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GENERAL BIOLOGY

Analysis of Geographical Variability of Morphogenetic Trajectories Using the Mole Vole (*Ellobius talpinus* Pall.) as an Example

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Absttract—Using the methods of geometric morphometrics, we have revealed the phenomenon of geographical variability of morphogenetic trajectories when doing side-by-side comparisons of mandibular shapes in individuals of different ages from three southern Trans-Ural populations of the mole vole (*Ellobius talpinus* Pall.) in the common morphospace.

Keywords: variability, morphogenesis, mole vole

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Geographical variability usually characterizes stable interpopulation differences for a particular feature, as well as manifestation of intraspecies differentiation and divergence [1, 2]. Geographical variability between different stages of postnatal morphogenesis has not been investigated up to now. Geometric morphometrics [3–5], which allows separate investigation of size and shape variability, assumes morphogenetic interpretation of changes in the shape of biological objects as a single multimeric character [3, 5] and can contribute to solving this problem.

Previously, Alberch et al. [6] substantiated the concepts of *ontogenetic trajectories* developed later on by Mina [7, 8], which characterize the consequence of phenotypic changes in individuals at different stages of postnatal ontogenesis.

Geometric morphometrics makes it possible to describe the changes in the shape (except for the size) of objects in ontogenesis; in this context, the case in hand is morphogenetic changes [3–5]. Hence, we proposed to define successive changes in the shape of object in the morphospace at different stages of its postnatal development as a *morphogenetic trajectory* [5]. The hypothetical morphogenetic trajectories of geographically distant populations can be represented in the morphospace as the following probable types: **a**, syntopic, when trajectories are almost identical; **b**, parallel, i.e., shifted relative to each other without divergence; **c**, divergent, when trajectories diverge with age; **d**, equifinal, when initially distant trajectories finally converge; **e**, allotopic, if trajectories are almost parallel but shifted relative to each other; and **f**, allotopic–divergent, i.e., the same but with the divergence of trajectories (Fig. 1).

The study was aimed at verification of the hypothesis that geographical variability can manifest itself at the level of not only individual phenotypic characteristics, but also morphogenetic trajectories. The main problem thereupon was to use the methods of geomet-

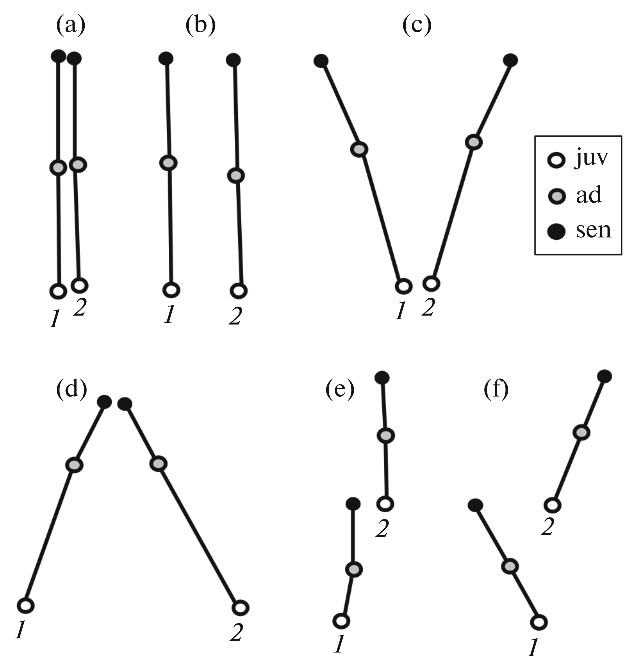

Fig. 1. The hypothetical types of morphogenetic trajectories (the stages of morphogenesis: juv, juvenile; ad, adult; sen, senile) of geographically distant populations of the species (*1, 2*) in the common morphospace: (a) syntopic, (b) parallel, (c) divergent, (d) equifinal, (e) allotopic, (f) allotopic-divergent.

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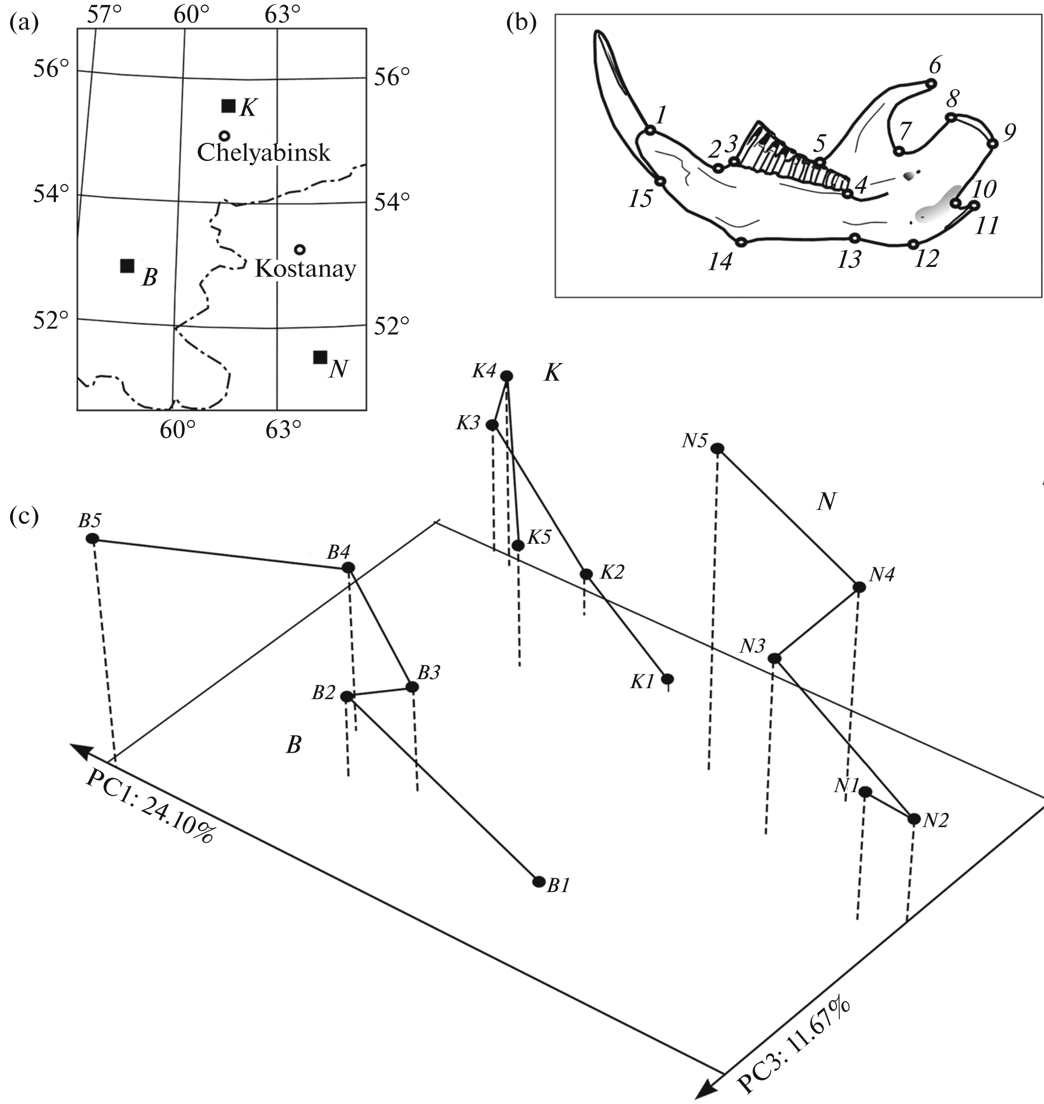

Fig. 2. The geographical positions of the Kunashak (*K*), Baymak (*B*), and Naurzum (*N*) populations of the mole vole in the Southern Trans-Urals (a); the location of landmarks (*1–15*) on the lingual side of the right mandible (b); the ordination of centroids of age groups (*1–5*) and the constructed trajectories of changes in the shape of the mandible in the common morphospace along the first three principal components: PC1–PC3 (c).

ric morphometris in the study of geographical variability of mandibular shape in groups of individuals of different ages from geographically distant populations of the model rodent species, the mole vole (*Ellobius talpinus* Pall., 1770), in the Southern Trans-Ural region.

The collections from the Museum of the Institute of Plant and Animal Ecology of the Ural Branch of Russian Academy of Sciences, used in the study included the samples from three distant populations of the mole vole: (1) Kunashak (Kunashak settlement, Chelyabinsk oblast, 95 individuals: 55°35′ N, 61°40′ E); (2) Baymak (Baymak settlement, the Republic of Bashkortostan, 106 individuals: 52°33′ N, 58°13′ E); and (3) Naurzum (Naurzum State Nature Reserve, northern Kazakhstan, 106 individuals: 51°31′ N, 64°29′ E). The geographical positions of the populations are shown in a schematic map (Fig. 2a). The southern Naurzum population is at approximately the same longitude as the northern Kunashak population, while the geographically intermediate (Baymak) population is slightly shifted westwards.

The age was determined by the stage of root development of the first lower cheek tooth, m1 [9]. The samples are represented by individuals of five age groups: (1) young-of-the-year or 0+, (2) 1+, (3) 2+, (4) 3+, (5) a pooled group of old animals (4+ and older, up to 6 years old). The mandible was chosen as a research object because the mole vole actively uses the lower cutting teeth for digging and foraging for food, and its morphological variability represents functional adaptation to the local conditions [10]. By using the TPS software [11, 12], the configurations of 15 landmarks were put onto digital images of the right (lingual) side of the mandible to characterize its shape variability (Fig. 2b). The least-squares generalized Procrustean analysis (GPA) was used [3], and the Procrustes shape coordinates characterizing the variability of mandibular shape were used for intergroup comparison. Statistical analysis was performed using the TPS [11, 12], PAST 2.17c [13], and MorphoJ 1.6d [4] software.

The method of principal components was used for ordination of the Procrustes shape coordinates and then the mean values of each subsequent age group were connected with a line in three-dimensional morphospace formed by the first three principal components (PC1–PC3) to construct the "morphogenetic trajectories" for the three compared populations (Fig. 2c).

The proportion of variance explained along the first three principal components was 51.1%. There were no significant Spearman correlations between the axis values and sex; hence, that it was possible to compare combined-sex samples.

The localization of morphogenetic trajectories of three populations in the common morphospace is largely consistent with their mutual geographical positions in the Southern Trans-Ural region. The ordinates along the first and third axes are significantly related to geographical positions of the populations (PC1 to latitude $r_{sp} = 0.72$, $p = 0.0025$ and longitude $r_{sp} = 0.70$, $p = 0.0037$; PC3 only to longitude $r_{sp} = 0.68$, $p = 0.0054$), while those along the second axis (PC2) are related only to age ($r_{sp} = 0.80$, $p = 0.0003$). The fourth (PC4) and fifth (PC5) components are also significantly related to the geographical position and age ($p < 0.01$). However, their contribution to total dispersion is low (7.7 and 6.9%, respectively) and hence they are not considered here separately. Nonparametric multidimensional two-way analysis of variance (PERMANOVA) with 10000 permutations in the complex of the first five principal components has shown significant effects of geographical positions of the samples with regard to latitude ($F = 16.63$; $p < 0.0001$) and age ($F = 5.46$; $p < 0.0001$), but the interaction between these factors proved to be nonsignificant ($p = 0.9306$).

The morphogenetic trajectories of the populations occupy different areas of the morphospace (see Fig. 2c); therefore, it can be considered that mandibular morphogenesis is specific for each population. The trajectory of the Kunashak population is shifted relative to the Naurzum population, while the trajectory of the Baymak population takes an intermediate position in the figure with a leftward shift from the former two. If we compare the positions of ordinates of the same age groups of three populations in the morphospace, the shape of the mandible at each successive stage of morphogenesis will be different in proportion to their geographic remoteness. Thus, the localization of ordinates of all age groups forming morphogenetic trajectories in the common morphospace of the three compared populations represents the geographical variability of ontogenetic changes in mandibular configuration. At the same time, the general direction of morphogenetic trajectories is the same: in all populations, the trajectories of changes in the shape of the mandible are almost parallel from the youngest to senile groups. This direction is partially consistent with the shift of northern samples relative to southern samples, because the groups of young animals in all populations are conditionally more "southern" in the morphospace, while the groups of senile animals are more "northern." Since the positions of morphogenetic trajectories in the morphospace correlate with their geographical positions, the revealed pattern of changes in the trajectories best corresponds to the allotopic or allotopic-divergent type described above (see Fig. 1). Finally, it can be concluded that this digging species, while gradually penetrating from southern parts of the species area to its northern parts (the Kunashak population inhabits the northern boundary of the area), has developed the peculiarities of postnatal mandibular morphogenesis specific for each local population at almost all stages of development. Thus, the population structure and differentiation of this species can exemplify the initial stages of geographical formation, and the morphogenetic differences between the populations probably reflect the successive stages of microevolutionary changes in the mole vole when the species inhabited the steppe and forest steppe landscapes of the Southern Trans-Ural region.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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