

Evolutionary–Ecological Analysis of Trends in Phenogenetic Variation of Homologous Morphological Structures: From Populations to Ecological Series of Species

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Abstract—An evolutionary–ecological analysis of homologous variations in cranial morphological structures (phenes) has been performed at the level of populations and subspecies exposed to technogenic, climatic, and landscape–geographic changes in the environment, as well as with ecological series of 46 species and infraspecific forms differing in ecological specialization within the family Cricetidae. On this basis, consistent manifestations of phenogenetic variation have been revealed. Species with the same ecological specialization show parallel directional changes in the frequencies of homologous phenes and their individual combinations. These changes apparently have adaptive significance and result from rearrangements in the ancestral epigenetic system. It is shown that similar ecological requirements imposed by the environment historically lead to unidirectional transformations of homologous morphological structures in different species, which may account for high incidence of homoplasy as well as for the parallel and, in part, directional evolution of closely related taxa with similar ecological specialization.

Key words: evolutionary ecology, phenogenetic variation, homologous morphological structures, nonmetric characters, rodents.

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The leading role of ecological factors in evolutionary rearrangements of developmental processes, as understood by Shvarts (1980), has gained due recognition in world science only in recent years (Gilbert et al., 1996; Gilbert, 2003; etc.). This concerns not only the understanding of evolution as an ecological phenomenon (Pianka, 1981), but also the realization that evolutionary rearrangements are associated with changes in the process of development at the level of populations and species. The probability of evolutionary–ecological changes is especially high in new technogenically altered environments and, primarily in transformed communities (Moyne and Neige, 2007). Studies in evolutionary ecology (Smirnov, 2006) show that the ecological component of these rearrangements is of special significance.

Hardly any region of the world has escaped some degree of landscape transformation caused by long-term anthropogenic impact. This impact on the environment is increasing, and acceleration of microevolutionary transformations in populations of animals, plants, and microorganisms can well be expected under such conditions (Vasilyev and Bol'shakov, 1994; Vasilyev and Vasilyeva, 2005). This concept agrees in part with the results of studies by Zherikhin (2003), who revealed abrupt, catastrophic changes in the com-

position of entomofauna in the Mesozoic, at the Upper Cretaceous boundary. This author also considers that the signs of impending global biocenotic crisis distinctly manifest themselves today, against the background of increasing landscape transformation under anthropogenic impact.

In the light of these views, it appears highly relevant to perform an evolutionary–ecological analysis of trends in the phenogenetic variation of homologous morphological structures (phenes) in the outpost populations of species colonizing areas with new environmental conditions (including technogenic) and also of intraspecific covariation in sympatric species and of parallel morphological transformations in the taxa representing different ecological series and life forms. Remember that homologous phenes of bilateral characters are analyzed on each body side separately (i.e., one body side is taken as an observation unit); therefore, such studies deal with intraindividual variation, which is of epigenetic nature (Berry and Searle, 1963; Astaurov, 1974; Zakharov, 1987; Vasilyev, 2005). Following Krenke (1933–1935), who described intraindividual variation of bilateral structures in plants, we term this phenomenon as phenogenetic variation (Korona and Vasilyev, 2000; Vasilyev, 2009). Phenoge-

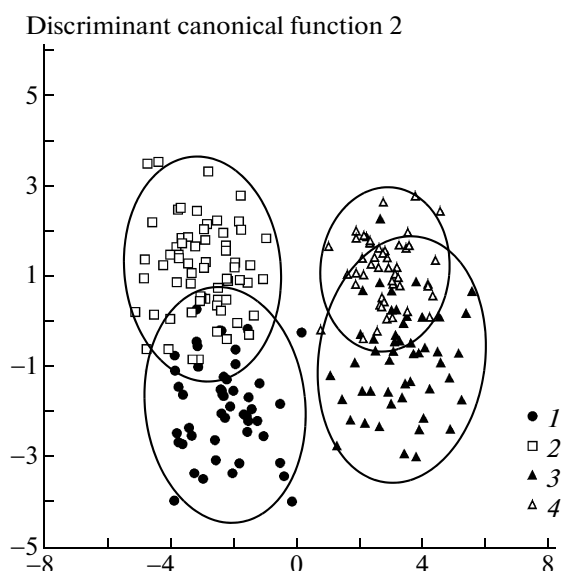


Fig. 1. Results of canonical discriminant analysis of principal components for individual compositions of homologous nonmetric cranial phenes in the northern and southern subspecies of root and narrow-skulled voles: (1) *Microtus oeconomus hahlovi*, (2) *M. o. oeconomus*, (3) *M. gregalis*, and (4) *M. g. gregalis*.

netic variation is accounted for by two components, organizing and stochastic: the former is epigenetic variation (Vasilyev, 2005), which is governed by epigenetic thresholds established for each population or taxon; the latter is realizational variation (Strunnikov and Vyshinskii, 1991), which is accounted for by random fluctuations in the epigenetic system and provides the possibility of choice (switch) between alternative developmental pathways (Vasilyev, 2009). Therefore, an evolutionary–ecological analysis of manifestations of phenogenetic variation in homologous morphological structures can aid in solving the problem and understanding the ecological basis of parallel evolutionary changes (Tatarinov, 1987; Rautian, 1988).

In previous studies (Vasilyev and Vasilyeva, 1995; Vasilyeva et al., 2003), we described parallelism in the manifestation of homologous discrete variations in nonmetric skeletal characters (phenes) of rodents from natural populations exposed to chronic irradiation at different dose rates in the impact zone of the Eastern Ural Radioactive Trace (EURT), which was formed in the Southern Urals after the 1957 accident at the NPO Mayak radiochemical plant in Kyshtym. In the pygmy wood mouse (*Sylvaemus uralensis*), for example, a comparative analysis of northern and southern impact samples (from areas located along the EURT axis) and control samples (from beyond the EURT) revealed parallel changes in the occurrence frequencies of 17 out of 34 aberrant morphological structures studied: these frequencies were increased in

both northern and southern impact samples, with their excess over the control level being similar in both cases (Vasilyeva et al., 2003). A discriminant analysis of the impact and control samples with respect to principal components (PCs) of intraindividual phene compositions showed that the centroids of geographically distant (southern and northern) impact samples were located close together in the morphospace formed by the discriminant functions, whereas the centroids of control samples proved to be distributed in the pattern proportional to that in the field. In other words, similar unidirectional phenogenetic transformations took place in both impact populations, despite that the corresponding levels of chronic radiation exposure differed by almost three orders of magnitude (Vasilyeva et al., 2003). Similar phenomena were also observed in groups of red voles from the EURT area (Vasilyev and Vasilyeva, 1995; Vasilyev, 2005).

In view of these data, the main problem can be formulated as follows: whether the parallel phenogenetic modifications of homologous morphological structures at the intraspecies and species levels take place under the effect of similar changes in ecological conditions?

The purpose of this study was to perform an evolutionary–ecological analysis of phenogenetic variation in homologous variants (phenes) of cranial morphological structures in model rodents at different levels of taxonomic hierarchy: from intraspecific forms of different species to aggregations of species with similar ecological specialization within the family Cricetidae. Multidimensional ordination of homologous cranial phenes was used as a means to solve two problems: (1) to compare the directions of phenogenetic variation in sympatric southern and northern subspecies of two vole species, the root vole (*Microtus oeconomus*) and the narrow-skulled vole (*M. gregalis*), and (2) to make an attempt to differentiate the groups of rodent (Cricetidae) species differing in ecological specialization by the frequencies of homologous cranial morphological structures.

MATERIAL AND METHODS

At the preliminary stage, we identified and homologized 107 phenes of nonmetric cranial characters in 46 species and intraspecific forms of the family Cricetidae (Vasilyeva, 2006). These were discrete variations in the skull structure: the appearance, duplication, or reduction of certain foramina for nerves or blood vessels; reduction of bone fragments; appearance of intercalary bone elements; reduction of buccal teeth; etc. Studies were performed with the skulls of male and female animals from the craniological collection kept at the Laboratory of Evolutionary Ecology, Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences. On the whole, 1502 skulls were examined, including 104 skulls of animals from

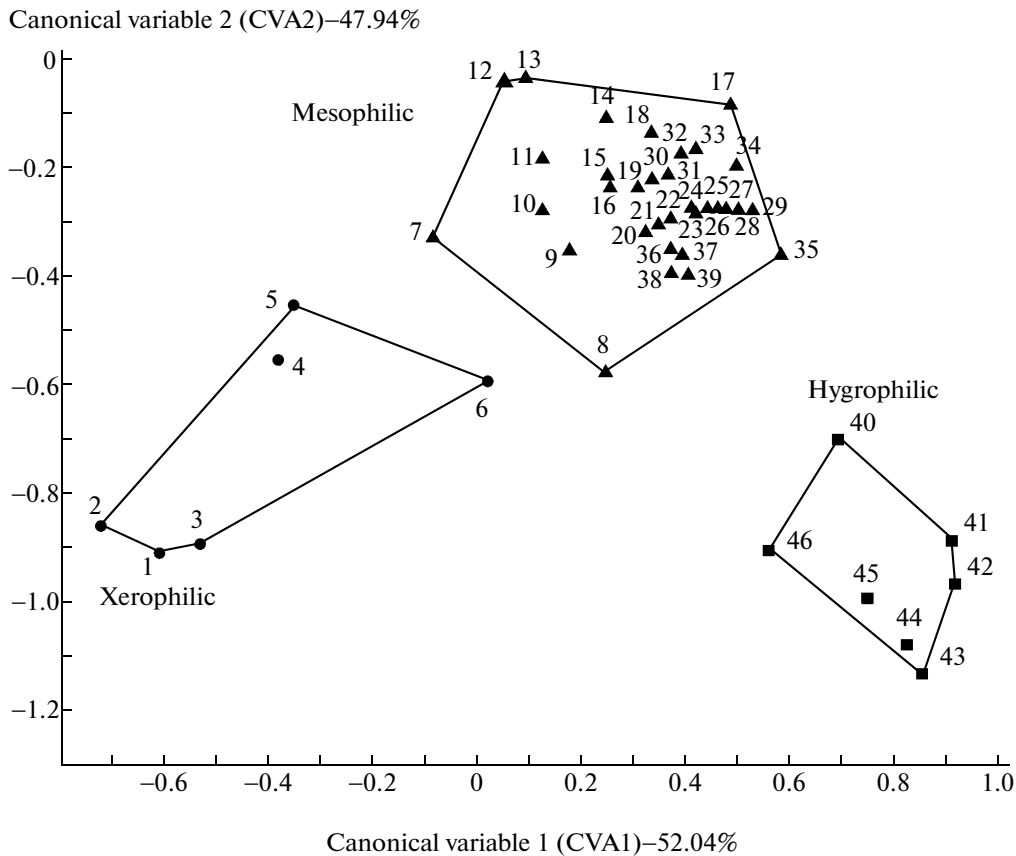


Fig. 2. Results of canonical discriminant analysis of principal components for occurrence frequencies of nonmetric cranial phenes in (1–6) hygrophilic, (7–39) mesophilic, and (40–46) xerophilic rodent species: (1) *Cricetulus migratorius*, (2) *Mesocricetus auratus*, (3) *Ellobius talpinus*, (4) *Lagurus lagurus*, (5) *Lasiopodomys brandti*, (6) *Microtus socialis*, (7) *Cricetus cricetus*, (8) *Microtus gregalis*-1*, (9) *Prometheomys schaposchnikovi*, (10) *Microtus carruthersi*-1, (11) *Myopus schisticolor*, (12) *Microtus transcaspicus*-1, (13) *Microtus majori*, (14) *Myodes gapperi*, (15) *Alticola macrotis*-1, (16) *Myodes rutilus*-1, (17) *Alticola strelzowi*, (18) *Microtus carruthersi*-2, (19) *Alticola lemminus*-1, (20) *Microtus juldaschi*, (21) *Dicrostonyx torquatus*, (22) *Microtus ilaeus*-1, (23) *Microtus pennsylvanicus*, (24) *Chionomys gud*, (25) *Alticola argentatus*, (26) *Microtus arvalis*, (27) *Microtus levis*, (28) *Microtus gregalis*-2, (29) *Microtus ilaeus*-2, (30) *Alticola lemminus*-2, (31) *Alticola fetisovi*, (32) *Myodes rufocanus*, (33) *Chionomys roberti*, (34) *Myodes glareolus*, (35) *Myodes rutilus*-2, (36) *Lemmus lemmus*, (37) *Microtus agrestis*, (38) *Microtus transcaspicus*-2, (39) *Alticola macrotis*-2, (40) *Microtus middendorffi*, (41–43) *Microtus oeconomus*, (44) *Microtus maximowiczii*, (45) *Ondatra zibethicus*, and (46) *Arvicola terrestris*

*Numerals after species names indicate intraspecific forms.

vivarium colonies of the northern and southern subspecies of the root vole (*Microtus oeconomus hahlovi* and *M. o. oeconomus*) and the narrow-skulled vole (*Microtus gregalis major* and *M. g. gregalis*). The colonies of both species were derived from the samples of founder animals trapped in populations inhabiting geographically close regions: the Polar Urals and Yamal Peninsula in the north and the Chelyabinsk and Kurgan regions in the south.

The presence or absence of homologous phenes was coded 1 or 0, respectively. As recommended by Astaurov (1974), bilateral structures were analyzed on each body side separately; therefore, the occurrence frequencies of bilateral phenes were calculated relative to the number of body sides, whereas those of medial phenes, relative to the number of individuals examined.

In intergroup comparisons of intraindividual (phenetic) variation in narrow-skulled and root vole subspecies, we initially employed the PC method for multidimensional ordination of phene compositions on the left and right sides of the skull and then used the values of PCs for canonical discriminant analysis. The groups of Cricetidae species differing in ecological specialization were compared with respect to the occurrence frequencies of arbitrarily chosen phenes (we decided to take 43 phenes with even ordinal numbers from a random part of the frequency matrix for all 107 phenes). The matrix of these frequencies (by species) was ordinated by the PC method. Then, according to the Jolliffe cut-off value, ordinates of taxa for 27 first PCs were taken to perform canonical analysis of the ecological groups of species. All calculations were

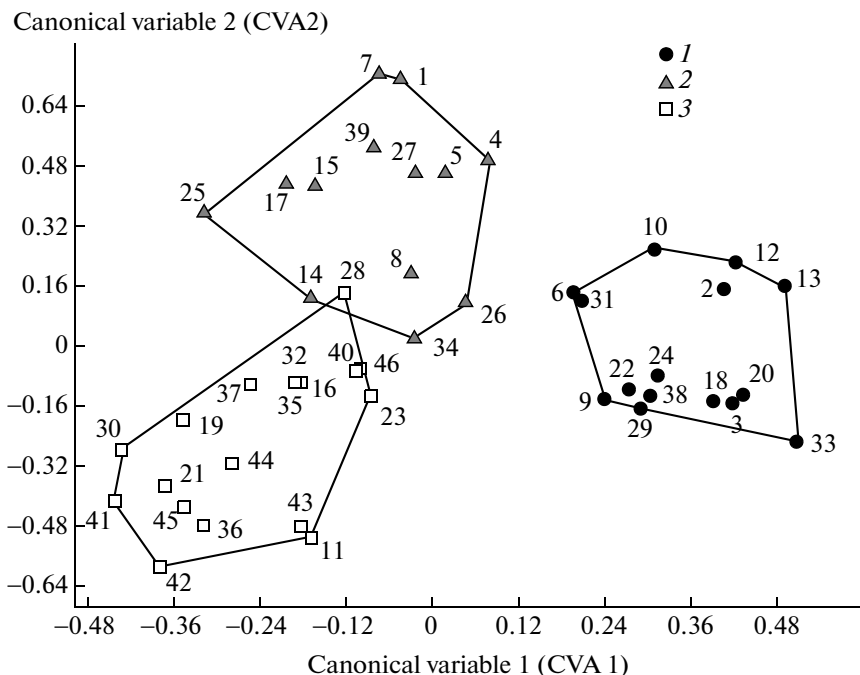


Fig. 3. Results of canonical discriminant analysis of principal components for occurrence frequencies of nonmetric cranial phenes in rodents of (1) southern, (2) temperate, and (3) northern latitudes. Species are numbered as in Fig. 2.

made with programs Statistica 5.5 è PAST 2.0 (Hammer et al., 2001).

RESULTS AND DISCUSSION

Previously, we revealed the phenomenon of parallel, unidirectional rearrangements in the epigenetic system marked by homologous phenes of nonmetric cranial characters in neighboring rodent populations. This provided a basis for analyzing the above phenomenon at a higher level of infra- and supraspecific hierarchy, by comparing representatives of the northern and southern subspecies of different rodents. Accordingly, we considered variation patterns of homologous phenes on the natural model of southern and northern subspecies of the root vole and narrow-skulled vole, the species representing epigenetically remote subgenera *Pallasiinus* and *Stenocranius*.

In such a comparative study, it was interesting to estimate the relative degree of epigenetic differentiation between the northern and southern subspecies of these voles. It could be assumed in advance that this differentiation would be stronger in the narrow-skulled than in the root vole, taking into account the long-term spatial isolation of its subspecies—probably, since the development of the forest zone (Fadeeva and Smirnov, 2008)—and obvious morphological differences between them (in body size, proportions of the skull, etc.). On the other hand, we could check whether unidirectional, parallel changes in the epigenetic system take place when two rodent species of the same genus (*Microtus*) develop adaptations to envi-

ronmental conditions of the north. Such changes could be estimated from unidirectional displacement of sample centroids for the northern and southern subspecies of the voles compared, since calculations in both cases were made by the same method and with the same set of homologous phenes.

To check this hypothesis, we made a comparison involving the two subspecies of each vole, northern (*M. oeconomus hahlovi* and *M. gregalis major*) and southern (*M. o. oeconomus* and *M. g. gregalis*). Canonical discriminant analysis revealed three statistically significant functions. Interspecific differences between the samples of the narrow-skulled and root voles manifested themselves along the axis of the first discriminant canonical function (DCF1), which accounted for 75.7% of the total variance (Fig. 1). Along the DCF2 axis, unidirectional differences between the centroids of samples representing the northern and southern subspecies were observed (15.4% of the variance in intergroup differences): in both species, the ellipsoids covering 95% of variance in the coordinates of individuals were displaced downward in the northern subspecies and upward in the southern subspecies (Fig. 1). Since differences between the samples of northern and southern subspecies along this axis have the same direction, they indicate that both vole species have undergone similar phenogenetic changes related to their acclimation in the north. In fact, this is an example of unidirectional, parallel transformations of the epigenetic system in different species that took place during the development of corresponding adaptations.

Differences between the centroids of intraspecific forms that have different directions in the two species manifested themselves along the third axis (8.9% of the variance), characterizing species-specific responses of their epigenetic system to the same habitat conditions. It may well be that different epigenetic systems historically operating in the same environment, either in the north or in the south, have provided for the formation of different combinations (compositions) of certain homologous phenes.

The level of intraspecific differentiation in the expression of phenes between the northern and southern subspecies in the narrow-skulled vole proved to be only slightly higher than in the root vole, with the squared Mahalanobis distance (used as an indirect measure of epigenetic divergence) being $D^2 = 11.9$ vs. 10.6, respectively. Since these forms of the narrow-skulled vole have long been spatially isolated from each other (Fadeeva and Smirnov, 2008) and live in environments with sharply differing conditions (tundra vs. forest–steppe), a much higher degree of differentiation between them could be expected.

Species diagnosis by individual phene compositions is 100% reliable, which is not surprising: the taxa studied belong to two different subgenera, and the level of epigenetic divergence between them averages $D^2 = 38.93$, being several times higher than the average level of intraspecific divergence in either species ($D^2 = 11.25$). The accuracy of individual identification within the species is also high, ranging from 89% in the root vole to 92% in the narrow-skulled vole, which is evidence for a fairly high level of intraspecific epigenetic divergence.

The expression of phenes is highly resistant to the direct impact of various ecological factors, which makes it possible to use the phenomenon of phenogenetic variation for indirectly estimating the extent of epigenetic differences between the animal groups of interest. The measure of epigenetic divergence is additive and includes at least two components, phylogenetic and evolutionary–ecological. The phylogenetic component is accounted for by the inertia and phylogenetic stability of the regulative epigenetic system, which result in the phenomenon of transitive polymorphism (Meyen, 1988). The evolutionary–ecological component, in turn, has two aspects: species-specific (taxon–environment interactions) and ecological–historical (parallelism in phene expression as a result of historical adaptation of taxa to similar ecological conditions).

The above example of parallel comparison between the northern and southern subspecies of the narrow-skulled and root voles (both of the genus *Microtus*) can be used to illustrate the relationship between these components. The intergroup phenetic differences between the species (the phylogenetic component of epigenetic divergence) accounted for about 76% of the total variance in phene expression; the evolutionary–ecological component, for about 24%, with 15% being

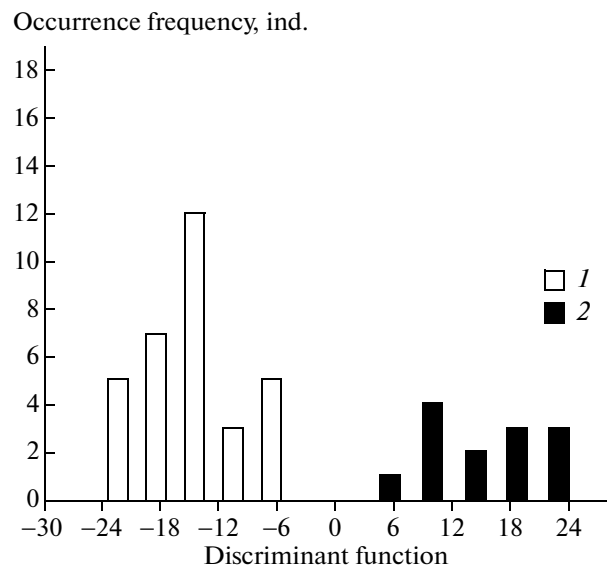


Fig. 4. Results of canonical discriminant analysis of principal components for occurrence frequencies of nonmetric cranial phenes in rodents of the family Cricetidae: (1) widespread plain species, including inhabitants of foothills; (2) specialized mountain species.

attributed to parallelism in phene expression (the ecological–historical aspect) and 9%, to differences in the morphogenetic response of syntopic subspecies to the same environmental conditions (the species–specific aspect). This example shows that the phylogenetic component is many times superior to the evolutionary–historical component in its contribution to the general measure of epigenetic divergence.

Thus, an analysis of intraspecific forms revealed unidirectional, parallel changes attributable to similar adaptive transformations of the epigenetic system in different species. Hence, it could be expected that similar parallel phenomena would be revealed by comparing the series of species differing in ecological specialization. We considered three aspects of general ecological specialization: hygrophily, expansion to northern latitudes, and adaptation to life in the mountains.

Let us first consider the results of comparison of 46 species and intraspecific forms with respect to the degree of hygrophily. All these taxa were conditionally divided into three groups: hygrophilic (the water vole *Arvicola terrestris*, muskrat *Ondatra zibethicus*, root vole, etc.), mesophilic (the majority of species), and xerophilic (the Brandt's vole *Lasiopodomys brandti*, steppe lemming *Lagurus lagurus*, gray dwarf hamster *Cricetulus migratorius*, etc.). As described in Material and Methods, the matrix of homologous phene frequencies in the ecological groups of taxa was ordinated by the PC method and subjected to canonical discriminant analysis, which revealed significant differences between these groups along the axes of two canonical variables, CVA1 and CVA2 (Fig. 2). Along the CVA1

axis, these differences manifest themselves in the formation of three distinct clusters, from xerophilic taxa on the left to hygrophilic taxa on the right. Along the CVA2 axis, the dominant mesophilic cluster is above two other clusters located at approximately the same level.

In the second ecological series, the taxa were ranked into three classes with respect to the degree of latitude marking the northern boundaries of their ranges: (1) southern (up to 50° N), (2) temperate (50 to 65° N), and northern taxa (above 65° N). This series could be conditionally regarded as reflecting the historically acquired levels of general cold tolerance.

The results of canonical discriminant analysis revealed significant differences between the taxa of these classes (Fig. 3). Along the CVA1 axis, which accounts for 79.9% of the intergroup variance, they are segregated into three distinct clusters differing in cold tolerance: northern taxa on the left (in the zone of negative values), temperate taxa in the middle, and southern taxa on the right, in the zone of high positive values. Along the CVA2 axis (20.0% of the variance), certain specificity of temperate taxa relative to northern taxa manifests itself. It is noteworthy that, regardless of long-term spatial isolation of the northern *M. gregalis* subspecies, which apparently dates from the Late Pleistocene (Fadeeva and Smirnov, 2008), its ordinate in the plot (no. 28) joins the cluster of temperate taxa, approaching the ordinate of the normative subspecies (no. 8). This fact indirectly indicates that adaptive epigenetic rearrangements in the northern subspecies have not yet been completed: it retains some features of the southern form and, therefore, can still be classified with the taxa of temperate latitudes.

The results of these two comparisons show that different species that belong to different supraspecific taxa but are similar in ecological specialization (with respect to aquatic or riparian mode of life) or cold tolerance are characterized by similar patterns of phene frequencies, which reflect unidirectional (parallel) adaptive phenogenetic transformations of these taxa. It is as yet unclear what exactly accounts for such similarity of phene frequency patterns in the vole species studied, but the very fact of their convergence indicates that this phenomenon is not accidental and can be interpreted as evidence for similar rearrangements of the epigenetic system in each ecological series of species.

In the third ecological "series," taxa were grouped with respect to the degree of specialization for life in the mountains. In this case, we managed to distinguish only two groups: inhabitants of plains and foothills (further subdivision was difficult) and specialized inhabitants of high mountains. The latter group included Asian mountain voles of the genus *Alticola* (except *A. strelzowi*); endemics of the Caucasus such as the long-clawed mole vole *Prometheomys schaposchnikovi*, Caucasian snow vole *Chionomys gud*, and Robert's snow vole *Chionomys roberti*; and some other spe-

cies. The results of discriminant analysis revealed significant differences between these groups (Fig. 4), with their magnitude being similar to that in previous comparisons. The attribution of taxa to one or the other group proved to be 100% correct. Therefore, specialization for life in the mountains in different rodent species is also associated with the formation of a similar, unidirectional pattern of phene frequencies, which apparently reflects the adaptive nature of epigenetic divergence of mountain forms.

CONCLUSIONS

The results of this study agree with the evolutionary–ecological theory of geographic speciation as understood by Shvarts (1980). This author considered that "species are species not because they do not interbreed, but they do not interbreed because they are species," thereby emphasizing the leading role of ecological (rather than molecular genetic) factors in the evolutionary process and the occurrence of irreversible morphophysiological shifts in the norm of reaction to an altered environment. At the same time, our data do not contradict the views of N.I. Vavilov, N.P. Krenke, and S.V. Meyen, confirming the existence of phenogenetic series of homologous variation in morphological structures, the rule of related deviations of homologous characters in distant taxa (Krenke's rule), and the phenomenon of transitive polymorphism (according to Meyen).

Our comparative analysis have shown that unidirectional, parallel changes in the pattern of homologous phene frequencies manifest themselves at different hierarchical levels, from neighboring populations and intraspecific forms to supraspecific ecological groups. Such changes are accounted for by similarity of ecological requirements and unity of ancestral epigenetic systems of different hierarchical levels (from subspecies to taxa of different subfamilies) that have been formed within the family Cricetidae in the course of evolution.

Long ago, Henry F. Osborn (1933; cited from Rautian, 1988) described the theoretical possibility of independent parallel rearrangements in taxa of close origin, which he named aristogenesis. This author regarded the profound structural unity of independently and parallelly formed homoplastic properties as a manifestation of limitations imposed due to intrinsic, hereditary properties of organisms. It may be hypothesized that these parallel micro- and macro-evolutionary changes in the expression of homologous phenes are related to epigenetically conditioned transitive polymorphism (Meyen's term) translated in the series of phyletic lines and operating as a factor restricting and governing subsequent morphological evolution at the level of species and, possibly, supraspecific taxa. Our results can be interpreted as indirect evolutionary–ecological evidence for the possibility of parallel but independent aristogenetic trans-

formations of homologous morphological structures in closely related taxa. This may lead to mass incidence of homoplasy, i.e., to the parallel and, in part, directional evolution of related taxa with similar ecological specialization.

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