THEORETICAL PAPERS
AND REVIEWS

Chromosomal Evolution of the Common Shrew *Sorex araneus* L. from the Southern Urals and Siberia in the Postglacial Period

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Abstract—This paper summarizes a series of studies on chromosomal geography of the common shrew *Sorex araneus* L. in Siberia and the Southern Urals. Chromosomal races inhabiting the Southern Urals and the Western Siberian Plain sequentially replace each other in the latitudinal direction. In this region, karyotypes of each two adjacent races differ from each other by a single whole-arm reciprocal translocation. In the Eastern Siberian and Altai branches, the neighboring races differ mainly in the number or set of metacentric chromosomes. Analysis of the race distribution in the common shrew in the context of paleoecology of the glacial and postglacial period allowed us to reconstruct the sequence of events leading to the establishment of the present-day structure of the species *S. araneus*.

INTRODUCTION

Karyotypic variation in the common shrew *Sorex araneus* L. is characterized by polymorphism for Robertsonian translocations: the number of autosomal arms is constant (FNa = 36) but the number of autosomes varies from 2Na = 18 to 2Na = 30. According to the standard nomenclature of this species, each chromosomal arm is designated by a letter of the Latin alphabet [1]. Autosomes af, bc, and tu are invariant metacentrics. The remaining autosomal arms, g, h, i, j, k, l, m, n, o, p, q, and r, either are present in the karyotypes as acrocentric chromosomes or form metacentrics in various pairwise combinations [2, 3]. The karyotype of each common shrew population is characterized by a particular combination of variable arms of metacentric chromosomes. Groups of populations with identical karyotypes inhabiting the same territory were termed chromosomal races [3]. At present, virtually the entire range of *S. araneus* has been studied. It has been shown that the karyotypic structure of this species is a mosaic of parapatric chromosomal races. By now, more than 50 races has been described [2, 3].

Karyotypes of the overwhelming majority (nine out of eleven) of the races inhabiting Scandinavian Peninsula contain exclusively metacentric chromosomes. These races consecutively replace each other, and each subsequent race differ from the preceding one by a single whole-arm reciprocal translocation [4, 5]. In the remaining part of Europe, only 4 out of 26 races have an entirely metacentric karyotype. The races inhabiting the southern margin of the *S. araneus* European range (Switzerland, Turkey) have the lowest number of metacentrics [2, 3].

Hypotheses on the *S. araneus* evolution explain the origin of the chromosomal races by the global climatic changes during the last glaciation [6–8]. These hypotheses are based on the assumption that in the original ancestral karyotype of the common shrew, all variable chromosomes were acrocentric. During the glaciation, the range of *S. araneus* was fragmented. This resulted in the appearance of several small, isolated populations, in which Robertsonian translocations occurred and the resulting metacentrics were fixed. Later, during the climatic warming, the areas of these populations expanded and merged; at the places of contact, narrow intergradation zones appeared [3, 7, 9]. On the territory of Scandinavia, the races were formed consecutively, one after the other, as shrews colonized the peninsula [4, 5, 10].

When these hypotheses were being developed, evidence on chromosomal differentiation of *S. araneus* in Siberia and the Urals was scarce and generally not taken into account in phylogenetic reconstructions. By 1995, four chromosomal races of these species were described in Siberia based on a few findings [11–14]. The distribution of these races was unclear.

In 1995–1997, in the course of several expeditions, we found five new chromosomal races in Siberia and the Urals. Geographical ranges of several new and previously described races were roughly established. The present paper summarizes all our results on the geographical distribution of chromosomal variants in the common shrew. All races that we found and the meth-
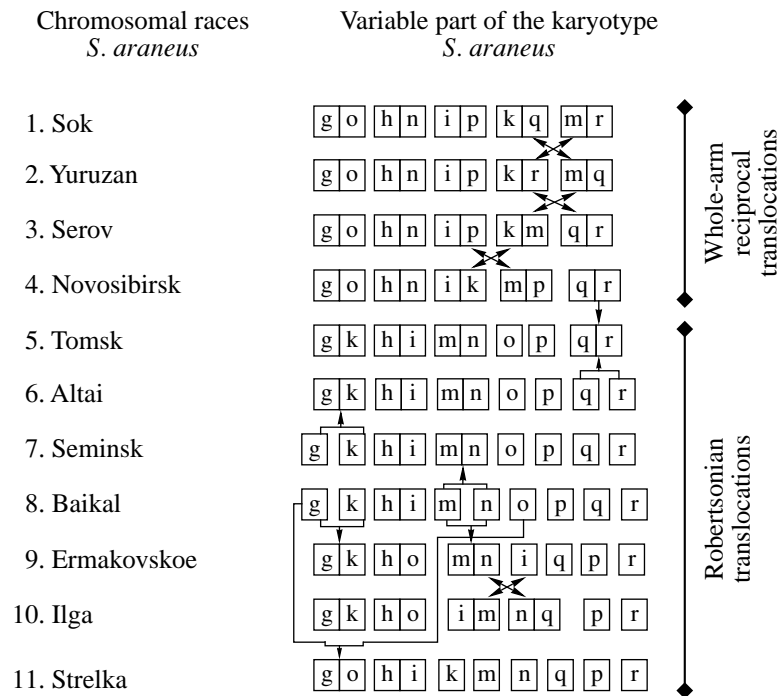
Chromosomal races *S. araneus*	Variable part of the karyotype *S. araneus*	

Fig. 1. Phylogenetic relationships in the Southern Urals and Siberian chromosomal races of the common shrew.

ods used for their analysis have been described in a series of publications [15–21].

Based on this evidence, we discuss evolution of *S. araneus* in Siberia and the Urals and develop views on the formation of the entire species structure.

KARYOTYPES OF CHROMOSOMAL RACES OF *S. ARANEUS* FROM THE SOUTHERN URALS AND SIBERIA AND THEIR DISTRIBUTION

The eastern edge of the *S. araneus* range is populated by at least two races of the common shrew: the Baikal [13, 14] and the Ilga [21] races (Figs. 1, 2 and table); the latter of these races was discovered by us. The Baikal race is the "most acrocentric" in Siberia: only four out of twelve arms of the variable karyotype part are united in metacentrics hi and jl. The locality of description of the Ilga race is situated about 300 km north of the Baikal race locality. In contrast to the latter, the Ilga race is rich in metacentrics: in this race, only two small arms p and r remain as acrocentrics.

The karyotype of the Ermakovskoe race, which was recorded only in one locality (Figs.1, 2 and table), is also rich in metacentric chromosomes [12]. In this respect, as well as in the set of metacentrics, the Ermakovskoe and the Ilga races are very similar differing only by one whole-arm reciprocal translocation.

To the north of the locality of the Ermakovskoe race, we found a new race named Strelka (Figs.1, 2 and table) [21]. This race is probably distributed along the

right bank of the Enisei River north of its right-hand tributary, the Mana River.

The left bank of the Enisei River is inhabited by the Altai and Tomsk races of *S. araneus* (table) [12, 13, 15, 18, 22]. The only difference between these races lies in the fact that in the Altai race, chromosomes q and r are always acrocentric and in the Tomsk race, they are typically included in the qr metacentric. The southern boundary of the area inhabited by shrews having the qr metacentric in their karyotype approximately coincide with the 54° N [15]. This indicates that the territory between the Enisei and Ob' to the south and north of 54° N is inhabited respectively by the Altai and Tomsk races.

The boundary between the Altai and Tomsk races, on the one hand, and the completely metacentric Novosibirsk race, on the other, lies to the west [11–13, 15, 16, 18, 22]. The eastern boundary of the Novosibirsk race goes northward along the right bank of the Ob'. After 55° N, this boundary deviates to the east and reaches the Tom' River [12, 13, 15, 18, 22]. The karyotypes of the Novosibirsk race, on the one hand, and the Tomsk–Altai group, on the other, dramatically differ in the metacentric chromosome set. This is probably one of a few known cases of such drastic differences between chromosomal compositions of the neighboring races.

The Novosibirsk race occupies virtually the entire Western Siberian Plain to the north of the Ob'. The areas of the Novosibirsk and of the Serov race (first described by us) are divided by the Tobol and Irtysh riv-

Localities of sampling different chromosomal races of *S. araneus*

Race	Locality	Coordinates	Reference
Altai	Teletskoe Lake, Altai	51°45′ N/87°30′ E*	[12]
Altai	Sema settlement, Altai	51°37′ N/85°47′ E	[15]
Altai	Krasnogorsk settlement, Altai	52°18′ N/86°00′ E	[15]
Altai	El'tsovka village, Altaiskii Krai	53°15′ N/86°15′ E	[15]
Altai	Turochak settlement, Altai	52°17′ N/87°02′ E	[15]
Altai	Belyi Etap settlement, Kemerovo oblast	54°07′ N/87°28′ E	[12]
Altai	Chuvashka village, Kemerovo oblast	53°36′ N/87°49′ E	[12]
Altai	Maina village, Krasnoyarsk Krai	52°53′ N/91°30′ E	[12]
Baikal	Baikal Lake, Irkutsk obl	53°40′ N/108°00′ E*	[13, 14]
Ermakovskoe	Ermakovskoe village, Krasnoyarsk Krai	52°53′ N/91°22′ E*	[12]
Ilgink	Zhigalovo village, Irkutsk oblast	54°45′ N/104°56′ E*	[21]
Novosibirsk	Novosibirsk	54°49′ N/83°06′ E*	[11, 15]
Novosibirsk	Kurgan	55°30′ N/65°20′ E	[15]
Novosibirsk	Zavodoukovsk, Tyumen' oblast	56°30′ N/66°30′ E	[15]
Novosibirsk	Petropavlovsk	54°25′ N/68°35′ E	[15]
Novosibirsk	Khanty-Mansiisk, Tyumen' oblast	61°00′ N/69°00′ E	[15]
Novosibirsk	Abatskii settlement, Tyumen' oblast	56°20′ N/70°30′ E	[15]
Novosibirsk	Cherlak settlement, Omsk oblast	54°00′ N/74°30′ E	[15]
Novosibirsk	Nizhnyaya Omka settlement, Omsk oblast	55°28′ N/74°57′ E	[15]
Novosibirsk	Kuibyshev, Novosibirsk oblast	55°30′ N/78°30′ E	[15]
Novosibirsk	Kargasok settlement, Tomsk oblast	59°00′ N/81°00′ E	[15]
Novosibirsk	Kolomino village, Tomsk oblast	57°50′ N/83°18′ E	[12]
Novosibirsk	Uspenka village, Novosibirsk oblast	55°27′ N/83°15′ E	[12]
Novosibirsk	Tal'menka village, Altaiskii Krai	53°48′ N/83°36′ E	[15]
Novosibirsk	Novobibeevo village, Novosibirsk oblast	55°42′ N/83°45′ E	[12]
Novosibirsk	Proskokovo village, Kemerovo oblast	55°50′ N/84°43′ E	[12]
Novosibirsk	Kaftanchikovo village, Tomsk oblast	56°20′ N/84°52′ E	[12]
Novosibirsk	Yurga, Kemerovo oblast	55°42′ N/85°05′ E	[12]
Novosibirsk	Novoromanovo village, Kemerovo oblast	55°40′ N/85°20′ E	[12]
Novosibirsk	Berezovo village, Kemerovo oblast	55°14′ N/86°15′ E	[12]
Serov	Kedrovyi settlement, Tyumen' oblast	61°28′ N/68°14′ E	[20]
Serov	Serov, Sverdlovsk oblast	59°50′ N/60°22′ E*	[17, 20]
Serov	Chelyabinsk	55°59′ N/61°15′ E	[17, 20]
Serov	Miass, Chelyabinsk oblast	55°15′ N/61°50′ E	[20]
Sok	Sok River, Samara oblast	53°35′ N/50°30′ E*	[20]
Sok	Usen' River, Bashkortostan	54°30′ N/54°00′ E	[20]
Strelka	Novoangarsk, Krasnoyarsk Krai	58°07′ N/93°30′ E*	[21]
Strelka	Narva settlement, Krasnoyarsk Krai	55°26′ N/93°44′ E	[21]
Tomsk	Khaldeevo village, Tomsk oblast	56°38′ N/85°36′ E*	[12]
Tomsk	Kolarovo village, Tomsk oblast;	56°20′ N/84°58′ E	[12]
Tomsk	Krapivinskii settlement, Kemerovo oblast	55°00′ N/86°50′ E	[12]
Tomsk	Berikul' settlement, Kemerovo oblast	55°32′ N/88°07′ E	[12]
Tomsk	Komsomol'sk, Kemerovo oblast	55°37′ N/88°10′ E	[12]
Tomsk	Kolmogorovo, Krashoyarsk Krai	59°16′ N/91°08′ E	[15]
Tomsk	Ust'-Pit settlement, Krasnoyarsk Krai	59°00′ N/91°50′ E	[15]
Tomsk	Divnogorsk, Krasnoyarsk Krai	56°00′ N/92°45′ E	[15]
Yuruzan	Yuruzan, Chelyabinsk oblast	54°50′ N/58°20′ E*	[20]

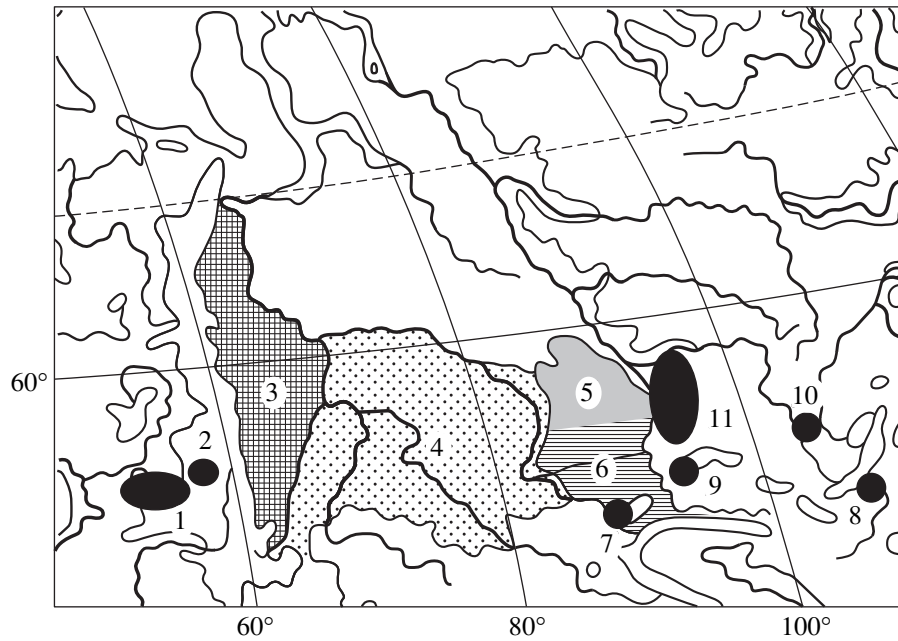* Locality of the first description of the chromosomal race.

Fig. 2. The present-day distribution of the Southern Urals and Siberian chromosomal races of the common shrew. The races are numbered in the same order as in Fig. 1.

ers [17, 19, 20]. According to our results (see table), the Serov race is distributed over the entire eastern foothills of the Urals. It also occurs on the right bank of the Ob' River, north of the confluence of the Ob' and Irtysh. The karyotypes of the Serov and Novosibirsk races consist exclusively of metacentric chromosomes. We found two more new races, the Yurusan and Sok, on the western Urals slopes (table) [20]. The areas of these races are yet to be verified. Their karyotypes are also entirely "metacentric". Note that the Sok, Yuruzan, Serov, and Novosibirsk races, as Scandinavian ones, consecutively replace one another: each of them differs from the neighboring one by one whole-arm reciprocal translocation (see Fig. 1). Interestingly, the Sok and Yuruzan races from the Urals have the same chromosome composition as the races Kumo and Ilomantsi, respectively, which terminate the sequence of the Scandinavian races at the east.

PHYLOGENETIC ASSOCIATIONS BETWEEN THE EXAMINED CHROMOSOMAL RACES OF THE COMMON SHREW

Based on the karyotypic variation within the species *S. araneus* in Siberia and the Urals, two independent phyletic branches can be identified. One of them includes the Sok, Yuruzan, Serov, and Novosibirsk chromosomal races consecutively replacing each other in the latitudinal direction, from the Southern Urals to the eastern borders of the Western Siberian Plain. The character of karyotypic variability in this race group was considered above. The other phyletic branch includes the races from East Siberia and Altai. This race group

has more complex spatial configuration than the other. The adjacent races comprising the Eastern Siberian group differ mainly in the number and composition of metacentric chromosomes having arisen by Robertsonian fusions (see Fig. 1).

According to our views, the Baikal race was the first in the Eastern Siberian race sequence (Fig. 1). This race inhabits the southeastern edge of the range. The variable part of its karyotype contains only two metacentrics, hi and jl. The most genetically close to the Baikal race, judging by the number of metacentrics in the karyotype, is the Altai race (gk, hi, jl, mn); this race could originate from the former via two centric translocations. Note that the sample from the Sema locality (hi, jl, mn) at the southern margin of the Altai race area [15, 21] may be regarded as a transitional form between the Baikal and Altai races. The area of the Tomsk race (gk, hi, jl, mn, qr) is north of the Altai race are; the former differ from the latter by the presence of the qr metacentric. The appearance of this metacentric in the Tomsk race karyotype is alternatively explained by (1) fusion q + r ⟶ qr and fixation of the metacentric chromosomes in the marginal northern populations of the Altai race or by (2) introgression of the qr chromosome from the more western Novosibirsk race, in which this metacentric is common [15]. Further studies are needed to choose between these hypotheses.

The Strelka race distributed along the right bank of the Enisei probably originated from the Baikal race. In addition to metacentrics hi and jl characteristic of the Baikal race, the karyotype of the Strelka race also contains the go metacentric (Fig. 1).
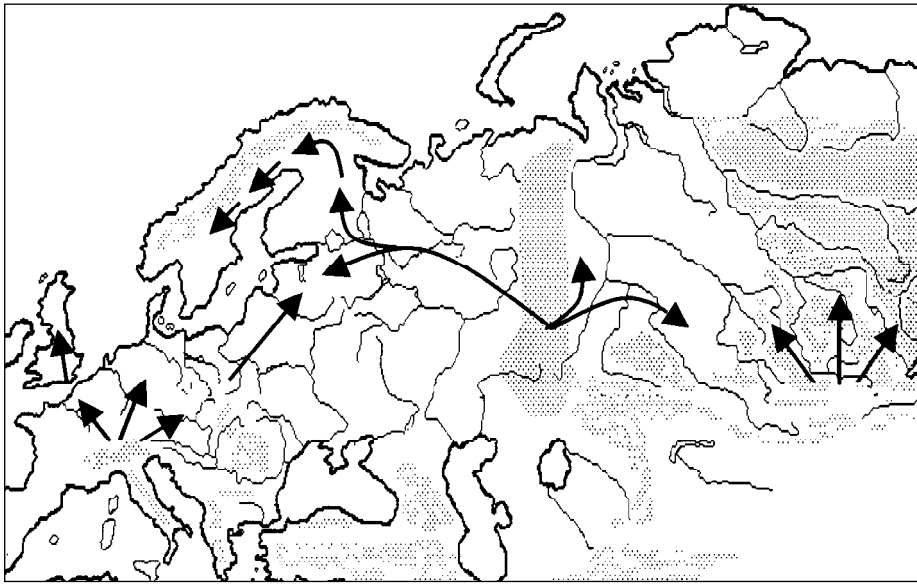
Fig. 3. The dispersal pathways of *Sorex araneus* in the postglacial period.

To establish the origins of the Ermakovskoe and Ilga races, additional evidence is required. They are probably related to the Baikal–Tomsk branch. The Ermakovskoe race may have originated from the neighboring Altai race via one whole-arm translocation (hi, o $\longrightarrow$ ho, i) whereas the Ilga race may be derived from the Ermakovskoe race via one centric fusion (i + q $\longrightarrow$ iq). As an alternative explanation, we can assume the independent origin of these races from a hypothetical ancestral form having the gk, ho, jl, i, m, n, p, q, r karyotype through two Robertsonian fusions i + m $\longrightarrow$ im, n + q $\longrightarrow$ nq in the case of the Ilga race and one Robertsonian fusion m + n $\longrightarrow$ mn in the case of the Ermakovskoe race.

The proposed scenario of the *S. araneus* karyotype evolution by sequential accumulation of metacentrics explains the characteristic feature of the geographic karyotype distribution in the Asian part of the species range, i.e., the northward increase in the number of metacentrics.

PALEOECOLOGY AND RACE FORMATION IN THE COMMON SHREW

The late macrocycle of the tertiary lasted about 130 thousand years and included the interglacial and the subsequent glacial period. During the interglacial period, when the species *S. araneus* probably was formed [23], the zonal structure in Siberia was generally similar to the modern one. We can assume that the population structure of the common shrew with regard to karyotypic variability did not differ to the present-day structure in the sense that the latitudinal gradient in the metacentric number existed, i.e., their number increased northward.

In the period of maximum cooling 20 to 18 thousand years ago, the Siberian climate was extremely severe.

This was the age of a massive expansion of the permafrost, whose southward movement completely destroyed the forest belt. Because of the continuous glacial front at the north, which hindered free drainage to the Kara Sea, the Western Siberian Plain was covered by a gigantic lake. Drainage could take place only via the Turgai flexure. At that time, Siberia had only three vegetation zones: periglacial, tundra–steppe, tundra, and forest–tundra. The latter was situated north of 56° N in the parts of the plain close to the Urals and the Enisei, and on the southern bank of the glacial water reservoir [24]. Thus, fragmentary forests were preserved only along the southern border of the Palearctics [25, 26]. The hills and mountains of the Southern Urals and Southern Siberia could serve as refugia for arboreal plants [27] and animals connected to them [28]. Apparently, the distribution of the common shrew was restricted to these refugia. A decrease in the northern area of the common shrew must have led to a reduction in karyotype variability of this species. Metacentric-rich chromosomal races whose area was limited by the glacier at the north of the range were preserved only in the Southern Urals. At the extreme south of the range in the Sayan and Altai refugia, acrocentric races similar to the modern Baikal race were retained. After the warming of the Siberian climate, forests started spreading northward. This was followed by an expansion of the common shrew range (Fig. 3). At the northern margin of the range, in the most extreme and unstable environmental conditions, isolated populations may have periodically appeared. In these populations, chromosome rearrangements were likely to be fixed. The latitudinal karyotype gradient in chromosomal races of the Eastern Siberian group probably resulted from the sequential formation of new metacentrics via Robertsonian

fusion of acrocentrics during the colonization of northern areas by the common shrew.

In contrast to shrews from the southern Siberian refugia, animals inhabiting the Southern Urals refugia probably had completely "metacentric" karyotypes. After the retreat of the glacier, the Urals forms dispersed westward (via northern Eastern Europe to Finland and further to Sweden) and eastward (to the eastern edge of the Western Siberian Plain). The race formation in the common shrew was determined by fixation of whole-arm reciprocal translocations between metacentric chromosomes.

The Novosibirsk race apparently was derived from the Serov race and moved eastward from the eastern Urals colonizing territories liberated as the Western Siberian glacial lake was drying out. At the east, the area of the Novosibirsk race converged with that of the Tomsk–Altai race group. A still-existing hybrid zone formed at their border [15, 22]. This accounts for the drastic difference in chromosome composition between the Novosibirsk race and the Altai–Tomsk group. These are separated by several thousand years of independent evolution. In meiosis, a chain of nine elements must form in hybrids between the Novosibirsk and Tomsk races. Such disturbances lead to formation of unbalanced gametes and, consequently, to complete sterility or extremely low fertility in hybrid individuals [22, 29].

Summarizing the above discussion, we can conclude that chromosomal races of the common shrew in Siberia were formed step by step, as the territories became available and colonized after the postglaciation climate warming. The general principles of the karyotype evolution in the common shrew may have been similar in Europe and Siberia. Monotonous landscapes and severe climate of Siberia led to the formation in this region in the postglaciation period of a simpler structure of the common shrew species than the structure of this species observed in Europe, which made phylogenetic relationships between the Siberian races more distinct. In Europe, the postglaciation migration of *S. araneus* probably followed a more complex pattern, which resulted in less regular geographical distribution of the race areas. However, the meridional gradient in the metacentric frequency in karyotypes of the European chromosomal races is similar to the Siberian one. In view of this, we can reasonably assume that the karyotype evolution in the common shrew started in Europe, as in Siberia, from the southern range margin and consisted in accumulation of metacentrics as the range expanded northward [30]. Scandinavia and Eastern Europe were colonized by chromosomal races of the Urals origin. These two phylogenetic branches, the southern European and Urals ones, converged in the region of the modern Poland. There, the only hybrid zone (between the Drnholek and Belovezh races) has been described. By differences in the races forming it, this zone is comparable to the hybrid zone between the Novosibirsk and Altai races in Siberia [31].

REFERENCES

1. Searle, J.B., Fedyk, S., Fredga, K., *et al.*, Nomenclature for the Chromosomes of the Common Shrew (*Sorex araneus*), *Memoires de la société vaudoise des sciences naturelles*, 1991, vol. 19, pp. 13–22.

2. Zima, J., Fedyk, S., Fredga, K., *et al.*, The List of the Chromosome Races of the Common Shrew (*Sorex araneus*), *Hereditas* (Lund, Swed.), 1996, vol. 125, pp. 97–107.

3. Searle, J.B. and Wojcik, J.M., Chromosomal Evolution: The Case of *Sorex araneus*, *Evolution of Shrews*, Wojcik, J.M. and Wolsan, M., Eds., Bialowieza: Mammal Res. Inst., Polish Academy of Sciences, 1998, pp. 219–268.

4. Halkka, L., Kaikusalo, A., and Vakula, N., Revision of *Sorex araneus* L. Chromosome Nomenclature, and Race N New to Finland, *Ann. Zool. Fennici*, 1994, vol. 31, pp. 283–288.

5. Fredga, K., The Chromosome Races of *Sorex araneus* in Scandinavia, *Hereditas* (Lund, Swed.), 1996, vol. 125, pp. 123–135.

6. Searle, J.B., Three New Karyotypic Races of the Common Shrew *Sorex araneus* (Mammalia, Insectivora) and a Phylogeny, *Syst. Zool.*, 1984, vol. 33, pp. 184–194.

7. Wojcik, J.M., Chromosome Races of the Common Shrew *Sorex araneus* in Poland: A Model of Karyotype Evolution, *Acta Theriol.*, 1993, vol. 38, pp. 315–338.

8. Wittenbach, A. and Hauser, J., The Fixation of Metacentric Chromosomes during the Chromosomal Evolution in the Common Shrew (*Sorex araneus*, Insectivora), *Hereditas* (Lund, Swed.), 1996, vol. 125, pp. 209–217.

9. Searle, J.B., Chromosomal Hybrid Zones in Eutherian Mammals, *Hybrid Zones and the Evolutionary Process*, Harrison, R.G., Ed., New York: Oxford Univ. Press, 1993, pp. 309–353.

10. Halkka, L., Soderlund, V., Scaren, U., and Heikkila, J., Chromosomal Polymorphism and Racial Evolution of *Sorex araneus, Hereditas* (Lund, Swed.), 1987, vol. 106, pp. 257–275.

11. Kral, B. and Radjabli, S.I., Banding Patterns and Robertsonian Fusion in the Western Siberian Population of *Sorex araneus* (Insectivora, Soricidae), *Zool. Listy*, 1974, vol. 23, pp. 217–227.

12. Aniskin, V.M. and Volobuev, V.T., Chromosome Polymorphism in Siberian Populations of Shrew of the *araneus–arcticus* Complex (Insectivora, Soricidae): III. Three Chromosomal Forms of the Common Shrew *Sorex araneus* L., *Genetika* (Moscow), 1981, vol. 17, no. 10, pp. 1784–1791.

13. Kral, B., Aniskin, V.M., and Volobouev, V.T., Karyotype Variability in Siberian Populations of *Sorex araneus* (Soricidae, Insectivora), *Folia Zool.,* 1981, vol. 30, pp. 23–37.

14. Zima, J., Macholan, M., Filippucci, M.G., *et al.*, Karyotypic and Biochemical Status of Certain Marginal Populations of *Sorex araneus, Folia Zool.*, 1994, vol. 43, suppl. 1, pp. 43–51.

15. Polyakov, A.V., Borodin, P.M., Volobuev, V.T., and Searle, J.B., Karyotypic Races of the Common Shrew (*Sorex araneus*) with Exceptionally Large Ranges: The Novosibirsk and Tomsk Races of Siberia, *Hereditas* (Lund, Swed.), 1996, vol. 125, pp. 109–115.

16. Polyakov, A.V., Chadova, N.B., Rodionova, M.I., *et al.*, Novosibirsk Revisited 24 Years on: Chromosome Polymorphism in the Novosibirsk Population of the Common Shrew *Sorex araneus* L., *Heredity,* 1997, vol. 79, pp. 172–177.

17. Polyakov, A.V., Borodin, P.M., Lukacova, L., *et al.*, The Hypothetical Old-Northern Chromosome Race of *Sorex araneus* Found in the Ural Mountains, *Ann. Zool. Fennici*, 1997, vol. 34, pp. 139–142.

18. Polyakov, A.V., Rogacheva, M.B., and Borodin, P.M., Chromosome Geography of Natural Populations of Shrew *Sorex araneus* and *Suncus murinus, Genetika* (Moscow), 1997, vol. 33, no. 8, pp. 1126–1132.

19. Borodin, P.M., Ladygina, T.Yu., Polyakov, A.V., and Rogacheva, M.B., Chromosome Pairing in Robertsonian Heterozygotes of Common *Sorex araneus* and Musk *Sorex murinus* Shrew, *Dokl. Ross. Akad. Nauk*, 1997, vol. 356, no. 1, pp. 132–134.

20. Polyakov, A.V., Zima, J., Searle, J.B., *et al.*, Chromosome Races of the Common Shrew, *Sorex araneus*, in the Ural Mountains: A Link between Siberia and Scandinavia?, *Acta Theriol.*, 2000, vol. 45, suppl. 1, pp. 19–26.

21. Polyakov, A.V., Zima, J., Banaszek, A., *et al.*, New Chromosome Races of the Common Shrew (*Sorex araneus*) from Eastern Siberia, *Acta Theriol.*, 2000, vol. 45, suppl. 1, pp. 11–18.

22. Aniskin, V.M. and Luk'yanova, I.V., A New Chromosome Race and Analysis of the Hybrid Zone of Two Karyomorphs of *Sorex araneus* (Insectivora, Soricidae), *Dokl. Akad. Nauk SSSR*, 1989, vol. 309, pp. 1260–1262.

23. Gureev, A.A., Insectivores: Hedgehogs, Moles, and Shrews (Erinaceidae, Talpidae, Soricidae), in *Fauna SSSR. Mlekopitayushchie* (Fauna of the Soviet Union: Mammals), Leningrad: Nauka, 1970, vol. 4, no. 2, p. 503.

24. Velichko, A.A., *Razvitie landshaftov i klimata severnoi Evrazii* (Development of the Landscape and Climate of Northern Eurasia), Moscow: Nauka, 1993, no. 1, p. 102.

25. Grichuk, V.P., Main Types of Vegetation (Ecosystems) during the Maximum Cooling of the Last Glaciation, *Atlas of Palaeoclimates and Palaeoenvironments of the Northern Hemisphere*, Frenzel, B., Pecsi, B., and Velichko, A.A., Eds., Budapest: Hung. Acad. Sci., 1992.

26. van Campo, E., Guiot, J., and Peng, C., A Data-Based Re-Appraisal of the Terrestrial Carbon Budget at the Last Glacial Maximum, *Global and Planetary Change*, 1993, vol. 8, pp. 189–201.

27. Frenzel, B., Vegetation during the Maximum Cooling of the Last Glaciation, *Atlas of Palaeoclimates and Palaeoenvironments of the Northern Hemisphere*, Frenzel, B., Pecsi, B., and Velichko, A.A., Eds., Budapest: Hung. Acad. Sci., 1992.

28. Baryshnikov, G.F. and Markova, A.K., Main Mammal Assemblages of the Upper Pleniglacial of the Last Glaciation, *Atlas of Palaeoclimates and Palaeoenvironments of the Northern Hemisphere*, Frenzel, B., Pecsi, B., and Velichko, A.A., Eds., Budapest: Hung. Acad. Sci., 1992.

29. Gropp, A. and Winking, H., Robertsonian Translocations: Cytology, Meiosis, Segregation Patterns and Biological Consequences of Heterozygosity, *Symp. Zool. Soc. London*, 1981, vol. 47, pp. 141–181.

30. Hewitt, G.M., Some Genetic Consequences of Ice Ages, and Their Role in Divergence and Speciation, *Biol. J. Linn. Soc.*, 1996, vol. 58, pp. 247–276.

31. Fedyk, S., Banaszek, A., Chetnicki, W., *et al.*, Reassessment of the Range of the Drnholec Race: Studies on Meiosis in *Sorex araneus* Hybrids, *Acta Theriol.*, 2000, vol. 45, suppl. 1, pp. 59–67.