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ULTRASTRUCTURE OF THE MOLAR ENAMEL IN REPRESENTATIVES OF THE GENUS *ELLOBIUS* (RODENTIA) IN THE PLEISTOCENE AND HOLOCENE OF UKRAINE

Leonid Rekovets[1,2], Vitalii Demeshkant[1]

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Affiliations

[1] Wrocław University of Environmental and Life Sciences (Wrocław, Poland); [2] National Museum of Natural History, NAS of Ukraine (Kyiv, Ukraine)

Correspondence

Leonid Rekovets; Department of Vertebrate Ecology, Wrocław University of Environmental and Life Sciences; ul. Kożuchowska 5b, 51-631 Wrocław, Poland; Email: leonid.rekovets@upwr.edu.pl; Orcid: 0000-0001-9934-7095

Abstract

New data on the enamel ultrastructure of molars of selected extinct and extant representatives of the genus *Ellobius* (Arvicolinae, Rodentia) from the Pleistocene of the south of Eastern Europea, mainly from the territory of Ukraine, are presented. Among the analysed species are the extinct *E. tiliguliensis*, *E. paleotalpinus*, *E. tarchankutensis*, *E. tauricus*, and *E. melitopoliensis*, some extinct populations of *Ellobius talpinus* from the Late Pleistocene, as well as the extant *E. talpinus* and *E. fuscocapillus*. It was revealed that the enamel of molars of these species has the same structure as the enamel of Cricetidae and it belongs to three types described by Koenigswald (1980): radial, tangential, and lamellar. Radial enamel is the prevailing type in *Ellobius*, which is the initial form in the evolutionary process of other types. According to Kilic et al. [1997], radial enamel can also be divided into three groups (I, II, and III) by the arrangement of the interprismatic matrix (IPM) and prismatic enamel (PE) in its structure. The first type is characterised by an almost linear arrangement of IPM and PE, whereas the second type is reticulate, and the third one is always located near the enamel-dentin junction (EDJ) and is connected to dentin, the matrix of enamel formation. It was shown that in the lineage of the subgenus *Ellobius* and in the formation of the species *E. talpinus* the second type of radial enamel predominated, whereas weakly expressed lamellar enamel of various levels of evolutionary development is present only on the tips of conids (primitive and progressive enamel). In contrast, in the lineage of the subgenus *Bramus* (= *Afganomys*) and the formation of the species *E. fuscocapillus* monotypic (according to the density of IPM and PE) first type radial enamel predominates and lamellar enamel is absent. This line of development by morphological characters has traditionally been considered as progressive evolution of the genus, although (as it turned out) it is characterised by a more primitive enamel structure (lack of lamellar enamel). As a result, we were able to further substantiate the phylogeny of the genus *Ellobius* with new data from the morphologocal analysis of molars and to outline the prospects for possible use of the enamel structure as a character in the taxonomy and phylogeny of species of Cricetidae.

Cite as

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Ультраструктура емалі кутніх зубів у представників роду *Ellobius* (Rodentia) в плейстоцені й голоцені України

Леонід Рековець, Віталій Демешкант

Резюме. Представлено нові дані про ультраструктуру емалі корінних зубів вибраних вимерлих та сучасних представників роду *Ellobius* (Arvicolinae, Rodentia) з плейстоцену півдня Східної Європи, переважно з території України. Це вимерлі види: *E. tiliguliensis*, *E. paleotalpinus*, *E. tarchankutensis*, *E. tauricus*, *E. melitopoliensis* та деякі вимерлі популяції *Ellobius talpinus* з пізнього плейстоцену, а також сучасні види: *E. talpinus* і *E. fuscocapillus*. Встановлено, що емаль їх зубів відповідає структурі емалі Cricetidae і відноситься до трьох, описаних раніше Кьонігсвальдом (1980), типів: радіальна, тангенціальна та ламелярна. Переважаючою в структурі *Ellobius* є радіальна емаль як вихідна для формування в процесі еволюції її інших типів. Згідно з даними Кіліка з кол. (1997) вона теж поділяється на три типи (I, II, III), за способом укладення міжпризматичної матриці (IPM) та призматичної емалі (PE) в структурі цієї емалі. Перший тип має переважно лінійчату структуру укладення IPM та PE, другий — сітчастоподібну, третій — завжди розміщений біля емаль-дентинової границі (EDJ) та поєднаний з дентином — матрицею формування емалі. Показано, що в філетичній лінії підроду *Ellobius* та становлення виду *E. talpinus* домінуючим у структурі радіальної емалі є її другий тип, а на вершинах конідів зубів є слабо виявлений ламелярний тип емалі різного еволюційного рівня (примітивна та прогресивна емаль). В той час як у філетичній лінії підроду *Bramus* (= *Afganomys*) та становлення виду *E. fuscocapillus* переважаючою є монотипова (за щільністю структури IPM та PE) радіальна емаль першого типу та відсутність ламелярної емалі. Цю лінію розвитку за морфологічними ознаками традиційно розглядали як прогресивна в еволюції роду, але (як виявилося) вона має примітивну структуру емалі (брак ламелярної емалі). В підсумку вдалося додатково обґрунтувати філогенію роду *Ellobius* новими даними морфологічного аналізу зубів та окреслити перспективи можливого використання структури емалі як ознаки для цілей таксономії і еволюції видів Cricetidae.

Ключові слова: *Ellobius*, емаль, радіальна структура, ламелярна структура, плейстоцен, філогенез.

Introduction

The remains of *Ellobius* species are consistently encountered in Pleistocene deposits across many locations in the southern part of Eastern Europe. This is evidenced by numerous publications starting from the second half of the 20th century, which have been included in the catalogue of *Pleistocene Fauna of Ukraine* [Krokhmal & Rekovets 2010] and literature reviews on palaeomammalogy [Kovalchuk 2013]. Fossil remains of this genus are not rare and, in some cases, are even dominant, such as in the Crimea [Rekovets 1994 *a–b*], serving as indicators of arid climate and reflecting the existence of steppe ecosystems in the landscapes of that time.

An analysis of the literature indicates that in Eastern Europe a succession of several *Ellobius* species occurred at the beginning of the Pleistocene, including *E. tiliguliensis*, *E. paleotalpinus* (= *E. kujalnikensis*), *E. tarchancutensis*, and *E. tauricus*, which appeared almost simultaneously from the east and the Mediterranean region [Topachevsky, 1963, 1965 *a–b*; Nesin & Nadachowski 2001; Rey-Rodríguez *et al.* 2021]. Their remains in archaeozoological sites are often identified as '*Ellobius* species', i.e. without species identification.

Phylogenetically, the genus originates from a group of morphologically similar taxa predominantly known from the Pliocene of Western Europe (*Ungaromys*, *Betfiomys*, and *Germanomys*) [Topachevsky & Rekovets 1982; Rey-Rodríguez *et al.* 2021]. It is most likely that these taxa are related to the Mediterranean subgenus *Bramus*, while the ancestors of the subgenus *Ellobius* may be forms originating from Asia [Topachevsky & Rekovets 1982].

The identification of fossil remains of extinct forms is primarily based on the characteristics of molars, which exhibit distinct morphological gaps. This enabled the identification of a new *Ellobius* species, *E. pomeli* (established by A. Tesakov), for the studied region of Europe during the Middle Pleistocene (Tiraspol faunal complex, MQR 7 chronozone), as a phylogenetic intermediary between

E. tarchancutensis and *E. lutescens*. For extant species, genetic [Coskun 2016; Charakheloo & Kivanc 2003] and molecular [Kuprina *et al.* 2023] differentiation criteria have been developed. Additionally, the ecological and morphological features of the most widespread species in the studied region of Europe are relatively well studied [Coskun 2016; Artemieva 2022; Korobchenko 2008; Korobchenko *et al.* 2008, 2014].

The most comprehensive information on the phylogenetic relationships of *Ellobius* taxa during the Pleistocene, reflected in monophyletic lineages (morphological clades) and their schematics, was provided in earlier publications [Topachevsky & Rekovets 1982; Rekovets 1994 *a–b*]. A brief analysis of the data suggests that the evolution of the genus *Ellobius* in Eastern Europe includes at least four phyletic lineages that define the development of modern species: *tancrei*, *talpinus*, *fuscocapillus*, and *lutescens*. The primary morphological features of molars considered were size, presence/absence of a prismatic fold on m1, degree of track development, root development level, crown height, and simplification of M3.

The goal of this study was to introduce additional criteria—specifically, the morphological characteristics of the ultrastructure of molar enamel—to characterise the evolution of the genus *Ellobius*. This analysis encompassed both extinct (*E. tiliguliensis*, *E. paleotalpinus*, *E. tarchancutensis*, *E. tauricus*, and *E. melitopoliensis*) and extant (*E. talpinus*, *E. fuscocapillus*) species. The objective stemmed from the hypothesis that enamel structure, as a highly functional trait, could provide supplementary evidence for existing taxonomic and phylogenetic diversity, not only within *Ellobius* but also across rodents (Rodentia) as a whole.

General information about teeth enamel of mammals

As an integral component of the digestive system and a defensive mechanism, teeth serve as the first point of contact (following movements and gaits) between an organism's body and the external environment. The formation of enamel, dentin, and cement structures in teeth occurs through the activity of odontoblasts (ameloblasts and cementoblasts), which collectively form the dental and enamel structures within the periodontal complex [Du Toit 2008]. Dentin is known to act as a matrix for the production of radial enamel with the involvement of ameloblasts.

Enamel is classified into three primary structural types: radial, tangential, and lamellar. These types differ in the arrangement of their crystals, which contribute to the stratification of the enamel structure within its boundaries, the enamel-dentine junction (EDJ), and the outer enamel surface (OES). The main structural components of enamel are the interprismatic matrix (IPM) and the prisms of the prismatic enamel (PE), which can exhibit various organisational modifications depending on taxonomic and functional factors [Koenigswald & Sander 1997].

In Arvicolinae, radial enamel is considered the simplest form (with uniform distribution of IPM and PE) and is viewed as the ancestral structure from which other types evolved. It is paragenetically and functionally connected to the derived forms. Based on prism arrangement, radial enamel is subdivided into three types [Kilic *et al.* 1997 *a–b*].

> Type I consists of elongated and almost parallel IPM, interspersed with crystals or bundles of PE (Fig. 1 *b–c*). Type II features a reticulated arrangement of IPM with PE prisms, which are generally coarser than the IPM (Fig. 1 *a*). Type III, characterised by coarse IPM and a narrow band of PE, is always located near the EDJ and is consistently associated with dentin, which serves as the primary source for enamel formation (Fig. 1 *c–d*).

The morphological stability of radial enamel is determined by genetic characteristics, while the noticeable variability of tangential and lamellar enamel is influenced additionally by functional requirements, which play a crucial role in dietary specialisation [Herrmann, 2002; Korobchenko & Zagorodniuk 2008]. Lamellar enamel represents a highly modified and advanced form of radial enamel, exhibiting significant structural variability (both primitive and advanced forms). It is always found on the anterior walls of tooth conids (T 1–9) near the EDJ boundary and is absent on their posterior walls, where tangential enamel is consistently present near the OES boundary and is not associated with dentin [Koenigswald *et al.* 1994].

Material and Methods

The material for this study consisted of a series of molar teeth of both extinct and extant species of the genus *Ellobius* from the Pleistocene and Holocene. These specimens are part of the collection of the Department of Palaeontology of the National Museum of Natural History, NAS of Ukraine (Kyiv). A total of 14 molar teeth from upper and lower jaws (two teeth per species) were analysed and compared. The ultrastructure of the teeth was studied using a Zeiss® EVO LS 15 scanning electron microscope at the University of Wrocław (Poland).

The study employed established and tested methodologies for specimen preparation and experimental procedures [Koenigswald 1980; Demeshkant & Rekovets 2021] and involved the creation of a corresponding digital database. The primary structural elements of enamel types (IPM and PE) were visually compared and analysed using computer images (photographs), and the results were summarised in the form of conclusions. Additionally, comparisons were made with ecologically similar fossorial forms from the genera *Anomalomys* and *Spalax* [Nowakowski *et al.* 2018]. The study also incorporated the naming conventions for molar tooth elements in Arvicolinae and the stratigraphic scheme of the Pleistocene proposed by Krokhmal *et al.* [2023: fig. 2–3]. In the text and the figures (Fig. 1–9), the following abbreviations were used:

BSA, LSA—names of conids according to Krokhmal *et al.* [2023: fig. 1]; D—dentin; EDJ—enamel-dentine junction; IPM—interprismatic matrix; L—lamellar enamel; OES—outer enamel surface; PE—prismatic enamel; PL—primitive lamellar enamel; PLEX—prismless external layer of enamel; PT—primitive tangential enamel; R—radial enamel (types I, II, and III); and T—tangential enamel.

Results

The first insights into the enamel structure of *Ellobius* were published in the monographs by Koenigswald [1980] and Kalthoff [2000], while later studies primarily focused on the mechanics of teeth during burrowing and foraging. In general, the enamel of *Ellobius* molars is composed predominantly (90%) of radial enamel. A significantly smaller proportion (around 5–7%) consists of primitive lamellar enamel, described as 'diskreter lamellenschmelz' [Koenigswald 1980: figs 11, 26], while tangential enamel or irregular enamel may sporadically appear on certain conids. According to our research, this enamel structure is characteristic of both extinct and extant representatives of the genus. However, it simultaneously exhibits distinct structural features.

Genus *Ellobius* Fischer, 1814

In the Palearctic, the genus is divided into two subgenera—*Ellobius* s. str. (four species) and *Bramus* (= *Afganomys*) (two species)—and there are 9 extinct species of the genus. The structure of tooth enamel in representatives of both groups, which belong to six species from the Pleistocene of Ukraine, is considered.

Subgenus *Ellobius* Fischer, 1914

In Ukraine, one modern species of the subgenus exists (*Ellobius talpinus*) and four extinct species (*E. tiliguliensis*, *E. tauricus*, *E. palaeotalpinus*, and *E. melitopoliensis*) and one subspecies (*E. t. palaeoucrainicus*) have been described.

Ellobius tiliguliensis Topachevsky & Rekovets 1982, (Tylihul), MIS 63–64 (Fig. 1)

The species was described from the Tylihul locality near the village of Morske (Tylihul Estuary), early Pleistocene, early Taman faunas [Topachevsky & Skoryk 1977]. It occupies a basal position in the phylogenetic scheme of the genus [Topachevsky & Rekovets 1982: fig. 1]. Across all tooth conids and along their perimeter within the boundaries of the enamel-dentine junction (EDJ) and the outer enamel surface (OES), highly structured radial enamel of the first (linear arrangements of IPM and PE) and second (a mesh-like arrangement of IPM and PE) types predominates. The third type, located near the EDJ boundary, is well-developed (thick IPM with nearly absent PE), demonstrating a close association with dentine ameloblasts (Fig. 1 *a–c*).

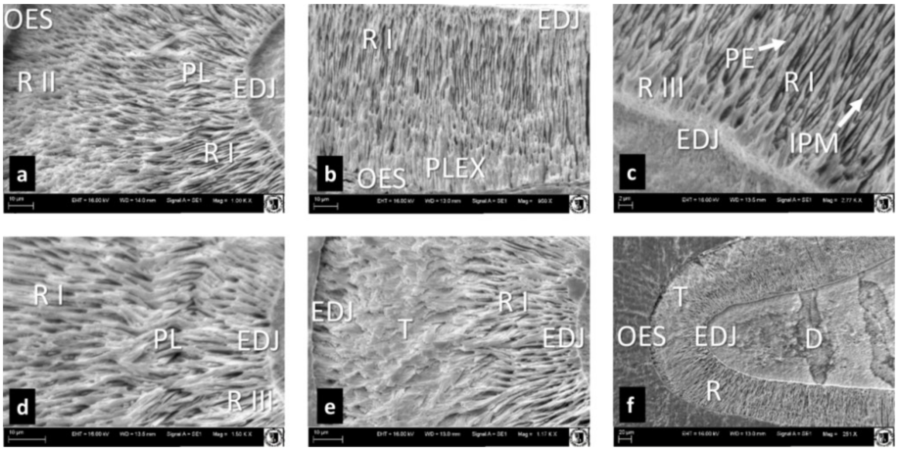

Fig. 1. Enamel structure in *Ellobius tiliguliensis*, early Pleistocene, Tylihul.

Рис. 1. Структура емалі у *Ellobius tiliguliensis*, ранній плейстоцен, Тилігул.

A notable feature of the enamel structure in this species is the presence of barely visible crystals of primitive lamellar enamel among the prisms of radial enamel at the apical tips of the conids (BSA, LSA), exhibiting a specific interwoven structure of irregular IPM enamel (Fig. 1 *d*). A similar enamel structure for this type in *Ellobius* was also noted by Koenigswald [1980: fig. 26]. However, the most distinctive characteristic of the enamel in *Ellobius tiliguliensis* is the well-developed, albeit primitive tangential enamel on the LSA 1 conid. This tangential enamel is strikingly similar to the irregular enamel typical of Ochotonidae, which is a rare feature for the genus in general (Fig. 1 *e–f*). Additionally, the local presence of irregular PLEX-type enamel near the OES boundary was observed (Fig. 1 *b*).

***Ellobius palaeotalpinus* Schevtschenko, 1965, Taman faunal complex, MIS 22–62 (Figs. 2–3)**

In the literature, this species is also known as *Ellobius kujalnikensis* Topachevsky 1965. This name continues to appear in publications even after its synonymisation in 1982. The species is recognised in two chronopopulations: the early Taman chronopopulation (*E. p. palaeotalpinus*, Kryzhanivka, Taman faunal complex Zhevakhova Hora[1]) and the late Taman chronopopulation (*E. p. progressus*, Nohaisk[2]) [Topachevsky & Rekovets 1982].

Ellobius palaeotalpinus (s. str.) Schevtschenko, 1965 (Zhevakhova Hora), MIS 36–62 (Fig. 2). The species differs from the *E. tiliguliensis* by a denser arrangement of radial enamel prisms between the boundaries of the EDJ and OES, a rather weak development of primitive lamellar enamel on the cusps of the conids, and the absence of tangential enamel type (Fig. 2 *c*). Another distinguishing feature is the weakly expressed first-type enamel, with the second type being dominant, while the third type is notably developed, showing a dense connection with the dentin (Fig. 2 *a–b*). Near the OES boundary, a well-developed layer of unstructured PLEX-type enamel is observed (Fig. 2 *d*).

Ellobius palaeotalpinus progressus Topachevsky 1973 (Nohaisk), MIS 22–35 (Fig. 3). The structure of radial enamel prism arrangement and its characteristics are quite similar to those of the nominal subspecies (Fig. 3 *a–b*). The main distinction lies in the weak development of primitive lamellar enamel on the cusps of the LSA and BSA conids, which exhibits a more advanced weaving pattern of prisms compared to the nominal subspecies (Fig. 2 *c*; Fig. 3 *c*). Additionally, the subspecies from Nohaisk has a poorly developed layer of third-type enamel near the EDJ boundary. Overall, this species is characterized by the dominance of second-type enamel with a mesh-like structure and the presence of primitive lamellar enamel, named as 'Little ordered lamellar enamel' [Koegigswald 1980: fig. 11]. The PLEX-type is rather weakly developed.

[1] The Zhevakhova Hora locality (= Zhevakhova Gora) is near the city of Odesa.

[2] Since 1964 as Prymorsk, in Berdiansk Raion of Zaporizhzhia Oblast.

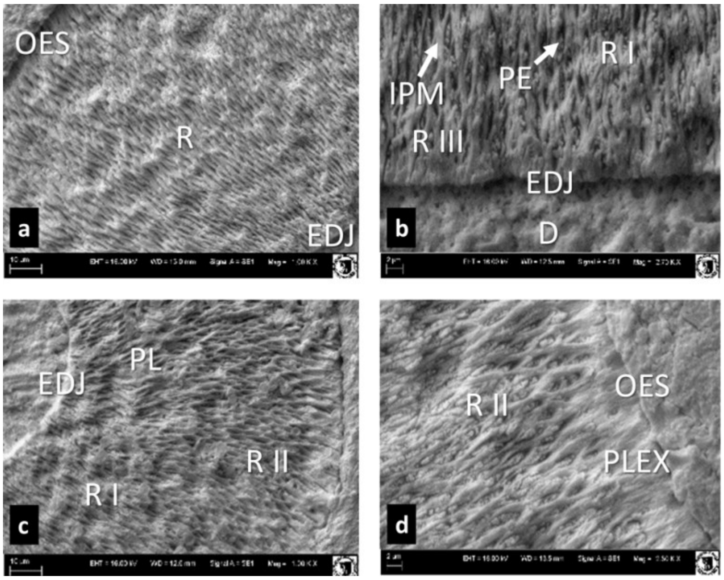

Fig. 2. Enamel structure in *Ellobius palaetalpinus* (s. str.), early Pleistocene, Zhevakhova Hora.

Рис. 2. Структура емалі у *Ellobius palaetalpinus* (s. str.), ранній плейстоцен, Жевахова гора.

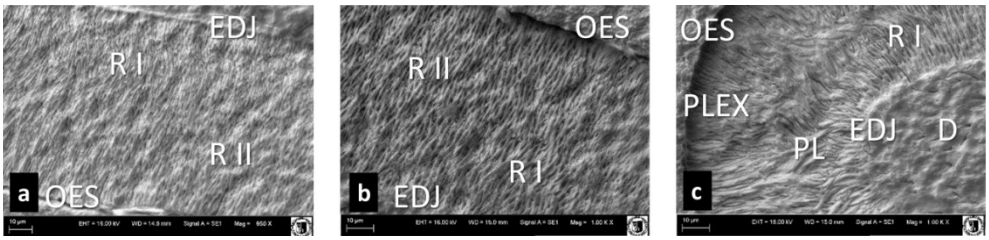

Fig. 3. Enamel structure in *Ellobius palaeotalpinus progressus*, late early Pleistocene, Nohaisk.

Рис. 3. Структура емалі у *Ellobius palaeotalpinus progressus*, пізній ранній плейстоцен, Ногайськ.

***Ellobius tauricus* Topachevsky 1965 (Tarkhankut), MIS 36–40 (Fig. 4)**

The species was described from the late Tamansk faunas of the Eopleistocene of the Crimea, specifically from the Tarkhankut locality [Topachevsky 1973]. In terms of structure and characteristics, the tooth enamel of this species is more similar to that of *Ellobius tiliguliensis*. It features a distinctly developed first-type enamel with parallelly arranged IPM and elongated PE prisms. The second-type enamel, with a mesh-like structure, is also well developed, while the third-type enamel is weakly represented (Fig. 4 *a–b*). Lamellar enamel and PLEX are virtually absent (Fig. 4 *c*).

On one of the external conids (BSA 3) near the OES boundary, irregular enamel is clearly observed (similar to that in Ochotonidae) and is quite comparable to the primitive tangential type found in some *Allophaiomys* (Fig. 4 *d*). This type of enamel was also noted in *E. tiliguliensis* (Fig. 1 *e–f*). Based on these features, the enamel of this species is distinctly different from that of *E. palaeotelpinus* and more similar to that of *E. tiliguliensis*.

***Ellobius melitopoliensis* Topachevsky 1973 (Tychonivka, Luzanivka), MIS 20-21 (Fig. 5)**

The species was described from the Tiraspol faunas of the middle Pleistocene, Tykhonivka, in southern Ukraine [Topachevsky 1973]. Overall, the enamel structure of this species is quite similar to that of *E. palaeotalpinus*, with a predominance of the second-type enamel (Fig. 5 *a*).

However, it shows a possibly more advanced development of lamellar enamel, although it resembles irregular enamel (Fig. 5 *b–c*). The third-type enamel is moderately developed and closely integrated with dentin. In the enamel structure, IPM elements dominate, while PE prisms are arranged in lens-shaped bundles. The third-type enamel and PLEX are weakly represented.

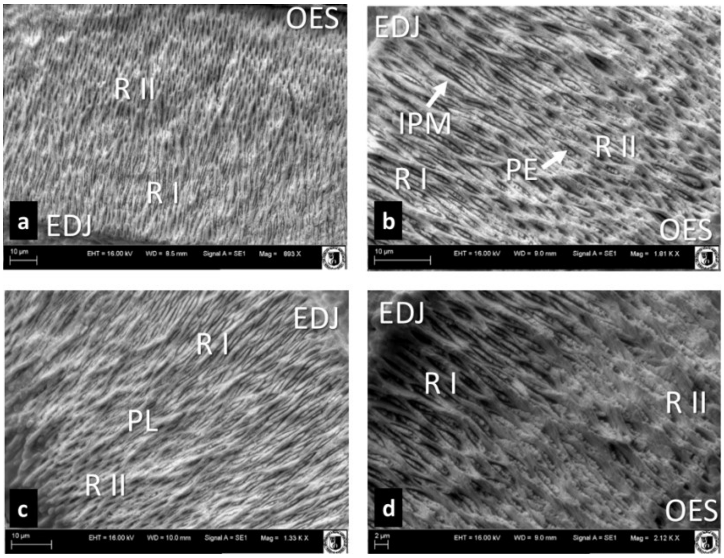

Fig. 4. Enamel structure in *Ellobius tauricus*, early Pleistocene, Tarkhankut.

Рис. 4. Структура емалі *Ellobius tauricus*, ранній плейстоцен, Тарханкут.

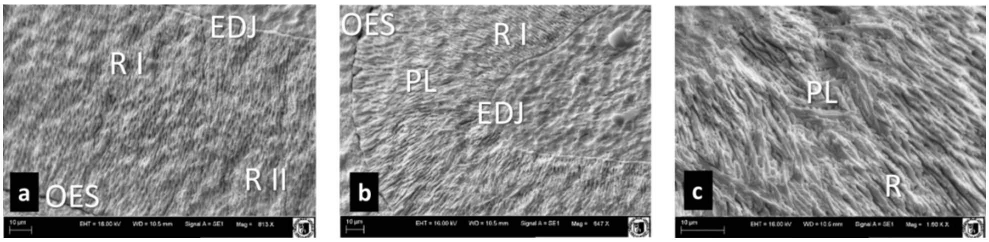

Fig. 5. Enamel structure in *Ellobius melitopoliensis*, middle Pleistocene, Luzanivka.

Рис. 5. Структура емалі у *Ellobius melitopoliensis*, середній плейстоцен, Лузанівка.

***Ellobius talpinus palaeoucrainicus* Rekovets, 1985 (Dnipro alluvium, Late Pleistocene), MIS 4–5 (Fig. 6)**

The subspecies was described from modern alluvial deposits of the Lower Dnipro based on the morphology of molar teeth [Rekovets 1985]. The enamel of this subspecies does not fundamentally differ from that of the extant species (Fig. 6 *a*–*b*). The third-type enamel is weakly developed, and lamellar enamel is primitive, appearing primarily on the walls of the tooth cones (Fig. 6 *c*–*d*). PLEX-type enamel is also poorly developed. A comparison was made with *Ellobius talpinus* from cave deposits in the Crimea (Emine-Bair-Khosar) dated to the Late Pleistocene. No significant differences in the enamel structure were found. In general, in the extinct forms of the subgenus *Ellobius*, second-type radial enamel predominates, while lamellar enamel is relatively weakly expressed.

***Ellobius talpinus* Pallas 1770, recent, Lower Dnipro area (Fig. 7)**

The enamel of teeth of the extant species from the western part of its range (Ukraine) exhibits typical subgeneric characteristics with a predominance of the second-type enamel (Fig. 7 *a*–*c*) and a relatively progressive lamellar type. This type is present throughout the periphery of the cusps in the form of primitive (on the cusps' walls, Fig. 7 *b, f*) and more progressive (on the cusp tips, Fig. 7 *d*–*e*) variations. The lamellar enamel appears at the boundary between the first and second types of radial enamel, especially near the EDJ boundary as enlarged and tilted bundles of prisms towards the cusp tips (Fig. 7 *g*–*h*). The progressive structure is characterised by a higher level of prism bundling and extends onto the front and back walls of the cusp tips. The PLEX enamel type is present (Fig. 7 *i*), and the third-type enamel is weakly developed (Fig. 7 *a, d*). All these enamel features are typical of the modern *E. talpinus* species. A preliminary analysis suggests that the enamel of the extant species compared to the described extinct species shares similar characteristics but with more advanced features, especially for the lamellar enamel.

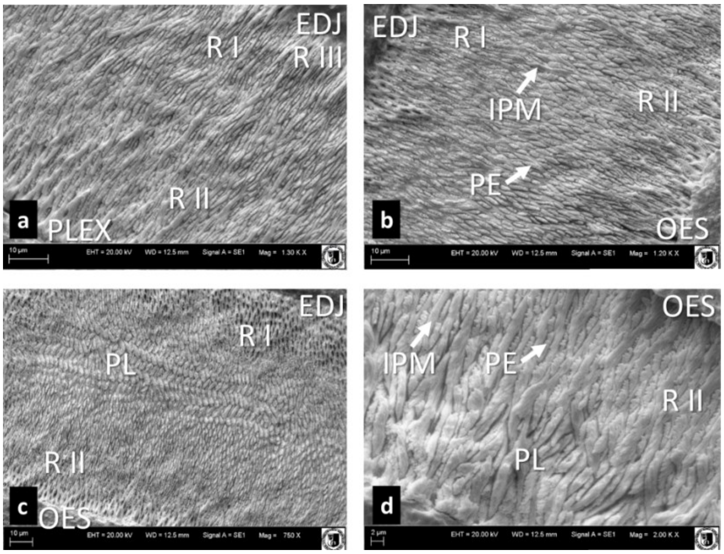

Fig. 6. Enamel structure in *Ellobius talpinus palaeoucrainicus*, Late Pleistocene, Middle Dnipro alluvium.

Рис. 6. Структура емалі у *Ellobius talpinus palaeoucrainicus*, пізній плейстоцен, алювій Середнього Дніпра.

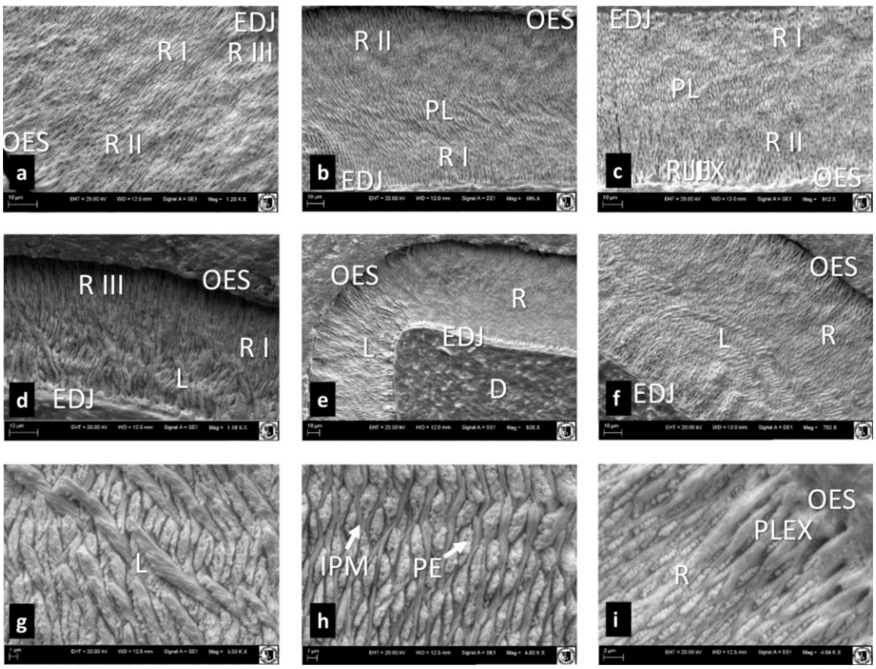

Fig. 7. Enamel structure in *Ellobius talpinus*, recent, western part of the range, Ukraine.

Рис. 7. Структура емалі у *Ellobius talpinus*, сучасний, західна частина ареалу, Україна.

Subgenus *Bramus* (= *Afganomys*) Pomel 1892

There are two modern species known outside of Ukraine (*Ellobius fuscocapillus*, *E. lutescens*) and two extinct species (including one from Ukraine, *E. tarchancutensis*, the enamel of which has been studied).

Ellobius tarchancutensis Topachevsky 1973 (Tarkhankut, Zhevakhova Hora), MIS 36–40 (Fig. 8)

The species belongs to a different evolutionary lineage of the genus, as indicated by morphological features and data from previous studies [Topachevsky & Rekovets 1982; Gharakheloo & Kivans 2003], as well as our analysis of enamel ultrastructure.

The species is known from the Taman faunas of the Crimea (Tarkhankut) and the Black Sea coastal region of Odesa (Zhevakhova Hora), middle Eopleistocene. This species is considered ancestral to modern *E. fuscocapillus* and possibly *E. lutescens*. The enamel of the extinct species exhibits the typical structure of the genus but with certain unique characteristics. Within the EDJ and OES boundaries, the enamel is dominated by that of the first type with linearly and densely arranged IPM and PE. Near the EDJ boundary, there is a weakly visible layer of third-type enamel (Fig. 8 *a–b, d*). The primitive lamellar (?) enamel, more reminiscent of primitive tangential enamel, is barely noticeable on the hypoconid of m1 (BSA 1) (Fig. 8 *c*). Its structure does not form the intertwining typical of lamellar enamel, with IPM prisms arranged in a leaf-like and somewhat irregular (chaotic) manner closer to the EDJ.

Notable features of the enamel of this extinct species include monotypy (mainly only the first type) and a dense structure with elongated and not thickened IPM and lens-shaped bundles of PE (Fig. 8 *a–b, d*). The enamel differs from that of species of the *Ellobius* subgenus in its monotypic construction, weak development of IPM and PE, linearly and parallelly arranged, low mesh structure, and near-absence of lamellar enamel. The presence of tangential enamel is unclear.

***Ellobius fuscocapillus* Blyth 1843, recent, from the Eastern Caspian area (Fig. 9)**

This species from the Caspian region differs from other species of the genus by having somewhat progressive features (absence of prismatic fold, high coronoid process, high level of ridges, etc.) and, together with *E. lutescens*, forms an independent lineage [Topachevsky & Rekovets 1982].

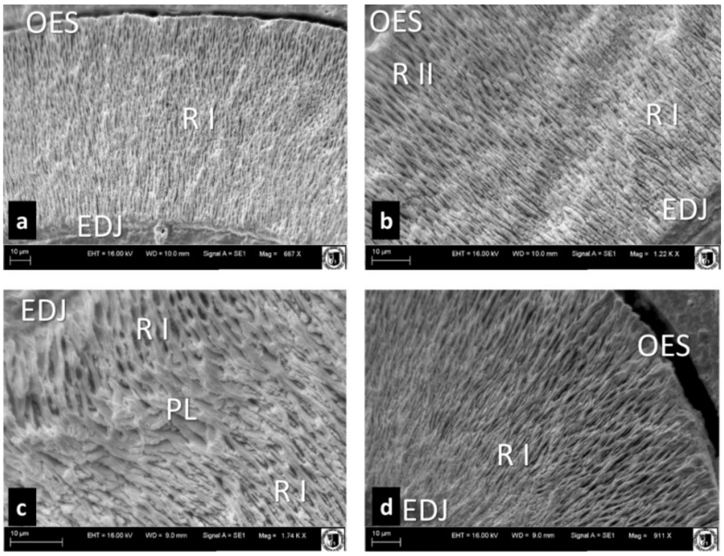

Fig. 8. Enamel structure in *Ellobius tarchankutensis*, early Pleistocene, Tarkhankut.

Рис. 8. Структура емалі у *Ellobius tarchankutensis*, ранній плейстоцен, Тарханкут.

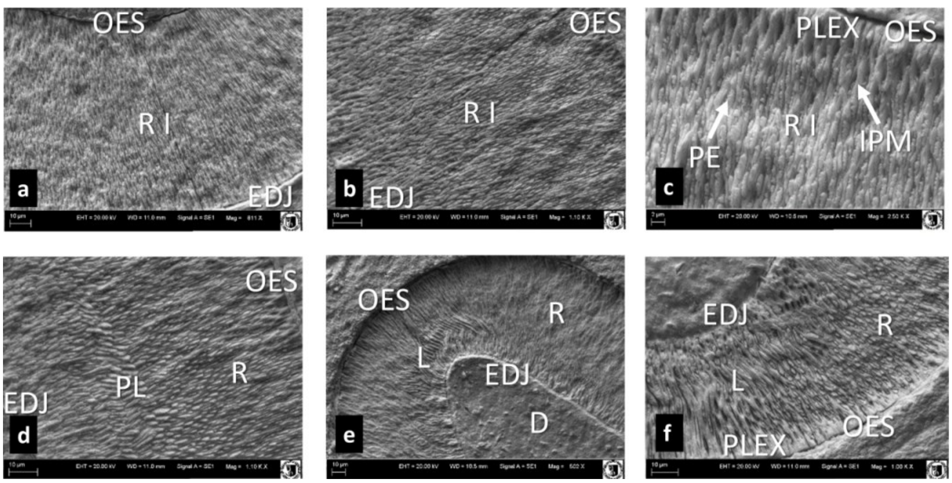

Fig. 9. Enamel structure in *Ellobius fuscocapillus*, recent, Eastern Caspian area.

Рис. 9. Структура емалі у *Ellobius fuscocapillus*, сучасний, Східний Каспій.

In the enamel structure, it is quite similar to the extinct *E. tarchancutensis*, which is also confirmed by our studies, while at the same time differs from *E. talpinus* and other species of the subgenus *Ellobius*. The species is characterised by a monotypic enamel structure, similarity in IRM arrangement and prisms of PE, and weak development of the third-type enamel near the EDJ (Fig. 9 *a–b*). The difference between them also lies in the fact that in the modern species the enamel on the apices of the cones is lamellar, which should be attributed to the progressive type (Fig. 9 *e–f*), but, at the same time, there is also enamel of primitive type on the walls of the cones (Fig. 9 *d*).

The PLEX-type enamel is notably developed (Fig. 9 *c, f*). The fact of the evolutionary formation of lamellar enamel (possibly through a stage of irregular enamel) in this monophyletic lineage (clade) is well-known in the literature [Koenigswald 1980: fig. 70].

Discussion

The results of the conducted studies have allowed us to establish and trace the evolutionary variability of such an apparently stable trait as the enamel structure of molars within the phylogenetic lineage of the genus *Ellobius* in Eastern Europe during the Pleistocene. Once again, it has been confirmed that enamel has its species-specific structural characteristics and patterns of morphological transformations over time [Koenigswald 1980: fig. 70], as well as dependencies on functional loads. The enamel structure predominantly features radial enamel (first and second types), with less developed primitive lamellar enamel, and occasionally unstructured tangential enamel, along with PLEX-type enamel or other irregular forms. The latter type is also characteristic of Ochotonidae [Rabiniak *et al.* 2017] and Spalacidae [Nowakowski *et al.* 2018], which exhibit a *Bramus*-like arrangement of radial enamel (dense arrangement of the first type).

For previously established clades within the genus *Ellobius* [Topachevsky & Rekovets 1982], specific enamel structures have been noted, which might indicate morphological (and possibly phylogenetic) relationships among the examined forms. For example, the similarity between *E. tiliguliensis* and *E. tauricus* is observed in the almost 50 : 50 ratio of the first (linear type) and second (reticulated type) types of radial enamel, while in other species of this branch, including *E. talpinus*, the second type predominates. In species of the subgenus *Ellobius* (starting from *E. tiliguliensis*), we observe the emergence and progressive development of lamellar enamel over time, an increase in the density of IRM and PE arrangements in radial enamel, and the presence of PLEX-type enamel. Based on these traits, the species *E. tauricus* shows differences and diverges from the lineage of *E. talpinus* at the level of *E. tiliguliensis*, rather than at the level of *E. palaeotalpinus* [Topachevsky & Rekovets 1982: fig. 1].

The evolutionary branch of *E. tarchancutensis–E. fuscocapillus* in the subgenus *Bramus*, although considered more progressive than the previous one, does not exhibit lamellar enamel as a progressive feature of the subgenus *Ellobius*. Moreover, *Bramus* is characterised by a monotypic structure of radial enamel (predominantly only the first type). In this context, it would be interesting to compare the enamel of *E. pomeli* (middle Pleistocene) and the extant *E. lutescens*, which currently is not feasible.

In sum, we can conclude that for the existing phylogenetic scheme of the genus *Ellobius*, based on morphological traits, scientific reliability has been confirmed, substantiated by additional morphological features, which are the structural components of molar enamel. These data also support the views that Miocene–Pliocene species of the genera *Ungaromys*, *Stachomys*, and *Germanomys*, which are considered as possible ancestors of *Ellobius*, have a small amount of primitive lamellar enamel on the apices of cones, a trait found even in some modern species, for example, *Prometheomys*. It has been confirmed that enamel structure as a morphological trait can be utilised in the practice of taxonomy and systematics of various evolutionary forms.

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