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Variants of Tooth Mesowear in *Microtus* Voles as Indicators of Food Hardness and Abrasiveness

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Abstract—Methodological approaches to the description of variants and degrees of hypselodont tooth mesowear in voles are proposed on the basis of studies on the collection of skulls of two vole species trapped in the field (narrow-headed vole, $n = 38$; common vole, $n = 22$) and two species from laboratory colonies (narrow-headed vole, $n = 46$; root vole, $n = 76$). Trends in the manifestation of different mesowear variants have been analyzed in experiments on feeding root voles from the laboratory colony with "hard" and "soft" foods. It has been found that animals kept on low-abrasive diet show signs of wear due to tooth-to-tooth contact, such as low crown height, relatively obtuse wear angle and more upright position of m/1 in the jaw, shallow occlusal surface relief, and lateral wear facets. Chewing hard food items requires application of vertical occlusal pressure, which result in the formation of a depression in repair dentin, while denser dentin at the anterior enamel wall of prisms remains unworn.

Keywords: mesowear, molars, *Microtus* voles, experimental ecology, diet, paleoecology
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An interesting aspect of the paleoecology of Late Cenozoic terrestrial vertebrates concerns analysis of their food spectra. Indirect methods for estimating the type of animal feeding have become widespread in recent years. They are based on analysis of the micro- and mesoreliefs of the masticatory tooth surface, which acquire a certain pattern depending on animal diet and therefore can provide an idea of physical characteristics of food items, particularly hardness and abrasiveness. Such an approach provides limited information but is applicable to the teeth of mammals, the most abundant material available to paleozoologists: microwear reflects a short period of time relative to the animal's life span and provides information about its "last meals," while variants of mesowear reflect tendencies in feeding over weeks to few months. Mesowear analysis can help to answer questions concerning the average diet of an animal from a certain location (Fortelius and Solounias, 2000). Tooth chilling and anomalous wear patterns can provide information about specific features of foods (Harvely et al., 2009; Kropacheva et al., 2012; Smirnov and Kropacheva, 2015). Mesowear is mainly studied in hypsodont teeth of large herbivorous mammals and brachyodont teeth of primates (Kaiser and Fortelius, 2003; Kaiser at al., 2013; Faith, 2011; Fortelius and Solounias, 2000; Taylor et al., 2014; Semprebon and Rivals, 2010; Rivals at al., 2009; etc.).

Herbivorous rodents and lagomorphs are important and widely available objects of studies in paleoecology of Late Cenozoic terrestrial mammals. Most species of this group are small mammals, the structure of their teeth is diverse, and studies on tooth mesowear in these animals are at the initial stage (Lee and Houston, 1993; Guerecheau et al., 2010; Kropacheva et al., 2012; Sibiryakov, 2013; Müller et al., 2014; Ulbricht et al., 2015). Even the search for tooth wear features indicative of characteristics of animal diet is still underway. Methods for evaluating different variants of mesowear are being developed on the basis of experience in analyzing the sharpness and depth of occlusal surface relief in large herbivores (Ulbricht et al., 2015). Variants of mesowear identified as specific for *Microtus* voles include the slope angle of m/1 occlusal surface, a depression in dentin on the occlusal surface of enamel prisms, and lateral wear facets (Guerecheau et al., 2010; Kropacheva et al., 2012; Smirnov and Kropacheva, 2015; Sibiryakov, 2013).

The molars of these voles are of hypselodont type; i.e., they have no roots and are characterized by continuous and rapid growth and wear. Therefore, it can be expected that their mesorelief readily changes in response to modifications of animal diet. A great variety of relief variants are possible, since vole teeth include components of different densities and have a complex outline of the occlusal surface.

This study was aimed at developing methodological approaches to the description of variants and degrees of mesowear in hypselodont molars of voles in order to use these characteristics for indication of hardness and abrasiveness of foods consumed by recent and fossil rodents.

To this end, we made a review of the relevant literature, performed experiments with a laboratory colony of narrow-headed voles, and analyzed the skulls of voles trapped in the field. Our purposes were as follows:

(1) to identify and describe a series of variants of permanent tooth mesowear in several vole species;

(2) develop methodological approaches to the description of forms and degrees of each mesowear variants;

(3) compare the teeth of captive narrow-headed voles receiving "hard" and "soft" foods in order to test the hypothesis that the manifestation of certain mesowear variants depends on the composition of food;

(4) evaluate the dependence of the degree of mesowear in different variants on the time of feeding one or another diet to the voles;

(5) reveal interrelation between manifestation of different mesowear variants; and

(6) to compare the frequency and degree of mesowear in voles from experimental groups with those in voles trapped in nature.

MATERIAL AND METHODS

The search for variants of tooth mesowear and development of methodological approaches to their assessment were based on analysis of the collections of skulls of three vole species: the narrow-headed vole *Lasiopodomys* (*Stenocranius*) *gregalis gregalis*, common vole *Microtus arvalis obscurus*, and root vole *Microtus oeconomus oeconomus*. Narrow-headed voles (n = 38) were trapped near the village of Zverinogolovskoe, Kurgan oblast; common voles (n = 22), near the city of Dvurechensk, Sverdlovsk oblast. The founders of the laboratory colony of root voles (n = 76) were trapped in Sverdlovsk and Chelyabinsk oblasts. Experiments on the manifestation of certain mesowear variants depending on food abrasiveness were performed with narrow-headed voles from the laboratory colony maintained at our institute. Its founders (17 ind.) were trapped in Beloyarskii raion of Sverdlovsk oblast. The voles born in captivity (n = 46) were fed special diets beginning from the age of 1 month.

Standard containers for laboratory animals have lids made of metal grating, and the animals periodically gnaw on them. To avoid tooth damage, standard lids were replaced by fine steel mesh. The voles from each litter included in the experiment were divided into two groups so that the group sex ratio was equal. These groups received diets with different contents of abrasive components (phytoliths). The diet of the first group ("soft food") was poor in phytoliths but contained solid components. It included cleaned dandelion leaves, carrots cleaned of soil (to remove extraneous abrasive components), and cored apples. The second group received "hard food" with high phytolith contents, such as monocot leaves and hay, and also carrots without cleaning them of soil. The voles were kept on the diets for 1 month (9 ind. from group 1 and 8 ind. from group 2), 2 months (7 and 6 ind.), and 3 months (8 and 8 ind.).

Lateral images of vole jaws were taken with a Leica EZ4 binocular microscope, placing the jaw so that the tooth row was parallel to the microscope stage and objective lens (Yaklovskaya et al., 2014). Dimensional and angular parameters were measured twice, and their average values were calculated. Measurements were performed with the TPS program package (TPS Util and TPS Dig2). Images of teeth were made under a TESCAN VEGA3 scanning electron microscope. The data were processed statistically using Statistica 7.0 program.

Methodological Approaches to the Study of Mesowear

(1) *Tooth height above the alveolus* (mm). The height of molars in hypselodont voles depends on the ratio between the rates of their growth and wear. Such a relationship has been demonstrated in a series of studies on large and small herbivores (Skogland, 1988; Wolf and Kamphues, 1996; Rinaldi and Cole, 2004; Kubo et al., 2011; Taylor et al., 2014; Kubo and Yamada, 2014; Müller et al., 2014; Pérez-Barbería et al., 2015).

The height of maxillary M1/ and M2/ was measured in lateral images of the skull from the occlusal surface to the alveolus along the lateral side of BSA1 (here and below, designations according to Borodin, 2009) (Fig. 1, measure *1*). To measure mandibular m/1 (Fig. 1, measure *2*), an orientation line was drawn on lateral images of the mandible along the upper buccal edges of the alveoli, from m/3 to m/1 (Fig. 1, line *a*), and the distance from this line to the occlusal surface was measured along the labial tooth surface.

(2) *The angle of occlusal surface wear in m/1 and M1/* relative to the labial tooth surface. This character in *Microtus* voles shows seasonal and geographic variation (Guerecheau et al., 2010; Kropacheva et al., 2012; Sibiryakov, 2013). The biomechanics of mastication in these rodents is characterized by the prevalence of rostrocaudal movement of the mandible relative to the maxilla (Gromov and Polyakov, 1977; Kesner, 1980; Charles et al., 2007; Cox et al., 2012). Therefore, the loading on the occlusal surfaces of different teeth and different parts of the same tooth may be uneven, with consequent variation in the wear angle. This angle for the M1/ occlusal surface (Fig. 1, measure *3*) was measured between two straight lines connecting the most prominent points on the occlusal surface, in the zones of triangle T4 and anterior loop (AL) (Fig. 1, line *b*), and on the labial AL surface, at the boundary with the occlusal surface and at the edge of the alveolus (Fig. 1,

Fig. 1. Scheme of measurements of teeth in voles: (*1–5*) lines of measurements, (*a–e*) orientation lines.

line *c*). To measure the wear angle for the m/1 occlusal surface (Fig. 1, measure *4*), the corresponding lines were drawn between the most prominent points on the occlusal surface, in the zones of posterior loop (PL) and anterior cap (AC) (Fig. 1, line *d*), and on the labial AC surface, at the boundary with the occlusal surface and at the age of the alveolus (Fig. 1, line *e*).

(3) *The angle of m/1 inclination relative to the alveoli* (Fig. 1, measure *5*) was measured between line *e* and orientation line *a* (see above).

(4) *Occlusal surface relief* is formed because tooth components differing in location and density are worn to different extents, with consequent development of facets on the occlusal surface. The degree of their development is the key parameter used for mesowear analysis in large herbivores. Animals feeding on the leaves of shrubs and green shoots have a prominent occlusal surface relief with sharp cutting edges of the facets, indicating that the main cause of wear is tooth-to-tooth contact (*attrition*). Facets in animals feeding mainly on grass are largely obliterated, with blunt edges, which is indicative of wear by food-to-tooth contact (*abrasion* (Kaiser and, Fortelius, 2000). Mesowear analysis has recently been applied to some lagomorphs (Leporinae) and murine rodents (Murinae) (Ulbricht et al., 2015).

The occlusal surface of molars in voles consists of enamel prisms filled with dense dentin at the periphery and soft (repair) dentin in the central part. It has been shown that the distinctness of depression in dentin on the occlusal surface of buccal teeth in voles depends on the frequency and intensity of vertical chewing strokes used to crush non-green food items (Lee and Houston, 1993; Sibiryakov, 2013).

The surface relief of each prism in m/1 was examined for the level of manifestation of four characters: (1) dense dentin wear at the anterior (thick) enamel wall, (2) the presence and features of depression in dentin, (3) the degree of wear of the posterior (thin) enamel wall, and (4) relief depth.

Seven variants of relief were distinguished based on combinations of characters 1–3:

(1) The occlusal surface is flat (Fig. 2, panel *1*).

(2) Dense dentin at the anterior wall is not worn, the depression is mainly confined to repair dentin; the posterior wall throughout its length rises above the depression bottom level (Fig. 2, panel *2*).

(3) Dense dentin at the anterior wall is not worn, the depression is mainly confined to repair dentin; the posterior wall or its part is worn down to the depression bottom level (Fig. 2, panel *3*);

(4) Dense dentin at the anterior wall is not worn, the depression is indistinct; the occlusal surface is flat and sharply inclined toward the thin enamel wall; the lowest point of the posterior wall is the lowest point of the relief (Fig. 2, panel *4*);

(5) Dense dentin at the anterior wall is worn down below the enamel level, the depression extends over both repair and dense dentin; the posterior wall throughout its length rises above the bottom level of depression in repair dentin (Fig. 2, panel *5*);

(6) Dense dentin at the anterior wall is worn down below the enamel level, the depression extends over both repair and dense dentin; the posterior wall or its part is worn down to the bottom level of depression in repair dentin (Fig. 2, panel *6*);

(7) Dense dentin at the anterior wall is worn down below the enamel level, the depression is indistinct; the occlusal surface is flat and sharply inclined toward the thin enamel wall; the lowest point of the posterior wall is the lowest point of the relief (Fig. 2, panel *7*).

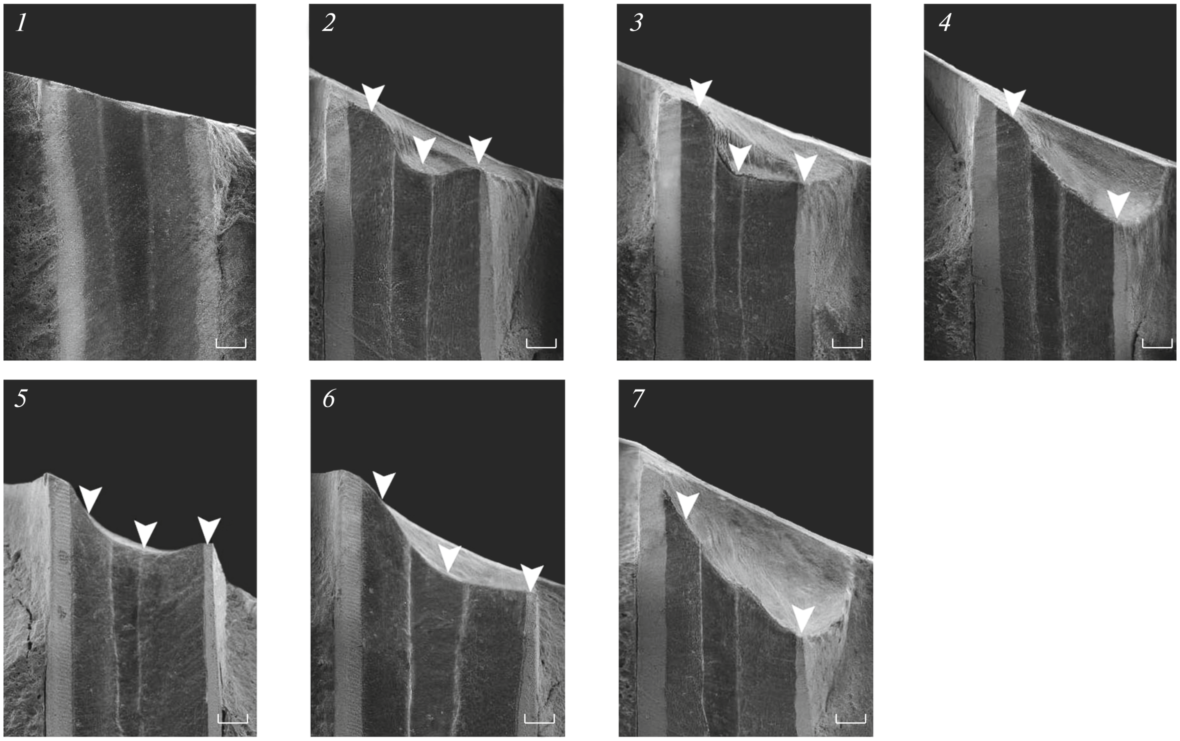

Fig. 2. Variants of occlusal surface relief of prisms in m/1 teeth of voles. Scale bar 50 μm.

Relief depth in each prism was measured as the distance from the enamel surface of the anterior (thick) wall to the lowest point of depression on the occlusal surface and graded as follows: (0) the occlusal surface is flat or slightly inclined toward the thin wall; (1) the deepest point of the relief is at a depth equivalent to no more than one-third of the maximum prism width; (2) the deepest point of the relief is at a depth equivalent to one-third to two-thirds of the maximum prism width; and (3) the deepest point of the relief is at a depth equivalent to more than two-thirds of the maximum prism width.

(5) *Chips on the occlusal surface enamel*. The enamel may be chipped both while chewing soft food, due to tooth-to-tooth contact, and against extraneous abrasive particles such as grains of sand (Walker, 1984; Fortelius and Solounias, 2000). Chips on each prism were counted under a binocular microscope at 3× magnification.

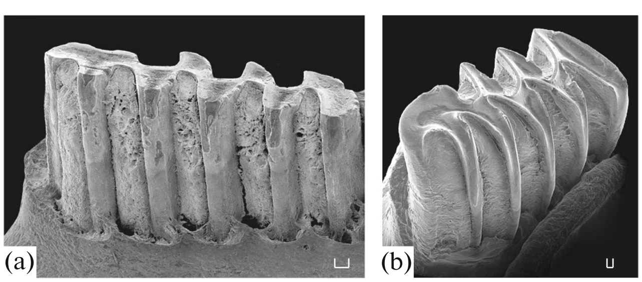

Fig. 3. Lateral wear facets on m/1 teeth of (a) narrow-headed vole from soft-diet group and (b) root vole trapped in the field. Scale bar: (a) 100 μm, (b) 50 μm.

(6) *Lateral wear facets* are furrows of different depths (in the enamel alone or both enamel and dentin) on the lateral walls of prisms that taper downward from the occlusal surface boundary and disappear before reaching the alveoli (Fig. 3). They appear due to functional changes upon switching to insufficiently hard food. Analysis of their occurrence in 15 species from 10 genera of the subfamily Arvicolinae has shown that this pathology is widespread (Smirnov and Kropacheva, 2015).

The degree of lateral facet development was graded as follows: (1) the initial stage, facets confined to the boundary with the occlusal surface; (2) facets extending over the upper one-fourth of the lateral surface; and (3) facets extending over more than one-fourth of the lateral surface.

RESULTS

The height of m/1, M1/, and M2/ above the alveoli was significantly smaller in narrow-headed voles kept on the soft diet than in those on the hard diet (m/1: $F = 14.14$, $p < 0.001$; M1/: $F = 20.87$, $p < 0.001$; M2/: $F = 25.51$, $p < 0.001$). The m/1 height significantly differed between the animals that were kept on a certain diet for different periods of time ($F = 6.69$, $p < 0.05$), with the time dependence in this case being nonlinear: the minimum height in both groups was recorded after 2 months. No such differences were observed in the heights of M1/ and M2/. Field-trapped voles did not differ significantly from the hard-diet group in the height of m/1, but their teeth were significantly higher than in the soft-diet group ($F = 6.37$, $p < 0.05$) (Table 1).

Voles kept on the soft diet had a more obtuse angle of occlusal surface wear in m/1 ($F = 38.57$, $p < 0.001$) and a more acute angle in M1/ ($F = 15.30$, $p < 0.001$). These angles differed between animals kept on a certain diet for different periods of time (m/1: $F = 6.52$, $p < 0.05$; M1/: $F = 14.4$, $p < 0.001$). The maximum angle of m/1 and the minimum angle of M1/ in both groups were recorded on the second month of the experiment. The angles of m/1 surface wear in field-trapped voles were more acute than in voles of the soft-diet group ($F = 55.26$, $p < 0.001$) but only slightly differed from those in the hard food group ($F = 4.18$, $p < 0.05$) (Table 2).

The m/1 inclination angle was smaller in voles that received soft food than in the hard food group; i.e., the tooth had an approximately upright position in the former and was slanted forward in the latter ($F = 24.83$, $p < 0.001$) (Table 3). No difference in this parameter was revealed between animals kept on a certain diet for different periods of time. The average inclination angles in voles trapped in nature did not differ from those in the hard-diet group but were more obtuse than in voles that received soft food ($F = 31.94$, $p < 0.001$).

The frequencies of variants of the occlusal surface relief (see Fig. 2) significantly differed between all three groups of voles ($\chi^2 = 285.5$, df = 12, $p < 0.001$). The first and second most frequent variants were as follows: variants 2 and 3 in the soft-diet group, variants 6 and 3 in the hard-diet group, and variants 5 and 6 in field-trapped voles.

Differences in the depth of the occlusal surface relief between the three groups were also significant ($\chi^2 = 336.6$, df = 4, $p < 0.001$). A shallow relief (grade 1)

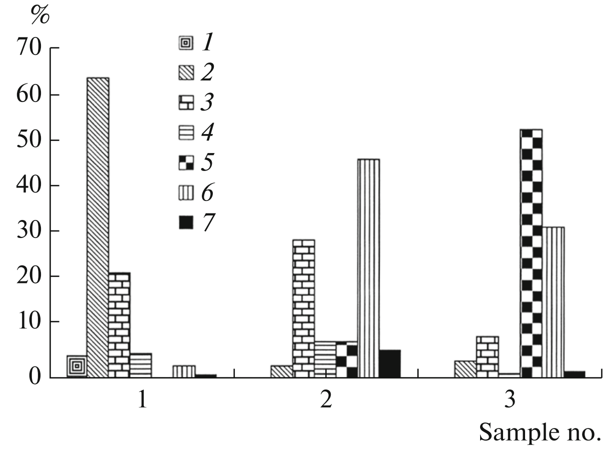

Fig. 4. Ratios of surface relief variants (*1*–*7*) recorded in all prisms of molar teeth in voles from (1) soft-diet group ($n_{prism} = 116$), (2) hard-diet group ($n_{prism} = 116$), and (3) field-trapped group ($n_{prism} = 193$).

was prevalent in the soft diet group (more than 90% of all prisms). It also prevailed in the hard diet group (70%), where the proportion of prisms with a deeper relief (grade 2) reached 30%. In the group trapped in nature, 75% of prisms had grade 2 relief, and 5% of prisms, grade 3 relief. The occlusal surface of prisms was not always worn uniformly all over the tooth.

The number of chips on the enamel was significantly greater in animals kept on the soft diet ($\chi^2 = 9.73$, df = 1, $p < 0.001$). Lateral wear facets were found in 19 out of 24 animals from this group. The degree of their manifestation varied but showed no dependence on the duration of the diet. This form of mesowear was not recorded in the hard diet group.

The pattern of correlations between different forms of mesowear (Table 4) is apparent from data on specific features of their manifestation in the two experimental groups.

Table 1. Molar tooth heights (mm) in narrow-headed voles from laboratory colony and in field-trapped voles

Tooth	Sample no.	n	Tooth height, mm		
			$M \pm SD$	min	max
m/1	1	24	1.02 ± 0.14	0.78	1.29
	2	22	1.16 ± 0.14	0.10	1.53
	3	17	1.16 ± 0.22	0.79	1.63
M1/	1	24	1.14 ± 0.08	1.01	1.34
	2	22	1.22 ± 0.06	1.07	1.38
M2/	1	24	0.96 ± 0.07	0.76	1.10
	2	22	1.03 ± 0.06	0.84	1.12

Sample numbers: (1) soft-diet group, (2) hard-diet group, (3) field-trapped group (here and in Tables 2, 3).

Table 2. Angles of occlusal surface wear in molar teeth of narrow-headed voles from laboratory colony and in field-trapped voles

Tooth	Sample no.	n	Wear angle, deg		
			$M \pm SD$	min	max
m/1	1	24	77.7 ± 2.87	70.5	81.50
	2	22	72.86 ± 3.08	65.0	77.0
	3	38	70.89 ± 3.86	61.39	77.05
M1/	1	24	113.1 ± 3.07	108.0	118.0
	2	22	115.7 ± 3.03	109.3	120.7

Table 3. Inclination angles of m/1 relative to the alveoli in narrow-headed voles from laboratory colony and in field-trapped voles

Sample no.	n	Inclination angle, deg		
		$M \pm SD$	min	max
1	24	93.0 ± 2.84	86.0	100.0
2	22	97.6 ± 3.21	92.0	106.0
3	37	97.3 ± 2.83	92.6	104.9

DISCUSSION

The identified forms of mesowear have proved to be manifested to different extends depending on the density and hardness of food components and can serve as indicators of diet composition.

The data presented above show that the rate of tooth wear by attrition (tooth-to-tooth contact) in hypselodont voles feeding on soft foods is higher than the rate of wear by abrasion (food-to-tooth contact) in the case of feeding on hard foods. At first glance, this contradicts the results of studies on large hypsodont herbivores and hypselodont lagomorphs, in which tooth wear was higher in animals feeding on abrasive foods and the prevailing type of tooth wear (Skogland, 1988; Kubo et al., 2011; Taylor et al., 2013; Kubo and Yamada, 2014; Müller et al., 2014; Pérez-Barberia et al., 2015). However, observations on animals kept for a long time on a soft diet were beyond the scope of these studies; conversely, they were focused on the effect of intrinsic (phytoliths) or extraneous (e.g., sand) abrasive food components. We devoted more attention to the effect of soft diet, and the hard diet was free of extraneous abrasive components, which otherwise could have accelerated the rate of tooth wear.

An increase in the angle of tooth wear in response to a soft diet is probably explained by specific features in the biomechanics of mastication and the distribution of masticatory loading over different tooth parts. The directions of vectors of jaw movement and loadings on different muscles (Kesner, 1980; Cox et al., 2012) suggest that greater loading is placed on the posterior part of the occlusal surface, which is therefore worn more strongly and at a more acute angle when chewing hard foods. If the abrasiveness of food is low, the loading on the posterior tooth part is attenuated and distributed more evenly, and the angle of wear becomes more obtuse. Moreover, this angle cannot be acute if the tooth height above the alveolus is low.

Differences in food hardness may be responsible not only for different variants of mesowear but also for changes in the m/1 inclination relative to the alveoli.

Lateral wear facets were found in the majority of voles kept on the soft diet. These animals were also characterized by features such as low tooth height above the alveoli, relatively obtuse angle of occlusal surface wear, and more upright position of m/1 in the alveolus. A special biomechanical study is needed to answer the question as to which of these features is more responsible for the development of malocclusion and lateral wear facets.

Diets of different compositions proved to have different effects on the occlusal surface relief. It is known that a depression in dentin appears due to application of vertical occlusal pressure (Lee and Houston, 1993; Sibiryakov, 2013). Therefore, it appears that the characteristic occlusal surface relief in voles kept on the soft diet—with unworn dense dentin at the anterior prism wall and a distinct depression with steep walls in repair dentin (variant 2)—is formed due to vertical chewing strokes used to crush solid food items (apples and carrots), while the enamel and dense dentin are worn mainly by tooth-to-tooth contact in the course of chewing soft green food components.

In the most frequent variant of occlusal surface relief in the hard-diet group, the dense dentin of prisms was worn down below the enamel level at the

Table 4. Coefficients of correlation between dimensional and angular parameters of teeth in voles from laboratory colony

Form of mesowear	m/1 height	M1/ height	M2/ height	m/1 wear angle
M1/ height	0.54	–	0.82	–0.51
M2/ height	0.53	0.82	–	–0.55
m/1 wear angle	–0.65	–0.51	–0.55	–
M1/ wear angle	0.53	0.30	–	–0.53
m/1 inclination angle	–	0.47	0.50	–0.76

A dash (–) indicates the absence of statistically significant correlation.

anterior wall, a distinct depression extended over both repair and dense dentin, and the posterior enamel wall was also worn down (variant 6). The second most frequent was the variant where the dense dentin at the anterior wall was unworn, the posterior enamel wall was worn down, and a distinct depression in repair dentin had a steep anterior wall similar to that in animals from the soft-diet group but with more oblique wall margins (variant 3). This similarity may be explained by the fact that the hard diet also included carrots, which implies the necessity for vertical chewing strokes to chew them.

Variants of tooth mesowear in voles trapped in the field were similar to those in the hard-diet group in tooth height, occlusal surface wear angle, and tooth inclination angle, but characteristics of the occlusal surface relief were different. Its depth was greater, and the most frequent was the variant with dense dentin at the anterior wall being worn down below the enamel level, a depression extending over both repair and dense dentin, and the posterior wall rising above the bottom level of depression in dentin (variant 5). Variant 6 (dominant in the hard-diet group) was the second most frequent.

Differences in all test characters between the two experimental groups from the laboratory colony were already noted after 1 month, becoming increasingly distinct as the animals continued to feed on different diets. This was probably due to fine tuning of tooth growth to masticatory loading.

Thus, characters such as low tooth height above the alveoli, more obtuse wear angle of m/1, its more upright position in the jaw, shallow occlusal surface relief, and lateral wear facets appear as a result of tooth-to-tooth contact during feeding on low-abrasive foods; on the other hand, unworn dense dentin at the anterior prism wall and a depression confined mainly to repair dentin are indicative of feeding on solid dietary components that need vertical chewing strokes to chew them.

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