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Growth Rate of Cheek Teeth in Narrow-Skulled Vole (*Lasiopodomys gregalis*) Depending on Food Abrasiveness

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Abstract—The growth rate of the first lower molar and its wear features have been studied in narrow-skulled vole individuals (n = 39) that received hard and soft feeds under laboratory conditions. Using tetracycline markers, we have found that the tooth height increases by 0.33–0.56 mm throughout the day. Voles that received soft feed, in general, had a lower rate of molar growth, a lower crown, and a more obtuse wear angle of the chewing surface than the animals feeding on hard feed; they were also characterized by the appearance of lateral wear facets. As these signs of wear developed in animals fed soft food, the growth rate of the molar increased.

Keywords: molars, paleoecology, diet, *Microtus* voles, rate of tooth growth, experimental ecology

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The dentition of herbivorous mammals is a complex of interacting biomechanical structures for treating large forage masses. The generic and species specific features of their implementation in cheek teeth are expressed in the ratio of enamel, dentin, and cement elements: their shape, number, and relative position. Researchers pay attention to these features during the solution of problems of the origin and relationship of taxa of different levels, including the intraspecific level. Particular attention is given to the enamel pattern of the chewing surface and other features, the variation of which is highly dependent on the hereditary component [1, 2]. At the same time, the dental system has a number of characteristics, the features of which are formed as a reaction to environmental influences. They can have an adaptive or pathological pattern and be reversible. It is this class of characteristics that attracts attention as an indicator of feeding conditions, especially in those study areas where it is difficult or impossible to directly assess them, primarily in paleoecology.

The development of indirect methods for reconstructing animal nutrition on the basis of the wear features of the tooth chewing surface is a promising study area, since it significantly advances the possibilities of paleoecological reconstructions. Different taxonomic and ecological groups of mammals have significant specific features of tooth growth and wear.

The object of our research was narrow-skulled vole (*Lasiopodomys gregalis*). This species is widespread in the forest-steppe and steppe communities of Eurasia and its remains are represented by mass odontological material in paleontological collections from Late Pleistocene and Holocene localities throughout Europe and North Asia [3, 4].

The molars of *Microtus* voles are hypselodont; they are characterized by the absence of roots and by continuous growth and wear. The typical features of tooth wear were previously determined for narrow-skulled voles kept on feeds with different abrasive properties. These differentiating features include the value of the wear angle of the chewing surface, height of the tooth above the alveoli, appearance of lateral wear facets, and features of the micro- and mesorelief of the chewing surface [5–7]. Variations in the characteristics of the mesorelief of the upper cheek teeth are shown for this species from three areas along the latitudinal gradient of the ecological subzones of the Yamal Peninsula in the Russian Arctic [8].

A number of studies [9–11] have shown that the growth rate of teeth without roots (both cheek and incisor teeth) depends on the physical properties of the consumed food and slows down in low-abrasive diets. It has been assumed [8] that this pattern is also manifested in narrow-skulled vole. This study is devoted to testing this hypothesis. Data on the growth rate of cheek teeth are necessary to understand the process of formation of tooth wear variants in response to the consumption of feeds with different abrasive properties and determine the time interval reflected by different wear variants.

The purpose of this research is to estimate the growth rate of the first lower cheek tooth ($m/1$) in narrow-skulled vole individuals that were kept on the soft and hard diets and compare the data on the tooth growth rate with the parameters of tooth crown wear (tooth height above the alveoli, wear angle of the chewing surface, and lateral wear facets) and with previously published data on the micro- and mesorelief of the chewing surface in the same animals.

MATERIAL AND METHODS

The data are based on an experiment with narrow-skulled vole ($n = 46$) at the laboratory colony of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, in 2015. The founding animals of the colony were trapped in Beloyarskii raion of Sverdlovsk oblast, which corresponds to the range of the subspecies *L.g. gregalis* [12]. The purpose of this experiment was to reveal the variants of tooth wear in the animals consuming feeds with different abrasive properties. As a result, it was shown that voles that received low-abrasive foods had a larger area of enamel damage, a lower mesorelief, a lower crown height, and a more obtuse wear angle than the animals feeding on more abrasive foods. The detailed description of the experiment and results of studying the micro- and mesorelief were published earlier [5, 6]. The tooth growth rate was studied using part of a sample of animal skulls from this experiment ($n = 39$) that were sufficiently well preserved for measuring the tetracycline markers. The structure of the experimental groups is given in Table 1. Voles were born in May and June. Voles from each litter (nine litters, seven maternal lineages) were divided into two experimental groups so that the group sex ratio was equal when possible. The experiment involved individuals from the age of 1 month. The body length and weight of the animals were monthly measured.

The animals were kept in plastic containers that were covered with a fine metal mesh and contained sawdust litter. We used two feed compositions differing in the content of abrasive elements for the two experimental groups. The soft feed ($n = 20$) was maximally cleared of external abrasives (soil particles and dust) and included components with a low content of internal abrasives (plant phytoliths): dandelion leaves washed from dust and soil particles, carrots cleaned of soil particles by removing the periderm, and apples without a core. The food of the second group—hard feed ($n = 19$)—included components with a high content of plant phytoliths and dense components: monocotyledonous plant leaves, hay, and unpeeled carrots. Both internal and a small amount of external abrasives (soil particles) could naturally enter together with hard feed.

The height growth of the *m*/1 crown was evaluated using a tetracycline marker, which was subcutaneously injected at a rate of 20–25 mg/kg [13]. The animals were sacrificed 15 days after injection. The growth rate was recalculated per one day (mm/day). The tooth areas that grew during the period of tetracycline circulation in the body have yellow fluorescence during ultraviolet light examination. The position of the tetracycline marker was measured according to the photographs from its upper edge to the basal part of the tooth along the third buccal salient angle (BSA3) (hereinafter, the notations are given according to [1]) (Fig. 1(1)). To avoid damage of the tooth and its malposition in the jaw, we did not remove it from the alveoli. To photograph the marker, we cut out a piece of the mandibular bone using a dental drill and exposed the lower 2/3 of the tooth. This part of the tooth was most accessible using this approach and selected for measuring the marker (BSA3).

The wear angle of the chewing surface was measured relative to the anterior surface of the molar (in degrees) (Fig. 1(2)). The height of the tooth crown above the alveoli was measured on the buccal side from the chewing surface to the edge of alveoli in two regions: along the BSA1 and BSA3 angles (Figs. 1(3), 1(4)). Two measurements were taken to establish the relationship of the height of the anterior and posterior part of the tooth with the wear angle and determine the patterns of its formation. The tooth height was measured on the buccal side from the chewing surface to the basal part of the tooth along BSA3 (Fig. 1(5)). Based on this measurement, we calculated the theoretical time required for the renewal of tooth tissues at constant growth and wear rate.

We also studied the lateral wear facets, namely the abnormal manifestation of wear of vole teeth due to the occlusion disturbance. Facets occur both in voles kept under laboratory conditions and in voles from nature [7]. They are located on the inner salient angles of the lower molars and external salient angles of upper molars, which indicates the formation of lateral wear facets as a result of tooth-to-tooth friction. As a rule, lateral wear develops from the anterior to the posterior part of the tooth and from the anterior to the posterior molars (mostly recorded on *m*/1 and M1/) [7]. The degree of development of facets is evaluated in points: 1, initial stage, which covers only the edge of the chewing surface of the tooth; 2, wear covers the upper quarter of the lateral surface of the molar; and 3, wear covers more than one-fourth of the molar.

Vole jaws were photographed in lateral projection using a Leica EZ4 binocular microscope. Measurements were made using the TPS software package (TPS Util and TPS Dig2).

The statistical significance of the results of comparison of the angular and dimensional parameters and growth rate of teeth of the animals from the two experimental groups was estimated using a two-way analysis of variance (ANOVA, F) with the "experimental group" (soft and hard feed) and "diet duration" factors. The possible contribution of the hereditary component to the variability of the rate of tooth growth was estimated using an ANOVA with the "maternal lineage" and "experimental group" factors. The correlation between the tooth parameters in each of the experimental groups was determined using Pear-

Table 1. Structure of experimental groups

Experimental group	Soft feed									
Diet duration, months	1		2				3			
Age at the end of the experiment, months	2		3				4			
Maternal lineage no. (*n* individuals)	1(3)	2(2)	1(1)	3(2)	4(3)	5(1)	1(2)	3(1)	5(3)	7(2)
Litter no. (*n* individuals)	20(3)	22(2)	17(1)	16(2)	18(3)	19(1)	17(2)	16(1)	15(3)	14(2)
Sex composition: one male and two females (*n* individuals)	1(2), 2(1)	1(1), 2(1)	2(1)	1(1), 2(1)	1(2), 2(1)	2(1)	1(1), 2(1)	2(1)	1(2), 2(1)	1(2)

Experimental group	Hard feed										
Diet duration, months	1			2			3				
Age at the end of the experiment, months	2			3			4				
Maternal lineage no. (*n* individuals)	1(2)	2(1)	9(2)	3(2)	4(3)	5(1)	1(2)	3(1)	5(3)		7(2)
Litter no. (*n* individuals)	20(2)	22(1)	21(2)	16(2)	18(3)	19(1)	17(2)	16(1)	15(2)	19(1)	14(2)
Sex composition: one male and two females (*n* individuals)	1(2)	2(1)	1(1), 2(1)	1(1), 2(1)	1(1), 2(2)	2(1)	1(1), 2(1)	1(1)	1(2)	1(1)	1(1), 2(1)

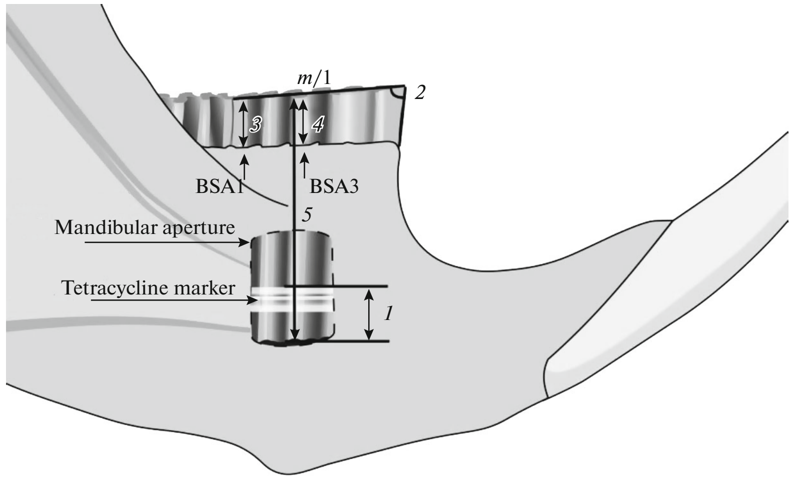

Fig. 1. Scheme of measurements of the first lower molar (*m*/1): (*1*) position of the tetracycline marker; (*2*) wear angle of the chewing surface; (*3*, *4*) height of the tooth crown above the alveoli, measured along BSA1 and BSA3, respectively; (*5*) height of the tooth from the basal part to the chewing surface, measured along BSA3.

son's correlation analysis (r). The relationship between the angular and dimensional parameters, growth rate of the molar, and degree of development of lateral wear facets in the group of animals that received soft feed was determined using an ANOVA with the "degree of facet development" factor (expressed in points). The data were statistically analyzed in Statistica 7.0.

RESULTS

The body length and weight did not statistically differ in the animals from the experimental groups that received different foods (the "experimental group" factor). The body length significantly increased in groups kept on the diets for different time periods ("diet duration") ($F(2; 33) = 6.47$, $p < 0.05$).

The rate of *m*/1 growth was statistically significantly lower in vole individuals kept on the soft diet than in the animals kept on the hard diet ("experimental group" factor) ($F(1; 33) = 23.27$, $p < 0.001$) (Table 2). If we assume that the rates of crown growth and wear remain continuous, the average time required for the complete renewal of tooth tissues is 75.7 days (from 48.9 to 97.3 days) for the animals kept on soft feed and 65.1 days (from 55.5 to 81.5 days) for the animals kept on hard feed. The differences between the tooth growth rate in animals that were kept on the diets for different time periods are also statistically significant ("diet duration" factor ($F(2; 33) = 7.37$, $p < 0.05$). The maximum growth rate in both groups was recorded for the animals that were kept on the diets for 2 months (the age of the animals was 3 months) (Fig. 2a). The two-way ANOVA with the "experimental group" and "maternal lineage" (lineages 1–5 and 7) factors showed statistically significant differences between the experimental groups ($F(1; 25) = 8.30$, $p < 0.05$), while the differences between the maternal lineages ($F(5; 25) = 0.45$, $p = 0.81$) and interaction of these factors ($F(5; 25) = 0.60$, $p = 0.70$) are statistically insignificant. These data suggest that there is no contribution of the hereditary component to the variability of the tooth growth rate.

The wear angle of the chewing surface is statistically significantly greater (more obtuse) in animals feeding on soft food ("experimental group" factor) ($F(1; 33) = 40.72$, $p < 0.001$). The "diet duration" factor is also statistically significant for them ($F(2; 33) = 5.29$, $p < 0.05$) (Fig. 2b).

The tooth crown measured along BSA1 and BSA3 is lower in animals that received soft feeds ("experimental group" factor) ($F(1; 33) = 9.86$, $p < 0.05$ and $F(1; 33) = 16.68$, $p < 0.001$, respectively) (see Table 1, Figs. 2c, 2d). The "diet duration" factor is statistically significant for BSA3 $F(2; 33) = 8.03$, $p < 0.05$) (Fig. 2c).

Lateral wear facets were found only in animals that received soft feed (in 12 of the 20 individuals). The degree of facet development was 1, 2, and 3 points. In the course of further analysis, the teeth with the second and third degrees of facet development were combined into one group (2 points) because of the small volume of material in each sample.

The relationship between the molar growth and wear parameters in the two experimental groups. No significant correlations between the tooth growth rate, crown height, and wear angle of the chewing surface were found in the group that received hard feed. The group that received soft feed showed a statistically significant negative correlation between the molar growth rate and crown height measured along BSA1 and BSA3 ($r = -0.47$, $r = -0.44$, $p < 0.05$), positive correlation between the growth rate and wear angle of the chewing surface ($r = 0.47$, $p < 0.05$), and negative correlation between the crown height measured along BSA1 and wear angle of the chewing surface ($r = -0.55$, $p < 0.05$). Therefore, the crown is lower and the angle is more

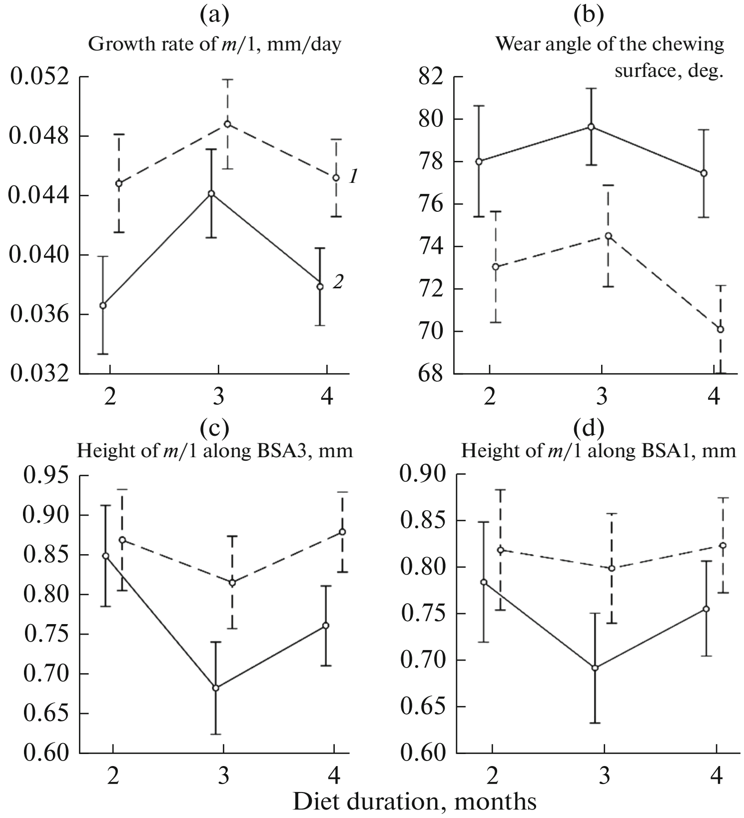

Fig. 2. Characteristics of the teeth of narrow-skulled vole individuals that were kept on the two diets for different periods (mean values and 95% confidence interval): (1) hard feed; (2) soft feed.

obtuse at a higher growth rate. The tooth growth rate increases as the facets develop from 0 to 2 points ($F(2; 17) = 7.29$, $p < 0.05$) (Fig. 3a). The wear angle becomes more obtuse ($F(2; 17) = 16.26$, $p < 0.001$) (Fig. 3b) and the tooth crown measured along BSA1 and BSA3 becomes lower ($F(2; 17) = 9.55$, $p < 0.05$ and $F(2; 17) = 8.63$, $p < 0.05$, respectively) (Fig. 3c, 3d).

DISCUSSION

Rate of *m*/1 growth. The results of estimation of the rate of *m*/1 growth were compared with the literature data on the growth rate of this tooth in other rodent species, obtained using tetracycline markers. The average rate of *m*/1 growth is slower in narrow-skulled vole than

Table 2. Parameters of the *m*/1 and body of narrow-skulled vole individuals kept on the soft (SF, $n = 20$) and hard (HF, $n = 19$) feeds

Parameter	Diet	M ± Std Dev.	min	max
Rate of *m*/1 growth, mm/day	SF	0.040 ± 0.0058	0.033	0.056
	HF	0.046 ± 0.0035	0.041	0.053
Height of *m*/1 above the alveoli, mm:				
BSA1	SF	0.74 ± 0.076	0.60	0.85
	HF	0.82 ± 0.07	0.70	1.0
BSA3	SF	0.75 ± 0.09	0.60	0.94
	HF	0.86 ± 0.07	0.75	1.05
Height of *m*/1, mm: BSA3	SF	2.96 ± 0.25	2.55	3.45
	HF	2.99 ± 0.19	2.65	3.40
Height of *m*/1, mm: BSA	SF	78.65 ± 3.31	72.0	85.0
	HF	72.42 ± 2.95	66.00	76.00
Wear angle of the *m*/1 chewing surface, deg.	SF	15.71 ± 3.40	11.10	22.50
	HF	17.24 ± 3.82	13.00	26.80
Body length, mm	SF	102.05 ± 6.10	95.00	116.00
	HF	101.42 ± 4.20	92.00	115.00

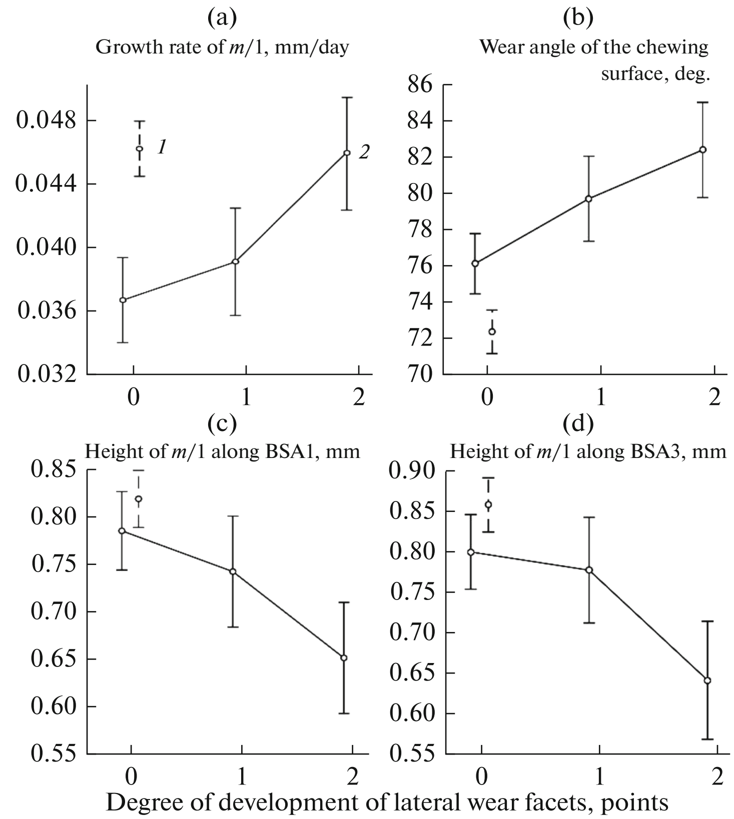

Fig. 3. The relationship between the parameters of the teeth of voles kept on the low-abrasive diet (mean values and 95% confidence interval): (*1*) hard feed; (*2*) soft feed.

in other hypselodont voles, in which cement is deposited in the reentrant corners of the molars [14, 15].

Comparison of the animals feeding on different foods showed that the rate of tooth growth was higher in the variant with hard feed. The body weight did not differ between the animals kept on different diets; therefore, the lower rate of tooth growth in the animals feeding on soft food is not determined by lack of nutrients. As in natural conditions, the growth and development of animals born in laboratory conditions have seasonal variability. All the animals involved in the experiment were born at the laboratory within two months, in May and June; therefore, the influence of the birth season on growth processes was similar in all individuals. No contribution of the hereditary component to the variability of the tooth growth rate was revealed. Therefore, it is most likely that the observed differences in tooth growth in the two experimental groups are determined by different food compositions, which caused different loads on the molar during chewing.

***M*/1 wear parameters.** The height of continuously growing teeth is determined both by the growth rate and wear rate. Narrow-skulled vole individuals kept on soft feed had a lower crown. This could be determined by at least two interrelated causes: first, the formation of the low crown might be due to the fact that the rate of tooth growth was lower in individuals kept on the soft diet as a result of low tooth load; second, it might be formed due to a more intensive tooth wear. The highly abrasive diet in our experiment was similar to the natural diet (albeit not the same due to the presence of carrots). It was previously shown that the characteristics of the crown mesorelief and height were similar between the animals kept on this diet and animals captured in nature [5]. The low-abrasive diet was probably extremely soft for this species. Narrow-skulled vole individuals kept on this diet had a lower crown and a more obtuse wear angle and were characterized by the presence of lateral wear facets resulting from tooth-tooth friction. It was previously shown [6] that the area of damage of the enamel as a result of its shearing was larger in animals feeding on low-abrasive food than in animals feeding on more abrasive food. Therefore, the wear parameters indicate a high level of tooth tissue wear, which might result from tooth-tooth contacts friction during the consumption of food with a small amount of abrasive components.

The differences in the values of the angles of wear when keeping voles on the two diets are probably associated with the biomechanics of the chewing movements of the lower jaw, which are directed from front to back, the distribution of food particles in the oral cavity, different loads during chewing on the front and back of the tooth, and the position of the tooth in the jaw [8, 12, 17, 18]. Presumably, the posterior part is worn down more significantly during the consumption of hard feed, thereby forming a sharper angle. In the case of a low abrasive feed, the load on the back of the tooth is reduced, but wear on both the front and back of the tooth is increased due to the interaction of the tooth with the tooth, which probably together leads to an obtuse angle of wear. In addition, the obtuseness of the angle increases with the development of facets, which begin to spread from the anterior part of the tooth. It can be assumed that occlusion is disturbed primarily in the anterior tooth part and increases the obtusion of the wear angle.

Diet duration. Differences in the studied parameters were recorded between the animals kept on the two diets for different time periods. These changes are nonlinear, but synchronous in both groups, which excludes their randomness. The 3-month-old individuals kept on the diets for 2 months had a higher rate of tooth growth, a lower crown height, and a more obtuse wear angle in both experimental groups. It is worth noting the directions of trait changes within the groups kept on different diets: the increase in the growth rate accompanied by an increase in the wear angle and a decrease in the crown height.

Interestingly, individuals with a sharp wear angle and a high crown also occurred in the group that received soft feed, and half of the animals from this group did not have lateral wear facets. This might be due to the preference of only one of the food components (carrots or dandelions) by voles or, more likely, due to the adaptation of some of the animals to this food type owing to the peculiarities of the anatomy and biomechanics of chewing movements. Both these hypotheses require testing in special studies.

Relationship between the studied *m*/1 parameters in animals feeding on soft food and comparison with literature data. The intragroup analysis of the animals feeding on soft food showed that the rate of crown growth increased with the development of tooth wear, probably due to the tooth-tooth contact. The extreme manifestation of this wear is the appearance of lateral wear facets. The development of facets is combined with a faster growth rate of the tooth, a more obtuse wear angle, and a lower tooth crown.

We compared our data with the results of experiments on hypselodont animals [9, 16, 19]. The study involving guinea pigs showed that the teeth of the animals were lower and had deeper sockets in the dentin in the variant with highly abrasive food (bamboo leaves) than in the variant with less abrasive food (timothy and alfalfa leaves) [19]. Narrow-skulled vole individuals feeding on hard food also had a deeper mesorelief of the chewing surface of molars than the animals kept on soft feed [5]. However, the teeth were higher in voles feeding on hard food, since hard feed was not extremely abrasive for this species and did not cause increased molar wear.

The experiment on rabbits [9, 16] showed that the teeth of the animals that received highly abrasive food including external abrasive (sand) had a low and round mesorelief of the chewing surface and a more pronounced microrelief than the teeth of the animals that did not receive the external abrasive (alfalfa, monocotyledonous plant leaves, and monocotyledonous plant leaves together with rice husks). The rate of tooth growth and wear was higher in the variant with highly abrasive food than in the variant with softer feeds. The tooth crown was lower in animals that received sand with food than in animals that did not receive it, since the growth rate did not fully compensate for the wear [9, 16].

In our experiment, the height, mesorelief, and microrelief of the teeth of voles kept on soft feed are somewhat similar to the respective parameters for rabbits that received food with sand [9, 16]: signs of strong wear of the enamel [6], low mesorelief [5], and low crown; at the same time, they also had a trait that was not found in rabbits, namely, lateral wear facets. Presumably, extremely soft feeds, causing tooth-tooth contacts during chewing, leads to the appearance of wear similar to severe tooth wear when the animals are kept on an extremely hard diet, including external abrasive, with prevailing tooth-food contacts.

On the whole, the growth rate of molars in the individuals of the experimental group was lower in the variant with soft feed than in the variant with hard feed. Apparently, the low-abrasive diet provokes a decrease in the load on the teeth during chewing and leads to a decrease in the rate of their growth. At the same time, the group feeding on soft food also had signs of severe wear of tooth tissues. The degree of manifestation of these features differed in different individuals. The animals without high wear of the crown had the minimum rate of tooth growth. Voles with signs of severe molar wear had a higher rate of molar growth. In the case of maximum wear, the tooth growth rate was close to the value for the animals kept on the hard diet.

The results of our research indicate that the consumption of extremely low-abrasive food, provoked a decrease in the molar growth rate; however, it probably caused an excessive tooth-to-tooth contact in some individuals. This was accompanied by a severe wear of the teeth, which probably led to an increase in the chewing force and was compensated by the acceleration of the growth. The growth rate of teeth was higher in voles feeding on hard food than in voles feeding on soft food. Hard feed did not provoke an increased tooth wear, since it was not extremely abrasive for this species. The range of individual changes in the growth rate of teeth and pattern of their abrasion in response to the consumption of feeds with different abrasive properties can be evaluated by studying the same animals based on a sequential change of diets with different abrasive properties and in vivo assessment of the studied parameters.

Our results confirm the hypothesis that the growth rate of the molars of narrow-skulled vole depends on the physical properties of the consumed food. The morphological responses of teeth to deviations from a certain "normal" proportion of foods with different levels of hardness for the species suggest that there is a species specificity of cheek tooth characteristics determining the ability to treat foods with a certain range of abrasiveness. Probably, the deviation from this range affects the pattern of abrasion of the chewing surface and tooth growth rate. Comparative study of these processes in different taxonomic and ecological groups of herbivorous mammals is an important and relevant problem in functional tooth morphology, the solution of which will make it possible to significantly advance the possibilities of paleoecological reconstructions.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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