

Postglacial recolonisation of European Russia by the common shrew *Sorex araneus*

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ABSTRACT. The present distribution of common shrew chromosome races indicates that the region covered by the Late Valdai ice sheet was subsequently recolonised by populations from refugia near the glacial front. The similarity of chromosome races from Finland and the Urals can be considered convergent: identical karyotypes have been formed independently on the basis of metacentrics in common and the canalisation of karyotypes. Chromosome races that survived the glaciation in southern refugia (Kiev, Neroosa, Penza and Sok) did not contribute to the postglacial recolonisation of the region vacated by the ice sheet.

KEY WORDS: *Sorex araneus*, chromosome races, postglacial recolonisation.

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Послеледниковая реколонизация Европейской России обыкновенной бурозубкой *Sorex araneus*

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РЕЗЮМЕ. Современное распространение хромосомных рас обыкновенной бурозубки указывает на то, что в прежней ледниковой области Восточной Европы расселение популяций шло из рефугиумов в непосредственной близости от ледниковой области. Сходство хромосомных рас Урала и Финляндии трактуется как конвергентное: идентичные кариотипы формировались независимо на базе общих метацентриков и канализованности эволюционных изменений кариотипов. Популяции, пережившие оледенение в южных рефугиумах (Киев, Нерусса, Пенза, Сок), не принимали участия в реколонизации ледниковой области Восточной Европы.

КЛЮЧЕВЫЕ СЛОВА: *Sorex araneus*, хромосомные расы, послеледниковая реколонизация.

Introduction

There is a general perception that during the last glaciation (Late Weichselian or Late Valdai in European Russia) Northern and Eastern Europe was inhospitable for temperate forest mammal species, including populations of the common shrew *Sorex araneus*. Such species traditionally have been considered to have spread northwards from refugia in Southern Europe at the end of the glaciation (Hewitt, 1999). However, mitochondrial DNA studies on some widespread species of small mammal suggest that colonisation may have occurred from glacial refugia in central Europe (Bilton *et al.*, 1998; Deffontaine *et al.*, 2005). Chromosome studies on the common shrew suggest that postglacial colonisation of Northern Europe may have occurred from the Urals (Polyakov *et al.*, 1997, 2000) and from “a refugium near the Black Sea coast” along the northern slopes of the Carpathian Mts. (Brünner *et al.*, 2002).

Here, we present additional karyotypes of the common shrew from areas that were covered by ice at the height of the Late Valdai glaciation. The ice sheet covered some of the Russian Plain including parts of the following river basins: Pechora, Mezen and North Dvina. The ice sheet flowed southwards to the Upper Volga River and West Dvina River drainage (Velichko *et al.*, 1993) (Fig. 1).

Material and methods

Original data on 13 karyotypes from 8 new geographical sites are presented. Common shrews were caught with live traps during 2001–2005 in different regions of European Russia. The localities and chromosomal characteristics of these populations are given in Tab. 1 and Fig. 1, together with similar data from previously published studies.

Air-dried chromosome preparations were made from bone marrow and spleen after *in vivo* or *in vitro* treatment with colchicine (following a modified method ac-

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Table 1. Locations, sample sizes and diagnostic chromosomes of karyotyped common shrews.

No.	Site name	Coordinates	Number of specimens	2NA	Diagnostic chromosomes	Race	Ref.
1	Izborsk*	N 57°45', E 27°50'	1	18	<i>gm, hk, ip, jl, nr, oq</i>	Pskov (Ps)	5
2	Sebezhd	N 56°20', E 28°50'	2	18	<i>gm, hk, ip, jl, nr, oq</i>		5
3	St.Petersburg, 50 km to S, Kartashevskaya*	N 59°25', E 30°05'	3	20	<i>g, hk, ip, jl, mq, nr, o</i>	St.Petersburg (Sp)	9
4	St.Petersburg, 30 km to W, Novij Peterhof	N 59°50', E 29°30'	1	20	<i>g, hk, ip, jl, mq, nr, o</i>		10
5	Soltsy	N 58°10', E 30°15'	1	21	<i>g, hk, ip, jl, m/q, nr, o</i>		10
6	Okulovka	N 58°25', E 33°20'	1	21	<i>g, hk, ip, jl, mq, nr, o</i>		10
7	Valdai	N 58°00', E 33°15'	1	20	<i>g, hk, ip, jl, mq, nr, o</i>		1
			1	24	<i>g, h/k, ip, j/l, m, nr, o, q</i>		1
8	Lake Seliger *	N 57°10', E 33°30'	2	20, 21	<i>g, hn, ik, jl, mq (m/q), o, pr</i>	Seliger (Sl)	8
9	Pertozero	N 61°45', E 34°25'	5	20–23	<i>g, hn, ip (i/p), jl, kr (k/r), mq (m/q), o</i>	Ilomantsi (Il)	8
10	Salmy, 10 km to S, Karkku	N 61°40', E 32°00'	1	22	<i>g, hn, i/p, jl, kr, m/q, o</i>		1
11	Zapadnaya Dvina*	N 56°15', E 32°00'	3	18	<i>gm, hk, ip, jl, no, qr</i>	West Dvina (Wd)	9
12	Toropets, 25 km to N	N 56°45', E 31°30'	1	18	<i>gm, hk, ip, jl, nr, oq</i>		1
			1	18	<i>gm, hi, jl, kr, no, pq</i>	Moscow (Mo)	1
13	Lake Sterzh	N 57°15', E 32°40'	5	18	<i>gm, hi, jl, kr, no, pq</i>		6
14	Selizharovo	N 56°35', E 33°30'	1	19	<i>g/m, hi, jl, kr, no, pq</i>		6
15	Rzhev	N 56°10', E 34°30'	12	18	<i>gm, hi, jl, kr, no, pq</i>		3, 8
16	Izdeshkovo, 15 km to E	N 55°10', E 33°50'	3	18	<i>gm, hi, jl, kr, no, pq</i>		7
17	Serpukhov	N 54°50', E 37°20'	5	18	<i>gm, hi, jl, kr, no, pq</i>		8
18	Zvenigorod	N 55°45', E 36°50'	2	18	<i>gm, hi, jl, kr, no, pq</i>		7
19	Moscow	N 55°40', E 37°00'	2	18	<i>gm, hi, jl, kr, no, pq</i>		3, 8
20	Moscow, 40 km to NE, Chernogolovka*	N 55°55', E 38°30'	3	18	<i>gm, hi, jl, kr, no, pq</i>		2
21	Sergiev Posad	N 56°20', E 38°00'	2	18	<i>gm, hi, jl, kr, no, pq</i>		3
22	Savelevo	N 56°50', E 37°25'	1	18	<i>gm, hi, jl, kr, no, pq</i>		1
23	Paleh	N 56°50', E 41°50'	1	18	<i>gm, hi, jl, kr, no, pq</i>		12
24	Yuzha	N 56°35', E 42°15'	1	18	<i>gm, hi, jl, kr, no, pq</i>		12
25	River Mologa, Lesnoe, 30 km to E*	N 58°20', E 36°00'	6	18–20	<i>g/m, hn, i/o, jl, kr, p/q</i>	Mologa (Ml)	3, 7, 8
26	Vladimir, 30 km to E, (right bank of Klyazma River)	N 56°05', E 40°55'	1	18	<i>gm, hn, io, jl, kr, pq</i>	Penza (Pn)	1
27	Kovrov (right bank of Klyazma River)	N 56°20', E 41°25'	1	18	<i>gm, hn, io, jl, kr, pq</i>		8
28	Velsk	N 61°00', E 42°00'	6	18	<i>go, hi, jl, kq, mn, pr</i>	Manturovo (Ma)	7
29	Krasnoborsk	N 61°42', E 46°41'	1	18	<i>go, hi, jl, kq, mn, pr</i>		11
30	Syctyvkar	N 61°30', E 51°00'	2	18	<i>go, hi, jl, kq, mn, pr</i>		7
31	Gorodets	N 56°33', E 43°53'	2	18	<i>go, hi, jl, kq, mn, pr</i>		11
32	Buj	N 58°30', E 41°30'	4	18	<i>go, hi, jl, kq, mn, pr</i>		1

Table 1 (continued).

No.	Site name	Coordinates	Number of specimens	2NA	Diagnostic chromosomes	Race	Ref.
33	Kostroma, 15 km to N	N 57°55', E 41°00'	1	18	<i>go, hi, jl, kq, mn, pr</i>		1
			1	18	<i>(go, gm, mn, no), jl, hi, kq, pr</i>	F1 Manturovo ? Kirillov	1
			1	18	<i>gm, hi, jl, kq, no, pr</i>	Kirillov (Kr)	10
34	Kirillov*	N 59°50', E 38°25'	3	18	<i>gm, hi, jl, kq, no, pr</i>		10
35	Onega, 15 km to S	N 63°50', E 38°15'	1	18	<i>gm, hi, jl, kq, no, pr</i>		13
			2	19	<i>gm, hi, jl, k/q, no, pr</i>		1
			1	20	<i>g/m, hi, jl, k/q, no, pr</i>		1
			1	20	<i>g, m, hi, jl, kq, no, pr</i>		1
36	Severodvinsk, 20 km to S	N 64°20', E 40°00'	3	18	<i>gm, hi, jl, kq, no, pr</i>		10
37	Severodvinsk, Island Yagry*	N 64°35', E 40°00'	3	18	<i>go, hi, jl, kq, mp, nr</i>	Yagry (Ya)	10
38	Kanin Peninsula*	N 68°20', E 45°13'	1	18	<i>gp, hi, jl, kq, mn, or</i>	Kanin (Kn)	4
39	Pechora, 50 km to N *	N 65°30', E 57°00'	2	18	<i>gi, hn, jl, kq, mo, pr</i>	Pechora (Pt)	7

The type sites (*) for each chromosome race are indicated. Locality number (No.) refers to Fig. 1. References: 1 — present study; 2 — Aniskin & Lukianova, 1989; 3 — Orlov *et al.*, 1996; 4 — Fredga, 1996; 5 — Zaitsev & Bulatova, 1999; 6 — Bulatova *et al.*, 1999; 7 — Kozlovsky *et al.*, 2000; 8 — Bulatova *et al.*, 2000; 9 — Bulatova *et al.*, 2002; 10 — Orlov & Kozlovsky, 2002; 11 — Bystrakova *et al.*, 2003; 12 — Orlov *et al.*, 2003; 13 — Orlov *et al.*, 2004.

according to Ford & Hamerton, 1956; Orlov & Kozlovsky, 1969; Kozlovsky, 1974). G-band staining was applied by a modified version of Seabright's (1971) technique. Chromosome nomenclature follows Searle *et al.* (1991).

Results

Within the Russian Plain, 12 chromosome races have been described in the vicinity of the former ice sheet and near its southern boundary.

Pskov race: XX/XY₁Y₂ *af, bc, gm, hk, ip, jl, nr, oq, tu*

This race was described by Zaitsev & Bulatova (1999) from a region in north-western European Russia (localities 1 and 2). The Pskov race has been assigned to the Baltic Karyotypic Group (*hk*) and to the West Dvina Karyotypic Family (*gm, hk, ip*) (Orlov *et al.*, 2004).

St. Petersburg race: XX/XY₁Y₂ *af, bc, g, h/k, ip, j/l, m/q, n/r, o, tu*

The St. Petersburg race was originally described from Kartashevskaya, Leningrad district (locality 3) (Bulatova *et al.*, 2002), from New Petergof near St. Petersburg and from Novgorod district (localities 4–7, our data). The distribution range of this race can, therefore, be extended from the Gulf of Finland to the Valdai Heights. This race may be placed in the Baltic Karyotypic Group (*hk*) and the East Baltic Karyotypic Family (*hk, ip, nr*) (Orlov *et al.*, 2004). Polymorphism for chromosomes *mq* and *nr* was found in this race for the first time.

Seliger race: XX/XY₁Y₂ *af, bc, g, hn, ik, jl, m/q, o, pr, tu*

This race was described by Bulatova *et al.* (2000) from the Valdai Heights in one site (locality 8). This

race has been placed in the East European Karyotypic Group (Orlov *et al.*, 2004).

Ilomantsi race: XX/XY₁Y₂ *af, bc, g/o, hn, i/p, j/l, kr, m/q, tu*

This race was described by Halkka *et al.* (1987) in the east of Finland and from southern Karelia (Bulatova *et al.*, 2000; our data; localities 9–10), but the limits of its advance to the south is unknown. The race may be placed in the East European Karyotypic Group and in the Finnish Karyotypic Family (*go, hn, ip*) (Orlov *et al.*, 2004).

West Dvina race: XX/XY₁Y₂ *af, bc, gm, hk, ip, jl, no, qr, tu*

This race was described by Bulatova *et al.* (2002) in the vicinity of the Zapadnaya Dvina railway station, upper West Dvina River basin (locality 11). The West Dvina race has been assigned to the Baltic Karyotypic Group (*hk*) and to the West Dvina Karyotypic Family (*gm, hk, ip*). According to our new data the West Dvina race reaches the nearest Lovat River basin (locality 12). At this point individuals of both the West Dvina and Moscow races were found.

Moscow race: XX/XY₁Y₂ *af, bc, gm, hi, jl, kr, no, pq, tu*

Two metacentrics (*gm* and *hi*) of this race are typical of the West European Karyotypic Group (Aniskin & Lukianova, 1989; Orlov *et al.*, 1996). Four metacentrics are shared by this race and the Vaud race. We suggest that they are closely related. The Moscow race might have migrated from Western to Eastern Europe during the warm Mikulino (Eemian) interglacial 130,000–100,000 years ago.

The area of the Moscow race covers much of the Upper Volga River basin from the Upper Volga River



Figure 1. Localities of chromosome races of the common shrew in the context of the Late Valdai glacial period (Velichko *et al.*, 1993). 1 — Late Valdai loess; 2 — maximum extent of ice sheet. Locality number refers to Tab. 1.

in the north (localities 13, 14, 22) to the Oka River in the south (locality 17) and from the Upper Dnepr River in the west (locality 16) to the Upper Volga in the east (localities 23 and 24). According to our new data the Moscow race reaches the Lovat River basin in the west (locality 12). At this point the Moscow race is in contact with the West Dvina race.

Mologa race: XX/XY₁Y₂ *af, bc, g/m, hn, i/o, jl, kr, p/q, tu*

The Mologa race was first described in the Mologa River basin (Orlov *et al.*, 1996) on the southern border

of the ice sheet (locality 25). However, Bulatova *et al.* (1999, 2000) and Bystrakova *et al.* (2003) also found the race in localities much further to the south in the Middle Volga River basin. Orlov *et al.* (2003) suggested that the northern population from the Mologa basin is isolated and should not be grouped with the southern, Middle Volga, population. These populations are separated by the Moscow race occupying most of the lowland between the Upper Volga and the Oka rivers (Fig. 1).

From the above reasoning we may interpret the northern and southern populations of the previously-

described Mologa race as distinct races. The name “Mologa” should be reserved for the northern population, and the southern populations should be described as a new Penza race.

Penza race: XX/XY₁Y₂ *af, bc, gm, hn, ilo, jll, kr, p/q, tu*

This race and the Moscow race have three metacentrics (*gm, kr, pq*) in common. The Penza race (and the Mologa race) have been classified as part of the East European Karyotypic Group (Orlov *et al.*, 2004). Type locality: Zemetchino, Penza Province, the right bank of the Lengas River (N 53°20', E 42°40') (Bulatova *et al.*, 1999). Difference from the Mologa race: geographical isolation and the fixation of the metacentric *gm*.

Distribution: this is certainly a widespread race in the Middle Volga River (right bank) basin (Bystrakova *et al.*, 2003) (Fig. 1). We suggest that the Moscow/Penza interracial boundary passes along the small Klyazma River (localities 23, 24 — the Moscow race and 26, 27 — the Penza race).

Kirillov race: XX/XY₁Y₂ *af, bc, gm, hi, jl, kq, no, pr, tu*

The Kirillov race has been mentioned in literature (Orlov & Kozlovsky, 2002; Orlov *et al.*, 2004) but without a banded karyotype. Fig. 2 shows the fully metacentric karyotype but the Onega population is polymorphic (Tab. 1). Two metacentrics of this race (*gm* and *hi*) are characteristic of the West European Karyotypic Group. The Kirillov race is identical to the Oxford race (United Kingdom) and the Sjaelland race (Denmark). We suggest that they are closely related. The Kirillov race might have migrated from Western Europe to Eastern Europe during the warm Mikulino (Eemian) interglacial. The current chromosomal races of Northeastern Europe are probably the product of contact between the Kirillov race and native populations. Diagnostic metacentrics of the Kirillov race are found in the Yagry, Kanin, Manturovo and Pechora races. The similarity between the Kirillov race and other chromosome races of Northeastern Europe with respect to the cytochrome *b* gene (Balakirev *et al.*, 2007) might be due to their reticulate evolution.



Figure 2. G-banded karyotype of the Kirillov race. Male specimen from Kirillov, 2NA=18.

Type locality: Kirillov, Vologda Province (N 59°50', E 38°25') (locality 34). The Kirillov race is widespread in northern Russia (localities 33, 35, 36).

Manturovo race: XX/XY₁Y₂ *af, bc, go, hi, jll, kq, mn, pr, tu*

This race and the Kirillov race have three metacentrics (*hi, kq, pr*) in common. The Manturovo race may be placed in the East European Karyotypic Group and in the North Dvina Karyotypic Family (*go, hi, kq*) (Orlov *et al.*, 2004). This is a widespread race in the North Dvina and Upper Volga river basins (Bulatova *et al.*, 2000; Kozlovsky *et al.*, 2000; Bystrakova *et al.*, 2003). The Manturovo race has been found relatively close to the southern border of the former ice sheet (localities 28–30). It is likely that the Manturovo race occupies part of the area vacated by the Kola-Mezen and White Sea lobes of the ice sheet but the limits of its advance to the north are unknown. The Manturovo and Kirillov races and hybrid individuals were found in the vicinity of Kostroma city (locality 33).

Yagry race: XX/XY₁Y₂ *af, bc, go, hi, jl, kq, mp, nr, tu*

The Yagry race has been mentioned in the literature (Orlov & Kozlovsky, 2002; Orlov *et al.*, 2004) but without a banded karyotype. The fully metacentric karyotype is shown in Fig. 3. This race and the Kirillov race have two metacentrics (*hi, kq*) in common. The Yagry race has been placed in the East European Karyotypic Group and in the North Dvina Karyotypic Family (*go, hi, kq*) (Orlov *et al.*, 2004).

Type locality: Yagry Island (White Sea) in the vicinity of Severodvinsk, Arkhangelsk Province (locality 37). This race is only known so far from the Island of Yagry but may be widespread in the North Dvina River basin.

Kanin race: XX/XY₁Y₂ *af, bc, gp, hi, jl, kq, mn, or, tu*

This race was described by Fredga (1996) in the extreme north of European Russia (Kanin Peninsula) (locality 38). There are two metacentrics (*hi, kq*) in common between this race and the Kirillov race. The Kanin race has been assigned to the East European Karyotypic Group (Orlov *et al.*, 2004).

Pechora race: XX/XY₁Y₂ *af, bc, gi, hn, jl, kq, mo, pr, tu*

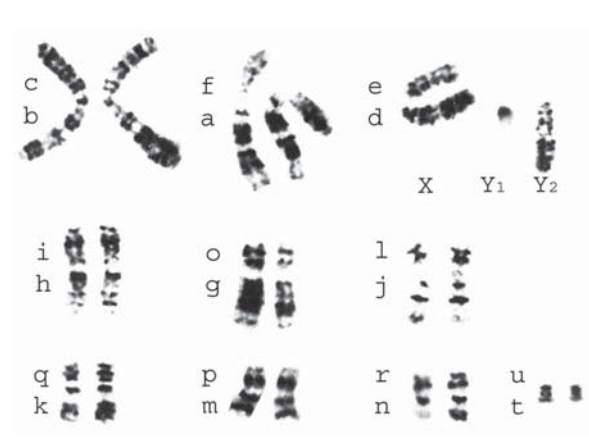


Figure 3. G-banded karyotype of the Yagry race. Male specimen from the Island of Yagry (White Sea), 2NA=18.

The Pechora race was found in one site in north-eastern European Russia (Kozlovsky *et al.*, 2000) near to the edge of the former ice sheet (locality 39). Two meta-centrics (*kq*, *pr*) are common to this race and the Kirillov race. The Pechora race has been considered part of the East European Karyotypic Group (Orlov *et al.*, 2004).

Discussion

A recent reconstruction of the Late Valdai ice sheet by Velichko *et al.* (1993) provides much detail about the behaviour of the ice sheet through time and about the nature of its margins. This information is summarised in Fig. 1.

The last glaciation in European Russia began with the advance of the Novaya Zemlya ice sheet to the Mezen River and the Pechora River basins (Fig. 1). There, the ice margin reached its maximum position by about 33–36,000 years ago and retreated by about 15–16,000 years ago. The Pechora race has been found in this area of the former ice sheet.

The ice of the Kola-Mezen and the White Sea lobes (Scandinavian ice sheet) flowed southeastward to the Onega, North Dvina and Mezen River basins (the maximum ice position was reached 24,000 years ago) (Fig. 1). The Yagry, Kirillov, Kanin and, possibly, Manturovo races are currently present in the area where these lobes occurred.

The Lake Onega – Karelia lobe moved southeastwards by compressive flow out of Lake Onega to the Upper Volga River drainage and the North Dvina River basin (the maximum extend of this lobe was reached 21,000–22,000 years ago). The Kirillov race is widespread in the area previously occupied by this lobe.

The two sublobes of the Lake Ladoga lobe flowed southwards farther to the west across the Russian Plain (with a maximum position about 17–18,000 years ago). Its eastern sublobe extended only as far as the Mologa River. At the same time its western sublobe moved onto the Valdai Heights and as far southwards as the West Dvina River basin. The ice of the Lake Chudskoe lobe flowed southwards into the West Dvina basin (with a maximum position about 17–18,000 years ago). Seven chromosome races are currently present in the area where these lobes occurred (Fig. 1).

The distribution of chromosome races in Eastern Europe seems paradoxical. The majority of races (about three quarters of all those known in Eastern Europe) are located in the former ice sheet area of the Late Valdai glaciation. In addition, races located in the former glacial area are characterised by endemic chromosomes (*gi*, *gp*, *mo* and *or*).

Twenty-three chromosome races of the common shrew have been found in the former Late Valdai glacial area (i.e. in Europe — to the east of the Vistula River and the Gulf of Bothnia), covering an area of about 1.5×10^6 km² (an average of 6.5×10^4 km² per race). On the other hand, only four chromosome races (Sok, Penza, Neroosa and Kiev) are widespread in the unglaciated area of the Late Valdai glaciation from the Carpathian Mountains to

the Southern Urals (an average of 6×10^5 km² per race, that is ten times larger than for races in the formerly glaciated area) (Orlov & Kozlovsky, 2002).

We suggest that the common shrew populations in the northern part of Russian Plain did not vanish during the Late Valdai glaciation. We believe that they survived the glacial maximum in refugia near the glacial front. Moreover, the ice sheet created conditions for the isolation of animal populations and for the origin of new forms. This conclusion agrees with what is known about the periglacial environment in the Russian Plain during the Late Valdai glaciation period.

The periglacial environment in Eastern Europe during the Late Valdai was characterised by a very dry climate, a mean annual temperature of about -2°C and colder, and widespread permafrost to the east of the Upper Volga River basin. The mean annual precipitation in the unglaciated area decreased to 200 mm (as in modern semi-deserts!), while the amounts of precipitation increased near the glacial front (the West Dvina, Upper Volga and North Dvina River basins) (Velichko *et al.*, 1993).

The temperate forest rodents *Clethrionomys glareolus* and *Microtus agrestis* have been found near the glacial front during the maximum of the Late Valdai glaciation (20,000 years ago). At that time, temperate forest species were not recorded in the southern part of the Russian Plain (to the south of the Oka River) (Markova *et al.*, 1995).

Late Valdai loess in the Russian Plain (Fig. 1) was inhospitable for temperate species. Loess-derived soils in the Russian Plain extend from the Black Sea eastwards to the Middle Urals. Late Valdai loess covers a large part of the Russian Plain to the south from the line L'vov – Kiev – Kaluga – Ryazan and forms the agricultural heartland of Ukraine and Russia. Under lower temperatures, a deficit of available moisture must have reduced plant cover with the resulting formation of eroded surfaces and eolian sand (Velichko *et al.*, 1993).

Shrub-tundra bordered the edge of the ice sheet in the West Dvina River basin during the Late Valdai (San'ko, 1987). Forest vegetation was present near the glacial front (the Baltic, Smolensk, Moscow and Valdai Heights) and in the northern periglacial area (the Vyatskie Uvaly and Severnye Uvaly Heights) throughout the Late Valdai. The transition from tundra to forest vegetation occurred in these northern regions of the Russian Plain approximately 14,000 years ago or later (Kozharinov, 1994).

The Lake Onega – Karelia lobe was retreating by about 15–16,000 years ago. Shortly after that time, the Onega River basin was deglaciated, leaving the residual ice in the lakes between the White Sea and Lake Onega. The extensive deglaciation in the Onega River basin made it possible for the Kirillov race to extend northwards. The final dissipation of the ice between the White Sea and Lake Onega did not take place until after 11,000 years ago (Velichko *et al.*, 1993). This prevented the Kirillov race from extending to the west (in Karelia).

The advance of the Lake Ladoga lobe was followed by extensive deglaciation of its eastern sublobe (15–16,000 years ago). The glacial front retreated from the

Mologa River to Lake Ladoga, whereas the ice of the western sublobe remained in the West Dvina River basin. The extensive deglaciation in the Mologa River basin made it possible for the range of the Mologa race to extend to the north. The deglaciation of the Lake Ladoga eastern sublobe and the Onega – Karelian lobe was followed by residual ice in the system of lakes between Lake Onega and the Upper Volga that separated the Mologa and the Kirillov races.

Only a small numbers of populations of the Moscow and the West Dvina races entered the area of the former ice sheet (the Lake Ladoga lobe). The Pskov race might have colonised the area of the former Lake Chudskoe lobe (Fig. 1) from refugia located in the West Dvina River basin 18–13,000 years ago. Hybrids between the Pskov race and other native populations were able to form the Tallinn race. The St. Petersburg race occupies the largest part of the western sublobe. The Pskov, St. Petersburg and Lemi races have three metacentrics (*hk*, *ip*, *nr*) in common. We suggest that these three races originated in glacial refugia near the glacial front.

The present cytogenetic study of chromosome races of the common shrew from the former Late Valdai ice sheet indicates that this region was recolonised by populations which survived in refugia near the glacial front.

Some populations survived during the Late Valdai glaciation period in southern refugia. The Kiev race might have survived during the glacial period in the Carpathian forest refugia and then extended eastwards to the loess area; the Neroosa and the Penza races – in the refugia of the Middle Russian and Middle Volga Heights (to the south of the Late Valdai loess region), the Sok race — in the Pre-Urals. Fossil remains of *Sorex* sp. collected from a series of new sites in the Perm Pre-Urals have been dated to the Late Pleistocene glacial maximum (Fadeeva, 2003). These four races did not contribute to the postglacial recolonisation of the Eastern Europe former ice sheet.

Recent studies have uncovered the similarity of some Finnish races and races from the Urals (Polyakov *et al.*, 1997, 2000). Two chromosome races from the Urals (Yuryuzan and Sok) appeared to have identical karyotypes to the races which had already been traced in Finland (Ilomantsi and Kuhmo). Polyakov *et al.* (1997, 2000) considered that the Finnish and Urals races are closely related and that during the last glaciation period the Urals must have been a refugium for some chromosome races which are currently distributed in Finland.

In our previous paper (Orlov & Kozlovsky, 2002) we presented evidence that the Northern European Karyotypic Group (NEKG) (Searle & Wójcik, 1998) did not form a continuous distribution between the Urals and Scandinavia.

The widespread occurrence of metacentric *hi* in the northeastern European populations of the common shrew (Kirillov, Manturovo, Yagry and Kanin races) suggests that there were no metacentrics with monobrachial homology with *hi* (namely, *hn* or *ip*, diagnostic chromosomes of races from Finland and the Urals) in this region. “A link” between Siberian and Finnish races could not be eliminated by the last glaciation, because

many native races and chromosome rearrangements of local origin (*gi*, *gp*, *mo* and *or*) still occur.

There are no populations of the common shrew near the former glacial front closely related to populations from the Urals. During postglacial colonisation, the Sok race expanded its range from the Urals to the Middle Volga in the west. Its advance northwestwards was limited by the Manturovo race (Bystrakova *et al.*, 2003).

Some populations have metacentrics that are diagnostic for the Urals and are widespread in Eastern Europe (metacentrics *ip* and *mq* in the St. Petersburg race and metacentrics *hn* and *kr* in the Mologa race). We suggest that chromosome races from Karelia and Finland might have originated during their postglacial colonisation from hybridisation of different populations, i.e. they are the product of reticulate evolution. The advance of metacentric *ip* to the north might have begun from the West Dvina basin (the Pskov race and the West Dvina race) and from the range of the St. Petersburg race. The advance of metacentrics *hn* and *kr* might have begun from the Upper Volga River basin (the Mologa race). Judging from the data concerning deglaciation, this could not occur earlier than 13,000 years ago (Velichko *et al.*, 1993). The hybridisation of the St. Petersburg race (metacentrics *ip* and *mq*) and the Mologa race (metacentrics *hn* and *kr*) might have resulted in the appearance of the Ilomantsi race (Orlov & Kozlovsky, 2002; Orlov *et al.*, 2004).

Metacentric *go* has not been found to the south of the Gulf of Finland and Lake Ladoga. However, its occurrence in the St. Petersburg race (with a frequency of 5%) and its penetration into Karelia from the south are not excluded. It should be noted that the frequency of metacentric *go* is as low as 5% in Finnish populations of the common shrew.

Metacentric *kq* is widespread in Western Europe. It might have been brought to the Finnish races (Savukoski and Kuhmo) from Scandinavia (Abisko race), because its spread from the east and south was prevented by metacentrics with monobrachial homology (*kr* and *mq* in the Ilomantsi race).

Therefore, the similarity of chromosome races from Finland and the Urals can be considered convergent: identical karyotypes have been formed independently on the basis of metacentrics in common and the canalisation of the evolutionary changes of karyotypes.

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