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Continuity of Y chromosome haplotypes in the population of Southern Poland before and after the Second World War

Marcin Woźniak [a,*], Tomasz Grzybowski [a], Jarosław Starzyński [a], Tomasz Marciniak [b]

[a] *Institute of Molecular and Forensic Genetics, Nicolaus Copernicus University, Collegium Medicum in Bydgoszcz, ul. M. Skłodowskiej Curie 9, 85-090 Bydgoszcz, Poland*
[b] *Institute of Sociology, Nicolaus Copernicus University, ul. Fosa Staromiejska 1A, 87-100 Toruń, Poland*

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Abstract

The Polish population is reported to be very homogenous as far as Y chromosome polymorphism is concerned. One of the hypotheses that explains this phenomenon is based on the assumption that massive migrations that took place in Poland after the Second World War might have evoked such an effect. Thus, knowledge of the pre-war frequencies of Y chromosome haplotypes in different parts of the country would be a useful tool in testing such a hypothesis. We have collected 226 DNA samples, together with family history data, from males living in the rural area of Małopolska, Polish Southern border region. Based on donors' family histories we were able to reconstruct an 'ancestral' subpopulation of 108 males whose ancestors had inhabited the area before both World Wars. We have analyzed 12 Y-STR loci: DYS19, DYS385, DYS389I&II, DYS390, DYS391, DYS392, DYS393, DYS437, DYS438 and DYS439 in all the collected samples. Comparisons of our contemporary and 'ancestral' population samples with other Polish and Central European populations showed that the population of Southern Małopolska is very closely related to other Polish and Slavic populations. The above-mentioned observations suggest that the population of Southern Poland could have been highly homogenous even before the Second World War.
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Keywords: Y chromosome; Y-STR; Polish population

1. Introduction

Poland is among those European countries whose history is especially rich in events such as wars, massive migrations and border shifts, particularly over the last 200 years [1]. Such events are usually regarded as important factors that promote mixing of human populations [2]. Indeed, two previous studies by Ploski et al. [3] and Kayser et al. [4] based on large sets of data coming from Y chromosome microsatellites (Y-STRs) and binary polymorphisms (Y-SNPs) in populations from different regions of Poland and Germany as well as from other Central European countries; reported extreme homogeneity of Polish populations and their distinctiveness; especially in comparison to their neighbouring German populations. Noticeably, no significant differences were observed among Polish populations samples coming from distant regions of the country even though such differences were observed in European countries much smaller than Poland; the Netherlands being the most prominent example [5].

Among a few explanations proposed for the observed homogeneity and distinctiveness of Polish Y chromosome lineages, there was a hypothesis that massive migrations that took place after the WWII could have evoked such an effect [4]. Indeed, due to the international agreements after the Second World War, the Eastern border of Poland was shifted westwards to the line of the Bug River (so called ''Curzon line''). Hence, the territory that used to belong to Poland was incorporated into Belarus, Ukraine and Lithuania. A part of a former German territory eastward from the Odra River was in turn attached to Poland. The consequences of the above-mentioned changes were massive eastward migrations of millions of the resettled Poles and Germans [1]. In the consecutive years, as a result of progressive urbanization of the country, many Polish families moved from the countryside to big cities, rendering the country's population migration patterns even more complex [6,7] (Fig. 1).

* Corresponding author. Tel.: +48 52 585 35 56; fax: +48 52 585 35 52.
E-mail address: marcinw@cm.umk.pl (M. Woźniak).

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Fig. 1. A schematic view of main post-war migration routes across the territory of Poland. White arrows represent an estimated figure of 8 million Germans resettled from Pomerania, Silesia and Prussia. Hatched arrows represent ca. 2 million Poles migrating from Lithuania, Belarus and Ukraine. Shaded area at the southern border of Poland indicates the region where samples were collected.

The post-war migrations described above are relatively recent events as they took place ca. 60 years ago. However, they influenced many individuals who had to move a few hundred kilometers away from their hometowns. Thus, collecting data on family history from individuals who volunteered to donate a DNA sample for scientific research should allow detecting such events by tracing birthplaces of the consecutive generations. Combining family history data with DNA polymorphism analysis could serve as a useful tool in tracing historical changes of regional DNA diversity.

The aim of this study is to test the possibility of using family history information provided by the sample donors for re-creating the recent history of Polish population and to gather evidence that detectable differences existed between pre-war and post-war populations inhabiting Poland. As most of the post-war Polish migrants had settled in the western part of the country and/or in relatively big cities like Wroclaw (former Breslau) or Szczecin (former Stettin) [6], the southernmost part of Małopolska region was chosen for sample collection (Fig. 1). The region comprises two relatively small, neighbouring subregions called Podhale and Beskid Sądecki, located in the mountains along the Southern border of Poland. The subregions are inhabited by a population that is distinctive with regard to their culture and dialect [8]. The rationale for the sampling strategy was the assumption that if there was a region in Poland that preserved at least some of the pre-war genetic structure it should be a rural area with a relatively low immigration rate. Podhale and Beskid Sądecki along with the surrounding areas seemed to fulfill this criterion.

2. Materials and methods

DNA donors were recruited among teenagers and teachers from secondary schools located in cities: Zakopane (N = 49°17′52.2″; E = 19°57′25.5″), Nowy Targ (N = 49°29′02.3″; E = 20°01′52.4″), Limanowa (N = 49°42′02.7″; E = 20°25′36.3″), Nowy Sącz (N = 49°36′22.2″; E = 20°42′18.1″). All donors were asked to fill in a questionnaire containing questions about their male lineage ancestors' place and year of birth. DNA samples and ancestry questionnaires were collected from 226 males. In ancestry analysis a sample was regarded to be of local origin if the donor's grandfather and/or great-grandfather in male lineage had been born inside the area confined by cities: Maków Podhalański (N = 49°43′53.8″; E = 19°40′45.7″), Dobczyce (N = 49°52′44.3″; E = 20°05′47.2″), Czchów (N = 49°50′12.9″; E = 20°40′48.2″) and Gorlice (N = 49°39′47.9″; E = 21°10′09.4″) (see Section 3 for the details concerning sample selection). Consecutive generations were named according to the following scheme—F0: sample donors generation; F-1: sample donors' fathers generation; F-2: sample donors' male lineage grandfathers generation; F-3: sample donors' male lineage great-grandfathers generation.

Buccal swabs were collected from the donors and DNA was isolated using standard organic extraction protocol with DNA salting-out [9]. 0.5 μL of the DNA solution was used for subsequent amplification.

Y-STR haplotypes for 12 Y-STR loci: DYS19, DYS385, DYS389I/II, DYS390, DYS391, DYS392, DYS393, DYS437, DYS438 and DYS439 were obtained using PowerPlex Y™ system (Promega, Madison, USA) following manufacturers' recommendations. Products of amplification were electrophoresed using ABI3100 Genetic Analyzer with an appropriate filter set prepared with the use of relevant PowerPlex® Matrix Standards provided by Promega [10]. Fifty-centimeter capillaries and POP-6 polymer were used for optimal resolution. One microliter of each sample was mixed with 9 μL of deionized formamide (Applied Biosystems) and 0.5 μL of Internal Lane Standard 60–600 (Promega). The results of the electrophoresis were analyzed using Genscan v. 3.7 and Genotyper v. 3.7 software (Applied Biosystems). Y Power Typer macro (Promega) was used to assign allelic names. Alleles were designated according to the recommendations of the DNA Commision of the International Society of Forensic Genetics [11]. In this publication complete haplotypes are coded in the form of a–b–c–d–e–f–g–h,i–j–k–l string where consecutive letters are replaced by alleles of Y-STR loci according to the following order: DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS385, DYS437, DYS438 and DYS439. The first nine positions in the string compose the so called ''minimal haplotype'' as defined by YHRD [12]. Haplotype data obtained in this experiment are available as electronic supplementary information.

Haplotype data for comparison purposes were extracted from the data set containing Y-STR haplotypes constructed from DYS19, DYS389&II, DYS390, DYS391, DYS392 and DYS393 loci in 12,700 donors from 91 different European locations, published by Roewer et al. [5]. The haplotypes of 5471 individuals were extracted from the dataset to represent populations of different regions of Poland as well as populations of other Central European countries neighboring Poland. The populations of Bydgoszcz, Gdansk, Krakow, Lublin, Warsaw, Wrocław were chosen to represent Poland, those of Vilnius, Riga and Tartu represented Baltic countries,

Table 1
Generation data retrieved from questionnaires collected from sample donors

	F0	F-1	F-2	F-3
N	226	222	202	142
Mean	1988.69	1957.84	1926.50	1892.92
S.D.	2.64	6.27	10.14	13.45
Median	1989	1959	1926	1896
Min.	1961	1926	1889	1844
Max.	1991	1968	1943	1918
95% percentile	Born after 1987	Born before 1966	Born before 1941	Born before 1913

F0: sample donors' generation data; F-1: sample donors' fathers generation data; F-2: sample donors' grandfathers generation data; F-3: sample donors' great-grandfathers generation data. *N*: number of questionnaires available containing data on particular generation; mean: year of birth mean value; S.D.: standard deviation; median: year of birth median value; min.: year of birth lowest value; max.: year of birth highest value.

the population of Kiev represented Ukraine, the two populations of Moscow and Novogorod represented Russia and the populations of Berlin, Chemnitz, Cologne, Duesseldorf, Freiburg, Greifswald, Hamburg, Leipzig, Magdeburg, Mainz, Munich, Muenster, Rostock and Stuttgart represented Germany.

Y-STR haplotype data were prepared for the analysis using MS Excel™ together with Microsatellite Toolkit add-in [13]. Calculations and statistical analyses were performed using Arlequin [14] and Statistica v. 7.0 [15] software.

3. Results

Out of the total 226 sample donors, 206 (91.15%) were able to provide necessary data on their grandfathers' date and place of birth, while 157 donors (70.72%) were able to provide the information on their great-grandfathers' place of birth and 142 donors (62.83%) provided also the information on their great-grandfathers' date of birth. Generation data retrieved from the questionnaires collected from the donors are summarized in Table 1. It is clearly observable that the majority of the F-2 generation (donors' grandfathers) were born before the Second World War while the majority of the F-3 generation (donors' great-grandfathers) were born before the First World War. Among all the 142 donors who were able to provide data on their male lineage great-grandfather data, 76% represented lineages whose Y chromosomes were present in the study area before the First World War. Among the 202 individuals who provided data on their male lineage grandfathers, 70% possessed Y chromosomes present in the area of interest before the Second World War. The difference between the two percentage values is insignificant in the double-sided test for difference between proportions ($p = 0.2208$). Based on the information concerning the place of birth of the sample donors and their ancestors provided in the questionnaires, the collected DNA samples were divided into groups (quasi-populations) representing particular generations and the geographic region they come from. G0 group contained all collected samples and represented the contemporary population of the sampled region. G1 group consisted of 140 samples and represented the set of Y chromosomes that had been present in the sampled region before the Second World War, thus, represented the grandfathers of the sample donors. G2 group contained 108 DNA samples representing chromosomes that had been present in the area of interest since at least World War I and thus represented the sample donors' great-grandfathers. G3 group consisted of samples representing 62 Y chromosomes that had not been present in the sampled area before the Second World War (Table 2). According to the historical information gathered from the donors the G3 group consisted of 26 chromosomes coming from regions of Małopolska other than the region under investigation. The remaining G3 group chromosomes came from other regions of Poland, from its Eastern and Southern parts mainly.

Standard diversity indices calculated using Arlequin software are summarized in Table 3. Different haplotypes constituted from 70% to 95% in each group, depending on its size, while standard diversity indices were similar among all groups. Haplotype frequencies were also calculated for each group. The frequency of most common haplotypes in each group was compared among groups as well as compared to the haplotypes frequencies in YHRD (Table 3). Two haplotypes

Table 2
Grouping of collected samples and standard diversity indices

Group	*N*	Grouping criterions	Number of different haplotypes	Gene diversity	Mean number of pairwise differences
G0	226	All sample donors	179	0.9955 ± 0.0014	6.979233 ± 3.291065
G1	140	F-2 and F-3 born inside SM or F-2 born inside SM and no information on F-3	112	0.9935 ± 0.0026	6.981295 ± 3.298691
G2	108	F-3 born inside SM	91	0.9939 ± 0.0030	6.839910 ± 3.242971
G3	62	F-3 born outside SM or no information on F-3 and F-2 born outside of SM	59	0.9984 ± 0.0033	7.004759 ± 3.331498

Grouping was performed on the basis of ancestry data provided by donors. Explanations—F-2: donor's grandfather; F-3: donor's great-grandfather; SM: Southern Małopolska region as defined in Section 2.

Table 3
Most frequent haplotypes in particular groups of chromosomes in the population of Southern Małopolska

	G0		G1		G2		G3		YHRD rel. 19
	Abs. freq.	Rel. freq.	Abs. freq.	Rel. freq.	Abs. freq.	Rel. freq.	Abs. freq.	Rel. freq	
Haplotypes most frequent in G1 and G2 groups									
17–13–30–25–11–13–10,14–14–11–10	10	0.044	8	0.057	6	0.056	1	0.016	192
16–13–30–25–10–11–13–11,14–14–11–10	7	0.031	4	0.029	3	0.028	1	0.016	161
16–13–30–25–10–11–13–10,14–14–11–10	6	0.027	6	0.043	5	0.046	0	0.000	63
15–13–29–22–10–13–13–11,14–15–12–12	3	0.013	3	0.021	3	0.028	0	0.000	2
Haplotypes most frequent in G3 group									
14–13–29–24–10–13–13–11,13–15–12–12	3	0.013	1	0.007	1	0.009	2	0.032	36
17–13–29–25–10–11–13-10,14–14–11–10	2	0.009	0	0.000	0	0.000	2	0.032	22
17–13–30–26–11–11–13–11,13–14–11–11	2	0.009	0	0.000	0	0.000	2	0.032	8

The last column represents absolute frequency of the ''minimal haplotype'' part of each haplotype in the YHRD release 19. Explanations—abs. freq: absolute frequency; rel. freq.: relative frequency.

were identified (17–13–29–25–10–11–13–10,14–14–11–10 and 17–13–30–26–11–11–13–11,13–14–11–11) that were present in the group of 62 chromosomes classified in G3 group while not present in chromosomes of G1/G2 group ($p = 0.035$ in double sided test for difference between proportions). Interestingly, the ''minimal haplotype'' part of the latter of the two haplotypes (17–13–30–26–11–11–13–11,13) was present exclusively in different Polish populations of Bydgoszcz, Gdańsk, Kraków, Szczecin and Wrocław at a frequency lower than 1%, as revealed by YHRD search. The most common minimal haplotype in groups G1/G2, that is in the group of chromosomes that had been present in the area of Southern Małopolska before the Second World War, was also very common in the whole Central Europe since 192 such haplotypes were present in the database. The third most frequent haplotype in the G1/G2 group differed from the most frequent one by only one repeat in DYS19 (16 instead of 17) and was present in 63 copies in the YHRD and also appeared frequently among populations of Poland and neighboring countries. However, it is worth noting that the only statistically significant differences between haplotype frequencies were observed for the most frequent haplotypes of G3 group compared to G1/G2 group.

An MDS plot of the inter-population haplotype frequency differences was constructed based on RST distances calculated in Arlequin and Microsat (Table 4). Populations grouped clearly according to linguistic criterion as all German populations clustering as one group, all Slavic populations clustered as another group, Baltic populations creating another group and the population of Tartu present as a singleton but relatively close to the cluster of German populations (Fig. 2, panel A). A close-up of the MDS plot section containing Slavic populations (Fig. 2, panel B) revealed a high degree of similarity among those populations. Significant differences among Slavic populations were observed in the study among population of Belarus and G1 and G3 groups as well as among population of Moscow and Polish populations of Lublin and Wrocław.

Table 4
R_{ST} distances among populations of Poland including quasi-populations G0–G3 (see text), Baltic countries, Belarus, Ukraine and Russia

	VIL	RIG	BYD	GDA	KRA	LUB	WAR	WRO	G3	G1	G2	G0	BEL	KIE	MOS	NOV	TAR
Vilnius (VIL)		−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Riga (RIG)	−0.001		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Bydgoszcz (BYD)	0.041	0.046		−	−	−	−	−	−	−	−	−	−	−	−	−	+
Gdansk (GDA)	0.035	0.039	−0.002		−	−	−	−	−	−	−	−	−	−	−	−	+
Krakow (KRA)	0.041	0.043	−0.006	−0.001		−	−	−	−	−	−	−	−	−	−	−	+
Lublin (LUB)	0.048	0.054	−0.004	0.000	−0.001		−	−	−	−	−	−	−	−	+	−	+
Warsaw (WAR)	0.036	0.041	−0.004	−0.002	−0.004	−0.001		−	−	−	−	−	−	−	−	−	+
Wroclaw (WRO)	0.041	0.049	−0.003	0.003	0.001	−0.006	0.000		−	−	−	−	−	−	+	−	+
G3	0.038	0.034	−0.004	−0.005	−0.005	0.000	−0.005	0.004		−	−	−	−	−	−	−	+
G1	0.034	0.035	−0.002	−0.003	−0.002	0.001	−0.003	0.004	−0.007		−	−	+	−	−	−	+
G2	0.034	0.036	−0.002	−0.003	−0.001	0.000	−0.003	0.003	−0.006	−0.008		−	+	−	−	−	+
G0	0.037	0.037	0.000	−0.002	−0.001	0.002	−0.002	0.005	−0.008	−0.005	−0.006		+	−	−	−	+
Belarus (BEL)	0.034	0.051	0.008	0.008	0.010	0.008	0.008	0.009	0.019	0.015	0.018	0.018		−	+	−	+
Kiev (KIE)	0.039	0.049	−0.005	−0.002	−0.006	−0.002	−0.003	0.001	0.000	0.002	0.004	0.003	−0.005		−	−	+
Moscow (MOS)	0.023	0.023	0.013	0.004	0.010	0.021	0.006	0.027	0.003	0.001	0.002	0.004	0.019	0.012		−	+
Novogorod (NOV)	0.036	0.051	0.002	0.008	0.004	0.010	0.002	0.008	0.016	0.015	0.015	0.017	0.002	−0.001	0.018		+
Tartu (TAR)	0.058	0.035	0.141	0.132	0.130	0.156	0.131	0.153	0.106	0.119	0.118	0.121	0.154	0.146	0.086	0.142	

Below diagonal: R_{ST} values calculated. Above diagonal: statistical significance of difference. German populations are excluded from this table as all distances among them and the remaining populations of Central and Eastern Europe under study were significant.

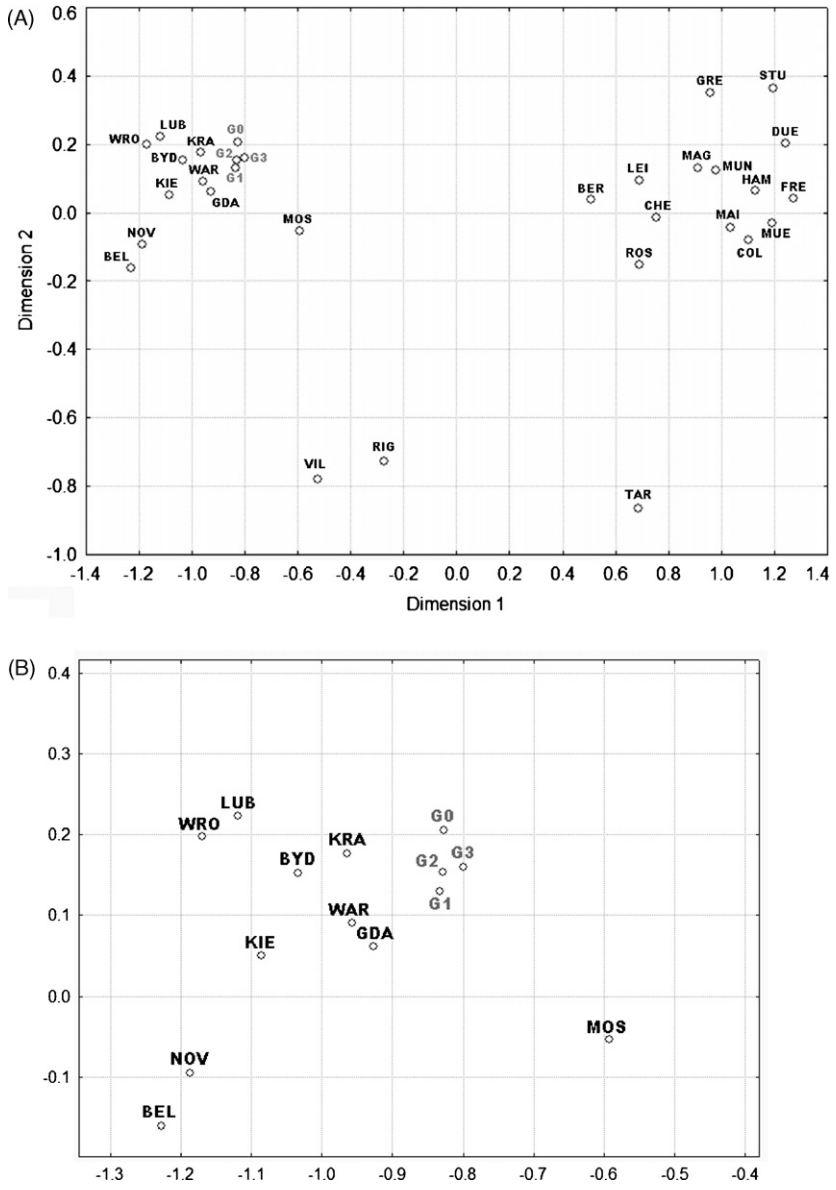

Fig. 2. MDS analysis of Central European Y-STR haplotypes based on R_{ST} distances. Explanation of population names—BEL: Belarus; BER: Berlin; BYD: Bydgoszcz; CHE: Chemnitz; COL: Cologne; DUS: Duesseldorf; FRE: Freiburg; GDA: Gdansk; GRE: Greifswald; HAM: Hamburg; KIE: Kiev; KRA: Krakow; LEI: Leipzig; LUB: Lublin; MAG: Magdeburg; MAI: Mainz; MOS: Moscow; MUN: Munich; MUE: Muenster; NOV: Novogorod; RIG: Riga; ROS: Rostock; STU: Stuttgart; TAR: Tartu; VIL: Vilnius; WAR: Warsaw; WRO: Wroclaw; G0: haplotypes of G0 group; G1: haplotypes of G1 group; G2: haplotypes of G2 group; G3: haplotypes of G3 group. Panel A: MDS plot of RST distances for all populations investigated. Panel B: close-up of the MDS plot portion containing Polish and other Slavic populations.

4. Discussion

The strategy applied to collect DNA samples for the study proved to be quite efficient in gathering family history information. Collecting most samples from teenagers at similar age allowed clear spacing of consecutive generations based solely on their date of birth (Table 1). The analysis of the family information gathered from sample donors seems to support the hypothesis of relatively low immigration rate in the Southern Małopolska region investigated as the generation-to-generation change in frequency of local versus non-local birthplaces of donors' ancestors is insignificant. However, one must remember that the calculated frequencies represented in fact a net result of all migrations. Moreover, the data available from the donors inhabiting one geographical area exclude possibility of inferences of separate emigration and immigration rates in the region under investigation.

Grouping of the haplotypes according to the criterion of the ancestors' birthplace (Table 2) enabled extracting ''ancestral populations'' from the entire set of the collected DNA samples. These groups represented Y chromosomes that were present in the region under investigation at the time when relevant ancestors had been born. It might be argued however, that such a grouping did not provide a representative population data as it failed to take into account those lineages that had disappeared in the meantime from the region under investigation due to

migration processes. However, to affect the population structure significantly in the relatively short period of the last 50–100 years such a migration would have to involve many individuals. In fact, no massive migrations were reported in the case of the Southern Małopolska region over the last 100 years. Moreover, one would expect that massive migration from the area of interest had lead to significant decrease of gene diversity indices in population sample of local origin. However, no such effect was observed either (Table 2, G3 group). It should be also emphasized that more than 60% of the contemporary male population of the Southern Małopolska are direct descendants of men that have lived in this region before the Second World War and this fact itself suggests lack of massive migrations from the area.

The analysis of the most frequent haplotypes present in the population of Southern Małopolska revealed the presence of the minimal haplotypes that are very common in Central Europe, including Poland. On the other hand, two haplotypes were detected that were present in the G3 group (i.e. group of chromosomes that had not been present in the Southern Małopolska region before the Second World War) but not present inside the area as represented by chromosomes of G1/G2 group. One of these haplotypes is particularly interesting as its ''minimal'' part is present exclusively in Polish populations according to the YHRD release 19. Presence of the above-mentioned haplotype frequency differences may indicate existence of some substructure between Polish populations. However, one cannot exclude the possibility that the significance of haplotype frequencies differences is an artifact of relatively small number of chromosomes present in G3 group.

Genetic distances between haplotypes of Central European populations, including groups of haplotypes constructed on the basis of the Southern Małopolska population sample, were obtained based on R_{ST} calculation. As expected, the most prominent genetic distances were observed between populations of German origin and Slavic populations, with Baltic populations divided into the Baltic speaking populations of Lithuania and Latvia and Finno-Ugrian population of Estonia. The result repeated to a great extent the results of Ploski et al. [3] with one exception. Namely, the population of Moscow in our comparison grouped closer to other Slavic populations than in the previous paper of Ploski et al. As far as Slavic populations were concerned, statistically significant differences were observed between distances calculated for our sample of Southern Małopolska and Belarus and between population of Moscow and Polish populations of Lublin and Wrocław. R_{ST} distances among groups of haplotypes derived from the Southern Małopolska samples turned out to be insignificant. All groups of the Southern Małopolska haplotypes clustered together on the MDS plot and were situated in proximity to other Polish populations (Table 4 and Fig. 2). Noticeably, G1/G2 groups containing chromosomes present in the area of Southern Małopolska before the Second and First World Wars respectively appeared on the MDS plot very close to the G3 group, that is, to the group of chromosomes that had been brought to the area after the last World War. Close clustering of G1/G2 and G3 groups may be explained partially by the fact that almost 50% of chromosomes in the G3 group come from male lineages that were present before the World War Second in the areas relatively close to the Southern Małopolska. This observation suggests in turn that mean generation-to-generation male migration distances were relatively short in the area of interest during the last 100 years. Taking into consideration lack of significant differences between the population studied and other Polish/Slavic populations and regarding relatively short range of male migrations observed in the area of interest, one may speculate that the similarity of the population observed to other Polish and Slavic populations may be a product of long-term small-scale population processes rather than a product of rare single migration events. However, more subpopulations from different regions of Poland should be examined to make more general inferences as to the sources of observed homogeneity of Poles possible.

In conclusion it can be stated that no significant difference was observed between contemporary population of the region of Southern Małopolska and the population of males who had lived there ca. 100 years ago as represented by their descendants. The comparisons of the ancestral population samples represented among contemporary inhabitants of the area studied along with other Polish and Central European populations showed that the ancestral and contemporary populations of Southern Małopolska are very closely related to other Polish and Slavic populations. Thus, the hypothesis that the population of Southern Małpolska could have been highly homogenous before the Second World War seems plausible.

Sample collection accompanied by family history data acquisition from a set of donors has proved to be a useful tool in reconstructing haplotype frequencies and their changes over a few recent generations in a particular population. However, the interpretation of the results obtained in these experiments was limited due to several factors. First of all, only one region was sampled. Other regional samples are being collected in the same manner as the presented sample and will be added to the analysis. Secondly, no SNP polymorphism was tested so no information on haplogroup frequency in the population under investigation is available yet. After collecting more samples from different regions of Poland one should be able to recreate to greater extent the genetic landscape of pre-war Poland and compare it with present day diversity. Sampling the populations living on formerly German territory as well as sampling the German population in search for those individuals who trace their ancestry to that territory should give particularly interesting results. Having obtained the results presented in this paper we suggest that a large, international and inter-laboratory experiment based on sample collection coupled with ancestry data collection from the whole area of Central Europe would be of great value for elucidating the genetic history of the region.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at 10.1016/j.fsigen.2007.01.003.

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