Chromosome races of the common shrew *Sorex araneus* Linnaeus, 1758 (Mammalia: Insectivora) from the south part of Valdai Heights (Russia)

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Abstract. The chromosomes were studied in 126 common shrews, *Sorex araneus* L., from 20 localities in the south part of Valdai Heights. The geographic distribution and contact zones of three races (the Moscow, the West Dvina, and the Seliger) are described and discussed. The West Dvina and Seliger races appear to be restricted to the former last glacial area (Veps stage), and the Moscow race is widespread in unglacial area. These findings are considered in view of possibility of conservation of some icefree refugia within the limits of the last ice sheet.

Key words: common shrew, *Sorex araneus*, karyotypes, chromosome races, geographic distribution, contact zones, last ice sheet, Valdai Heights.

INTRODUCTION

The common shrew *Sorex araneus* L. displays exceptional chromosomal variability, usually assumed to be resulted from Robertsonian fusions. In karyotypes of different populations of the common shrew, the chromosome arms g-r combine together to form 41 different metacentrics (Wójcik et al., 2002). In total, 70 different chromosome races have so far been described in the common shrew, using the standard definition of a "race" (Hausser et al., 1994).

One of the major issues that needs to be addressed in the common shrew is the postglacial recolonization history (Polyakov et al., 2001; Brünner et al., 2002; Wójcik et al., 2002; Orlov, Kozlovsky, 2002; Orlov et al., 2006, 2007). The last glaciation (Late Valdai) began 24 000 years ago in European Russia. The ice margin has evidently reached its maximum position about 18 000-17 000 years ago on the Valdai Heights and retreated about 15 000-16 000 years ago (Veps glacial stage) (Velichko et al., 1993). The surprising thing is that the majority of races (about three quarters of their total number known in Eastern Europe) are located in the former ice sheet area of the last glaciation (Orlov, Kozlovsky, 2002). In addition, races located in the former glacial area are characterized by numerous "endemic" chromosomes. One hypothetical scenario is that some populations (races) survived the last glaciation in icefree refugia of the glacial area and spread southward when the ice retreated. In that case some races have come into contact at the last glacial boundary (Orlov et al., 2007).

In this paper, we define more precisely the distribution pattern of three chromosome races (Moscow, West Dvina, and Seliger) in the south part of Valdai Heights (60x60 km in Toropets and Andreapol districts) with respect to the last glacial boundary.



No.	Locality	Coordinates	No. of
			shrews
1	Andreapol	56°41'N/32°12'E	2
2	Volok (right bank Volkota)	56°51'N/31°40'E	24
3	Volok (left bank Volkota)	56°51'N/32°01'E	3
4	Dmitrovo	56°54'N/32°05'E	1
5	Lake Lutchanskoe (NE shore)	56°56'N/32°03'E	3
6	Bubonitsy	56°44'N/31°31'E	1
6	Bubonitsy	56°44'N/31°31'E	6
7	Toropets	56°45'N/31°30'E	2
8	Tchistoe	56°45'N/31°28'E	3
9	Bel'kovo	56°45'N/31°28'E	18
10	Shapkino	56°45'N/31°29'E	1
11	Zalezh'e	56°44'N/31°37'E	3
12	Kuznetsovo	56°49'N/31°37'E	2
13	Brosno	56°49'N/31°55'E	2
14	Goritsy	56°52'N/31°51'E	1
15	Vypolzovo	56°51'N/31°57'E	8
16	Volok (left bank Volkota)	56°51'N/32°02'E	2
17	Skudino	57°00'N/31°50'E	12
18	Lubino, 4 km to W	56°58'N/32°01'E	2
19	Borzovo (Lake Lutchanskoe)	56°57'N/32°00'E	19
20	Sharygino	56°57'N/31°57'E	12
20	Sharygino	56°57'N/31°57'E	1
21	Ryabkino	57°03'N/32°02'E	1

Table 1. Locations and sample sizes of karyotyped common shrews. All data included are new except for No. 7 (Pavlova et al., 2006)

$M {\rm ATERIAL} \ {\rm AND} \ {\rm METHODS}$

Common shrews were caught with live traps during 2005-2007. In total, karyotypes of 126 common shrews from 20 populations have been studied. The material studied is listed in Table 1, together with data from previously published studies.

Air-dried chromosome preparations were made from the bone marrow and spleen after *in vivo* treatment with colchicine (following a modified method according to Ford and Hamerton (1956), Orlov and Kozlovsky (1969), and Kozlovsky (1974). G-band staining was applied by a modified version of Seabright's (1971) technique. Chromosome nomenclature used follows Searle et al. (1991).

RESULTS AND COMMENTS

The results are summarized in Table 1, which gives the locality, number of specimens, and chromosome race. Our present knowledge of the distribution of three chromosome races in the study area is given in Fig. 1, b.

The Moscow race has the chromosome formula XX/XY₁Y₂*af, bc, gm, hi, jl, kr, no, pq, tu* (Fig. 2). This race was described by Aniskin and Lukianova (1989) in the vicinity of Moscow. The Moscow race belongs to the West European Karyotypic Group (Searle, 1984), which is characterized by the arm combinations *gm* and *hi*. The race is monomorphic with fully metacentric karyotype. Chromosome polymorphism in one population of this race (Bulatova et al., 2000) may be



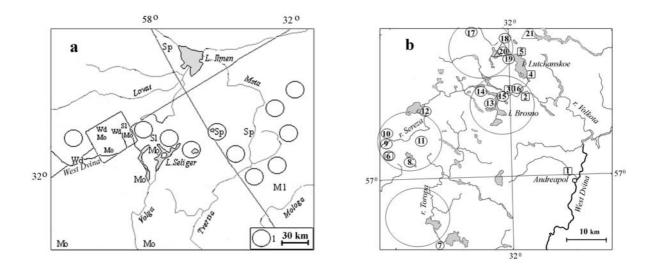


Fig. 1, a, b. Maps showing the distribution of chromosome races of *S. araneus* around the last glaciation boundary (Veps stage) on Valdai Heights (Orlov et al., 1996; Bulatova et al., 2000; Kozlovsky et al., 2000; our new collection sites). **a** - the total area under study. Localities of races: Mo – Moscow, Wd – West Dvina, Sl – Seliger, Sp – St. Petersburg, Ml – Mologa. 1 – Moraines of the last glaciation (Velichko et al., 1993). **b** - enlarged part of the distribution in the Upper West Dvina basin. Locality number refers to Table 1. Locality numbers within square mark the Moscow race; within circles – the West Dvina race; within triangles – the Seliger race. Large circles indicate the area of moraines of the last glaciation.

due to hybridization with a neighbouring race. Four metacentrics are shared by this race and the Vaud race from Western Alpes.

The Moscow race has a relatively wide distribution in the Upper Volga River basin from the Upper Volga River in the north to the Oka River in the south and from the Upper Dnepr River in the west to the Upper Volga in the east (Bulatova et al., 2000; Kozlovsky et al., 2000). According to our new data, the Moscow race is widely distributed in the West Dvina river basin (Fig. 1, b). It also reaches the Lovat river basin in the west (Fig. 1, b, locality 6) and comes into contact with the West Dvina race but this contact zone has not been thoroughly studied. Further to the east, the contact zone between the Moscow and West Dvina races runs along the river Volcota (Fig. 1, b, localities 2, 3 and 15, 16) and to the north from the lake Lutchanskoe (Fig. 1, b, localities 5 and 18, 19).

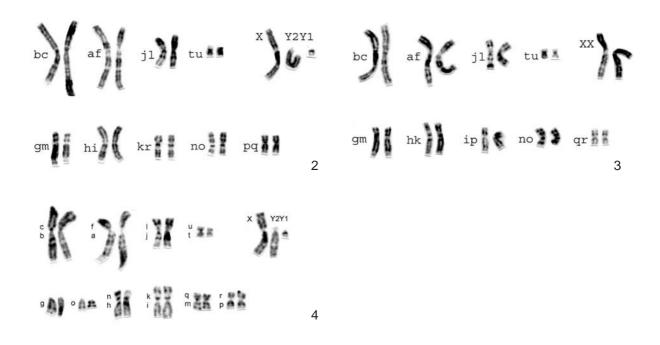
The West Dvina race has the chromosome

formula XX/XY₁Y₂ af, bc, gm, hk, ip, jl, no, qr, tu (Fig. 3). This race was described in the vicinity of the Zapadnaya Dvina railway station, the Upper West Dvina basin (Bulatova et al., 2002). The West Dvina race belongs to the Baltic Karyotypic Group characterized by the arm combination hk (Orlov et al. 2004). According to our new data, the West Dvina race is monomorphic with fully metacentric karyotype. The West Dvina race has a relatively wide distribution in the Lovat and West Dvina rivers basins (Fig. 1, b). Their distribution to the east is limited by the Moscow race.

The Moscow and West Dvina races differ by three Robertsonian metacentrics (Fig. 2, *hi*, *kr*, *pq* and Fig. 3, *hk*, *ip*, *qr*). Judging by karyotypes, their hybrids are expected to have 6 elements of ring configuration in meiosis I. It is probable that hybrids have lowered fertility due to production of aneuploid gametes.

The Seliger race has the chromosome for-





Figs 2-4. 2 - G-banded karyotype of the Moscow race. Male specimen from the NE shore of Lake Lutchanskoe, 2nA=18. **3 -** G-banded karyotype of the West Dvina race. Female specimen from Sharygino, 2nA=18. **4 -** G-banded karyotype of the Seliger race. Male specimen from Ryabkino, 2nA=20.

mula XX/XY₁Y₂*af, bc, g/o, hn, ik, jl, m/q, pr, tu* (Fig. 4). This race was described from the Valdai Heights in the vicinity of the lake Seliger (Bulatova et al., 2000). The Seliger race has a considerable degree of chromosomal polymorphism. This race belongs to the East European Karyotypic Group (Orlov et al., 2004). Two geographically separated races, Seliger and Bialowieza, share chromosomes *hn* and *ik* and are attributed to the subgroup Bialowieza (Orlov et al., 2004).

We have discovered this race southward from the lake Seliger (Fig. 1, b, localities 20 and 21). In this area further distribution of the Seliger race to the south is bounded by the West Dvina and Moscow races (Fig. 1, b). It is suspected that the Seliger race forms hybrids with the West Dvina race. Judging by their karyotypes (Figs 3, 4), hybrids are expected to have 10 elements of ring configuration and 9-10 elements of chain configuration in meiosis I. It is probable that hybrids have lowered fertility due to production of aneuploid gametes.

Recently, known distribution of five chromosome races (Moscow, Mologa, West Dvina, St. Petersburg and Seliger) of the common shrew on Valdai Heights (from the lake Onega to the West Dvina river basin) has been reported (Orlov et al., 2007). Chromosomal races from Valdai Heights differ by metacentrics with monobrachial homology (for example, *hi* in the Moscow race and *hk* in the West Dvina race). Such chromosomes must



necessarily replace each other in different populations. In hybrids, synapsis is expected to result in a multivalent (chain or ring) during meiosis. Because of this, hybrid zones are relatively narrow. and populations are isolated in a various degree. The contact zone between Moscow, West Dvina and Seliger races to the north from the lake Lutchanskoe has a rather small area (8x8 km). By way of example, the Oxford - Hermitage hybrid zone in Britain is roughly 300 km in length with a varying width of approximately 100 km. The diagnostic chromosomes distinguishing the Oxford and Hermitage races are kq and no in the former and ko in the latter (Searle, Wójcik, 1998). On the contrary, the Hällefors – Uppsala hybrid zone in central Sweden is 2.7 km wide and runs along the small river. In this area, both races dispay metacentric chromosomes and differ in two arm combinations, ko, pq and kp, oq, respectively (Narain, Fredga 1996). The Tomsk race (gk, hi, mn, o, p) comes into contact with the Novosibirsk race (g/ o, ik, hn, m/p) in the West Siberia. A relatively narrow contact zone between the races runs very close to the 200 m isocline (Polyakov et al., 2003).

We call attention that the contact zone between the West Dvina and Moscow races and between the Seliger and Moscow races seems to follow the last (Veps) glacial boundary in the study area (Fig. 1, b). Further to the north, the contact zone between the Seliger and Moscow races in the vicinity of the lake Seliger (Bulatova et al., 2000) is also located at the Veps glacial boundary (Fig. 1, a, Sl and Mo sites). It is likely that the contact zone between the St. Petersburg and the Mologa races (Fig. 1, a, Sp and Ml sites) runs very close to the Veps glacial boundary.

The West Dvina, Seliger and St. Petersburg races appear to be confined to the former last glacial area (Veps stage), and the Moscow and Mologa races are widespread in unglacial area. These findings are considered in view of possibility of conservation of some icefree refugia within the limits of the last ice sheet (Orlov et al., 2007). zones has not been essentially changed in postglaciation for the last 13 000 years. ACKNOWLEDGEMENTS We thank A.E. Balakirev, T.B. Demidova,

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It is safe to assume that some races recolonized the former glacial area when the ice retreated

from unglaciated area (the Moscow and Mologa

races) and other races (the St. Petersburg, Seliger

and West Dvina races) spread southward and

eastward from icefree refugia in the last glacial area.

Obviously, the current position of their contact

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References

- Aniskin V.M., Lukianova I.V. 1989. A new chromosome race and the analysis of hybridization zone of two karyoforms of *Sorex araneus* (Insectivora, Soricidae) // *Dokl. Akad. Nauk SSSR*. 309: 1260-1262. (In Russian).
- Brünner H., Turni H., Kapischke H.-J., Stubbe M., Vogel P. 2002. New Sorex araneus karyotypes from Germany and the postglacial recolonization of Central Europe // Acta Theriologica. 47(3): 277-293.
- Bulatova N., Nadjafova R. S., Krapivko T.P. 2002. Intraspecific phylogenetic relationships in *Sorex araneus* L.: the Southern Baltic Subgroup of chromosome races // *Genetika*. 38(1): 79-85. (In Russian).
- Bulatova N., Searle J.B., Bystrakova N., Nadjafova R., Shchipanov N., Orlov V. 2000. The diversity of chromosome races in *Sorex araneus* from European Russia // *Acta Theriologica*. 45(1): 33-46.
- Ford C.E., Hamerton J.L. 1956. A colchicine, hypotonic citrate squash sequence for mammalian chromosomes // *Stain Technol*. 31: 247-251.
- Hausser J., Fedyk S., Fredga K., Searle J.B., Volobouev V., Wójcik J.M., Zima J. 1994. Definition and



nomenclature of the chromosome races of *Sorex araneus* // *Folia* Zool. 43(Suppl. 1): 1-9.

- Kozlovsky A.I. 1974. The possibility for posthumous karyotyping of small mammals // *Zool. Zh.* 53(2): 1871-1872. (In Russian).
- Kozlovsky A., Orlov V., Okulova N., Kovalskaya J., Searle J.B. 2000. Chromosome studies on common shrew from northern and central parts of European Russia // Acta Theriologica. 45(1): 27-31.
- Narain Y., Fredga K. 1996. A hybrid zone between the Hällefors and Uppsala chromosome races of *Sorex araneus* in central Sweden // *Hereditas*. 125: 137-145.
- Orlov V.N., Bulatova N.Sh., Kozlovsky A.I., Balakirev A.E. 2004. Hierarchy of intraspecific taxa of the common shrew *Sorex araneus* L. (Insectivora), and taxonomic structure of species in mammals // *Zool. Zh.* 83(2): 199-212.
- Orlov V.N., Kozlovsky A.I. 1969. The chromosome complements of two geographically distant populations and their position in the general system of chromosomal polymorphism in the common shrew *Sorex araneus* L. (Soricidae, Insectivora, Mammalia) // *Tsitologiya.* 11: 1129-1136. (In Russian).
- Orlov V.N., Kozlovsky A.I. 2002. The role of glacial epochs in the formation of chromosomal polymorphism in the common shrew *Sorex araneus* L. (Insectivora, Mammalia) // *Dokl. Akad. Nauk.* (*Biol. Sci.*). 386: 462-465. (In Russian).
- Orlov V., Bulatova N., Kozlovsky A., Nadjafova R., Searle J.B. 1996. Karyotypic variation of the common shrew (*Sorex araneus*) in European Russia: preliminary results // *Hereditas*. 125: 117-121.
- Orlov V.N., Kozlovsky A.I., Potapov S.G., Illarionova N.A., Irchin S.Yu., Balakirev A.E. 2006. Refugial structure of species areas during the late Pleistocene – Holocene as inferred from molecular – genetic methods (pp. 174-179) // Dynamics of the recent ekosystems in Holocene. Proc. Russian Sci. Conf. Moscow, February 2-3, 2006. Moscow. 280 p. (In Russian).
- Orlov V.N., Kozlovsky A.I., Balakirev A.E., Borisov Yu.M. 2007. Endemism of chromosome races of the common shrew *Sorex araneus* L. (Insectivora

Mammalia) and the possibility of the conservation of refugia in the Late Valdai ice sheet area // *Dokl. Akad. Nauk.* (*Biol. Sci.*). 416(6): 727-730. (In Russian).

- Polyakov A.V., Panov V.V., Ladygina T.Yu., Bochkarev M.N., Rodionova M.I., Borodin P.M. 2001. Chromosomal Evolution of the Common Shrew *Sorex araneus* L. from the Southern Urals and Siberia in the Postglacial Period // *Genetika*. 37(4): 448-455. (In Russian).
- Polyakov A. V., Volobouev V. T., Aniskin V.M., Zima J., Searle J.B., Borodin P.M., 2003. Altitudinal partitioning of two chromosome races of the common shrew (*Sorex araneus*) in West Siberia // *Mammalia*. 67(2): 201-208.
- Pavlova S.V., Bystrakova N.V., Bulatova N.Sh., Nadjafova R.S., Polykov A.V. 2006. Materials for cadastre of the chromosomes races of the common shrew *Sorex araneus* L. // *Biogeography*. 13: 42-59. (In Russian).
- Seabright M.A. 1971. A rapid banding technique for human chromosomes // *Lancet*. 1(2): 971-972.
- Searle J. B., 1984. Three new karyotypic races of the common shrew *Sorex araneus* (Mammalia: Insectivora) and a phylogeny // Syst. Zool. 33: 184-194.
- Searle J.B., Fedyk S., Fredga K., Hausser J., Volobouev V.T. 1991. Nomenclature for the chromosomes of the common shrew (*Sorex araneus*) // *Mém. Soc. Vaud. Sci. Natur.* 19: 13-22.
- Searle J. B., Wójcik J. M. 1998. Chromosomal evolution: the case of *Sorex araneus* (pp. 219-268) // Wójcik J. M., Wolsan M. (Eds). *Evolution of shrews*. Bialowieza. 458 p.
- Velichko A.A., Borisova O.K., Doskach A.G., Morozova T.D., Spasskaya I.I., Faustova M.A. 1993. Russian plain (pp. 11-20) // Velichko A.A. (Ed.). Evolution of landscapes and climates of the Northern Eurasia. Late Pleistocene – Holocene. I. Regional paleogeography. Moscow. (In Russian).
- Wójcik J. M., Ratkiewicz M., Searle J.B. 2002. Evolution of the common shrew *Sorex araneus*: chromosomal and molecular aspects // *Acta Theriologica*. 47(Suppl. 1): 139-167.

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