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GENERAL BIOLOGY

Long-Term Morphogenetic Aftereffects of Muskrat Acclimatization in Western Siberia

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Acclimatization of invasive species is among the most topical problems in general biology [1–3]. In this regard, evolutionary and ecological research into long-term aftereffects caused by acclimatization of model species, including assessment of the rates and directions of their morphogenetic alterations, is most important.

Acclimatization is the adaptation of introduced species to new cenotic environment [4] associated with their morphogenetic alterations, on the one hand, and rearrangements in specific components of aboriginal communities caused by invasion of new species, on the other hand.

An adequate model for studying the basic processes in adaptation of a species to new abiotic and biotic environments is the muskrat (*Ondatra zibethicus* L.) acclimatization in Eurasia. The muskrat acclimatization may be regarded as an analog of geographic formation, and the rate and efficiency of the initial microevolutionary stages may be estimated according to population morphogenetic changes [4].

The goal of this study was to assess long-term morphogenetic consequences of the muskrat acclimatization in Western Siberia using geometric morphometry (GM) [5–7]. Several studies have demonstrated the efficiency of GM methods when clarifying specific features of morphogenetic processes in different species and intraspecific groups [6–8].

The muskrat acclimatization in Western Siberia started in 1929 after the first lot of animals originating from a northern Canadian population was released in the Dem'yanka River basin [3, 9]. Then, muskrats spread artificially and naturally to the lakes of Kurgan oblast and, later, in the northern part of Tyumen oblast. By the end of the 20th century and until now, the abundance of this species decreased everywhere, bringing it to the so-called third ("population") phase of acclimatization [10], which we believe to be more correctly referred to as the "population cenotic" phase.

Smirnov and Shvarts [9] compared the southern and northern muskrats with respect to their morphophysiological characters at the first stages of acclimatization in the 1950s and did not find any specific population features. However, we later examined the same material and detected considerable differences between the northern and southern muskrat populations in the morphometric and nonmetric skull characteristics, which remained until the late 20th century [3, 4]. The use of GM methods, making it possible to strictly separate the variations in shape and size, allowed us to obtain the first estimate of the morphogenetic component of muskrat variation during its acclimatization in the south and north, to clarify the degree of changes in shape and size, and to visualize the main morphogenetic transformations.

Allochronic age-matched muskrat samples from Kurgan oblast and the Yamal Peninsula collected at the initial (1954 and 1955; 35 and 59 individuals, respectively) and late (1979–1980, and 1989; 29 and 42 individuals, respectively) stages of muskrat acclimatization were analyzed. The variation in size and shape of the mandible as one of the organs important from ecological standpoint and directly associated with feeding and animal cenotic role was examined. Electron images of the right ramus lingual side were digitized (resolution, 1200 dpi) using the TPS software [11, 12]. The variation in shape was characterized using a configuration of 16 landmarks (Fig. 1). The variation of the total sizes of mandibles was assessed according to the centroid size (*CS*), determined as the square root of the sum of squared distances of a set of landmarks from the image center [5]. Preliminary analysis did not show any significant sex differences, allowing the male and female samples to be pooled.

Comparison of the allochronic muskrat samples from the northern and southern populations demonstrated that they differed in the mandible size as early as the first acclimatization stage, after 10–12 generations (Fig. 2). The animals of the northern, Yamal, population had significantly smaller mandibles as

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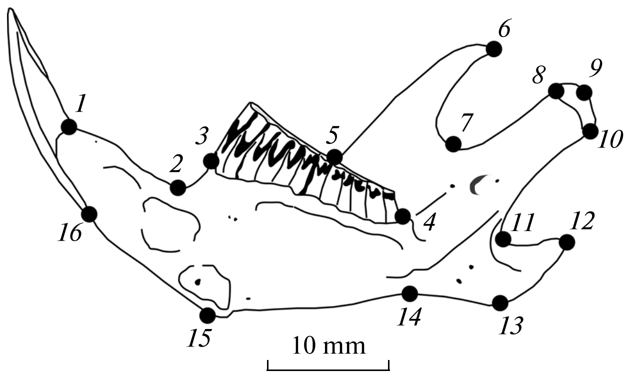

Fig. 1. Locations of 16 landmarks (*1–16*) on the lingual side of the muskrat mandible.

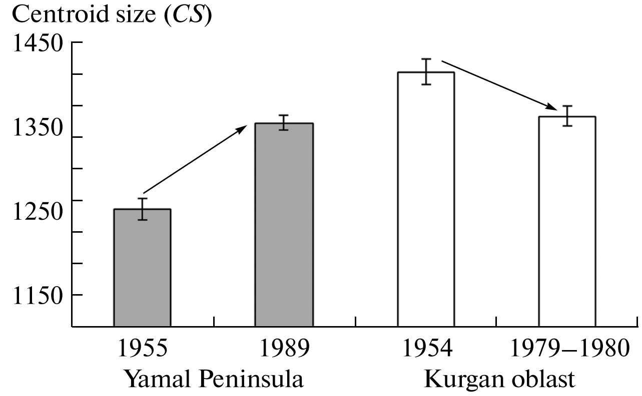

Fig. 2. Comparison of the centroid size (*CS*) characterizing the total mandible size in the allochronic muskrat samples of Yamal (1955 and 1989) and Kurgan (1954 and 1979–1980) populations; $M \pm m$.

compared with the representatives of the southern, Kurgan, population. However, the mandible sizes (proportional to *CS*) in the samples of these populations became almost equal 40–50 generations after beginning of acclimatization, by the end of the 20th century.

Canonical analysis of the Procrustes coordinates characterizing the variation in shape demonstrated that the northern and southern populations differed in the mandible shape both at the initial stage of acclimatization and at the end of the 20th century (Fig. 3). The between-group differences along the first two canonical axes are statistically significant and account for 87.8% of the between-group variation. The most pronounced transformation of the mandible in both populations is observed along the first canonical variable (CV1); this reflects the chronographic variation and accounts for 58.8% of the between-group variance. The range of morphogenetic changes in the allochronic samples of the northern group is higher as compared with the southern population, which is explainable by specific features of northern biocenoses and more severe conditions in the muskrat habitats of the Yamal forest–tundra. The chronographic changes comprise a decrease in the height of the mandible, elongation in its incisor part, and shortening of the angular and articular processes.

The morphogenetic specificities of the northern and southern populations are evident along the second, CV2, axis, which is retained at different acclimatization stages and associated with geographic variation. This variable accounts for 29.0% of the between-group variance, being twofold smaller as compared with CV1. The geographic variation appeared as a drastic increase in the incisor part and corpus mandibulae in the northern muskrats against the background of a relative lengthening of the dental arch and shortening of the coronoid, angular, and articular processes, which reflects adaptation of the northern animals to eating mechanically rougher feed [3]. The mandible in southern animals is more gracile displaying the opposite traits (Fig. 3).

The interaction between the factors "acclimatization stage" and "landscape–climate differences" is evident along the third axis, CV3; this interaction is rather small in the value of between-group variance (12.2%) and statistically nonsignificant.

Thus, a half-century-long muskrat acclimatization in Western Siberia has resulted in considerable morphogenetic changes detected in the newly established northern and southern muskrat populations. Since the chronographic changes are of almost the same direction, they suggest a similar direction of the adaptive changes in morphogenesis in both northern and

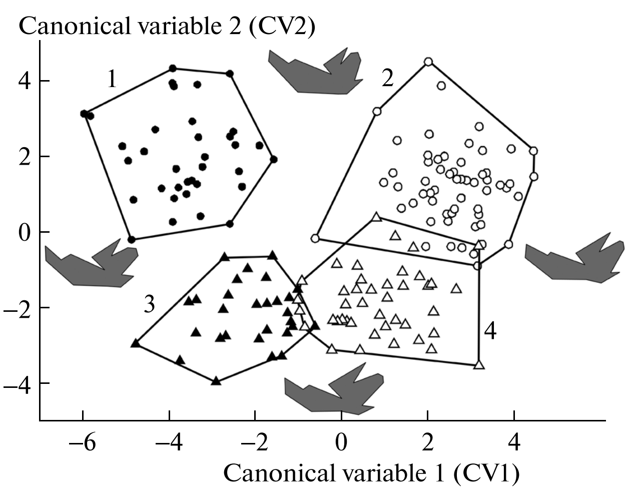

Fig. 3. Results of canonical analysis of the mandible shape variation in allochronic muskrat samples at different acclimatization stages in the Yamal (1, 1955 and 2, 1989) and Kurgan (3, 1954 and 4, 1979–1980) populations (shadow projections of mandible shape reflect its most pronounced changes along canonical axes).

southern areas. The initially formed range of morphological differences between the northern and southern populations has been retained, although the shape of the mandible in the representatives of these populations has changed. Therefore, the parallel chronographic changes in morphogenesis in both populations appearing after a half century are explainable by gradual integration of the muskrat into new biocenoses.

These results demonstrate a high potential of this species for rapid morphogenetic transformations, which determines the success of muskrat acclimatization in most of the Eurasian climatic zones. The detected long-term morphological aftereffects of acclimatization are an example of rapid directed microevolutionary transformation of morphogenesis in population of an acclimatized species under new cenotic conditions. This suggests that an uncontrolled acclimatization of invasive species may lead to rapid adaptive morphogenetic transformations on a historical rather than geological time scale at least in some of such species.

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