

Intra- and Interpopulation Odontological Variability in the Gray Red-backed Vole (*Craseomys rufocanus*) and Yu.I. Chernov's Compensation Principle

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Abstract—Methods of geometric morphometrics have been used to study geographic and chronographic forms of variation in the shape of the upper third molar (M3) in the gray red-backed vole *C. rufocanus*, a petrophilic rodent specialized to mountain habitats in the Urals. It has been shown that sexual dimorphism in M3 shape increases in the direction from the Southern to the Polar Urals. In the Middle Urals, differences in M3 shape (more distinct in males than in females) have been revealed between samples taken in years of high and low abundance of the species, which are apparently conditioned by a switch in tooth morphogenesis. This is suggestive of change in the morphofunctional properties of teeth and in related trophic preferences of males and females, i.e., in the possibility for them to consume different spectra of food resources. The increase in M3 sexual dimorphism in the south–north direction and in low-mountain biotopes (not common for the species) is in agreement with Chernov's compensation principle manifested at the intra- and interpopulation levels, as it helps to alleviate trophic competition between males and females. The phenotypic plasticity of teeth provides for population-cenotic stability of the species in climatically unfavorable years and in atypical biotopes and environmental conditions of the Polar Ural Mountains.

Keywords: gray red-backed vole, upper third molar, variation, sexual dimorphism, morphogenesis, geometric morphometrics

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A problem of evolutionary ecology that has been widely discussed in recent years in line with the concept of extended evolutionary synthesis [1–3] concerns rapid morphogenetic rearrangements in species resulting from epigenetic changes caused by environmental stress and fixation of these changes by mechanisms of transgenerational inheritance [4–6]. Therefore, it appears relevant to study the relationship between manifestations of chronographic and geographic forms of variation in eurytopic (unspecialized) and stenotopic (specializes) species. An evolutionary-ecological analysis of the relationship between these forms of variation is closely connected to the assessment of the evolutionary potential of the species, its phenotypic plasticity and evolvability [7, 8], i.e., the ability to undergo rapid evolutionary rearrangements upon climatic or anthropogenic changes in the environment [9, 10].

The search of adequate natural models for studying this evolutionary-ecological and ecomorphological problem consists in selecting situations where it is possible to bring into correlation the chronographic and geographic (intra- and interpopulation) forms of variation in nature.

Samples of the gray red-backed vole (*Craseomys rufocanus* Sundevall, 1846) collected in the Urals in the late 20th century may be regarded as such a model. Ecologically, *C. rufocanus* in the Ural region behaves as a specialized petrophile that is found mainly in mountain and low-mountain lithomorphotic biotopes and occurs from the Southern to the Polar Urals. This species inhabits mountain taiga landscapes, shows preference for conifer and deciduous crooked forests at the periphery of rock streams (corroms), and forms relatively isolated insular populations in the subgoltzy belt of the Urals [11].

According to molecular genetic data [12], the intra-specific genetic diversity of *C. rufocanus* in the greater part of the species range is expressed very slightly. In the European part of the range, including the Urals, these voles share a group of similar haplotypes of mtDNA cytochrome *b* gene (haplogroup C1), whose origin and expansion date from between 12000 and 31000 years BP. Therefore, it is interesting from the evolutionary-ecological standpoint to compare manifestations of geographic and chronographic forms of variation and morphological disparity in *C. rufocanus* as a specialized species in geographically distant pop-

ulations of the Urals, taking into account that carriers of haplogroup C1 have relatively recently appeared in this region.

According to the ecological compensation principle formulated by Chernov [13], the variability of a species should increase in oligospecific rodent communities (with an impoverished species composition) inhabiting mountain and, especially, northern polar biotopes and also under atypical conditions in low-mountain regions. We have previously observed such compensatory effects at the intrapopulation level in the bank vole *Clethrionomys glareolus*, a widespread eurytopic species [14], and in the northern mole vole *Ellobius talpinus*, a specialized burrowing species adapted to life underground [15].

The ecological specialization of a species is tightly connected with its trophic specialization and should therefore be reflected in the variability pattern of molar teeth. The shape of molars largely determines the morphofunctional capabilities of rodents for primary mechanical processing of food objects [16].

As shown in previous studies on several vole species under vivarium conditions [17, 18], the morphotypic variation pattern of molars in animals from laboratory colonies may change significantly, compared to that in animals from the initial (parental) natural populations inhabiting geographically distant parts of the range. However, experimental studies on odontological variation under different environmental conditions are very few in number [17, 19], and we are not aware of such neontological research performed on *C. rufocanus*. This study may provide the possibility to approach the solution of the ecomorphological problem under consideration.

Methods of geometric morphometrics, which allow analysis of variation in the shape itself of morphological objects, excluding the influence of their size, have been increasingly used in recent years to describe variation in the shape of vole teeth [10, 20, 21]. It should be emphasized that such an approach provides the possibility of interpreting the observed differences in morphogenetic terms [22]. This approach can also be used to test the hypothesis about the compensatory increase in the level of morphological disparity and variability of tooth shape in vole populations developing under unfavorable or atypical ecoclimatic or landscape-biotope conditions.

Therefore, in this study we applied the methods of geometric morphometrics to the assessment of chronographic and geographic variation in the shape of the upper third molar (M3) in samples of male and female *C. rufocanus* voles collected in the mountains of the Southern, Middle, and Polar Urals. The main purpose was to estimate stability in the pattern of M3 occlusal surface under different ecological conditions and specificity in the morphogenetic responses of males and females to the same environmental conditions. Special attention was given to analysis of intra- and

interpopulation variation in M3 shape with regard to animal sex.

MATERIAL AND METHODS

The study was performed with the series of *C. rufocanus* skulls from the collections kept at the Zoological Museum of the Institute of Plant and Animal Ecology (Ural Branch, Russian Academy of Sciences). Three samples included in analysis consisted of animals trapped in July and August in the Southern, Middle, and Polar Urals: (1) the Rai-Iz mountain range, Yamalo-Nenets Autonomous Area, the Polar Urals (66°53' N, 65°46' E); 81 ind. collected by V.S. Balakhonov in 1975 to 1977; (2) the Visim State Biosphere Reserve, Sverdlovsk oblast, the Middle Urals (57°28' N, 60°00' E); 95 ind. collected by K.I. Berdyugin in 1975 and 1977; (3) Mt. Iremel, Bashkortostan, the Southern Urals (54°30' N, 58°50' E); 73 ind. collected by O.F. Sadykov in 1978 and 1979. Geographic (between-population) variation was analyzed by comparing samples pooled over different years, males and females separately. Analysis of chronographic variation within populations was performed with the material from the Visim reserve, which was collected under favorable conditions in 1975 (high population size, 22.8 ind./100 trap-days; 22 males and 17 females) and under unfavorable conditions in 1977 (low population size, 3.2 ind./100 trap-days; 26 males and 30 females). The ratio of geographic and chronographic forms of variation was estimated by parallel comparisons of male and female samples collected in the Polar and Middle Urals in the same years (1975 and 1977).

In all geographic points, voles were trapped using snap trap lines set in relatively similar biotopes, at the boundaries between rock streams (corroms) and mountain taiga forests. Samples from the Visim reserve (the Middle Urals) were an exception: they were collected in conifer and deciduous crooked forests and mixed taiga forests growing in low-mountain areas. All samples consisted of male and female young of the year, with juvenile voles being excluded from analysis. The numbers of examined males and females in samples from the Southern to Polar Urals are shown in Table 1.

Variation in the shape of right M3 occlusal surface was assessed by methods of geometric morphometrics [10, 20, 23–25] in electronic images (2400 dpi) taken under an MBS-10 microscope with a Canon EOS 450 camera. The images were digitized with tpsUtil [26] and tpsDig2 [27] and analyzed with respect to the arrangement of 30 landmarks characterizing the above variation (Figs. 1a, 1b). Preliminary landmarking repeated twice revealed no bias of estimates resulting from personal errors.

The overall size of the occlusal surface was estimated indirectly, from the centroid size (CS) calculated as the square root from the sum of squared dis-

tances from the center of the image to each of the landmarks [23].

The superimposition of landmark configurations was performed by the method of generalized least-squares Procrustes analysis (GPA) [23] to calculate the Procrustes coordinates and relative warps (RWs) characterizing variation in the shape of the occlusal surface. Discriminant analysis of the Procrustes coordinates and canonical analysis of RWs were used to assess between-group differences in the configuration of landmarks. The hierarchy of between-group differences was evaluated by UPGMA cluster analysis of a matrix of squared generalized Mahalanobis distances D^2 based on the results of canonical analysis. An adequate distance metric for cluster analysis was selected by the highest value of the cophenetic correlation coefficient (R_{coph}).

The level of sexual dimorphism in different parameters was estimated by the formula $SDM = [(X_f/X_m) - 1] \times 100$, where X_f and X_m are the average values of a given parameter in females and males, respectively [28]. In multivariate analysis, squared generalized Mahalanobis distances D^2 (with estimates of their statistical significance) were used for this purpose.

Morphological disparity within the groups was evaluated by the nearest neighbor point pattern analysis within variation polygons [29, 30] plotted in the plane of the first two canonical variables. The mean nearest neighbor distance ($MNND$) between ordinates and its variance ($VarMNND$) characterized the level of morphological disparity. In terms of geometric morphometrics, an increase in these parameters was interpreted as evidence for a wider "fan" of individual morphogenetic trajectories within the group [10].

Multiple intergroup comparisons of individual parameters were made using one-way ANOVA. Pairwise differences between the samples were evaluated by Student's t -test and Tukey's post hoc Q -test.

The procedures of geometric morphometrics and statistical processing were performed using TPS [26, 27], PAST 2.17c [31], IMP [24], and MorphoJ 1.6d [25].

RESULTS

The centroid sizes (CS) of M3 teeth in the pooled samples of either males or females from the Visim population (the Middle Urals) were significantly greater than in the corresponding samples from the Southern and Polar Urals ($F = 10.85$, $d.f._{1,2} = 2, 246$; $p < 0.0001$). More detailed comparisons between samples from the Visim population showed that CS values in both females and males were higher in 1975 (high animal abundance) than in 1977 (low abundance), but the difference was significant only in males ($p < 0.01$), indicating that the growth of animals and, hence, their teeth was slightly inhibited under less favorable conditions of the latter year (Table 1). In both years, the

Table 1. Comparison of centroid sizes (CS \pm SE) of the upper third molar (M3) occlusal surface for samples of male and female gray red-backed voles from populations of the Polar, Middle, and Southern Urals

Locality: sex, year	Centroid size (ind.)
Polar Urals:	
males, 1975–1977	831.60 \pm 8.03 (42)
females, 1975–1977	846.48 \pm 8.24 (39)
Middle Urals:	
males, 1975 and 1977	857.16 \pm 6.96 (48)
females, 1975 and 1977	883.98 \pm 7.67 (47)
males, 1975	874.76 \pm 5.27 (22)
females, 1975	895.46 \pm 10.07 (17)
males, 1977	842.27 \pm 11.35 (26)
females, 1977	877.48 \pm 10.50 (30)
Southern Urals:	
males, 1978–1979	834.73 \pm 6.41 (38)
females, 1978–1979	847.78 \pm 8.98 (35)

average CS in females from the Visim population was greater than in males, and this difference in 1977 was statistically significant ($p < 0.01$). The tooth size showed a general tendency to be greater in females than in males in all the three populations compared, including samples taken in different years (Table 1), with the index of sexual dimorphism (SDM) in CS varying between the samples from 1.6 to 4.2%.

In pooled samples randomly standardized to the smallest sample size, CS averaged 837.21 ± 4.57 in males and 863.13 ± 5.30 in females ($t = 3.7$; $p = 0.00027$),

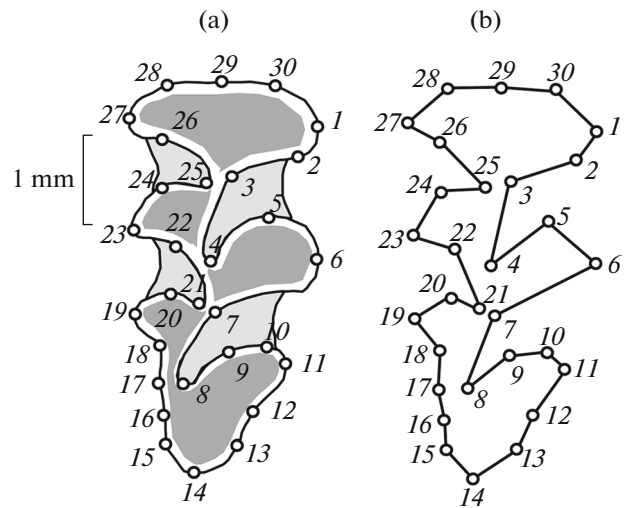


Fig. 1. (a) Locations of landmarks characterizing variation in the occlusal surface pattern of the upper third molar (M3) in the gray red-backed vole and (b) a wireframe scheme of the arrangement of landmarks 1–30.

Table 2. Results of canonical analysis of relative warps (RWs) characterizing variation in M3 shape in samples of male and female gray red-backed voles from three geographically distant Ural populations

Locality, sex	Canonical variable		
	CV1	CV2	CV3
Sample centroids ($\pm SE$)			
Polar Urals: males	1.544 \pm 0.167	0.425 \pm 0.199	0.361 \pm 0.184
Polar Urals: females	0.798 \pm 0.148	0.234 \pm 0.130	-0.497 \pm 0.150
Middle Urals: males	-0.176 \pm 0.154	-1.045 \pm 0.143	-0.246 \pm 0.149
Middle Urals: females	-0.378 \pm 0.135	-0.807 \pm 0.126	0.371 \pm 0.150
Southern Urals: males	-0.914 \pm 0.149	0.922 \pm 0.167	0.137 \pm 0.141
Southern Urals: females	-0.930 \pm 0.178	0.768 \pm 0.174	-0.111 \pm 0.152
Results of canonical analysis			
Wilks' Λ	0.0930	0.2137	0.4322
Eigenvalue	1.2981	1.0220	0.4692
Canonical correlation	0.75	0.71	0.57
Proportion of variance, %	39.28	30.92	14.20
χ^2 test	533.22	346.41	188.34
Number of degrees of freedom (d.f.)	205	160	117
Significance level	$p < 0.0001$	$p < 0.0001$	$p = 0.00003$

with SDM = 3.1%. The area of the occlusal surface delimited by landmarks was, on average, significantly greater in females than in males ($p < 0.001$). The highest level of sexual dimorphism in the size and occlusal surface area of M3 in the Visim population was observed in the samples collected in 1977.

The possible allometric effect of change in tooth shape depending on CS for male and female samples from each population was estimated by linear regression of the values of the first relative warp (RW1) on natural logarithms of centroid sizes (lnCS), as recommended [24]. A preliminary analysis of RW1 variation series showed that it was bimodal (i.e., with two peaks), reflecting differences between two M3 morphotypes characteristic of the species, *simplex* and *typica* [17, 18, 32]: in the former, the posterior loop has only one (third) salient angle on the lingual side; in the latter, there is also an additional (fourth) salient angle that begins to take shape or is already distinct. It has been shown that the boundary between these two tooth morphotypes passes in the zone of zero RW1 values.

Estimation of linear regression and correlation between RW1 and CS for each morphotype separately (with RW1 below zero formally corresponding to *simplex*, and above zero, to *typica*) did not reveal any relationship of tooth shape with its size: in both cases, Pearson's correlation coefficients were close to zero and lacked statistical significance. Therefore, no allometric effect was observed within the framework of each morphotype.

To evaluate geographic variation in M3 shape between male and female samples from the three Ural populations, we performed a canonical analysis of the values of the first 42 relative warps (RW1–RW42) accounting for 97.4% of the total variance. As a result, statistically significant between-group differences were revealed along the axes of the first four canonical variables explaining 96.8% of the total variance (Table 2, Fig. 2). Geographic differences manifested themselves mainly along the first canonical axis CV1 (39.28% of between-group variance). Spearman's coefficient of correlation between CV1 value and geographic location of samples was highly significant ($r_s = 0.73$, $p < 0.0001$). Along the CV2 axis (30.92% of the variance), centroids of male and female samples from the Middle Urals deviated from all others. Apparently, this reflected characteristic differences in M3 shape (depending on landscape-biotopic conditions and/or terrain elevation) between typically mountain populations from the Southern and Polar Urals, on the one hand, and low-mountain Visim population from the Middle Urals, on the other hand. Spearman's correlation coefficient characterizing the relationship between CV2 value and elevation at sampling sites also proved to be high and statistically significant ($r_s = 0.68$, $p < 0.0001$). Variation along the CV3 axis (14.20% of the variance) was mainly related to the animal's sex ($r_s = 0.38$, $p < 0.0001$).

Geographic variation (south to north) was manifested in the overall elongation of M3 posterior loop along with relative narrowing of the anterior unpaired

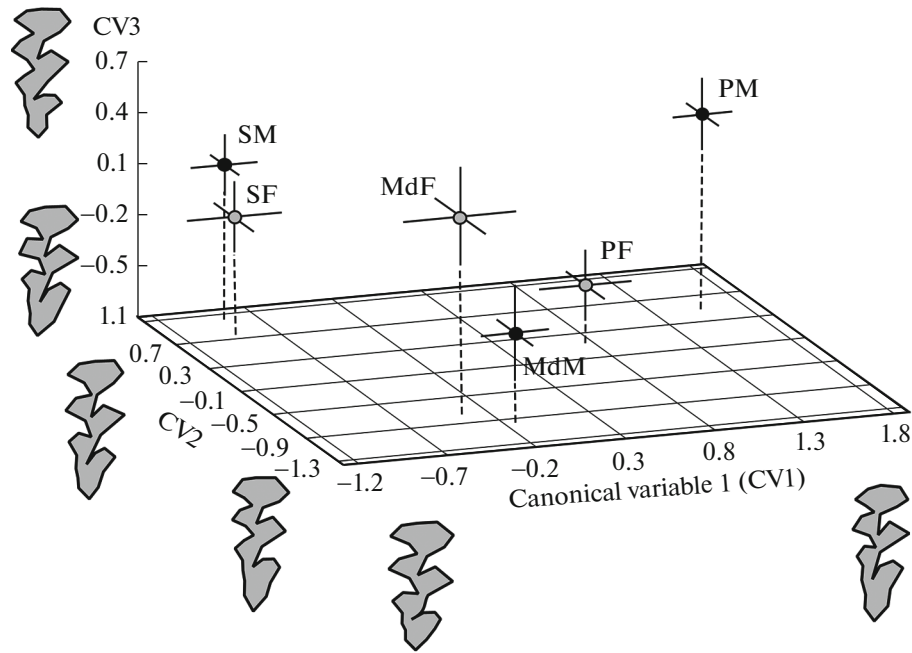


Fig. 2. Results of canonical analysis of relative warps (RWs) characterizing variation in M3 shape in samples of male (M) and female (F) gray red-backed voles from three populations of the Polar (P), Middle (Md), and Southern (S) Urals. Coordinates of sample centroids in the morphospace of the first three canonical variables (CV1–CV3) are shown with standard errors ($\pm SE$).

loop (Fig. 2). The landscape-biopic specificity of the low-mountain Visim population appeared to account for a general tendency toward an increase in the space between dentin fields in the frontal part of the posterior loop and the adjacent triangle. In turn, sex-related differences were mainly revealed in the shape of the posterior loop, which in females had a simpler configuration and often approached the *simplex* morphotype. A noteworthy fact is that these differences proved to increase from the south to the north, being minimum in the Southern Urals ($D^2 = 2.117$, $p = 0.2876$), intermediate in the Middle Urals ($D^2 = 3.488$, $p = 0.0001$), and maximum in the Polar Urals ($D^2 = 4.043$, $p = 0.0002$).

Since all samples included in the study could not be strictly collated by years, chronographic variation was evaluated using the example of males and females from the Visim population (the Middle Urals). A discriminant analysis of the Procrustes coordinates of these samples in years with high and low animal abundance revealed statistically significant between-group differences (Wilks' $\Lambda = 0.233$, $D^2 = 13.31$; Hotelling's $T^2 = 305.82$; d.f._{1,2} = 4, 90; $F = 74.02$; $p < 0.0001$). The wireframes shown in Fig. 3 refer to the contrasting landmark patterns that correspond to the lowest and highest values of the discriminant function and characterize M3 shape in different years. The differences were mainly manifested in the structure of the posterior loop, which proved to be more complex (with the fourth salient angle on the lingual side beginning to take shape) in the year of high animal abundance. The

proportion of relatively simple M3 morphotypes (with two entrant and three salient angles on the lingual side and three entrant and three salient angles on the buccal side) markedly varied between years: from $78.95 \pm 5.40\%$ in 1975 to $33.33 \pm 12.10\%$ in 1977 ($t = 3.44$, $p < 0.001$), which was in agreement with the results of discriminant analysis.

Discriminant analysis of tooth shape in males and females without regard to the year of sampling also revealed significant differences between them (Wilks' $\Lambda = 0.354$; $D^2 = 7.12$; Hotelling's $T^2 = 169.18$; d.f._{1,2} = 4, 90; $F = 40.92$; $p < 0.0001$). In particular, the posterior loop of M3 in males usually had a distinct third entrant angle on the lingual side, unlike in the majority of females.

Of special interest is the result of canonical analysis of relative warps characterizing variation in the pattern of M3 occlusal surface in allochronous samples of males and females from the Visim population (Fig. 4). Significant between-group differences manifested themselves along all the three canonical axes, with CV1 and CV2 accounting for 81.8% of between-group variance. As follows from this figure, male samples differ in the M3 shape to a greater extent than female samples: the corresponding variation polygons are distinctly separated along the CV1 axis (61.4% of between-group variance), while the polygons for female samples partially overlap in the plane of CV1 and CV2. It is noteworthy that significant sex-related differences in M3 shape were manifested in the Visim population at different levels of its abundance: the polygons for female

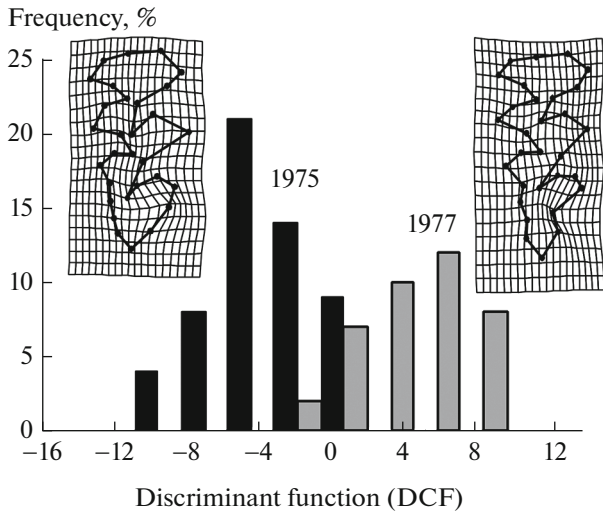


Fig. 3. Results of discriminant analysis of Procrustes coordinates characterizing M3 shape in gray red-backed voles from the Visim population in 1975 (high abundance) and 1977 (low abundance). Spline wireframes of landmark patterns at the maximum and minimum values of discriminant function are shown.

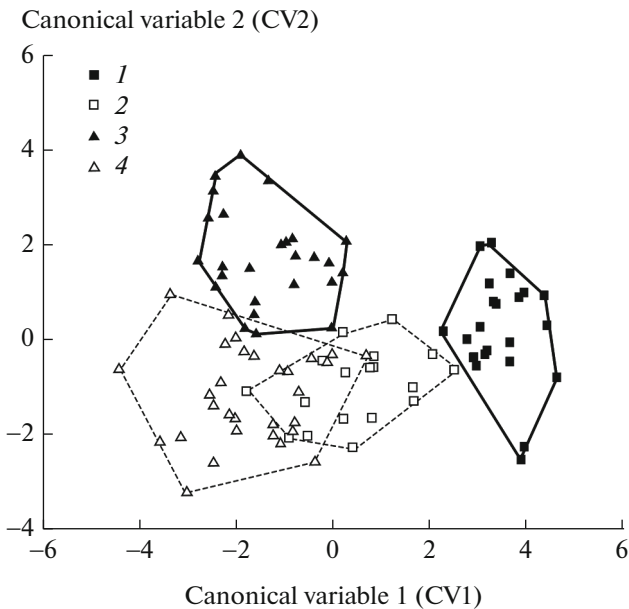


Fig. 4. Results of canonical analysis of relative warps (RWs) for M3 in samples of (1, 3) male and (2, 4) female gray red-backed voles from the Visim population taken in years of (1, 2) high and (3, 4) low abundance.

samples are displaced relative to those for male samples and occupy a specific region in the morphospace of CV1 and CV2 (Fig. 4). Thus, an abrupt switch in tooth morphogenesis at different levels of population abundance was revealed in both males and females. The phenotypic expression of sexual dimorphism in M3 differs depending on this level: sex-related differ-

ences in the 1975 samples (high abundance) are manifested along the CV1 axis, as do the differences in M3 shape between years, while in the 1977 samples (low abundance) they are more distinct along the CV2 axis.

It was of special interest to compare parameters of mean within-group morphological disparity (*MNND*) of M3 shape in males and females from the Visim population at different levels of its abundance. As follows from Fig. 5, this parameter in males in 1975 was lower than in 1977 and also significantly lower than in females. In contrast, the level of M3 morphological disparity in females was high in both 1975 and 1977. It is noteworthy that the variance of nearest neighbor distance between ordinates (*VarNND*) was also significantly higher in females than in males (1975: $F = 3.84$; $d.f._{1,2} = 17, 22$; $p < 0.01$; 1977: $F = 3.00$; $d.f._{1,2} = 30, 26$; $p < 0.01$). Therefore, it may be concluded that in 1975, under relatively favorable conditions, the level of M3 morphological disparity in males was low, and its variance was also lower; i.e., the process of tooth morphogenesis was relatively stable. The *MNND* value and the variance of *NND* increased significantly in 1977, against the background of low animal abundance, the latter providing indirect evidence for destabilization of tooth morphogenesis in males under unfavorable conditions. The same parameters in females are indicative of destabilization of M3 morphogenesis in both 1975 and 1977.

Finally, let us consider the results of canonical analysis of 14 relative warps (RW1–RW14) of M3 in samples of male and females synchronously collected in 1975 and 1977 from two populations of the Polar and Middle Urals, which provide the possibility to collate the geographic and chronographic forms of variation. Significant between-group differences were revealed along the first three canonical axes accounting for 89.2% of the total variance. According to Spearman's rank correlation test, CV1 (47.3% of the variance) was strongly correlated with the factor of geographic (south–north) location of sampling sites ($r_s = 0.77$; $p < 0.001$); CV2 (32.4% of the variance), with the factor of sampling year, mainly reflecting chronographic differences ($r_s = -0.63$; $p < 0.001$); and CV3 (9.5% of the variance), with animal sex ($r_s = 0.38$; $p < 0.001$). Based on the values of between-group variance along the three canonical axes, it may be concluded that geographic variation in this case is stronger than sex-related variation. However, this is an average effect that may manifest itself differently in each local population.

Based on these results, we performed UPGMA cluster analysis of a matrix of squared generalized Mahalanobis distances D^2 using the Chord distance metric, which was selected in view of the highest cophenetic correlation coefficient, compared to other metrics ($R_{\text{coph}} = 0.90$). Figure 6 shows that the structure of the resulting cluster, reflecting the phenomenon of geographic variation, hierarchically includes

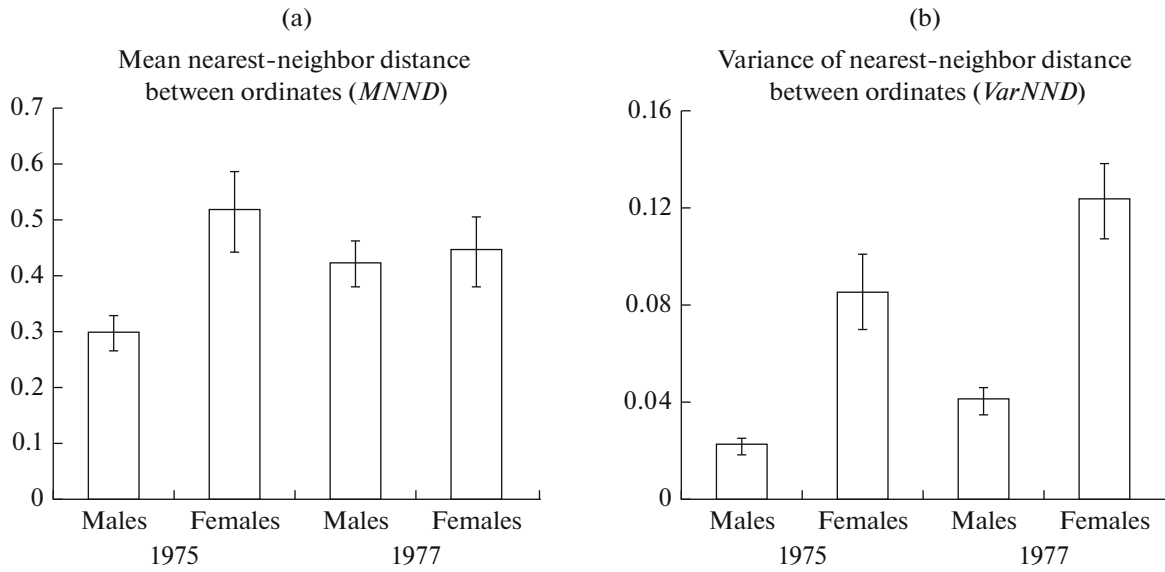


Fig. 5. Comparison of (a) the index of within-group morphological disparity (*MNND*) and (b) its variance (*VarNND*) in the morphospace of CV1 and CV2 ($\pm SE$) in samples of male and female gray red-backed voles from the Visim population taken in 1975 and 1977.

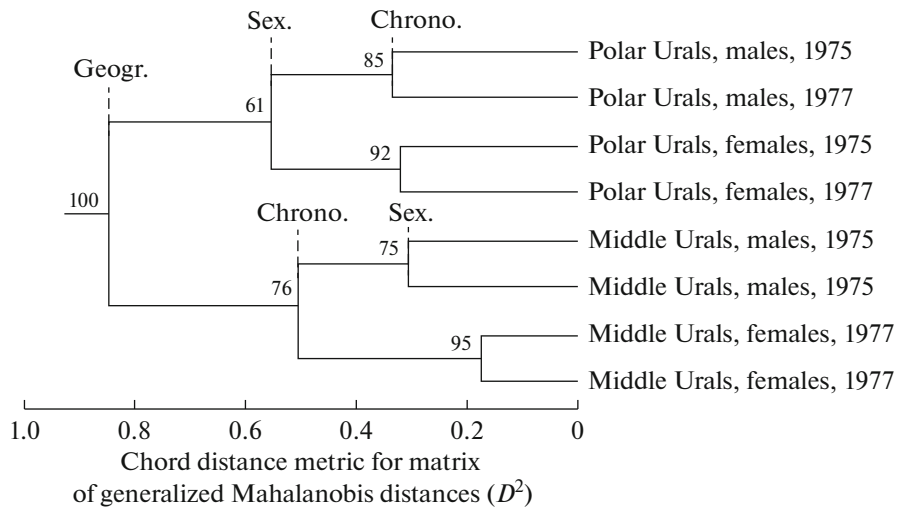


Fig. 6. Results of UPGMA cluster analysis of a matrix of generalized Mahalanobis distances D^2 (based on canonical analysis of relative warps for M3) between samples of male and female gray red-backed voles from the Polar and Middle Urals collected in parallel in 1975 and 1977. Ratios of the levels of geographic (Geogr.), chronographic (Chrono.), and sex-related (Sex.) between-group differences are indicated.

two large subclusters: one comprising all samples from the Polar Urals, and the other, all samples from the Middle Urals. The Polar Ural subcluster is distinctly divided into two hierarchically subordinate subclusters of male and female samples, and each of the latter is subdivided into the subclusters of samples taken in 1975 and 1977. The clustering of samples from the Middle Urals has a different pattern: the samples are first subdivided by years and then by sex. Thus, chronographic and sex-related differences and the relationship between them are not uniformly manifested in different populations of the Polar and Middle Urals.

DISCUSSION

In fact, the shape of teeth in *C. rufocanus* voles differs in many aspects between males and females. This is also indicative of their trophic specialization, since the degree of complexity, characterized by the numbers of salient and entrant angles of prisms, is closely related with their properties as tools for primary mechanical processing of food objects [16].

Our analysis of *C. rufocanus* voles from the Urals has revealed three forms of between-group variation in the shape and size of M3 tooth: geographic, chrono-

graphic, and sex-related variation. Geographic variation is expressed most distinctly, reflecting specific features of morphofunctional adaptation of the species to mountain biotopes at different latitudes, from the Southern to the Polar Urals. As follows from molecular genetic data [12], the intraspecific differentiation of populations accounting for this form of variation occurred in the Urals during a relatively short period of time, between 10000 and 30000 years, when this region was populated by voles of the same haplogroup C1. It is relevant in this context that haplotypes of mtDNA cytochrome *b* gene from populations of the Middle Urals (the environs of Shigaevo, Sverdlovsk oblast) and the Polar Urals (environs of Labytnangi, Yamalo-Nenets Autonomous Area) are almost identical [12]. In other words, molecular genetic changes have not yet taken place, whereas local adaptive morphogenetic rearrangements in M3 have already emerged and become fixed, with their range exceeding that of chronographic (between-year) fluctuations. It appears that the enhancement and fixation of intraspecific morphological (geographic) differences were facilitated by relative spatial and landscape-biotope isolation of local *C. rufocanus* populations in the Urals.

Different ratios of the two forms of M3 variation—chronographic and sex-related—in the typical mountain landscape of the Polar Urals and in the low-mountain taiga landscape (atypical for the species) of the Visim reserve in the Middle Urals (Fig. 6) may be interpreted as follows. In the Polar Urals, sexual dimorphism in M3 is in the forefront, while chronographic variation is less expressed. In other words, the species adapted to living in the mountains due to historically developed ability for switches in morphogenesis in a typically mountain biotope can thereby compensate chronographic (between-year) fluctuations in M3 shape and regulate their range. In the Middle Urals, conversely, the level of chronographic variation exceeds that of sex-related differences (Fig. 6). The morphogenetic compensation of chronographic variation due only to increasing sexual dimorphism is apparently difficult or impossible for the specialized species under these landscape-climatic conditions. Nevertheless, not only sex-related differences in M3 shape but also significant differences between males collected in different years have been revealed in *C. rufocanus* from the Middle Urals, with the overall size of teeth in these voles being also greater than in other mountain populations. A sharp increase in the total variety of M3 morphotypes is observed against this background: up to 16 discrete variants can be distinguished, compared to no more than 8 morphotypes found in any population from the Polar or Southern Urals [32].

It is noteworthy that within-group morphological disparity of M3 shape proved to be increased significantly in female samples from the Middle Urals. A possible explanation to this fact was that the development of females (unlike that of males) in the *C. rufo-*

canus population of the Visim reserve in 1975 was affected by a summer drought that occurred in most regions of the Urals and in many other parts of the country. As previously shown by Olenev [33] young-of-the-year bank voles *C. glareolus* (closely related to *C. rufocanus*) in the Ilmen Nature Reserve (Chelyabinsk oblast) failed to reach sexual maturity in the drought year (1975) and began breeding only in the next spring. Therefore, this drought might expectedly have an effect on *C. rufocanus* populations inhabiting more northern regions. Unlike in *C. glareolus*, however, breeding in the Visim population of *C. rufocanus* in 1975 was quite successful, and the abundance of voles was high. Therefore, destabilization of M3 shape in females from this population in 1975 and 1977 can more probably be explained by their inadaptive general morphogenetic response to development under low-mountain landscape-biotope conditions, which are atypical for the species.

Evidence for the phenomenon of switching in tooth morphogenesis in the Visim population comes from an abrupt reversal in the frequency ratio of the two characteristic M3 morphotypes, *simplex* and *typica*, between 1975 and 1977. This reversal within such a short period cannot be explained by the effect of selection alone, but it may well result from rapid stress-induced rearrangements in epigenetic DNA profiles leading to threshold switches in morphogenesis [4, 5]. The mechanisms and factors of such switch from the subprogram for *simplex* morphotype formation to the subprogram for *typica* morphotype are as yet unknown, but the results of this study show that they are not conditioned by direct allometric effects.

Morphogenesis of M3 in male *C. rufocanus* voles proved to be tolerant of the 1975 drought, unlike in females, but its destabilization in the ecologically unfavorable year 1977 was observed in both sexes. Female voles developing under atypical low-mountain landscape-biotope conditions in the Visim reserve were apparently exposed to stress either in the year of high population abundance or in the year of low abundance. Therefore, there are grounds to consider that this petrophilic species specialized to lithomorphic mountain biotopes has not yet adapted to the conditions of low-mountain taiga forests and can populate them only in certain years with favorable conditions.

CONCLUSIONS

The results of these studies are in good agreement with Chernov's compensation principle [13] at inter- and intrapopulation levels. In the Visim population, under low-mountain conditions atypical for the species, males and females show "compensatory" deviation from each other in the morphofunctional properties of teeth, thereby forming two or three trophically specialized "ecomorphs," depending on the level of population abundance. Thus, individuals with these M3 morphs compensate the role in the community of

other species that consume a different portion of trophic resources but have low abundance in a given year. In this respect, the ecomorphs play the role of additional, temporary “ecospecies” [6], contributing to the diversity of both population and community. The phenomenon of switching in morphogenesis at different population densities have already been observed in our previous study on chronographic variation in the shape of the mandible in a bank vole population from the Middle Urals [14].

Morphofunctional differences between sexes resulting from dimorphism in the shape of molar teeth are retained under relatively unfavorable conditions, when population abundance is low, but the program of tooth morphogenesis becomes different from that at a high level of abundance. Thus, a switch in M3 morphogenesis takes place, which modifies species capabilities for mechanical processing of food objects.

The polyvariant spectrum of potential morphogenetic subprograms historically formed in each local population of the species provides the possibility of rapid adaptive modifications of development in response to changes in environmental conditions. The range of variants of individual development in males and females may differ both within the population and between populations, which contributes to morphofunctional diversity and makes it possible to alleviate trophic competition between sexes and broaden the trophic potential of populations. The south-to-north increase in the sexual dimorphism of M3 shape in *C. rufocanus* populations can also be explained in terms of Chernov’s compensation principle [13]. The enhancement of intrapopulation diversity in the form of sexual dimorphism observed in severe mountain landscapes of the Polar Urals, under conditions of limited food resources and low cenotic diversity of rodents, can provide for alleviation of trophic competition in *C. rufocanus* populations. The ability for rapid differential switching in molar tooth morphogenesis revealed in male and female *C. rufocanus* voles allows this species to retain population-cenotic stability in climatically unfavorable years and also in outpost populations formed in low-mountain landscapes (atypical for the species) and severe conditions of the Polar Ural Mountains.

Thus, the phenomenon of morphogenetic plasticity of vole teeth should be taken into account not only in intraspecific diagnosis and paleoecological interpretations [34] but also in evolutionary synecology [6] as a manifestation of Chernov’s compensation principle [13] manifested at both intra- and interpopulation levels.

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