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The enamel characteristics of fossil and modern first lower molars of the European water vole (*Arvicola amphibius*, Arvicolinae, Rodentia) of the Perm Pre-Urals

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ABSTRACT

This article presents data on the enamel characteristics (thickness, enamel differentiation coefficient (SDQ)) of the first lower molars of the European water vole (based on the conditional groups “juvenile” and “adult”) from fossil and modern samples from the Perm Pre-Urals (Russia). Among the “adult” group teeth, samples from the Eemian (Mikulino) interglacial deposits had the highest mean SDQ values (91.5–94.8), while samples from the end of the Bryansk Interstadial, the Late Glacial, the Early Holocene deposits had the lowest (76.3–84.9).

1. Introduction

The search for marker species for biostratigraphic correlation of deposits is one of the most urgent problems in palaeontology today. Numerous teeth of small mammals found in the deposits of numerous localities of the Quaternary fossil fauna are the most suitable samples for studying evolutionary changes. Of particular interest are the morphological changes in the evolution of representatives of the genus *Arvicola*, whose modern range covers a vast area of Eurasia. Many studies have established that the Pleistocene is characterised by a change in the enamel thickness on the anterior and posterior walls of molars (Koenigswald, 1973, 1980; Janossy, 1976; Aleksandrova, 1976; Sutcliffe and Kowalski, 1976; Radulesko and Samson, 1977; Heinrich, 1978, 1982, 1987, 1991; Markova, 1981; Agadjanyan and Erbaeva, 1983; Yakovlev, 1988; Rekovets, 1989; Agadjanyan, 2009; Socha, 2014; etc.). However, the evolution of *Arvicola* vole molars is a quite complex process (Kolfschoten, 1990; Koenigswald and Kolfschoten, 1996; Maul and Markova, 2007; Escude et al., 2008; Ruddy, 2011), and when using morphological data of teeth from this genus for biostratigraphic purposes, it is quite important to determine regional differences (Röttger, 1987; Markova, 2006; Maul et al., 2018, 2020).

Identification of ontogenetic trajectories of morphological features of European water vole teeth within age groups and comparison of their enamel morphology is quite important for evaluating the application of these parameters in biostratigraphy (Ruddy, 2011). Differences between any samples of mammalian molars are reliable only upon comparison of the material of the same ontogenetic stage. For isolated teeth of unrooted voles (including the European water vole), there is a problem of determining individual age, the optimal solution for which has not yet been found (Maleeva and Elkin, 1986; Klevezal, 2007).

The European water vole (*Arvicola amphibius* (Linnaeus, 1758)) is currently a rare species throughout the Perm Pre-Urals (Perm Krai, Russia) (Voronov, 1971; Demidov and Demidova, 1990). The presence of this species in this area is confirmed by data on diet of the eagle owl, long-eared and short-eared owls (Shepel, 1992). Bone remains of this species have been found in the Late Pleistocene and Holocene deposits of karst cavities in the region (Fadeeva et al., 2000, 2005, 2005; Fadeeva and Bolotov, 2001; Fadeeva, 2002, 2005). The bones of European water voles account for up to 18% of the total number of small mammal bones in the Holocene deposits and up to 4% in the Late Pleistocene deposits. The most ancient deposits with bone remains of *Arvicola amphibius* found in the Makhnevskaya Ledyanaya Cave belong to the Eemian (Mikulino) Interglacial (Fadeeva et al., 2020).

In this paper, we investigated the morphometric characteristics of the enamel of fossil and modern first lower molars of the European water vole to determine the applicability of these parameters in regional biostratigraphic reconstruction.

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2. Localities and radiocarbon dating background

The study used samples of European water vole teeth from five fossils and three modern localities from the Perm Pre-Urals (Fig. 1, Table 1).

Materials from the Makhnevskaya Ledyanaya Cave were obtained from different types of deposits – mixed (excavations 2004–2012) and intact (excavations 2017–2018). Radiocarbon dates (Table 2) were obtained from samples from mixed deposits; that notwithstanding, the dating of the porcupine tooth cannot be considered reliable (low amount of collagen). The theriofauna from intact deposits of this cave is dominated by the bones of rodents and insectivorous mammals (including thermophilic species *Hystrix brachyura* Linnaeus, 1758, *Dryomys nitedula* (Pallas, 1778), *Apodemus flavicollis* (Melchior, 1834), *Crocidura leucodon* (Hermann, 1780)), amphibians and reptiles. The pollen spectra are dominated by pollen from woody plants, which contains taxa that are adventive for the modern vegetation of this area (oak, hazel, hornbeam). All this data shows that intact deposits of the grotto were formed during the Eemian (Mikulino) Interglacial (MIS 5e) (Fadeeva et al., 2020).

The fauna of small mammals from the Makhnevskaya-2 Cave deposits is dominated by the remains of three species of rodents (*Lasiopodomys gregalis* (Pallas, 1779), *Dicrostonyx* sp., *Lemmus sibiricus* (Kerr, 1792)). Radiocarbon dating (Table 2) shows that deposits from the studied depths of this cave were formed at the end of the Bryansk Interstadial – the beginning of the Last Glacial Maximum, in a cold and humid climate (Fadeeva, 2005).

Layers 8–9 of the Rasik Grotto were formed at the end of the Late Glacial (Table 2). The fossil fauna of layer 8 is characterised by a sharp predominance of bony remains of the narrow-skulled vole *Lasiopodomys gregalis* (70.1–74.1%). The species composition of small mammals from layer 9 is characterised by the predominance of the remains of two species *Lasiopodomys gregalis* (47.6%) and *Dicrostonyx* sp. (33.1%). Based on the fauna composition, the existence of periglacial tundra-steppes and an arid, cold climate at the end of the Late Glacial in the Perm Pre-Urals is obvious (Fadeeva et al., 2000).

The studied deposits of the Dyrovatiy Kamen Cave on Vishera River were attributed to the Holocene based on the analysis of the species composition and the ratio of species in the mammalian faunas (Fadeeva, 2002), as well as the correlation between changes in the theriofauna and the dynamics of the region's vegetation in the Holocene (Lapteva et al., 2017; Shumilovskikh et al., 2020). The bones of red-backed voles (*Craseomys rufocanus* (Sundevall, 1846), *Myodes rutilus* (Pallas, 1779), *M. glareolus* (Schreber, 1780)) are numerous throughout the depth of the exposed deposits. In the upper half of the deposits, many bone remains of shrews (*Sorex*) were found, while in the lower half, the bones of the tundra vole (*Alexandromys oeconomus* (Pallas, 1776)) predominate. The time of deposit formation is conventionally determined by the composition of small mammal faunas: 0–100 cm (depth) – Late Holocene; 100–185 cm – Middle Holocene; 185–245 cm – Early Holocene.

In the deposits of the Bolshaya Makhnevskaya Cave (depth 140–155 cm), about half of all bone remains belong to insectivorous mammals and bats; red-backed voles (*Craseomys rufocanus*, *Myodes rutilus*) predominate among rodents. The predominance of small mammal species in the dark coniferous taiga is evidence of the spread of forest formations during the formation of deposits (the Subboreal).

All modern teeth of the European water vole studied in this work

Table 1
Coordinates of localities and the amount of teeth from the fossil and modern collections of *Arvicola amphibius*, investigated in this study. Perm Pre-Urals, Russia.

Time	Locality	Coordinates	Number of examined first lower molars of *Arvicola amphibius*
Modern	Rocks Ambarnye, Berezovaya River	60°53′ N 57°17′ E	31
	Rocks Dyrovatye Rebra, Chusovaya River	58°12′ N 58°14′ E	69
	Ust-Turka, Iren River	57°13′ N 56°37′ E	60
MIS 1	Bolshaya Makhnevskaya Cave	59°27′ N 57°41′ E	11
	Dyrovatiy Kamen Cave, Vishera River	60°32′ N 57°41′ E	77
MIS 2	Rasik Grotto	59°04′ N 57°33′ E	14
MIS 3	Makhnevskaya-2 Cave	59°26′ N 57°41′ E	81
MIS 5e, 3?	Makhnevskaya Ledyanaya Cave	59°26′ N 57°41′ E	52
Total			395

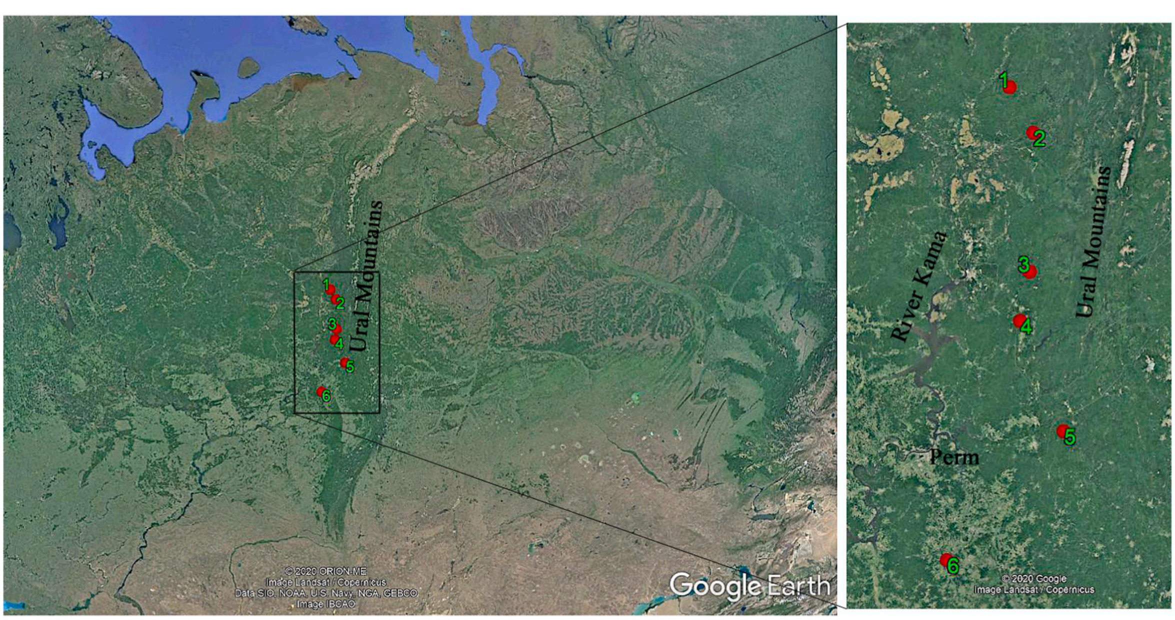

Fig. 1. The geographical position of the sites (Perm Pre-Urals, Perm Region, Russia). 1. Rocks Ambarnye, Berezovaya River; 2. Dyrovatiy Kamen Cave, Vishera River; 3. Makhnevskie Caves (Makhnevskaya Ledyanaya, Makhnevskaya-2, Bolshaya Makhnevskaya); 4. Rasik Grotto; 5. Rocks Dyrovatye Rebra, Chusovaya River; 6. Ust-Turka, Iren River.

Table 2
Radiocarbon dating. Perm Pre-Urals, Russia.

Locality	Layers	MIS	Date	Dating material
Bolshaya Makhnevskaya Cave	Depth 140–147 cm	1	3628 ± 86 IEMEG-1385	Bone of small mammals
Grotto Rasik	Layer 8 (square B)	2	11 060 ± 110 Spb-2336	Bone of small mammals
	Layer 9 (square B)	2	11 820 ± 120 SPb-2337	Bone of small mammals
Makhnevskaya-2 Cave	Depth 40–50 cm	3	24 760 ± 200 GIN 14242	Bone of small mammals
	Depth 50–70 cm	3	24 811 ± 426 IEMEG-1376	Bone of small mammals
Makhnevskaya Ledyanaya Cave	Mix deposits (excavation 2004–2012 years)	5e, 3?	>27 500 BP (AA-90664)	Porcupine teeth
			41 800 (+600, −500) BP (GrA-35461)	Porcupine teeth
			36 480 (+350, −310) BP (GrA-35460)	Mandible of water vole

were found in the enamel material of the eagle owl collected near the Berezovaya, Chusovaya and Iren (a tributary of the Sylva River) Rivers. In addition to the remains of this rodent species, bones of *Erinaceus* sp., *Talpa* sp., *Lepus* sp., *Mustela nivalis* Linnaeus, 1766, *Mustela erminea* Linnaeus, 1758, *Mustela sibirica* Pallas, 1773, *Mustela* sp., *Martes martes* (Linnaeus, 1758), *Microtus* cf. *arvalis*, *Microtus agrestis* (Linnaeus, 1761), *Alexandromys oeconomus*, *Myodes* sp., *Ondatra zibethicus* (Linnaeus, 1766), *Cricetus cricetus* (Linnaeus, 1758), *Apodemus uralensis* (Pallas, 1811), *Rattus norvegicus* (Berkenhout, 1769), *Sciurus vulgaris* Linnaeus, 1758, *Tamias sibiricus* (Laxmann, 1769) were found in the food spectrum of the owl (collection and identification were carried out by Professor A. I. Shepel).

3. Material and methods

The study included 395 fossil and modern first lower molars (m1) of the European water vole (only complete teeth). Most of the fossil teeth are isolated. Modern teeth are mostly preserved in the mandibles with varying degrees of damage. Fossil teeth were investigated from the collections of the Mining Institute of the Ural Branch of the Russian Academy of Sciences (Perm, Russia); modern teeth were studied from the collections of the Department of Vertebrate Zoology and Ecology of the Perm State National Research University. The following abbreviations for location names are used in the text: BER – Rocks Ambarnye,

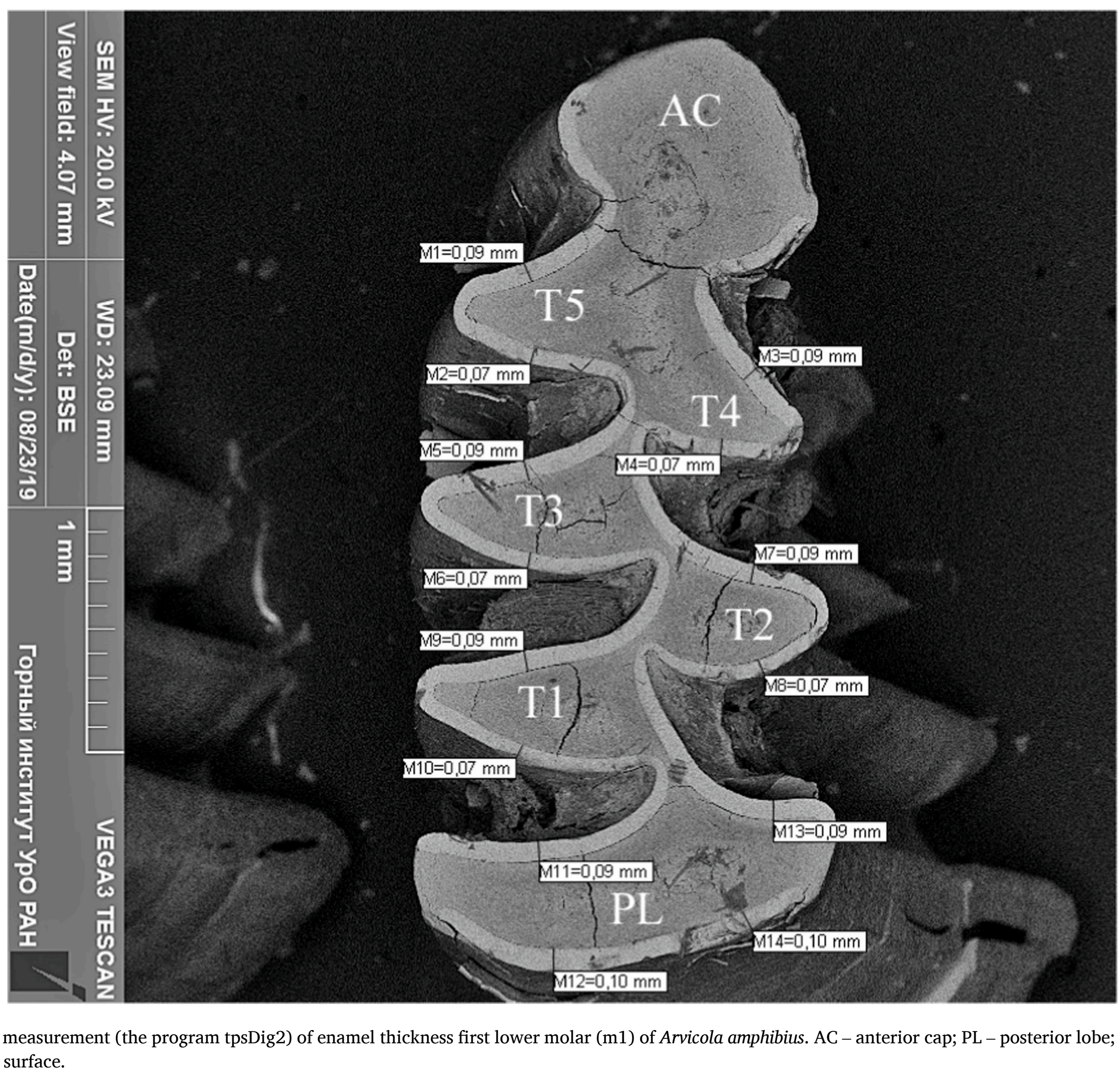

Fig. 2. The measurement (the program tpsDig2) of enamel thickness first lower molar (m1) of *Arvicola amphibius*. AC – anterior cap; PL – posterior lobe; T – triangles of occlusial surface.

Berezovaya River; CHUS – Rocks Dyrovatye Rebra, Chusovaya River; IREN – Ust-Turka Village, Iren River; BM – Bolshaya Makhnevskaya Cave; DKV (DKV 1 – Late Holocene; DKV 2 – Middle Holocene; DKV 3 – Early Holocene) – Dyrovatiy Kamen Cave, Vishera River; RAS – Rasik Grotto; M-2 – Makhnevskaya-2 Cave; ML int – Makhnevskaya Ledyanaya Cave, intact deposits; ML mix – Makhnevskaya Ledyanaya Cave, mix deposits.

All the material is additionally cleaned in a GB-10 LB ultrasonic bath. All teeth were digitised using a VEGA 3 LMH scanning electron microscope in the Laboratory of Geology of Mineral Deposits of the Mining Institute of the Ural Branch of the Russian Academy of Sciences. The thickness of the enamel walls was measured from digitised images using the tpsDig2 programme. The measurements were performed once on the middle sections of the enamel of the anterior and posterior walls of all five prisms and the posterior unpaired loop of the first lower molar (Fig. 2). The enamel differentiation coefficient SDQ (Schmelzband-Differenzierung-Quotient) of 7 triangular fields was calculated using the formula SDQTn = ebp/eba × 100. Statistical processing of the results was carried out using Statistika (version 13).

4. Results

4.1. Conditional ontogenetic groups

Among the studied material, two types of the first lower molars are identified that are conventionally called “juvenile” and “adult” (teeth with “juvenile” and “adult” features). These two groups differ morphologically in the structure of the anterior cap, the presence/absence of apical enamel, the degree of openness of the dentinal fields, and the development of cementum in the reentrant angles of the tooth.

The teeth of the conditional group “juvenile” belong to young individuals of European water voles in the postnatal period of development, which most likely have already switched to feeding on green food. A common characteristic of these teeth is the absence of cementum in the reentrant corners. Based on the morphological features of the occlusal surface of these teeth, we constructed a hypothetical series of ontogenetic changes (Fig. 3), the sequence of which is outlined in general terms by Hinton (1926). Teeth belonging to this group are characterised by the following features (description as per the serial number (Fig. 3)):

1 Open dentinal fields of prisms (T1, T2, T3); enamel boundaries between the anteroconid complex, prisms, and the posterior lobe are not distinguishable;
2. Enamel borders between the parts of the tooth are clearly distinguishable;
3. Open dentinal fields of the posterior lobe and prism T5 of the anteroconid complex; merging of the T1-T2 and T2-T3 prisms;
4. Partially open dentinal area of the anterior cap
5. Open dentinal area of the anteroconid complex; the presence of residual enamel islands – “marks”;
6. Dentinal fields of the posterior lobe and T1 prism, T3 prism and the anteroconid complex of the tooth are fused; the presence of a residual enamel “mark”;
7. The enamel contour of the posterior walls of the prisms (T1, T3, T4, T5) is straight, and the apical part of the anterior cap is covered with enamel;
8. The enamel contour of the apical part of the anterior cap is partially erased.

All teeth of the conditional group “adult” (Fig. 4) have cementum deposits of varying degrees of thickness in the reentrant angles and are characterised by the absence of enamel on the apical part of the anterior cap of the anteroconid complex. Based on this feature, we classified all the studied teeth of this group into three subgroups:

I. Cementum is not developed or is represented by a very thin layer in the reentrant corners of the anteroconid complex; the reentrant angles of the tooth prisms are filled with cementum of thickness ~1/3 of the length of the posterior walls of the prisms; the apical parts of the tooth prisms are triangular in shape;

II. Cementum is well developed in the reentrant angles of the anteroconid complex; in the other angles, the cementum thickness is ~½ of the length of the posterior walls of the prisms; the apical parts of the tooth prisms are triangular in shape;

III. Thick cementum deposits in the reentrant angles of the tooth prisms (more than ½ the length of the posterior walls of the prisms); the apical parts of the tooth prisms are rounded.

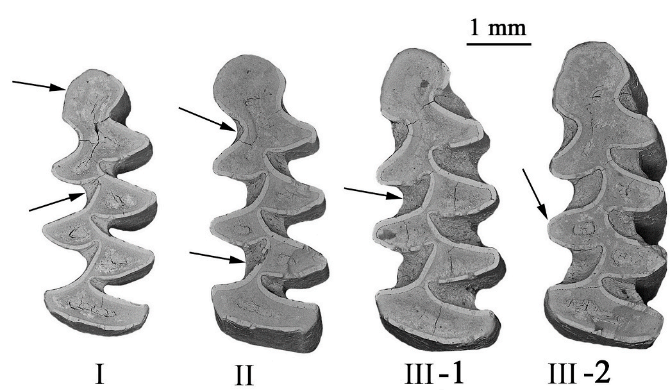

Fig. 4. First lower molars (m1) of *Arvicola amphibius* of the conditional group “adult”. I, II, III-2 (Makhnevskaya-2 Cave); III-1 (Dyrovatiy Kamen Cave). The arrows show the distinctive features of each tooth (comments are in the text).

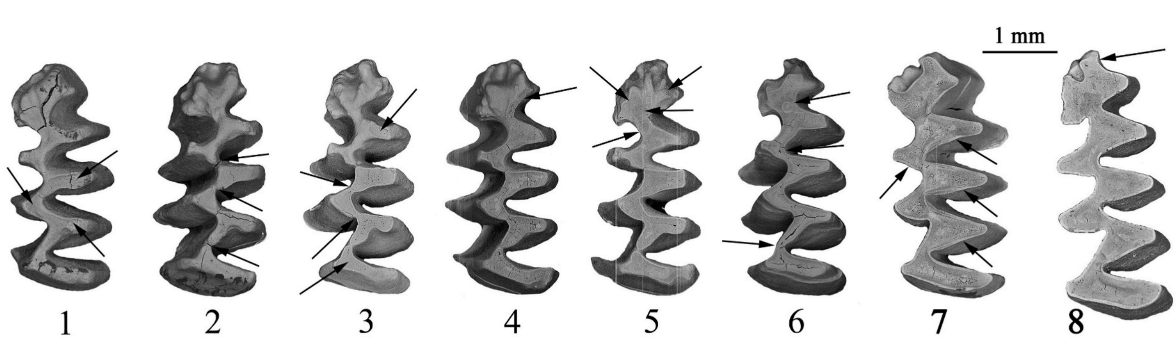

Fig. 3. First lower molars (m1) of *Arvicola amphibius* of the conditional group “juvenile”. 1–7 (Makhnevskaya-2 Cave); 8 (Dyrovatiy Kamen Cave). The arrows show the distinctive features of each tooth (comments are in the text).

4.2. Enamel

The thickness of the m1 *Arvicola amphibius* enamel increases with age in all samples. Its value is almost the same on both sides of the prisms in the conditional ontogenetic group “juvenile” (the study covered teeth only with open dentinal fields): 0.03–0.04 mm. The enamel is graded in all subgroups of the “adult” group (anterior walls of the prisms: “adult” I 0.07–0.08 mm; “adult” II 0.08–0.09 mm; “adult” III 0.09–0.10 mm; posterior walls of the prisms: “adult” I 0.06–0.07 mm; “adult” II 0.07–0.08 mm; “adult” III 0.08 mm).

Statistical analysis of the pooled subdivision samples (“juvenile”, “adult” I, “adult” II, “adult” III) showed significant differences in the SDQ coefficient (Table 3, Fig. 5). Differences are observed between the mean SDQ values of the “juvenile” and “adult” subdivisions; no differences were found within the “adult” division (Kruskal-Wallis test: $H (3, N = 395) = 19.15568$ $p < 0{,}05$).

In view of the statistical homogeneity of SDQ m1, samples from divisions “adult” I, “adult” II, “adult” III are combined into a single sample for all locations. The analysis identifies two groups of samples that differ well from each other but do not show statistically significant differences within the groups. Statistically significant differences were found between samples from the Interglacial (ML int, ML mix), Subboreal (BM), Late Holocene (DKV 1), Modern periods (CHUS) and samples from the end of Bryansk Interstadial (M-2), Late Glacial (RAS), Early and Middle Holocene (DKV 3, DKV 2), Modern periods (BER). The mean SDQ values of the first group of samples are higher than those in the second group of samples (Fig. 6, Tables 4 and 5).

5. Discussion

5.1. Conditional ontogenetic groups

Identification of ontogenetic changes in the morphology of molars of any mammalian species is an important step that precedes further sample analysis. Any comparisons between samples must be made in a graded manner, with subgroups of materials at equivalent stages of development being identified. The age structure for molars of the genus *Arvicola* is difficult to assess because the teeth do not have roots, grow throughout life, and are not suitable for determining the exact age (Klevezal, 2007).

In fossil samples of teeth, “juvenile” teeth are quite clearly graded, differing not only in their relatively small size, but also in the shape of the occlusal surface and the complete absence of cementum in the reentrant angles of the prisms. “Juvenile” teeth are typically quite fragile and are poorly preserved in the fossil state. Hinton (1926) noted that such teeth are quite rare in collections, and their structure shows signs (folds and islands of enamel) characteristic of teeth of representatives of the fossil genus *Mimomys*. In our work, based on the studied material, we presented a hypothetical series of development of juvenile teeth of the European water vole. Further studies of the collection material from this category will expand the understanding of successive ontogenetic changes in the structure of the teeth of the species.

The category of “adult” teeth includes specimens with an already well-formed occlusal surface and having cementum in the reentrant angles of the prisms. These teeth are relatively strong and belong to the young-of-the-year and overwintered individuals of the species. This “adult” sample is most often studied (size, enamel thickness ratio, etc.) and compared with other samples based on certain parameters. More fractional divisions of this sample by growth groups are possible for

Table 3
Values of the enamel thickness quotient (SDQ) of m1 of *Arvicola amphibius* (by groups). Fossil and modern collections. Perm Pre-Urals, Russia.

GROUPS	LOCALITIES	TIME	n	MEAN	MEDIAN	MIN	MAX	SD	CV
“juvenile”	DKV 1[a]	MIS 1	1	92.9	–	–	–	–	–
	DKV 2	MIS 1	1	117.9	–	–	–	–	–
	DKV 3	MIS 1	1	100.0	–	–	–	–	–
	M-2	MIS 3	4	95.7	98.8	82.9	102.4	8.8	9.2
	ML mix	MIS 3, 5e?	1	100.0	–	–	–	–	–
	ML int	MIS 5e	2	103.6	103.6	96.4	110.7	10.1	9.8
“adult” I	CHUS	Modern	4	91.4	91.9	85.0	96.6	5.1	5.6
	DKV 1	MIS 1	3	90.9	90.4	83.7	98.7	7.5	8.3
	DKV 2	MIS 1	13	86.5	87.0	77.8	97.2	6.0	7.0
	DKV 3	MIS 1	4	82.0	81.0	74.2	91.5	7.7	9.4
	M-2	MIS 3	19	82.1	82.1	70.4	93.5	6.5	7.9
	ML mix	MIS 3, 5e?	2	91.6	91.6	88.8	94.4	4.0	4.3
“adult” II	BER	Modern	25	84.4	82.9	70.5	104.0	8.9	10.5
	CHUS	Modern	62	88.1	88.5	77.0	102.1	5.3	6.0
	IREN	Modern	60	86.2	86.7	74.0	101.1	5.4	6.3
	BM	MIS 1	7	91.5	91.4	85.2	100.0	4.9	5.4
	DKV 1	MIS 1	13	86.5	87.0	77.8	97.2	6.0	7.0
	DKV 2	MIS 1	20	81.3	81.4	71.4	89.8	4.8	5.9
	DKV 3	MIS 1	18	76.3	74.8	62.5	91.9	7.4	9.7
	RAS	MIS 2	9	80.7	81.2	73.0	89.7	5.2	6.4
	M-2	MIS 3	46	82.1	79.7	70.6	104.8	7.4	9.1
	ML mix	MIS 3, 5e?	23	89.4	88.8	82.1	100.4	4.7	5.3
	ML int	MIS 5e	16	91.5	91.2	86.3	97.6	3.2	3.5
“adult” III	BER	Modern	6	77.6	78.0	69.7	82.0	4.2	5.5
	CHUS	Modern	3	92.6	93.4	90.7	93.7	1.6	1.8
	BM	MIS 1	4	87.6	88.5	80.8	92.7	5.8	6.6
	DKV 1	MIS 1	1	84.9	–	–	–	–	–
	DKV 2	MIS 1	3	82.9	80.6	79.4	88.7	5.1	6.1
	DKV 3	MIS 1	5	82.5	83.3	78.3	88.4	4.1	5.0
	RAS	MIS 2	5	83.0	81.8	76.7	91.5	5.4	6.5
	M-2	MIS 3	12	84.9	85.7	78.4	91.1	4.6	5.4
	ML mix	MIS 3, 5e?	6	92.9	91.6	83.0	101.2	6.8	7.3
	ML int	MIS 5e	2	94.8	94.8	92.4	97.2	3.4	3.6

[a] Hereinafter in the tables: BER – Rocks Ambarnye, Berezovaya River; CHUS – Rocks Dyrovatye Rebra, Chusovaya River; IREN – Ust-Turka Village, Iren River; BM – Bolshaya Makhnevskaya Cave; DKV (DKV 1 – Late Holocene; DKV 2 – Middle Holocene; DKV 3 – Early Holocene) – Dyrovatiy Kamen Cave, Vishera River; RAS – Rasik Grotto; M-2 – Makhnevskaya-2 Cave; ML int – Makhnevskaya Ledyanaya Cave, intact deposits; ML mix – Makhnevskaya Ledyanaya Cave, mix deposits.

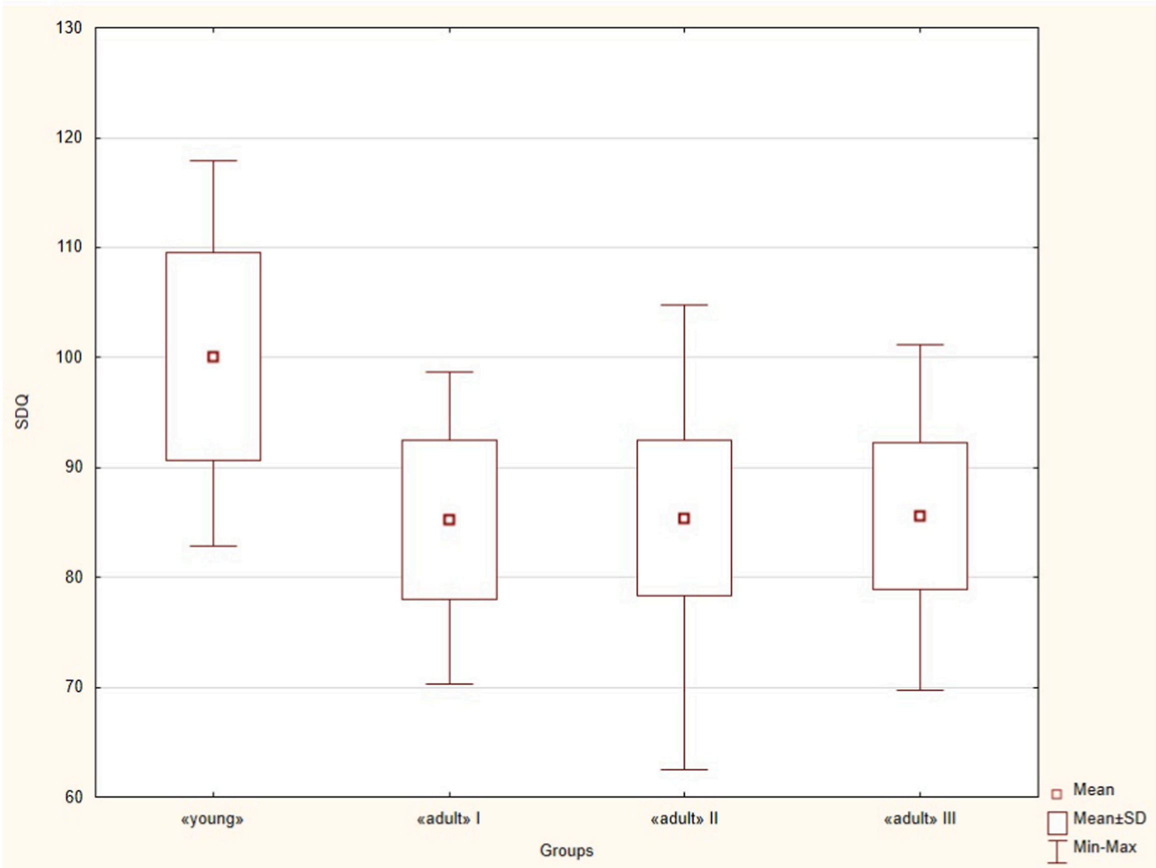

Fig. 5. The variations in SDQ values (mean, standard deviation, minimum-maximum) of m1 of *Arvicola amphibius* from groups "juvenile" and "adult". Fossil and modern collections (Perm Pre-Urals, Russia).

teeth that are preserved in the mandibles.

Hinton (1926) identifies six stages of development of the mandible of the European water vole that show changes in the morphology of the ascending branch of the mandible. By the nature of the fur molts, 5 age classes are distinguished, each of which is characterised by a change in the morphology of the angular process and varying degrees of severity of the alveolar tubercle of the mandible (Ventura and Gosalbez, 1992). The authors of several studies provide dimensional and visual characteristics of European water voles of different ages (Popov, 1960; Panteleev and Terekhina, 1976; Andera, 2001). However, these works do not discuss the age characteristics of the molars (except for the dentition length). Taking into account the ecogeographic variability of any rodent species, the use of such methods for determining the age is possible only for modern fully preserved skulls from collections from a certain territory. In addition, the growth and development of voles depends on the time of their birth. European water voles of the same absolute age but born in the spring and in the second half of summer will differ in the development of their cranial structures (Terekhina and Panteleev, 2001). Rodent skulls are rarely preserved in fossil zoogenic deposits and in modern materials of ornithogenic origin. The mandibles are present in such samples, but quite often have significant damage. For example, the alveolar tubercle, as an indicator of the age class, is often perforated. It is impossible to identify certain metric characteristics indicating the degree of development of this trait, and the descriptive characteristics (weakly developed tubercle, developed tubercle, strongly developed tubercle) do not have clear boundaries.

The sizes of hypseldont teeth of European water voles increase with age, factoring in the established fact of change in their lengths of maxillary and mandibular tooth rows (Popov, 1960; Andera, 2001). The amount of cementum in the reentrant angles of the teeth also increases and is always quite noticeable in adult and old hypselenodont vole forms (Borodin, 2009). Changes in the shape of the prism angles with age were recorded for forest voles (Olenev, 2009). In this paper, we conditionally divided the "adult" teeth into three groups according to the degree of cementum development and the prism angle shape. Teeth of the "adult" II subgroup predominate in all studied samples. Samples from modern localities were obtained from eagle owl enamel collected in June–July, with the proportion of such teeth in them ranging from 80 to 100%. The proportion of teeth in the "adult" II subgroup is slightly lower in the fossil samples (55–76%). It is possible that the teeth of subgroup "adult" II belong to individuals of the first spring and first summer generations, which make up the majority of individuals in the summer populations (Panteleev and Terekhina, 1976).

5.2. Enamel

Heinrich (1982, 1987, 1991) identified two species of water voles, namely the Middle Pleistocene species *Arvicola cantiana* (SDQ >100) and the Late Pleistocene species *Arvicola terrestris* (SDQ <100). At the boundary between Middle and Late Pleistocene, Central Europe was inhabited by another transitional form between these species with SDQ = 100. Based on this statement, Kratochvil (1980) proposed to consider the process of ontogenetic evolution as an analogy to the phylogenetic evolution of genus *Arvicola* in Central Europe, explaining the process of reverse differentiation of the enamel thickness by changes in diet. When commenting the equal enamel thickness of the young individuals of modern water voles, Agadjanyan (2001) noted, that from an evolutionary point of view the upper part of the crown is more ancient than its lower part. However, on the basis of SDQ data for *Arvicola amphibius* from the Pleistocene localities of Northwest and Central Europe,

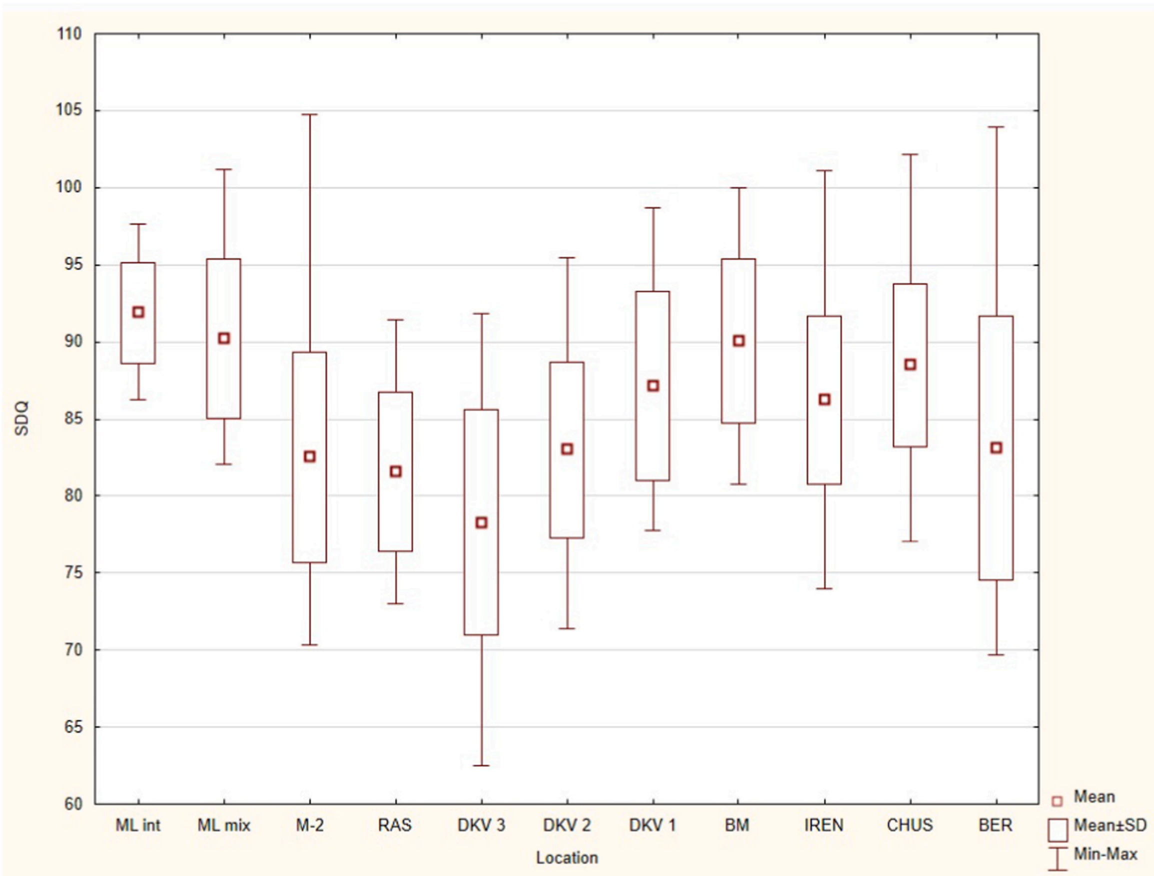

Fig. 6. Variation in SDQ values (mean, standard deviation, minimum-maximum) of m1 of *Arvicola amphibius* (group "adult") from different locations. Fossil and modern collections (Perm Pre-Urals, Russia).

Table 4
Results of the Kruskal-Wallis test: H (10, N = 385) = 108.6229 $p < 0.05$, showing significant differences between mean SDQ values of m1 (group "adult") *Arvicola amphibius*. Perm Pre-Urals, Russia.

	ML int	ML mix	M-2	RAS	DKV 3	DKV 2	DKV 1	BM	IREN	CHUS	BER
ML int[a]		1	**0.000**	**0.000**	**0**	**0.000**	1	1	**0.029**	1	**0.000**
ML mix	1		**0.000**	**0.004**	**0**	**0.002**	1	1	0.394	1	**0.001**
M-2	**0.000**	**0.000**		1	1	1	0.577	**0.018**	0.074	**0.000**	1
RAS	**0.000**	**0.004**	1		1	1	1	0.074	1	**0.016**	1
DKV 3	**0.000**	**0.000**	1	1		1	**0.015**	**0.000**	**0.00101**	**0.000**	1
DKV 2	**0.000**	**0.002**	1	1	1		1	0.125	1	**0.006**	1
DKV 1	1	1	0.577	1	**0.015**	1		1	1	1	1
BM	1	1	**0.018**	0.074	**0.000**	0.125	1		1	1	0.069
IREN	**0.029**	0.394	0.074	1	**0.001**	1	1	1		1	0.936
CHUS	1	1	**0.000**	**0.016**	**0**	**0.006**	1	1	1		**0.002**
BER	**0.000**	**0.001**	1	1	1	1	1	0.069	0.936	**0.002**	

[a] For the legend see Table 3.

Kolfschoten (1990) proved that the evolutionary trend in the enamel differentiation over time is not just progressive with decreasing SDQ values, but it demonstrates significant variations in values. The water vole teeth from the localities with Saale glaciation deposits (MIS 6, Saalian), as well as the Late Pleistocene deposits (MIS 5d–2, Weichselian), have "microtus" enamel (SDQ<100), however the water vole teeth dated to the Eemian interglacial (MIS 5e, Eemian) have "mimomys" enamel with SDQ > 100 (Coxon et al., 1980; Kolfschoten, 1990; Heinrich, 1991). Mean SDQ values < 100 were obtained for the teeth of the Middle and Late Pleistocene water voles (France, Italy), however over the integlacial period this value is higher than 100 (Desclaux et al., 2000). It is hypothesized (Kolfschoten, 1990; Koenigswald and Kolfschoten, 1996) that an increase in SDQ value in the Eemian populations is related to migration of water voles from other territories inhabited by populations with high SDQ. Extensive migration was possible during this period due to the opening of territories previously covered by a glacier (Koenigswald and Kolfschoten, 1996). Agadjanyan (2001) points out morphological similarity of the water vole teeth from the Eemian interglacial deposits of the Mikhailovsky Quarry and those of modern species *Arvicola sapidus* from the Iberian Peninsula, and believes that this species in the past had a much wider range (including the territory of Eastern Europe). When studying geographic and interspecies variation of the SDQ ranges for modern representatives of genus *Arvicola*, Rö;ttger (1987) showed that the value of this coefficient increases in populations from Western Europe to Iran. Markova (1981) indicates the uniqueness of the teeth (low enamel differentiation and small

Table 5
Values of enamel thickness quotient (SDQ) of teeth of the group "adult "
("adult" I + "adult" II +"adult" III) of m1 of *Arvicola amphibius*. Fossil and modern collections. Perm Pre-Urals, Russia.

LOCALITIES	TIME	n	MEAN	MEDIAN	MIN	MAX	SD	CV
BER[a]	Modern	31	83.1	82.0	69.7	104.0	8.6	10.3
CHUS		69	88.5	89.2	77.0	102.1	5.3	6.0
IREN		60	86.2	86.7	74.0	101.1	5.4	6.3
BM	MIS1	11	90.1	91.4	80.8	100.0	5.3	5.9
DKV 1		17	87.2	87.0	77.8	98.7	6.1	7.0
DKV 2		30	83.0	82.2	71.4	95.5	5.7	6.9
DKV 3		27	78.3	78.3	62.5	91.9	7.3	9.3
RAS	MIS 2	14	81.6	81.5	73.0	91.5	5.2	6.3
M-2	MIS 3	77	82.5	81.6	70.4	104.8	6.9	8.3
ML mix	MIS5e, 3?	31	90.2	89.0	82.1	101.2	5.2	5.7
ML int	MIS5e	18	91.9	91.9	86.3	97.6	3.3	3.6

[a] For the legend see Table 3.

dimensions) of the water vole populations from the southern European part of Russia (Kuban area, Southern Russia) in comparison with those from northern and temperate territories of this region and Siberia (though the author does not exclude a younger age of Kuban individuals). As per Kratochvil (1981), in modern mountain water vole population (1,160 m above sea level, Canton de Vaud, Switzerland) the SDQ value of the teeth is more than 110, while in populations from the territory of the Czech Republic it is < 100. The Late Pleistocene deposits of the Boquete de Zafarraya Cave (Spain) located at 1,022 m above sea level yield the water vole teeth with SDQ equal to 98.55–113.33–129.22 (Barosso et al., 2006). At the same time, there is a hypothesis that implies the existence of one single species *Arvicola cantiana* in the Pleistocene, whose teeth demonstrate high variability without any trends or patterns in the morphological space. This hypothesis questions the biochronologic grounds based on *Arvicola* (Escude et al., 2008). The authors of this hypothesis indicate that the patterns of the glacial and interglacial periods and migration (Kolfschoten van, 1990; 1992; Desclaux et al., 2000) lack clear evidence. Markova (2006) believes that though the tendency of the SDQ values to decrease from the Middle to the Late Pleistocene is apparent, this coefficient cannot be regarded as the only decisive argument in favour of a certain age of the fauna.

The mean SDQ value in all studied samples of "adult" teeth from the Eemian (Mikulino) Interglacial to the present does not exceed 94.8%. "Microtus" enamel is also typical for Late Pleistocene samples of European water vole teeth from zoogenic deposits of the Biśnik Cave (Poland), where the mean SDQ value does not reach 100 from the Eemian (Mikulino) Interglacial (MIS 5e) to Late Glacial (MIS 2) (Socha, 2014). For the majority of samples of the Eemian Interglacial period (except for the sample from the Chernianka locality, with a mean SDQ = 100) and all samples of later periods from Eastern Europe, a mean SDQ < 100 was also recorded (Markova, 2006).

Based on the mean SDQ values, the studied samples of "adult" group teeth of the Eemian (Mikulino) Interglacial (91.5–94.8) and the Subboreal period of the Holocene (87.6–91.5) are significantly higher than the SDQ of samples of the Late Bryansk Interstadial – Early Glacial Maximum and Late Glacial (80.7–84.9). The northernmost samples – the modern sample from the Berezovaya River and the samples of the first half of the Holocene from the Dyrovatiy Kamen Cave based on the mean SDQ values (77.6–84.4 and 76.3–86.5, respectively) are significantly less than the modern mountain sample from the Chusovaya River (88.1–92.6). However, all these samples do not differ from the southernmost of the studied samples – the modern plain sample from the Iren River. Fluctuations in the mean SDQ values were also observed in the Late Pleistocene samples of teeth from the Biśnik Cave species (Socha, 2014). Thus, weak differentiation of the tooth enamel of European water voles is typical for populations of relatively "warm" geological periods and for the modern population of the mountain region.

When studying teeth of the individuals of water voles that had left their nests (i.e. older than 1 month), Kratochvil (1980) found a significant increase in the enamel thickness with age. Water voles start eating green food at the age of 11–12 days (Andera and Rykhnovsky, 2001), so dentine fields of the prisms may start gradually open from this period. Ruddy (2011) found that up to 95.1% of variations in the enamel thickness in water voles are associated with ontogenetic age. Our data confirm the fact of a consistent increase in the enamel thickness on both sides of the prisms (minimum enamel thickness was recorded for teeth from the "juvenile" group and maximum enamel thickness for teeth from the "adult" group III). Most of the teeth from the "juvenile" group are characterised by the presence of "mimomys"-type enamel. Despite the established statistically significant differences between the SDQ of the teeth of the "juvenile" and "adult" groups, it is important to study a more representative sample of the "juvenile" group of teeth (the data that was obtained in our study was only for 10 specimens of teeth) for a more objective conclusion. Isolated teeth having a "mimomys"-type of enamel are also found in fossil and modern samples of "adult" group teeth. "Microtus"-type enamel is typical for the vast majority of the studied teeth of the group. When teeth from samples of all three "adult" subgroups were compared, no significant differences were found in the enamel thickness ratios (SDQ); therefore, the relative constancy of this coefficient in the middle and late stages of ontogenetic development of European water vole individuals is clear.

6. Conclusion

The studied material on the European water vole *Arvicola amphibius* from the Perm Pre-Urals covers several periods of the Late Pleistocene, Holocene and Modern Time. A graded approach to the study of the material (allocation of conditional ontogenetic groups) showed significant differences in the mean values of the SDQ enamel ratio index for the teeth of the "juvenile" (>100) and "adult" (<100) groups. There are no significant differences in the SDQ values within the three subdivisions of the last group. Most of the teeth in the studied fossil samples (including the oldest of the deposits of the Eemian (Mikulino) Interglacial deposits) have "microtus"-type enamel. Weaker grading of tooth enamel of European water voles is typical for samples from populations of relatively "warm" geological periods and for the modern population of the mountain region. Based on the results obtained, it is still premature to draw conclusions about any trends in the ratios of the enamel thickness of European water voles over time in the region. For a more substantial interpretation of these significant differences, additional studies of representative samples of European water vole teeth of different temporal and spatial relationships must be conducted.

CRediT authorship contribution statement

Tatyana Fadeeva: Conceptualization, Methodology, Formal analysis, Writing - original draft. **Pavel Kosintsev:** Investigation, Resources, Writing - original draft. **Elena Chirkova:** Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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