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ZOOLOGY

Morphometric Distances and Population Structuring in the Common Shrew *Sorex araneus* L. (Lipotyphla: Soricidae)

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Abstract—The skulls of shrews of genus Sorex from eight samplings from the European part of Russia and two from the vicinity of Novosibirsk were compared. The characteristics were identified using 22 marks on the axial skull. It was found that the centroid size differs significantly in the common and Laxmann's shrews S. caecutiens and the pygmy shrew S. minutus, while for selected marks, the common and Laxmann's, as well as pygmy, shrews were significantly different in form, but the differences were very small between Laxmann's and pygmy shrews. The characteristic features of the biology of the shrews Sorex are discussed, which may contribute to understanding the general laws of the morphological evolution of the genus.

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INTRODUCTION

The common shrew is a species possessing a phenomenal chromosomal polymorphism with multilevel divisions. One-type karyomorphs parapatrically localized in space are called chromosome races and, to date, 74 such races have been described in the species' range (Orlov and Borisov, 2009; Pavlova, 2010; White et al., 2010). Hybrid zones form between the races, the standard width of which is proportional to the discrepancy between their karyotypes, which suggests a limit in the interracial gene flow associated with karyotypic differences (Searle and Wójcik, 1998; Bulatova et al., 2011). The bimodality of the hybrid zones, i.e., the lack of hybrids observed in many hybrid zones, also testifies in favor of restriction of interracial gene flow. Moreover, according to the authors of the term, bimodality is the beginning of the way to species-formation, as it attests to a significant limitation of the gene flow between the hybridizing forms (Jiggins and Mallet, 2000). This allows us to discuss the first stages of divergence and to consider the separation of the common shrew into different chromosome races as the initial stage of chromosome speciation. However, the results of morphological, enzymatic, and molecular studies show similar genetic distances between the samples of the local populations of one race and the populations of different races (Ratkiewiz et al., 2003; Anderson, 2004; Polly, 2007). The interracial gene flow was assessed on the basis of Wright's relative magnitude of variation of genetic markers (F_{st}) (Wright, 1951). The similar levels of population differentiation within races and between them, which are associated with the differences in the karyotype, are considered as evidence of a lack of limits to the gene flow (Horn et al., 2012).

Thus, there is a paradox between the visible spatial localization of the karyotypes, which implies a restriction of the flow of genes between different forms and gene flow estimation based on an analysis of variation (frequency differences) of the genetic markers. We assume that the paradoxical estimates obtained by different methods can be explained not only by the lack of restrictions of flows through the hybrid zone, but also by the presence of gene flow restrictions between the local populations within races.

If the restrictions in the flow of genes between the races may be due to selection against the karyotypic heterozygotes, indicating the formation of "intense" hybrid zones (Barton and Hewitt, 1985), the restriction of gene flow between populations within a race can be associated only with limited migration between neighboring populations. A population system, i.e., a system of local populations with limited interpopulation migration in a homogeneous medium, is known, for example, in the Euroean anchovy (Altukhov, 2003). The restriction of the gene flow in this case may be due, for example, to the peculiarities of functioning of the population as a specific biological system (Shchipanov, 2003). It can be expected that the common shrew also belongs to a species the population subdivision of which is due to intrapopulation processes.

The population structuring is evaluated on the basis of frequency differences of genetic markers. Currently, microsatellite DNA is used as a genetic marker. However, such research is expensive and time-consuming, which complicates the study of population structuring in the species range. Craniological material is a by-product of traditional censuses with withdrawal. Geometric morphometry methods allow us to evaluate the morphological distance using the (Q_{st}) index, which is similar (but not identical!) to Wright's F_{st} (Spitze, 1993). We assumed that in the case of population structuring associated with a limited gene flow, differences similar to the estimates derived from using molecular markers will be obtained. The difficulty of using phenotypic characteristics is associated with the fact that variability is determined by both genetic and environmental factors (genetic and epigenetic variability), and environmental factors contribute significantly to the variability of the common shrews (Wójcik et al., 2003). However, it was found that epigenetic variability does not reveal a direct connection to the type of habitat, as shrews move in the course of ontogenesis and the samples represent a mixture of animals from different habitats.

The aim of this study is to assess the morphometric distances using Q_{st} between the samples from one and from different chromosome races of the common shrew. A unique feature is the fact that part of the closely spaced samples of the Moscow race was collected in the areas where the genetic distances between local samples had been previously determined using molecular markers, microsatellites.

MATERIALS AND METHODS

The animals were caught on the lines of specialized traps according to the standard protocol of capturing shrews (Shchipanov et al., 2000). The samplings were taken on a line of 50 traps (length 325 m) in 1 day. The distance between the samples in each sampling did not exceed 300 m.

The material was collected in the European part of Russia in the upper reaches of the Volga in the interval from the town of Staritsa, Tver oblast, to the village of Borok, Yaroslavl oblast. The craniological material is stored in the collection of the Institute of Ecology and Evolution, Russian Academy of Sciences. The belonging of *S. araneus* to a particular race for all the samples collected below the town of Kimry was confirmed by karyotyping (Pavlova et al., 2014), and the habitation of the Moscow race at a station in the Staritskii district of Tver oblast had been established earlier (Bulatova et al., 2000). Two samplings were carried out at a distance of 2 km from each other on the banks of the Novosibirsk reservoir, near the hybrid zone between the Tomsk and Novosibirsk races (Polyakov et al., 2011), but on the side of the Novosibirsk race. Unfortunately, in this case, the individuals were not karyotyped and are treated by us as one race, conventionally called "Novosibirsk." According to published data, *S. araneus* from the environs of Novosibirsk are likely to belong to the Novosibirsk race. Polyakov et al. (Polyakov et al., 2003, 2011) found an association between the distribution of these races and height: the Tomsk race was distributed at altitudes >200 m. Our samplings were taken at the heights of 140 and 190 m. However, some individuals could belong to the Tomsk race and include hybrid individuals; therefore, we consider the characteristics of both these races.

Samplings 1 Mo, 3 Mo, 5 Mo, and 6 Mo of the Moscow race at the station in the Staritskii district were carried out in the area where samples for the analysis of microsatellites had previously been collected. The genetic distances between the samplings measured by the frequencies of microsatellites were given earlier (Shchipanov et al., 2011). Sampling 5 Mo of the Moscow race was carried out in a spruce forest with green mosses, samplings 1 Mo and 6 Mo were collected in a spruce forest with ferns and small grasses, and the 3 Mo sampling was from a mixed motley grass forest. The remaining samplings of the Moscow and Mologa races were also carried out in various mixed floodplain forests with grasses in the lower tier.

The samplings of Laxmann's (*S. caecutiens*) and pygmy (*S. minutus*) shrews were collected along the way and were insufficient in volume for the same detailed analysis as for the common shrew. However, they allow us to assess the interracial and interpopulation differences in the common shrew at the level of interspecies differences. The coordinates of the sampling locations identified using a portable GPS-navigator and the race to which they belong are given in Table 1.

The skull of each sample was scanned in the ventral position using an Epson Perfection V30 tablet scanner with a resolution of 2400 dpi (Epson, Japan). In this paper, we selected the same positions of the markers (Fig. 1) as had previously been used in the study of the common shrew skull variability (Polly, 2007; Shchipanov et al., 2014). The digital images of the skulls were processed in the MorphoJ program package (Klingenberg, 2011). The centroid size (CS) and the relative deformation (RW) were calculated using standard methods (Bookstein, 1991; Zelditch et al., 2004) in the TPSrelw program (with the inclusion of the "affine transformations" module).

The structuring of the population was determined using Q-statistics, which evaluates the ratio of intra- and intergroup variation. We consider Q_{st} as a measure of the morphometric distance, which is analogous to F_{st} used to estimate the genetic distance. The Q_{st} designation was suggested for calculations on the basis of quantitative data, as opposed to the designation F_{st}, which is used to evaluate the molecular data (Spitze, 1993). We use the Q designation to emphasize that these are phenotypic rather than genetic characteris-

Table 1. General characterization of the samplings

Site (place)	Coordinates		Habitat	Species, race, sampling code	*n*, ind.
	N	E			
Tver oblast, Zubtsovskii district, environs of the village of Zabrovo (right bank of the Volga River)	56°17′	34°53′	Spruce forest with ferns and motley grasses	*S. araneus,* Moscow, 1 Mo *S. minutus* *S. caecutiens*	10 5 6
Environs of Novosibirsk, bank of the water reservoir	54°47′	83°08′	Grass and shrub pine forest	*S. araneus,* *, 2 No *S. minutus*	12 3
Tver oblast, boundary of the Zubtsovskii and Stritskii districts (right bank of the Volga River)	56°18′	34°53′	Birch and alder mixed forest with motley grasses	*S. araneus,* Moscow, 3 Mo *S. minutus*	8 7
Yaroslavl oblast, environs of the village of Sinitsino (right bank of the Volga River)	57°54′	38°30′	Floodplain pine forest with shrubbery, morley grasses and mosses	*S. araneus*, Mologa, 4 Ml *S. minutus*	13 3
Tver oblast, Staritskii district, environs of the village of Krutitsy (right bank of the Volga River)	56°19′	34°53′	Spruce forest with green mosses	*S. araneus*, Moscow, 5 Mo *S. minutus* *S. caecutiens*	6 6 3
Tver oblast, Staritskii district, environs of the village of Bakanovo (right bank of the Volga River)	56°00′	34°01′	Spruce forest with ferns and motley grasses	*S. araneus*, Moscow, 6 Mo *S. minutus* *S. caecutiens*	7 5 3
Yaroslavl oblast, Myshkinskii district, environs of the village of Sera (left bank of the Volga River)	57°41′	38°23′	The same	*S. araneus*, Mologa, 7 Ml *S. caecutiens*	7 3
Yaroslavl oblast, Uglichskii district, environs of the village of Maimery (right bank of the Volga River)	57°24′	38°08′	Mixed aspen and alder forest with small grasses	*S. araneus*, Mologa, 8 Ml *S. minutus*	5 4
Environs of Novosibirsk, 2 km from the bank of the reservoir	54°79′	83°12′	Spruce forest with ferns and motley grasses	*S. araneus*, *, 9 No *S. minutus*	7 9
Tver oblast, environs of the village of Strel'chikha	57°03′	37°31′	Floodplain spruce forest with motley grasses	*S. araneus*, Moscow, 10 Mo *S. minutus*	4 6

(*n*) Size of the samplings.
* Karyotyping of the specimens was not performed.

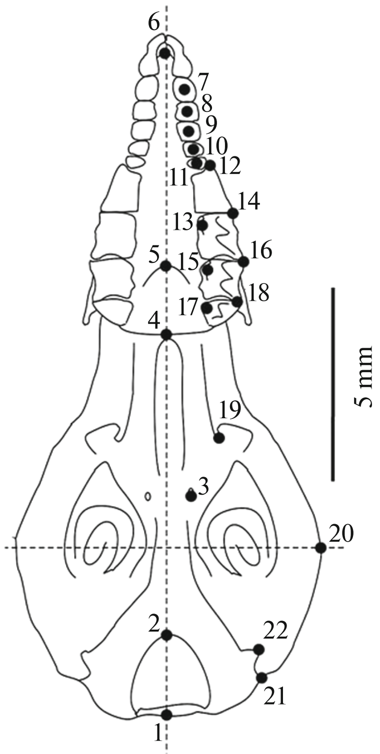


Fig. 1. Skull in the ventral position. 1–22 marks used in the study; for Figs. 1, 6, 7.

tics. The calculation involves alignment of short series using the random culling procedure of one of the group members (jackknife), 1000 iterations per sampling. To obtain comparable results, we used the formula given previously (Polly, 2007):

$$Q_{st} = (n - 1 - k)\mathrm{SSB}/(k - 1)(\mathrm{SSW} + \mathrm{SSB}),$$

where SSB is the sum of the squares of the differences between the mean in the group and the total mean, SSW is the sum of the squares of the differences between the group mean and individual values, n is the sampling size, and k is the number of groups. Like Polly (Polly, 2007), we characterize the magnitude of variation, giving a standard deviation, so the estimates obtained by us and presented in the paper by Polly, which summarizes data on 24 chromosome races of the common shrew, can be compared. The differences were evaluated using CS, and the differences of forms were assessed using the RW value.

Isolation by distance was evaluated by comparing the pairwise Q_{st} and the geographical distance between the samplings. Like Polly (Polly, 2007), we evaluated the correspondence of the geographical and genetic distances using Pearson's linear correlation coefficient (r). The correspondence of the genetic and morphological distances were assessed using Spearman's conformity coefficient (R_s). The CS dimensions were compared using one-way ANOVA followed by (post hoc) Tukey's test.

RESULTS

According to the Shapiro–Wilk's test, the distribution of CS and RW values is not different from the normal ($p > 0.05$), and the hypothesis of the equality of variances tested using Leuven's test was rejected for all samplings.

Size. The three study species differed considerably in CS (Fig. 2a). A comparison of the chromosomal races revealed that the sampling from Novosibirsk environs was represented by larger animals (Fig. 2b), as the ANOVA revealed significant differences ($p < 0.01$) from the Moscow and Mologa races. A comparison of the samplings with each other revealed significant differences in samplings 2 No and 5 Mo. The animals in the sampling 2 No were reliably larger, while from the sampling 5 Mo, they were significantly smaller ($p < 0.05$). Note that sampling 9 No did not differ in CS values from the other samples, but the variation in the size of the animals is the highest in it (Fig. 2c).

The morphometric distances between the populations of one race (Table 2) are similar to those found by Polly (Polly, 2007). The distance between the samplings of different races were considerably greater than those within a race, if the Novosibirsk samplings were included in the analysis. The distances between the samplings of the Moscow and Mologa races did not differ from the intraracial ones. Distances between races also depend on the inclusion of the samples from Novosibirsk in the analysis. Interestingly, the distance between three one-dimension species from the *araneus* group (*S. coronatus* and *S. antinorii*) in the study by Polly (Polly, 2007) were, on the contrary, less than the interpopulation differences and comparable to interracial ones (Table 2).

The differences in CS values in the samplings from the European part of Russia and Novosibirsk are substantial and reliable ($p < 0.01$); it may appear that they are correlated with the distance (Fig. 3a). However, this distribution of differences was due only to the presence of large shrews in the Novosibirsk samplings. The correlation with the distance was almost nonexistent for the matrix of normally distributed distances in the European part (Fig. 3b). Among the Moscow race samplings from the vicinity of the station, the morphometric differentiation levels estimated using the CS did not correlate with the distance and genetic distances estimated by microsatellites ($p > 0.3$).

Form. As a form variable, we used the relative deformation. Most of the explained variance accounted for RW1 (Fig. 4). Each deformation can carry different information, so the correlation with the genetic distances was checked. It was found that a good correlation ($r = 0.95$, $p < 0.03$) was shown only by RW1 (Figs. 5, 6). The other deformation did not

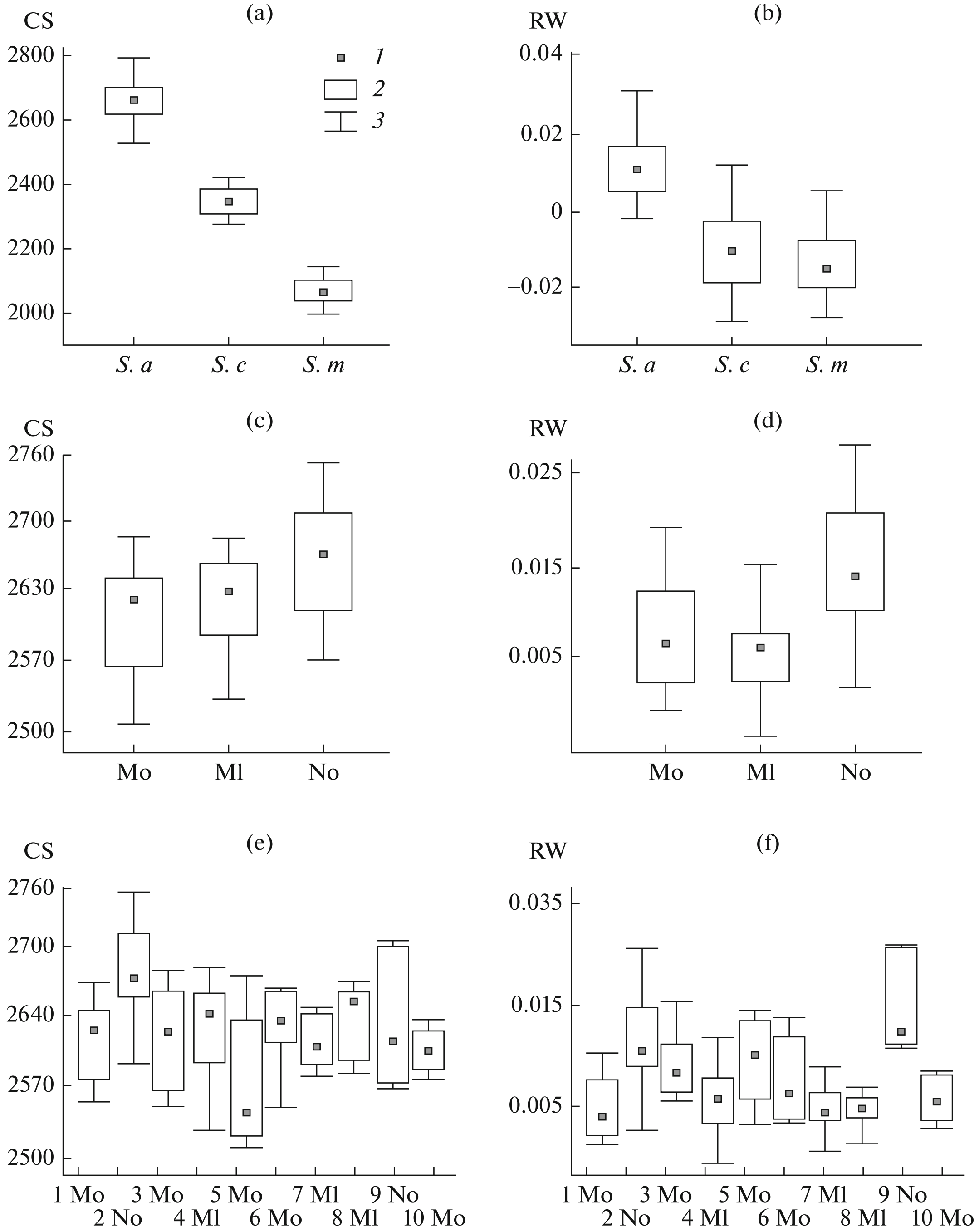


Fig. 2. Centroid size (CS) and form (RW) of the skull of the common shrew. (*1*) Median, (*2*) 25–74%, (*3*) extreme values. (*S. a*) *Sorex araneus*, (*S. c*) *S. caecutiens*, and (*S. m*) *S. minutus*. (Mo, Ml, No) Moscow, Mologa, and Novosibirsk Races (Mo, Ml, No are codes of samplings (Table 1)); for Figs. 2 and 7.

correlate with the genetic distance, and with an increase in the serial number of the deformation, the relative distances between the samplings grew, whereas the association with the genetic variable was lost. Figure 5 shows only the first 10 RW, but the tendency to decrease in the correlation with the level of differences measured using microsatellites can be seen clearly.

To scale the differences, we evaluated the interspecies morphometric differences. They were significant and reliable ($p < 0.001$) between the common and pygmy shrews; however, the pygmy and Laxmann's shrews hardly differed in RW with our choice of RW marks (Fig. 2e). The differences between the races are reliable owing to the significant deviations of the samplings from the environs of Novosibirsk (Fig. 2f). The

Table 2. Morphometric distances

Category of comparison	Compared groups	CS	RW1
Between samples of the same race	All samplings	0.1 ± 0.03	0.22 ± 0.05
	24 races*	0.11 ± 0.014	0.11 ± 0.014
Between samples of different races	All samplings	0.31 ± 0.05	0.58 ± 0.08
	Moscow–Mologa	0.08 ± 0.03	0.24 ± 0.09
Between races	All samplings	0.36 ± 0.14	0.31 ± 0.14
	Moscow–Mologa	0.07 ± 0.011	0.001 ± 0.001
	24 races*	0.04 ± 0.019	0.01 ± 0.002
Between species of *araneus* group*	Species*	0.06 ± 0.011	0.04 ± 0.004

(CS) Size, (RW1) shape.
* Data published previously (Polly, 2007).

Novosibirsk samplings differ significantly from the Moscow ($p < 0.002$) and Mologa ($p < 0.001$) races. Among the populations, both Novosibirsk samplings differ significantly ($p < 0.05$) (Fig. 2f).

The distances between the populations of the same race were larger than the average for the samplings of 24 races (Table 2). The differences in the comparison of populations of different races significantly exceeded the interpopulation differences within a race. This, as in the case of the size, depended on the inclusion of the Novosibirsk samplings in the analysis. After the exclusion of these sampling, the Q_{st} values for the interracial and intraracial comparisons were virtually indistinguishable. The differences between the races

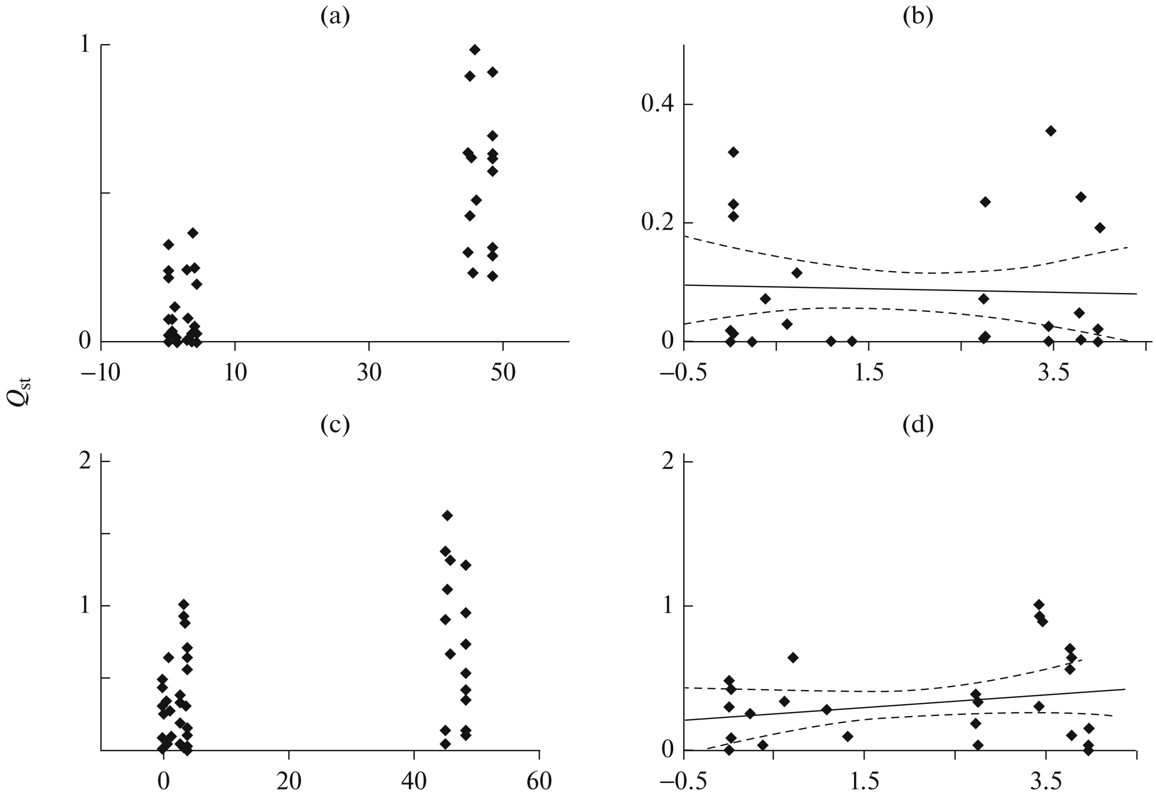


Fig. 3. Ratio of the morphometric (Q_{st}) and geographical distances between the samplings of chromosome races by size (a and b) and shape (c and d). On the left, including Novosibirsk, on the right, the correlation for the Moscow and Mologa races is given (size: $r = -0.09$, $p > 0.5$; form: $r = 0.22$, $p > 0.2$).

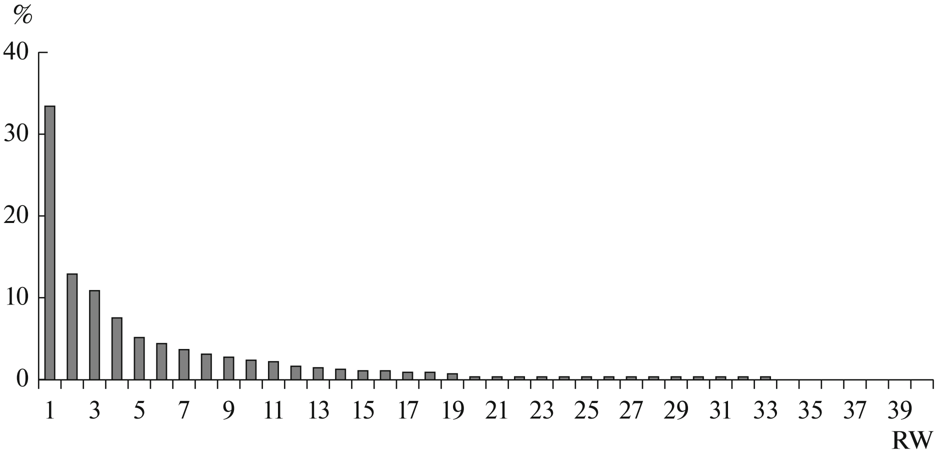


Fig. 4. The share of the total dispersion (ordinate axis) explained by each of the main components (RW).

were also largely determined by the Novosibirsk samplings. Races Moscow and Mologa were almost indistinguishable in form.

The increase in differences with the distance, as in the case of size, was observed only when comparing the groups of European and Novosibirsk samplings, but the differences were insignificant and unreliable. The correlation with the distance for the matrix of normally distributed distances in the European part, as in the case of CS, was unreliable (Fig. 3b).

DISCUSSION

An analysis of the CS of the skull reveals significant and highly reliable differences between the three sympatrically living species of shrews; however, significant differences in the shape of the skull were found only between the common and Laxmann's shrews, but were not found between the pygmy and Laxmann's shrews. In our view, this phenomenon reflects the general trend of the evolution of the genus *Sorex*. These trends are important for understanding the differences that arise in races and populations of the common shrews. Therefore, first of all, we discuss some aspects of biology, which, in our view, determine the main directions of the morphological variability of the genus.

The shrews of the genus *Sorex* are represented by small and very small animals. The animals are characterized by a metabolism level that is the highest among terrestrial mammals (Taylor, 1998). Reserves for physiological adaptations are practically absent, so the shrews are constantly functioning at the limit of their physiological capacity (Ochosińska and Taylor, 2005). Unlike the white-toothed shrews Crocidura, the *Sorex* shrews are not capable of surviving harsh periods by lowering their metabolism, i.e., while in torpor (Gębczyński, 1977; Genoud, 1985). To maintain a high level of metabolism all the time, shrews constantly have to eat high-calorie animal food, and they can be called voracious predators of invertebrates (Churchfield, 1990). The maximum period of fasting for the common shrew is 8.8 hours (Hanski, 1994). During this time, the animals have to eat food amounting to approximately 0.3 of their body mass. However, despite the apparent limitations of the living space, shrews managed to occupy a very profitable food niche. Their food resources are the various invertebrate animals inhabiting the ground layer (aboveground and litter soil layer), the total abundance of which is always high (Churchfield, 1982; Churchfield and Brown, 1987).

However, one of the features of the food niche occupied by them is the impossibility to adapt to specific groups of objects. The dominant species and groups of species of invertebrates are constantly changing throughout the season. The food preferences of the shrews vary depending on the prevalence of prey (Rudge, 1968). Laboratory experiments with *S. araneus* show that the animals selected the largest prey (Barnard and Brown, 1981). The peculiarity of the majority of the prey is their "vitality." The animals are forced to simultaneously hold and eat strong and relatively large prey.

According to Zaitsev (2005), it is the lack of special mechanisms of killing prey that left an imprint on the formation of the masticatory apparatus of the animals. The chewing mechanism of shrews can be defined as "horizontal cutting" as opposed to "vertical cutting" inherent in other insectivores and predators. A prey is captured and fixed by a pair of incisors (I1-I2, i1) and the directly hypertrophied front vertices of I1 owing to the work of the temporal muscle. The prey is then disjointed with small movements of the lower mandible mainly in the horizontal plane with the teeth barely open, which is possible due to the specific location of an entire complex of muscles, one of which is digastric (Nikol'skaya, 1965). This mechanism "enabled shrews

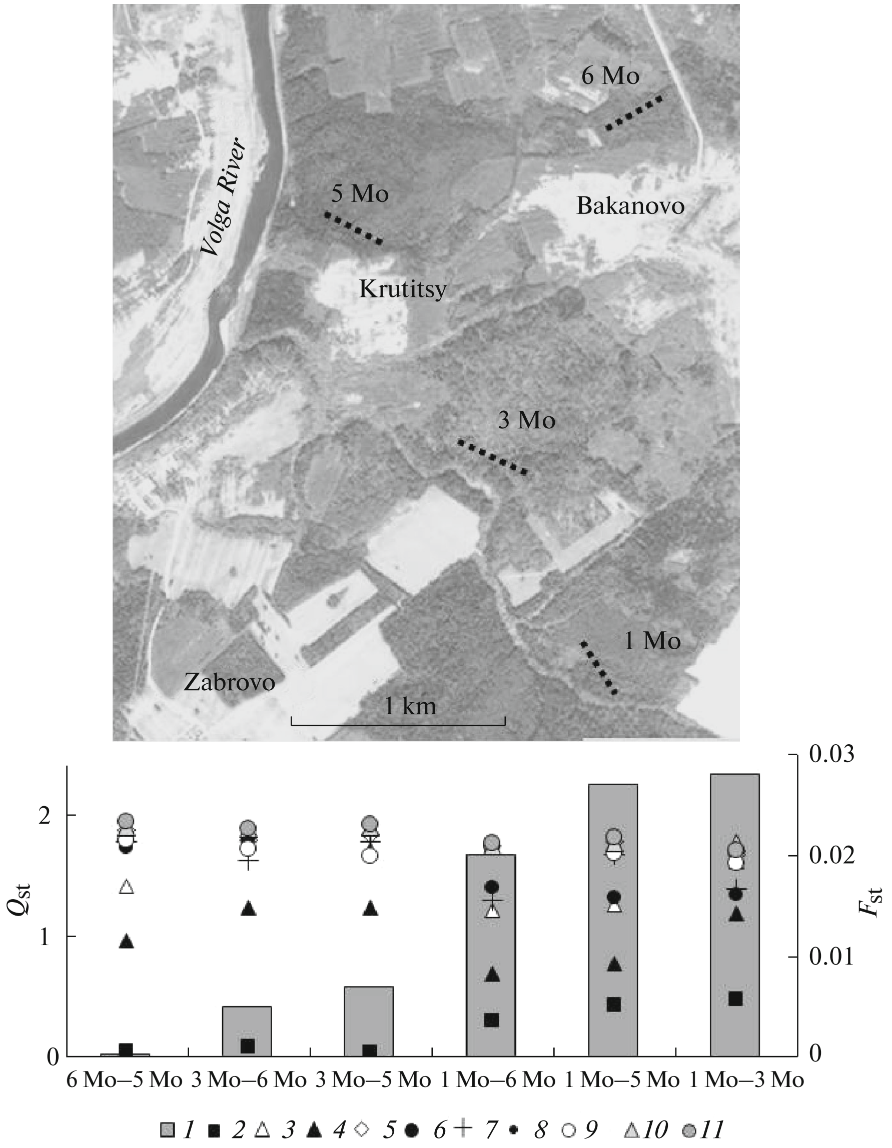


Fig. 5. A map of the mutual location of the samplings. The morphometric (the form by the first 10 RW) and genetic distances between the samplings in the station area. (*1*) F_{st}, (*2*) RW1, (*3*) RW2, (*4*) RW3, (*5*) RW4, (*6*) RW5, (*7*) RW6, (*8*) RW7, (*9*) RW8, (*10*) RW9, (*11*) RW10.

to consume large amounts of high-calorie food ... and ultimately ensured the evolutionary success of *Soricidae* as an independent group" (Zaitsev, 2005, p. 142). Evidently, the unique jaw movement mechanism is associated with the development of the respective muscles which should optimally be streamlined in space, have specific attachment points, etc. Thus, the conservative cranial skeleton of shrews can be predetermined to a large extent by their particular ecological niche.

The coexistence of sympatric species occupying the same ecological niche is impossible. However, judging by the occurrence of the food objects, the food niches of shrews overlap significantly. In the Yenisei taiga, food niches overlap by 54–91% (Chirchfield and Sheftel, 1994), and in some areas in Europe, the niches of different species are almost entirely the same in terms of the range of food consumed (Klenovsek et al., 2013a, 2013b). Apparently, the possibility of diverging into different ecological niches is mainly associated with changes in the size of the prey. Hanski (Hanski, 1994), having analyzed the costs and benefits, showed that the species of different size groups have specific size groups of their prey, which keeps their energy balance optimal. The optimum size of prey and its localization in the soil correspond to the average body length of the coexisting species. Small species prefer surface arthropods, whereas larger ones procure larger prey from the soil.

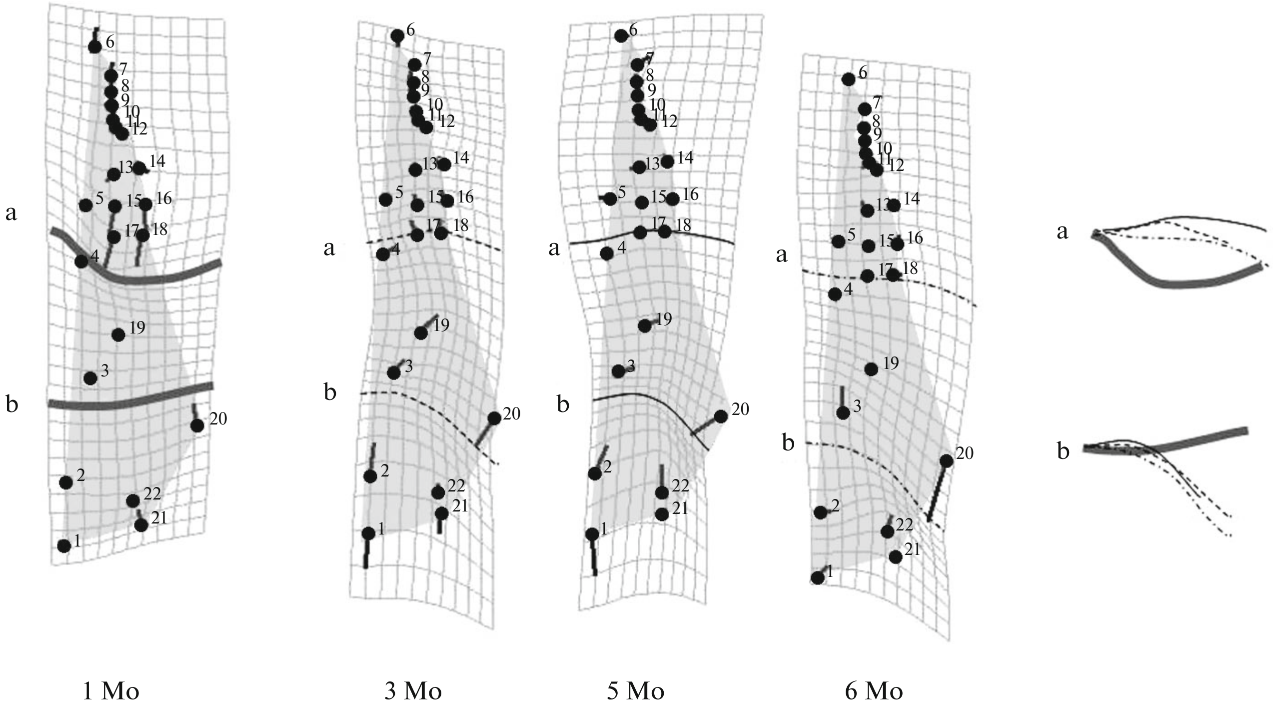


Fig. 6. Visualization of the change in form (RW1) in the Moscow race samplings (Mo) at the Tver station (Fig. 5). (a and b) Lines, emphasizing the distortions.

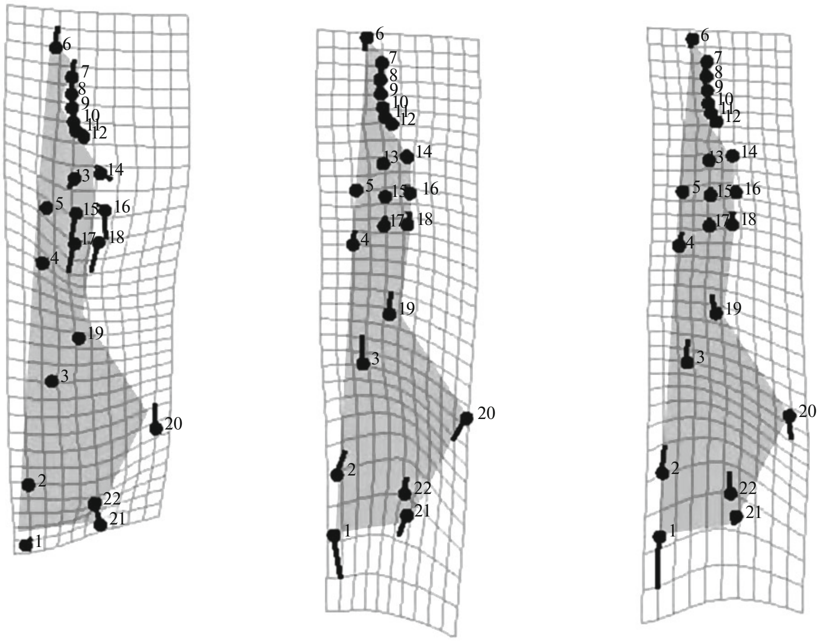
The hypothesis is that the general rule for *Sorex* shrews consists in filling three dimensional niches (Kirkland, 1991; Fox and Kirkland, 1992).

The considered species represent three size groups: large species (condylobasal length >18 mm), i.e., the common shrew with the condylobasal length of the skull being 19.5 mm; mid-size species (>18 > 16 mm), i.e., Laxmann's shrew with the condylobasal length of 17.2 mm; and small species (<16 mm), i.e., the pygmy shrew with a condylobasal length of 14.9 mm (Sheftel, 2005). The coexistence of these species is known for a vast range. Thus, it is the difference in size, rather than the form of the skull, that is the determining factor of ecological divergence in the present context.

The high similarity between the pygmy and Laxmann's shrews in shape with a significant difference between these two species and the common shrew (Fig. 7) may reflect the phylogenetic relationships of these species. In any case, the similarities and differences in form correspond to the position of the species in the *Sorex* genus cluster, which was drawn according to their karyotypic characteristics. During clusterization, among the Old World shrews, two groups of species were distinguished: the *araneus* and *minutus* groups (Laxmann's shrew belongs to the latter). These groups separated around 3 million years ago (Biltueva et al., 2011). The segregation of these two compact clusters is also confirmed by molecular studies (Fumagalli et al., 1999).

The *araneus* group of species is marked by a sexual trivalent, and its further evolution is clearly traced by the formation of new chromosomes. Inside the *araneus* group, 400000–500000 years ago, a cluster of related species was formed, the further evolution of which was related to the formation and subsequent fixation of metacentric chromosomes. Finally, the common shrew itself is divided into chromosome races. The separation into the modern races is, apparently, due to the last glaciation and dates back 12000–8000 years (Searle and Wójcik, 1998). The *minutus* group segregated approximately 100000 years ago. It was found that the karyotypes of the Laxmann's and pygmy shrews are similar and differ only in six centromeric shifts and one inversion (Biltueva et al., 2000). Thus, the observed similarities in the shape (RW1) of the skull of the pygmy and Laxmann's shrews, as well as the significant differences between the common and pygmy and common and Laxmann's shrews correspond to their position in the different groups of species that have long been divided (Biltueva et al., 2000, p. 60).

The chromosomal races of *S. araneus* studied by us represent different karyotype groups. The Moscow race belongs to the West European karyotypic group (WEKG), and the Mologa race belongs to the Eastern European group (EEKG). The Novosibirsk race belongs to the northern group (NEKG) (Searle and Wójcik, 1998) or is isolated as a subgroup (EEKG) (Orlov et al., 2004). The Tomsk race belongs to the



S. araneus *S. minutus* *S. caecutiens*

Fig. 7. Visualization of the change in the form of the shrew's skull by RW1.

Siberian karyotypic group (SKG) (Searle and Wójcik, 1998). Between themselves the races differ in the number of Rb-rearrangements. Thus, the karyotypes of the Moscow and Mologa races differ in two pairs of metacentrics, and with the Novosibirsk and Tomsk races, they differ in at least four pairs of metacentric chromosomes. They are either maximum for the races, as in the Mologa and Tomsk races or in the Moscow and Novosibirsk races (5 metacentrics), or are similar to those in the pairs Moscow–Novosibirsk and Moscow–Tomsk (four different metacentrics). Moreover, these groups of races have different biogeographical histories. The NEKG and SKG races presumably survived glaciation in refugia isolated from the European races (Polyakov et al., 2001).

Polly (Polly, 2007) found that a discriminant analysis reveals no significant differences between WEKG, EEKG, and NEKG in CS and a weak difference in shape (the Tomsk race was not present in this analysis). However, if the percentage of correct shape definitions of the NEKG races is ~60%, for EEKG it amounts to zero. The latter is due to the position of EEKG within the WEKG range. The peculiarity of our sampling of the Siberian races (regardless of whether they are represented by the Novosibirsk or Tomsk races or their hybrids) is their larger size. Thus, the Novosibirsk race was among the largest in a sampling of 24 races in the summary analysis (Polly, 2007), and the Tomsk race was reliably larger than the Novosibirsk one (Polyakov et al., 2002). Therefore, in our case, the marked contrast of the Novosibirsk sampling from the samplings of the Moscow and Mologa races by CS is due more to the specific set of races than to their belonging to different karyotypic groups. The lack of size differences between the Moscow and Mologa races is consistent with the results obtained previously (Shchipanov et al., 2014).

The difference in shape between the Moscow and Mologa races was very insubstantial, which is also consistent with the results of discrimination in the comprehensive analysis of the variability of races. The relatively large differences in shape between the smaller European races and the Novosibirsk sampling with larger individuals suggest that there is a connection between the form variability and CS in the common shrews. Earlier, we found an allometric effect associated with the altitude and mainly determined by the different sizes of the plain, foothill, and mountain populations of the Serov race (Shchipanov et al., 2014). The changes affected the skull size and shape of the jaw. An increase in the size of the skull with altitude is considered one of the two main trends of race variability in the common shrew (Polly, 2007). Note that when studying the variability of the Serov race, the dimensional differences that characterize the race as a whole were determined by the inclusion of the mountainous samplings in the analysis. The plain sampling of this race does not differ in size from the plain sampling of the Sok race carried out at the same height (Shchipanov et al., 2014). In our case, changes in the form were also associated with CS. The most different in CS pairs of races differed the most in form. Thus, the results obtained in this and in previous studies suggest a connection between the size and shape changes in the races of the common shrew. However, the existence of such a relationship can only be proved by the results of study of a larger number of samplings.

All samplings differ markedly and significantly in the size of the skull. These differences proved not to be related to the distances obtained in the analysis of the samplings using microsatellites. It can be assumed that, in our case, the size of the skull mainly reflects the epigenetic variability. For example, it is known that the race dimensions decrease toward the north (Ochocińska and Taylor, 2005; Polly, 2007). However, in our previous study, it was observed that, while the more southerly races on the whole were represented by larger specimens, the single and most northernmost Pechora race sampling was, on average, larger than the two more southerly samplings of the Sok race and the Manturovo race samplings. Apparently, the dimensional differences of shrews are associated with environmental factors, primarily the size of their main prey. Thus, when comparing the haplotypes (*cytb* mtDNA) of fossil giant shrews, previously regarded as a species ancestral to *S. araneus*, it was shown that this was not a separate species, but the giant form of the common shrews. At the same time, the authors of the publication found no direct correlation between the size and climate and assumed that the dimensions of the body are mainly associated with changes in the diet of the shrews (Prost et al., 2013).

Note that the sampling that was the smallest in CS (5 Mo) was also the southernmost, though obtained from a habitat of the boreal type: polytric and green moss spruce forest. Despite the very limited data, we paid quite a lot of attention to this aspect of variability, as we believe that a deeper study of this issue could contribute significantly to the understanding of the general laws of morphological evolution of shrews.

Comparing paired samplings, we found that the distance between the local samplings and the relative distortions by RW1 correlated. High and significant differences were found between the samplings 1 Mo and samplings 3 Mo, 5 Mon, and 6 Mo geographically close to them. These differences correspond to the previously marked areas with independent population dynamics, different compositions of micromycetes on the wool as a marker of the movements of individuals, and notions of the limited migration between these areas (Shchipanov, 2007). This suggests that the significant differences in RW1 can reveal areas with limited gene flow between their populations. Unfortunately, our assumptions are based on a small amount of material and should be treated with some caution. Apparently, the conjugation of the variability of molecular characteristics and relative deformations is of interest in a deeper analysis based on purposefully assembled material. Overall, however, we can assume that our findings show significant variability, if the local samplings are relatively independent (genetically) populations.

Note that the correlation with the level of differences measured by the frequencies of occurrence of microsatellites is demonstrated only by RW1. This variable describes a variability of ~30% and probably integrates the basic variability associated with the genetic characteristics of the animals. Previously, we showed that the differences between local populations are likely to be associated with the population drift. Each pair of populations, irrespective of belonging to a particular race, differs in different parameters (Shchipanov et al., 2011, 2014). Assuming that RW1 describes the variation in the largest number of genetically determined traits and the subsequent RW do the same for a decreasing number of characteristics, given that the differences are the result of a genetic drift, it is expected that these RWs will reflect the difference between rare alleles. It can be assumed that rare alleles are either present or absent in the sampling. Thus, for the discrimination of samplings by the differences in allele frequencies accumulated as a result of local processes and not aligned by migration, RW1 has the greatest value.

On the whole, it can be concluded that the analysis of our samplings demonstrates a tiered structuring of the population, which is known for the common shrews. The form most closely matches the genetic differences between the populations, and the correspondence is found only in RW1. The differences between the local populations are significant enough and do not differ in the samplings of populations of one race and of different races. The morphometric distance measured between the races depends on the specific samplings that are included in the analysis. An evaluation of the interracial morphometric distances performed without taking into account the population variation could reveal nonexistent differences and not reveal the actual differences. It is necessary to take into account the fact that population differences are likely to be determined by the genetic drift in local populations. Accordingly, the changes in characteristics are uncertain and uniting the samplings of different local populations increases the scale of variation and reduces the morphometric distance between the races. As a result, it may happen that the distance between the different races would be less than the interpopulation one. However, in this case, it will indicate a relatively high isolation of the local populations and will not attest to the free flow of genes between the common shrew races.

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