low with HH-index mostly below 1 (Fig. 16).

Paleoenvironmental remarks

The arvicolines, especially represented by extinct forms, are not among the strongest paleoenvironmental indicators. It is, however, possible to draw some general inferences on their biotopic position and to check it using the paleoecological information on the Kabakova Balka biotic assemblage. Believed to originate from predominantly granivorous (seed-eating) hamsters, voles progressively increased the role of green plants in their diet. As known from the extant fauna, voles with rhizodont cheek dentition (teeth with roots) commonly have a mixed diet combining herbivory, granivory, and sometimes rhizophagy. Many of these forms, like wood voles of the genera *Clethrionomys* and *Craseomys* pre-

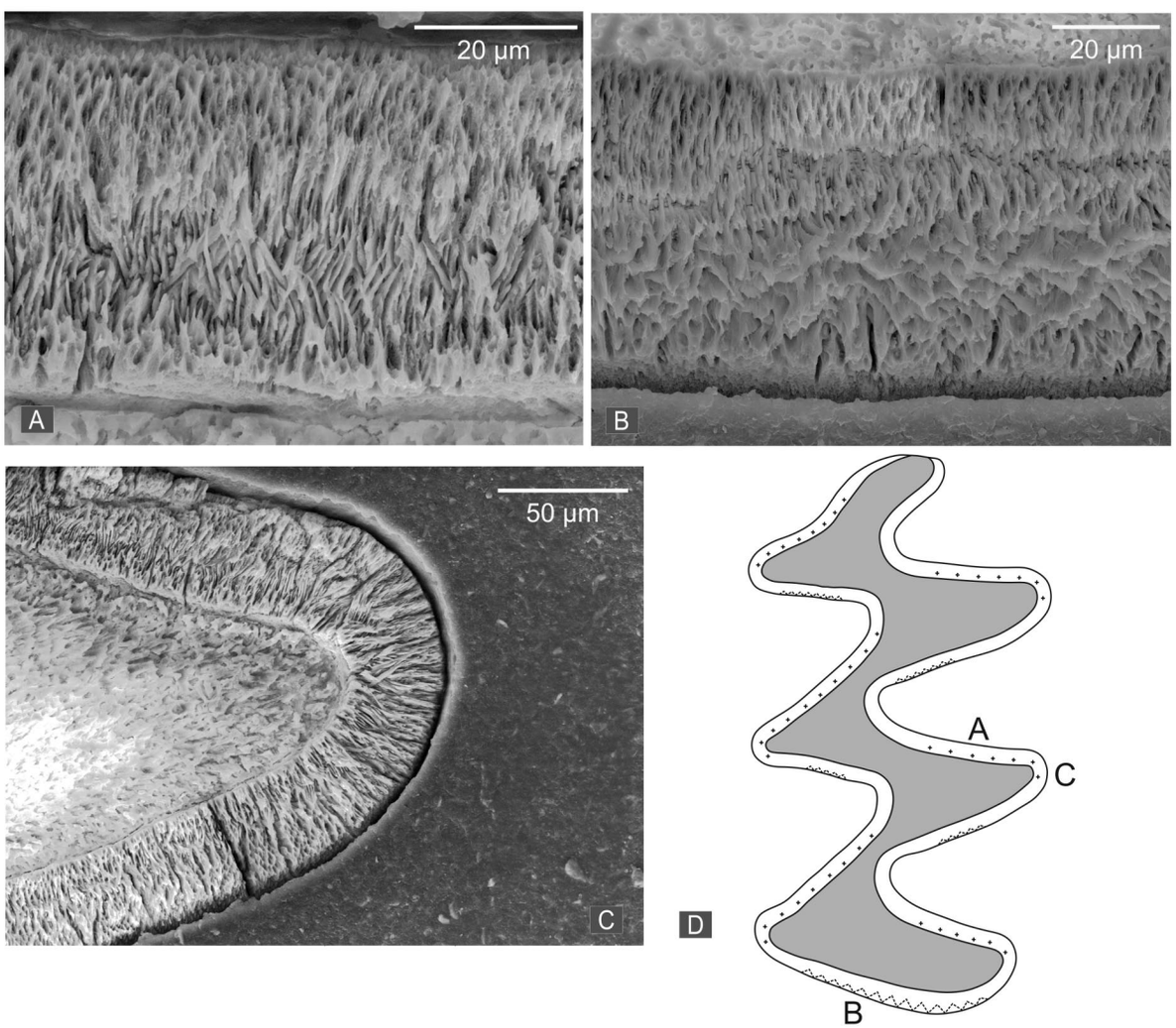

Fig. 15. Enamel microstructure of *Propliomys ucrainicus topacewskii* from Zhukovskiy Mayak, Late Pliocene, MN16a, m3 sin (GIN 1180/001). A — leading edge of triangle T1; B — closing enamel of posterior lobe; C — tip of triangle T1; D — overview image with the studied enamel parts and enamel types shown. Crosses stand for primitive lamellar enamel; dotted zigzag line is primitive tangential enamel; white space shows radial enamel.

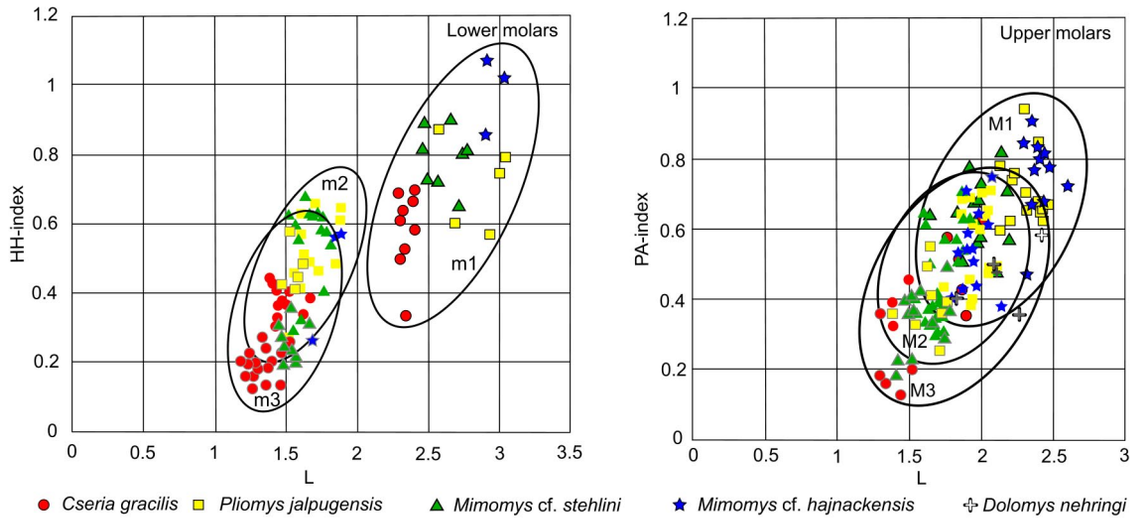

Fig. 16. Scatter diagrams of HH- and PA-index against L in lower (left graph) and upper (right graph) molars of arvicolines from Kabakova Balka.

fer mesic, closed biotopes with arboreal or shrubby vegetation. Voles with aquatic adaptations demonstrate larger body and dental size, and a delayed transition to rootless dentition like in the *Mimomys–Arvicola* lineage, or still retain molar roots as hydrobiont muskrats *Ondatra*. Fully herbivorous voles developed rootless, ever-growing molars by mid Early Pleistocene. With the actualistic examples in mind, we can therefore tentatively assume a notable share of granivory and a connection with closed forested, or mesic meadow biotopes for brachyodont mimomyine voles (*Promimomys gracilis*, *Mimomys* cf. *stehlini,* and *M.* cf. *hajnackensis*). The larger size and a very extensive range in Pliocene of Eurasia of the latter vole may indicate its aquatic adaptations. The same may be true for much more rare *Dolomys nehringi*. The best development of the advanced lamellar enamel type in these two largest voles of the fauna may point to their growing green-eating adaptations. The vole *Propliomys jalpugensis* shows complication of molars and angular reentrants that resemble Plio-Pleistocene lagurines. Sometimes this is taken as a sign of a connection with more open, steppe-like biotopes. A very primitive schmelzmuster and low hypsodonty clearly argue against any advanced herbivorous diet of this vole beyond a level of a mixed feeder still very closely connected with mesic biotopes. The general ecological picture inferred from the vole assemblage is strongly supported by the accompanying biota. First, the sediments that yielded mammal remains in this locality are overfilled with opercula of prosobranch land snail *Pomatias*. In the modern biota it is tightly connected with broad-leaved forests, especially dominated by beech (*Fagus*). Numerous shells of slugs (limacids s.l., and *Parmacella* sp.) indicate mesic, closed biotopes too. Among mammals, the most indicative is very diverse group of forest dwellers with four different size flying squirrels, a tree squirrel, and the Pliocene edible dormouse. This indicates a multi-layered forest with tall trees. Wood mice, moles, and capreoline deer further support the presence of mesic biotopes. In addition, the presence of periaquatic desmanines and beavers obviously indicates water bodies not very far from the burial. The forms that suggest a presence of open biotopes are much less numerous and include smaller hamsters, spalacids, and an ostrich, represented by a single fragment of egg shell. Therefore we can infer a warm temperate forest growing on hilly slopes and coastal lowlands, and freshwater streams flowing towards near-by brackish-water sea with occasional patches of open biotopes.

Biochronology

The biochronological position of the fauna (Fig. 17) is clearly in the late Ruscinian, MN15b, because all voles of Kabakova Balka are somewhat less evolved than their phyletic successors of the Early Villanyian.

The closest stratigraphic match of the fauna is the reference fauna of Csarnóta 2. In the regional biochronology of Eastern Europe (Tesakov, 2022) the fauna of Kabakova Balka typifies the regional zonal unit MNR7 (concurrent range zone of Propliomys jalpugensis and Promimomys gracilis). The combined evolutionary level of the fauna, reversed paleomagnetic signal and regressive character of the near-shore host deposits, as indicated by a fauna of brackish-water ostracods (Nikolaeva *et al.*, 2025), suggest the correlation of the fauna with the upper Gilbert Chron (C2Ar), late Zanclean, and terminal Kimmerian close to the transition to the Kujalnikian regional stage. Latest Ruscinian and the unit MN15b (zone *Mimomys hassiacus–M. gracilis*) of

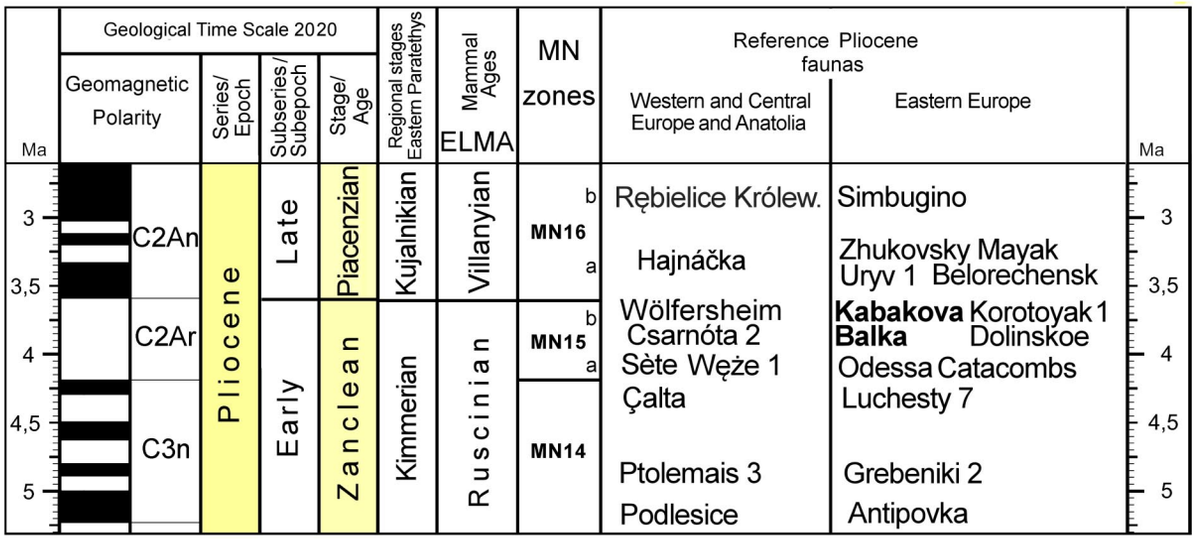

Fig. 17. Position of Kabakova Balka and other reference faunas in European biochronological scheme.

Fejfar *et al.* (1998) is the level of the fauna in the European biochronology. The age of the fauna is thus close or slightly older than 3.6 Ma.

Conclusions

The arvicolid association of Kabakova Balka provides the first insight into terminal Early Pliocene vole history in the North Caucasus region. This faunal level documents a period when Arvicolinae are diversified into five morphologically well defined forms and, as a group, dominate in number of remains in the burial over all other quite diverse small mammals of the latest Ruscinian fauna of Kabakova Balka. The fauna postdates early and mid Ruscinian faunas of the Euro-Siberian biogeographic region that correspond to a so called "lagomorph explosion", a period of diversity and abundance of pikas and rabbits that occurred near the Mio-Pliocene transition, and in the Early Pliocene (Erbajeva *et al.*, 2015). In Eastern Europe, the fossil assemblages of this period feature the very high role of remains of Ochotonidae and Leporidae, though decreasing in time with the coordinated increase of voles (Schevchenko, 1965; Agadjanian, 2009, etc.). The very brachyodont dental stages of all voles in Kabakova Balka immediately precedes the level of Early Villanyian faunas of the European Late Pliocene. The composition of the vole association is very similar to the coeval faunas of northwestern peri-Black Sea region and the Don River region. The presence of *Propliomys* ex gr. *jalpugenis-ucrainicus* distinguishes these faunas from synchronous Pliocene faunas of the Aegean-Anatolian region that feature a vicariant group of *Propliomys hungaricus-graecus*. The combination of voles specific for southeastern Europe, as *Propliomys* and *Dolomys*, and the widespread Eurasian mimomyine species emphasizes the important role of the new fauna for East-West faunal correlations.

ACKNOWLEDGEMENTS. The authors thank technical staff of GIN RAS and PIN RAS for their assistance in SEM imaging. Our colleagues P.D. Frolov, A.V. Ivanova, N.A. Orlov, S.A. Sokolov, A.D. Nikolaeva (GIN RAS), V.V. Titov (SSC RAS), E.V. Syromyatnikova (PIN RAS) are thanked for the work in the field and material sorting in the laboratory. Two reviewers are thanked for valuable comments and corrections. The work was financially supported by the grant № 22-17-00249-П of the Russian Science Foundation.

References

Agadjanian A.K. 1976. [Voles (Microtinae, Rodentia) of the Pliocene locality Uryv I, Middle Don] // Proceedings of the Zoological Institute of the Academy of Sciences USSR. Vol.66. P.58–97 [in Russian].

Agadjanian A.K. 2009. [Small mammals of the Pliocene-Pleistocene of the Russian Plain] // Proceedings of the Paleontological Institute. Vol.289. P.1–676 [in Russian].

Aleksandrova L.P. 1966. [New species of large fossil voles from the Lower Quaternary deposits of southwestern Ukraine (Kotlovina village)] // Byulleten Komissii po Izucheniu Chetvertichnogo Perioda. No.32. P.40–45 [in Russian].

Alfaro-Ibáñez M. P., Lira-Garrido J., Cuenca-Bescós G., Pons J. & Bover P. 2024. Insights on the evolution of the tribe Pliomyini (Arvicolinae, Rodentia): Ancient DNA from the extinct *Pliomys lenki* // Palaeontologia Electronica. Vol.27. No.3. Art.a47. DOI: 10.26879/1403

Andreescu I., Codrea V., Lubenescu V., Munteanu T., Petculescu A., Ştiucă E. & Terzea E. 2013. New developments in the Upper Pliocene–Pleistocene stratigraphic units of the Dacian Basin (Eastern Paratethys, Roma-

nia) // Quaternary International. Vol.284. P.15–29. DOI: 10.1016/j.quaint.2012.02.009

Bachelet B., Aenlle J.E. & Lopez-Martinez N. 1991. Révision des populations de *Mimomys* de petite taille (Rodentia, Mammalia) du Pliocène supérieur d'Europe sud-occidentale // Geobios. Vol.24. No.3. P.349–360. DOI: 10.1016/S0016-6995(09)90014-6

Beluzhenko E.V. & Pis'mennaya N.S. 2016. Upper Miocene–Eopleistocene terrestrial sediments of the northwestern Ciscaucasia region // Stratigraphy and Geological Correlation. Vol.24. No.4. P.407–426. DOI: 10.1134/S086959381604002X

de Bruijn H. & van der Meulen A.J. 1975. The early Pleistocene rodents from Tourkobounia-1 (Athens, Greece) // Koninklijke Nederlandse Akademie van Wetenschappen. Series B. Vol.78. No.4. P.314–338.

Chaline J. 1974. Un nuveau critère d'étude des *Mimomys*, et les rapports de *Mimomys occitanus–Mimomys stehlini* et *Mimomys polonicus* (Arvicolidae, Rodentia) // Acta Zoologica Cracoviensia. Vol.19. No.16. P.337–356.

Chaline J. & Laurin B. 1986. Phyletic gradualism in a European Plio-Pleistocene *Mimomys* lineage (Arvicolidae, Rodentia) // Paleobiology. Vol.12. P.203–216. DOI: 10.1017/S009483730001366X

Cohen K, Harper D, Gibbard P. & Car N. 2025. The ICS international chronostratigraphic chart this decade // Episodes. Vol.48. P.105–115. DOI: 10.18814/epiiugs/2025/025001

Erbajeva M., Flynn L.J. & Alexeeva N. 2015. Late Cenozoic Asian Ochotonidae: Taxonomic diversity, chronological distribution and biostratigraphy // Quaternary International. Vol.355. P.18–23. DOI: 10.1016/j.quaint.2014.10.064

Fahlbusch V. & Moser M. 2004. The Neogene mammalian faunas of Ertemte and Harr Obo in Inner Mongolia (Nei Mongol), China.— 13. The genera Microtodon and Anatolomys (Rodentia, Cricetidae) // Senckenbergiana Lethaea. Vol.84. No.1/2. P.323–349. DOI: 10.1007/BF03043475

Fejfar O. 1961. Die plio-pleistozänen Wirbeltierfaunen von Hajnáčka und Ivanovce (Slowakei), CSR. II. Microtidae und Cricetidae inc. sed. // Neues Jahrbuch für Geologie und Paläontologie. Vol.112. No.1. P.48–82.

Fejfar O. 1964. The Lower Villafranchian vertebrates from Hajnáčka near Filakovo in Southern Slovakia // Rozpravy Ustavu Geologickeho. Vol.30. P.1–116.

Fejfar O. 2001. The Arvicolids from Arondelli-Triversa: a new look // Bollettino Societa Paleontologica Italiana. Vol.40. No.2. P.185–194.

Fejfar O. & Heinrich W.-D. 1982. Zur biostratigraphischen Untergliederung des kontinentalen Quartärs in Europa anhand von Arvicoliden (Rodentia, Mammalia) // Eclogae Geologicae Helvetiae. Vol.74. No.3. P.997–1006.

Fejfar O., Heinrich W.-D. & Lindsay E.H. 1998. Updating the Neogene Rodent biochronology in Europe // Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO. Vol.60. P.533–554.

Fejfar O., Mein P. & Moissenet E. 1990. Early Arvicolids from the Ruscinian (Early Pliocene) of the Teruel Basin // Fejfar O. & Heinrich W.-D. (eds.). International Symposium: Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia). Prague: Geological Survey of Czechoslovakia. P.133–164.

Fejfar O. & Repenning C.A. 1998. The ancestors of the lemmings (Lemminae, Arvicolinae, Cricetidae, Rodentia) in the Early Pliocene of Wölfersheim near Frankfurt-am-Main, Germany // Senckenbergiana lethaea. Vol.77. No.1. P.161–193. DOI: 10.1007/BF03043739

Fejfar O. & Storch G. 1990. Eine pliozäne (ober-ruscinische) Kleinsäugerfauna aus Gundersheim, Rheinhessen. 1. Nagetiere: Mammalia, Rodentia // Senckenbergiana Lethaea. Vol.71. No.1/2. P.139–184.

Frolov P.D., Tesakov A.S., Ivanova A.V., Kurshakov S.V. & Sypomyatnikova E.V. 2024. [Between Two Seas: Late Pliocene of Taman] // Priroda. No.2. P.5–14 [in Russian]. DOI: 10.7868/S0032874X24020014

Gromov I.M. & Polyakov I.Ya. 1977. [The Fauna of the USSR. Mammals]. Vol.3. No.8. Voles (Microtinae). Leningrad: Nauka. 504 p. [In Russian]

Hammer Ø., Harper D.A.T. & Ryan P.D. 2001. PAST: Paleontological statistics software package for education and data analysis // Palaeontologia Electronica. Vol.4. No.1. P.1–9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Heinrich W.D. 1990. Some aspects of evolution and biostratigraphy of *Arvicola* (Mammalia. Rodentia) in the Central European Pleistocene // International Symposium on the Evolution, Phylogeny, and Biostratigraphy of Arvicolids. Prague. P.165–182.

Hellmund M. & Ziegler R.A. 2012. Ruscinian mammalian microfauna from a fissure filling near Sondershausen (Thuringia, Central Germany) // Swiss Journal of Palaeontology. Vol.131. No.1. P.77–94. DOI: 0.1007/s13358-011-0019-2

Hordijk K. & de Bruijn H. 2009. The succession of rodent faunas from the Mio/Pliocene lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece) // Hellenic Journal of Geosciences. Vol.44. P.21–103.

Kolfschoten T. van, van der Meulen A. & Boenigk W. 1998. The Late Pliocene Rodents (Mammalia) from Frechen, (Lower Rhine Basin, Germany) // Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO. Vol.60. P.161–172.

Kormos T. 1931. Öberpliozäne Wühlmäuse von Seneze (Haute-Loire) und Val d'Arno (Toscana) // Abhandlungen der Schweizerischen paläontologischen Gesellschaft. Vol.51. No.1. P.1–14.

Kormos T. 1932. Neue pliozäne Nagetiere aus der Moldau // Palaeontologische Zeitschrift. Vol.14. No.3. P.193–200.

Kowalski K. 1960a. Pliocene insectivores and rodents from Rębielice Królewskie (Poland) // Acta Zoologica Cracoviensia. Vol.5. No.5. P.155–194.

Kowalski K. 1960b. Cricetidae and Microtidae (Rodentia) from the Pliocene of Węże (Poland) // Acta Zoologica Cracoviensia. Vol.5. No.11. P.447–506.

Kretzoi M. 1955. *Promimomys cor* n. g., n. sp., ein altertumlicher Arvicolide aus dem Ungarischen Altpleistozan // Acta Geologica Academiae Scientiarum Hungaricae. Vol.3. No.1–3. P.89–94.

Kretzoi M. 1959. Insectivoren, Nagetiere und Lagomorphen der jungstpliozanen Fauna von Csarnota im Villanyer Gebirge (Sudungarn) // Vertebrata Hungarica. Vol.1. P.237–246.

Kretzoi M. 1962. Fauna und Faunenhorizont von Csarnóta // Annual Report of the Hungarian Geological Institute (1959). P.297–395.

Kretzoi M. 1969. Skizze einer Arvicoliden Phylogenie - Stand 1969 // Vertebrata Hungarica. Vol.11. No.1–2. P.155–193.

Lazarev S., Maul L., Kuiper K., Becker D., Bukhsianidze M., Hovakimyan H., Sahakyan L. & Vasilyan D. 2023. Pliocene volcanic terrain of the South Caucasus as a missing link in Eurasian palaeobiogeography: Dating and palaeoenvironments of vertebrate assemblages of the Jradzor locality, Armenia // Palaeogeography, Palaeoclimatology,

Palaeoecology. Vol.625. Art.111685. DOI: 10.1016/j.palaeo.2023.111685

Markova E.A., Nadirli L.V. & Zykov S.V. 2024. Dental enamel differentiation quotient of modern water voles of the genus *Arvicola* in Azerbaijan: variation and diagnostic value // Zoologicheskii Zhurnal. Vol.103. No.12. P.108–124. DOI: 10.31857/S0044513424120068

Martin R. 1987. Notes on the classification and evolution of some North American fossil *Microtus* (Mammalia; Rodentia) // Journal of Vertebrate Paleontology. Vol.7. No.3. P.270–283. DOI: 10.1080/02724634.1987.10011660

Martin R. & Tesakov A. 1998. Introductory remarks: Does *Allophaiomys* exist? // Paludicola. Vol.2. No.1. P.1–7.

Masini F. & Torre D. 1987. Review of the Villafranchian arvicolids of Italy // Geologica Romana. Vol.26. P.127–133.

Maul L. 1996. A discussion on the referral of *Mimomys occitanus* Thaler, 1955 (Rodentia, Arvicolidae) to the genus *Mimomys* // Acta Zoologica Cracoviensia. Vol.39. No.1. P.343–348.

Mayhew D.F. 2009. The type material and the enamel structure of *Villanyia exilis* Kretzoi, 1956 (Arvicolidae, Rodentia) // Acta Zoologica Cracoviensia. Vol.52A. No.1–2. P.81–94. DOI: 10.3409/azc.52a_1-2.81-94

Mayhew D.F., Dieleman F.E., Boele J., Verhaard L. & van den Hoek Ostende L.W. 2008. *Mimomys hajnackensis* from the Pliocene of the Netherlands // Netherlands Journal of Geosciences. Vol.87. No.2. P.181–188. DOI: 10.1017/S0016774600023210

Mehely L. v. 1914. Fibrinae Hungariae. Die tertären und quartären wurzelzänigen Wühlmäuse Ungarns // Annals of the National Nuseum of Hungary. Vol.12. P.155–243.

Mikhailov K.E. & Zelenkov N. 2020. The late Cenozoic history of the ostriches (Aves: Struthionidae), as revealed by fossil eggshell and bone remains // Earth-Science Reviews. Vol.208. Art.103270. DOI: 10.1016/j.earscirev.2020.103270

Minwer-Barakat R., García-Alix A., Martín-Suárez E. & Freudenthal M. 2008. The latest Ruscinian and early Villanyian Arvicolinae from southern Spain re-examined: biostratigraphical implications // Journal of Vertebrate Paleontology. Vol.28. No.3. P.841–850. DOI: 10.1671/0272-4634(2008)28[841:TLRAEV]2.0.CO;2

Mörs T., von Koenigswald W. & von der Hocht F. 1998. Rodents (Mammalia) from the late Pliocene Reuver Clay of Hambach (Lower Rhine Embayment, Germany) // Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO. Vol.60. P.135–160.

Nesin V.A. 1981. [A new species of vole *Dolomys ondatroides* sp. n. (Rodentia, Microtidae) from the Kotlovna locality] // Vestnik Zoologii. No.4. P.5–7 [in Russian].

Nesin V.A. 1983. [New finds of fossil voles of genus *Pliomys* (Rodentia, Microtinae)] // Vestnik Zoologii. No.6. P.41–45 [in Russian].

Nesin V.A. 1987. [A new species of vole from the Middle Pliocene of Ukraine] // Vestnik Zoologii. No.5. P.77–78 [in Russian].

Nesin V.A. 1988. [Analysis of molars of ancient Microtinae] // Vestnik Zoologii. No.2. P.84–87 [in Russian].

Nesin V.A. 1996. [An ancient fossil vole species (Rodentia, Cricetidae) from the Lower-Pontian of the South Ukraine] // Vestnik Zoologii. No.3. P.74–75 [in Russian].

Nikolaeva A.D., Tesakov A.S. & Tesakova E.M. 2025. [Ostracods from the Pliocene sediments of Kabakova Balka (Krasnodar Territory)] // Material of LXXI session of the Russian Paleontological Society. Saint Petersburg: Karpinsky Institute. P.195–197 [in Russian].

Piñero P., Agustí J. & Oms O. 2017. The late Neogene rodent succession of the Guadix–Baza basin (south-eastern Spain) and its magnetostratigraphic correlation // Palaeontology. Vol.61. P.1–20. DOI: 10.1111/pala.12340

Pogodina N.V. & Strukova T.V. 2016. Primitive Arvicolids (Early–Middle Pliocene) from Zverinogolovskoye locality (Southern Trans-Urals region) // Quaternary International. Vol.420. P.171–177. DOI: 10.1016/j.quaint.2015.10.083

Popov V.V. 2004. Pliocene small mammals (Mammalia, Lipotyphla, Chiroptera, Lagomorpha, Rodentia) from Muselievo (North Bulgaria) // Geodiversitas. Vol.26. No.3. P.403–491.

Qiu Zh. & Li Q. 2016. Neogene rodents from Central Nei Mongol, China // Palaeontologia Sinica, New Series C. Vol.30. P.1–684.

Rabeder G. 1981. Die arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. // Beiträge zur Paläontologie von Österreich. No.8. P.1–343.

Radulesco C. & Samson P. 1984. Les Micromammifères du Pliocène supérieur de Debren-1 (Bassin de Sf. Gheorghe, Dépression de Braşov, Roumanie) // Travaux de l'Institut de Spéologie "Émile Racovitza". Vol.23. P.39–47.

Radulescu C. & Samson P. 1987. *Dolomys* (Arvicolidae, Rodentia, Mammalia) in the Dacic Basin (Mammalia) // Travaux de l'Institut Spéologie "Émile Racovitza". Vol.26. P.45–53.

Radulescu C. & Samson P.-M. 1996. Pliocene and Early Pleistocene arvicolids (Rodentia, Mammalia) of the Dacic Basin, Romania // Acta Zoologica Cracoviensia. Vol.39. No.1. P.401–406.

Schevchenko A.I. 1965. [Reference complexes of small mammals of the Pliocene and lower Anthropogene in the southwestern part of the Russian Plain] // Nikiforova K.V. (ed.). [Stratigraphic Significance of the Anthropogenic Fauna of Small Mammals]. Moscow: Nauka. P.7–59 [in Russian].

Shotwell A. 1956. Hemphillian mammalian assemblage from northeastern Oregon // Bulletin of the Geological Society of America. Vol.67. P.717–738.

Şen Ş. 1977. La faune de Rongeurs pliocènes de Çalta (Ankara, Turquie) // Bulletin du Muséum National d'Histoire Naturelle: Sciences de la Terre. Vol.59. No.465. P.89–171.

Sen S. 1998. Pliocene vertebrate locality of Çalta, Ankara, Turkey. 4. Rodentia and Lagomorpha // Geodiversitas. Vol.20. P.359–378.

Skandalos P., Lansing K., Demirel F.A., Alçiçek M.C., Mayda S., Dieleman F. & van den Hoek Ostende L.W. 2023. Early Pliocene Arvicolinae and Cricetinae from the locality of Afşar, western Turkey // Turkish Journal of Earth Sciences. Vol.32. No.1. P.27–62. DOI: 10.55730/1300-0985.1826

Storch G. & Fejfar O. 1990. Eine pliozäne (ober-ruscinische) Kleinsäugerfauna aus Gundersheim, Rheinhessen. 1. Nagetiere: Mammalia, Rodentia // Senckenbergiana Lethaea. Vol.71. P.139–184.

Sulimski A. 1964. Pliocene Lagomorpha and Rodentia from Węże I (Poland) // Acta Palaeontologica Polonica. Vol.9. No.2. P.149–277.

Tesakov A.S. 2003. Early evolutionary stages of pitymyoid mimomyine voles (*Pitymimomys*, Arvicolinae, Cricetidae) from the Early Villanyian of Eastern Europe // Coloquios de Paleontologia. Vol.ext.1. P.659–668.

Tesakov A.S. 2004. [Biostratigraphy of the Middle Pliocene-Eopleistocene of Eastern Europe (based on small mam-

mals)] // Transactions of Geological Institute. No.554. P.1–247 [in Russian].
Tesakov A.S. 2005. Pliocene voles (*Pliomys*, Arvicolinae, Rodentia) from Odessa Catacombs // Russian Journal of Theriology. Vol.4. No.2. P.123–135. DOI: 10.15298/rusjtheriol.4.2.05
Tesakov A.S. 2021. [Evolution of small mammal faunas and continental biostratigraphy of the Late Cenozoic in southern Eastern Europe and Western Asia]. Dissertation for the degree of Doctor of Geological and Mineralogical Sciences in the form of a scientific report. 167 p. [In Russian]
Tesakov A.S. & Bondarev A.A. 2022. Down to the roots of lemmings: a new species of basal lemming from the upper Pliocene of West Siberia // Journal of Vertebrate Paleontology. Vol.41. No.5. Art.e2036173. DOI: 10.1080/02724634.2021.2036173
Tesakov A.S., Frolov P.D., Simakova A.N. & Titov V.V. 2026. Formation of the Greater Caucasus landform in the Late Oligocene, Miocene–Pliocene, and Early Pleistocene: A review of new paleontological data and biotic markers // Geotectonics. Vol.60. No.2. P.202–215. DOI: 10.1134/S001685212670011
Tesakov A.S., Frolov P., Simakova A., Yakimova A., Titov V., Ranjan P., Çelik H. & Trifonov V. 2024. Plio-Pleistocene small mammal-based biochronology of Eastern Anatolia and Transcaucasus // Quaternary. Vol.7. No.4. Art.42. DOI: 10.3390/quat7040042
Tesakov A.S., Ivanova A.V., Bondarev A.A., Sizov A.V., Yakimova A.A., Trofimova S.S., Frolov P.D., Kurshakov S.V., Dorogov A.L. & Sorokin A.D. 2024. Early Pliocene biotic locality Novaya Livenka in south of Western Siberia (Russia): Palynology, plant macrofossils, molluscs, small mammals, and biochronology // Fossil Imprint. Vol.80. No.2. P.239–257. DOI: 10.37520/fi.2024.019
Tesakov A.S., Titov V.V., Kurshakov S.V., Frolov P.D., Syromyatnikova E.V., Kazanov I.A. & Podvintsev V.G. 2018. [Kabakova Balka — a new locality of the Pliocene terrestrial vertebrates in Western Ciscaucasia] // Bogdanova *et al*. (eds.). Proceedings of LXIV session Paleontological society. VSEGEI. Saint Petersburg: Paleontological Society of Russian Academy of Sciences. P.236 [in Russian].
Topachevsky V.A. & Nesin V.A. 1989. [Rodents of the Moldavian and Khaprovian faunistic complexes of the Kotlovina locality]. Kiev: Naukova Dumka. 136 p. [In Russian]
Ünay E. & de Bruijn H. 1998. Plio-Pleistocene rodents ans lagomorphs from Anatolia // Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO. Vol.60. P.431–466.
van den Hoek Ostende L.W., Gardner J.D., van Bennekom L., Alçiçek M.C., Murray A., Wesselingh F.P., Alçiçek H. & Tesakov A. 2015. Ericek, a new Pliocene vertebrate locality in the Çameli Basin (southwestern Anatolia, Turkey) // Palaeobiodiversity and Palaeoenvironments. Vol.95. No.3. P.305–320. DOI: 10.1007/s12549-015-0202-3
van der Meulen A. 1973. Middle Pleistocene smaller mammals from the Monte Peglia (Orivieto, Italy) with special reference to the phylogeny of *Microtus* (Arvicolidae, Rodentia) // Quaternaria. Vol.17. P.1–144.
van de Weerd A. 1979. Early Ruscinian rodents and lagomorphs (Mammalia) from the lignites near Ptolemais (Macedonia, Greece) // Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, ser. B. Vol.82. No.2. P.127–170.
van de Weerd A., Reumer J.W.F. & de Vos J. 1982. Pliocene mammals from the Apolakkia Formation (Rhodes, Greece) // Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, ser. B. Vol.85. No.1. P.89–112.
Vasilyan D., Zazhigin V.S. & Böhme M. 2017. Neogene amphibians and reptiles (Caudata, Anura, Gekkota, Lacertilia, and Testudines) from the south of Western Siberia, Russia, and Northeastern Kazakhstan // PeerJ. Vol.5. Art.e3025. DOI: 10.7717/peerj.3025
von Koenigswald W. 1980. Schmelzstruktur und Morphologie in den Molaren der Arvicolidae (Rodentia) // Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft. Vol.539. P.1–129.
Yakimova A.A. & Tesakov A.S. 2026. [Small *Promimomys* vole from Early Pliocene of Cis-Caucasus] // Materials of LXXII Session of All-Russia Paleontological Society. Saint-Petersburg: Karpinsky Institute. P.338–339 [in Russian].
Yakimova A.A., Tesakov A.S. & Pogodina N.V. 2022. Morphology and evolutionary position of the Early Pliocene vole *Propliomys jalpugensis* from Eastern Europe // Russian Journal of Theriology. Vol.21. No.1. P.13–23. DOI: 10.15298/rusjtheriol.21.1.02
Yakimova A.A., Tesakov A.S. & Sokolov S.A. 2026. [Early Pliocene small mammals of the Kabakova Balka locality] // Materials of the XII congress of Theriological Society of the Russian Academy of Sciences, named after academician V.E.Sokolov. Moscow: KMK press. P.511 [in Russian].
Young C.C. 1935. Miscellaneous mammalian fossils from Shansi and Honan // Palaeontologica Sinica, ser. C. Vol.9. No.2. P.1–56.
Zazhigin V.S. 1980. [Rodents of the late Pliocene and Anthropogene of the south of Western Siberia] // Transactions of Geological Institute. Vol.339. P.1–156 [in Russian].
Zheng Sh., Zhang Y. & Cui N. 2019. Five new species of Arvicolinae and Myospalacinae from the Late Pliocene–Early Pleistocene of Nihewan Basin // Vertebrata PalAsiatica. Vol.57. No.4. P.308–324. DOI: 10.19615/j.cnki.1000-3118.190725
Zheng Sh., Zhang Y. & Cui N. 2024. Fossil Arvicolinae and Myospalacinae of China // Palaeontologia Sinica, New Series C. Vol.32(203). P.1–476.
Zykin V.S., Zazhigin V.S. & Prisyazhniuk V.A. 1987. [Stratigraphy of the Pliocene and Eopleistocene deposits in the Biteke river valley (North Kazakhstan)] // Geology and Geophysics. No.3. P.12–19 [in Russian].