

Maximization of the frequency of recombinants in the hybrid zones of *Sorex araneus* in northern Poland

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We studied populations of *Sorex araneus* Linnaeus, 1758 in the upper Drwęca River valley and in the vicinity of Lake Szelaż Wielki. We found that the cline of frequency of metacentric *np* decays in the Drwęca River valley, which results in a smooth transition between the Stobnica race (karyotype *hi, ko, gm, np*) and the Laska race (*hi, ko, gm*). However, on the west shore of Lake Szelaż Wielki the cline of frequency of metacentric *gm* disappears. Reduction of frequencies of autosomes *np* and *gm* makes possible broadening of the clines of metacentrics *gr* and *mn*, originating from the Łęgucki Młyn race. This results in a reduction of the number of hybrids and maximization of frequency of recombinants (*hi, ko, gr, mn*), which reaches the value of 1.0 in the populations located on the west shore of the lake. We compared studied populations with those in the Pasłęka River valley, and those between the Pasłęka and Drwęca Rivers valleys. We also discussed the maximization of the frequency of recombinants as a mechanism enhancing fertility of hybrid populations.

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Introduction

To date, eight chromosomal races of *Sorex araneus* Linnaeus, 1758 from NE Poland have been described. At first they were designated by Roman numerals (Fedyk 1986, Fedyk and Leniec 1987). Later, to conform with the rules set by ISAAC (Hausser *et al.* 1994), the numbers were replaced with geographical names of the area, in which a particular race was first described (Wójcik 1993, Banaszek 1994, Ratkiewicz *et al.* 1994, Fedyk 1995).

Hybrid zones are found between chromosomally different races that come into contact. One of the best studied contact zones between chromosomal races of common shrew in Poland is that of the Stobnica/Łęgucki Młyn. Fedyk *et al.* (1991) studied ten populations of the common shrews in the transect along the Pasłęka River, which enabled to preliminary describe the course of the zone. They also discriminated 5 subzones based on the hybrid index. The subzones differed in a

relative contribution of particular karyological categories. The Łęgucki Młyn race predominated in the northern part of the zone, while southern part was inhabited by the Stobnica race. Populations with the highest percentage of hybrids (complex heterozygotes) were found in the centre of the zone. Those hybrids form chromosomal complexes *kh/hilio/ok* (C1 hybrids), *r/r/g/g/m/m/n/n/p/p* (C2 hybrids), or even both of them, which segregate independently in meiosis (C1+C2 hybrids). Fedyk *et al.* (1991) also found that populations in the centre of hybrid zone were also characterized by a high frequency of recombinants with *hi*, *ko*, *gr*, *mn* karyotype. They do not form chromosomal complexes, which are likely to cause difficulties in meiosis, typical for complex heterozygotes (Gropp *et al.* 1982). Hence, maximization of the frequency of recombinants can be considered as a selection mechanism enhancing fertility in hybrid populations.

In the Drużno/Łęgucki Młyn contact zone, ca 70 km north from the studied area, the highest frequencies of recombinants were found in the populations outside the true hybrid zone. There recombinants form almost pure populations belonging to the Guzowy Młyn race (Banaszek 1994). This suggests that there is a continuous strip inhabited by recombinants and running along the contact zone between races Drużno/Łęgucki Młyn and Stobnica/Łęgucki Młyn.

In this paper we present a karyological analysis of the populations studied along the Drwęca River and Lake Szelaż Wielki (Figs 1, 2b). The aim of the study was to investigate the level of maximization of the frequency of recombinants. In the previous studies Fedyk *et al.* (1991) suggested that such maximization should occur at the expense of reduction of frequency of C1+C2 hybrids, which should lead to division of the contact zone into two zones (with C1 and C2 hybrids) separated by a strip inhabited by recombinants. Here we test this hypothesis.

Materials and methods

Studies were carried out in the upper Drwęca River valley and in the vicinity of Lake Szelaż Wielki (Figs 1, 2b). A continuum of the wet habitats lies along the banks of the river and extends along Lake Szelaż Wielki. In years 1993–94 we captured 68 shrews belonging to 10 populations named after nearest settlements (Table 1, Fig. 1). Shrews collected in sites located less than 0.5 km apart were treated as belonging to the same population. Every site is labelled a code number, hence it follows that some populations have double or even triple number marks, eg Zwierzewo – 162+164.

Animals caught at Ostrowin III (code 140) were assigned to a separate population, even though this site lies very close to Ostrowin A (137+139+142). This is because we found conspicuous differences in chromosomal frequencies at those two sites (Table 2). Population Ostrowin A consists of animals caught at three adjacent sites.

Chromosome preparations from the spleen were made by an *in vivo* method (Fedyk 1980) and stained for G-bands with Giemsa reagent after treatment with trypsin (Seabright 1971). We also investigated maximization of the frequency of recombinants in the whole area located in and between the valleys of the Pasłęka and Drwęca Rivers. In doing so, we used the data from earlier studies (Fedyk *et al.* 1991, Fedyk 1995).

Results

Karyological categories

We distinguished the following karyological categories in the study area (Fig. 1, Table 1):

(a) Laska race (diagnostic metacentrics *hi*, *ko*, *gm*) constitutes 8.8% of caught animals. Individuals with that karyotype were found in populations coded 140, 138, 141 and 162+164.

(b) Stobnica race (metacentrics *hi*, *ko*, *gm*, *np*) makes up 16.2% of the animals. They were trapped in populations coded 137+139+142 and 161.

(c) Hybrids (ie complex heterozygotes) occurred in two forms. C1 hybrids (meiotic ring *kh/hilolok*) were found in populations coded 149+151 and 150, and constituted 5.9% of caught animals. C2 hybrids with 5-element chain *g/gm/mn/np/p* were found in population 161, while hybrids forming four-element chains occurred in populations 140, 138, 161 (chain *g/gm/mn/n*), and 138 (chain *r/rg/gm/m*). Frequency of C2 hybrids reached 10.3%.

(d) The most numerous karyological category were recombinants (Guzowy Młyn race with metacentrics *hi*, *ko*, *gr*, *mn*), which made up 57.3% of all animals. They were found in all studied populations, except 138 and 150.

(e) Łęgucki Młyn race (metacentric *kh*, *io*, *gr*, *mn*) – a single individual belonging to this race was trapped in population 149+151.

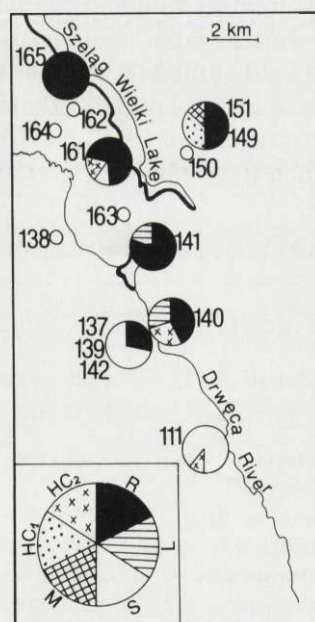


Fig. 1. Percentage contribution of particular karyotypic categories of *Sorex araneus* in the studied area. M, S, L – the Łęgucki Młyn, Stobnica and Laska races, respectively, HC₁ – C1 hybrids, HC₂ – C2 hybrids, R – recombinants, empty circle – the populations in which less than 5 individuals were identified; data from population 111 after Fedyk (1995).

Table 1. Number of individuals of particular karyotypic categories in the studied populations. L – Laska, S – Stobnica, M – Łęgucki Młyn races. * – the presence of homozygotes *nn*, *pp* in the population polymorphic for *np*.

Population		Karyotypic categories					
Name	Code numbers	L race	S race	HC ₁	HC ₂	R	M race
Dłużki	149, 151	0	0	3	0	4	1
Stare Jabłonki	150	0	0	1	0	0	0
Szeląg	165	0	0	0	0	7	0
Zwierzewo	162, 164	1	0	0	0	2	0
Nowe Siedlisko	161	0	1	0	3	9	0
Idzbark IV	163	0	0	0	0	2	0
Idzbark I	138	1	0	0	2	0	0
Idzbark II	141	2	0	0	0	8	0
Ostrowin III	140	2	0	0	2	3	0
Ostrowin A	137, 139, 142	0	10(8*)	0	0	4	0
Rychnowska Wola	111	0	9(5*)	0	1	0	0

Frequencies of diagnostic metacentrics

The frequencies of metacentrics were computed only for populations represented by at least 5 animals (Table 2). Metacentrics *hi* and *ko* reached identical frequencies (1.00 or 0.69) in all studied populations, except 141, where the frequencies were affected by polymorphism of *ko* pair. Chromosome *gm* reached the highest frequency of 0.32 in population coded 137+139+142. The frequency of *gm* metacentric decreased abruptly to 0.11–0.15 northwards, in populations coded 161, 140 and 141, and down to 0.00 in 149+151 and 165. Metacentric chromosome *np* occurred sporadically only in two populations: 161 and 137+139+142 with the frequencies of 0.04 and 0.07, respectively. Autosomes *hk* and *io* occurred with the same frequencies of 0.31 and were found exclusively in population 149+151. The

Table 2. Frequencies of diagnostic metacentrics. * – data from this population after Fedyk (1995).

Population		Diagnostic metacentrics							
Name	Code numbers	Stobnica race				Łęgucki Młyn race			
		<i>hi</i>	<i>ko</i>	<i>gm</i>	<i>np</i>	<i>hk</i>	<i>io</i>	<i>gr</i>	<i>mn</i>
Dłużki	149, 151	0.69	0.69	0.00	0.00	0.31	0.31	0.37	0.87
Szeląg	165	1.00	1.00	0.00	0.00	0.00	0.00	0.43	0.64
Nowe Siedlisko	161	1.00	1.00	0.11	0.04	0.00	0.00	0.15	0.50
Idzbark II	141	1.00	0.95	0.15	0.00	0.00	0.00	0.20	0.50
Ostrowin III	140	1.00	1.00	0.14	0.00	0.00	0.00	0.00	0.43
Ostrowin A	137, 139, 142	1.00	1.00	0.32	0.07	0.00	0.00	0.03	0.14
Rychnowska Wola*	111	1.00	1.00	0.55	0.20	0.00	0.00	0.00	0.20

frequency of metacentric *gr* varied from 0.00 and 0.03 in the southern populations: 140 and 137+139+142, respectively, to 0.15 and 0.20 on the west shore of Lake Szelał Wielki (populations 141 and 161, respectively) and reached the highest frequencies of 0.37 and 0.43 in 165 and 149+151. Metacentric *mn* occurred in all studied populations. Its frequency continuously decreased from 0.87 in 149+151 on the north of study area to 0.14 in 137+139+142 on the south. On the western shore of Lake Szelał Wielki the frequency of metacentric *mn* reached 0.50 and 0.64 in 161 and 165, respectively (Table 2).

Distribution of karyological categories of *Sorex araneus* in the area of Pasłęka and Drwęca Rivers

Tens of populations of *Sorex araneus* located in the Pasłęka River valley and between the Pasłęka and Drwęca Rivers have been studied since 1985. Here we take into account only those of samples which consist of at least 5 trapped animals. We divided the populations into 3 groups (Fig. 2b). Group A consists of 21 populations located in the area of the River Pasłęka and its tributaries. Group B comprises 5 populations located between the Pasłęka and Drwęca Rivers, while 11 populations located in the area of the upper Drwęca River and Lake Szelał Wielki were classified as the group C (Fig. 2b).

C1 hybrids predominated in populations of the group A. Their contribution varied from 10.5% in population 18 to 50% in populations coded 16+93+96 and 108. C1 hybrids were not found in the northernmost population 121 and in three populations located on south: 102, 101, and 10. Shrews belonging to the Łęgucki

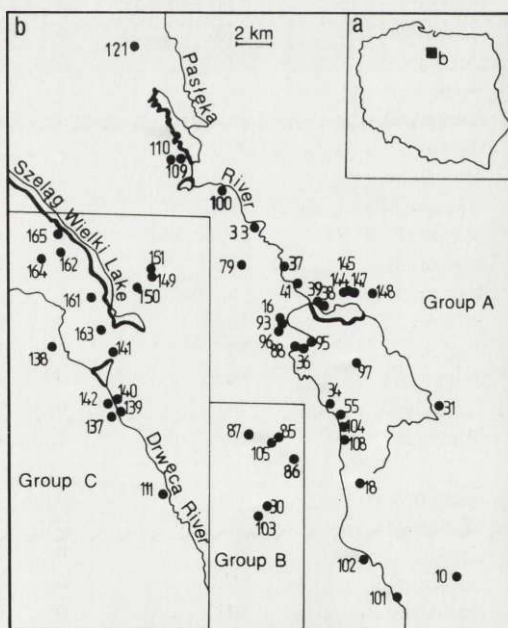


Fig. 2. The distribution of trapping sites along and between the Pasłęka and Drwęca Rivers valleys: (a) location of the studied area in northern Poland, (b) location of the groups of populations in the studied area.

Młyn race were trapped in all populations lying north of the population 55+104. They constituted the second most numerous karyological category in group A. Recombinants and shrews belonging to the Stobnica race were more rare than those of the Łęgucki Młyn race. Maximum of the frequency of recombinants occurred between the populations labelled 36+88+95 and 108. Individuals of the Stobnica race were exclusively trapped south of population 16+93+96. In two populations (102 and 10) their frequencies reached 100%. C2 and C1+C2 hybrids were the most rare and occurred slightly south of the centre of the hybrid zone. The range of occurrence of C2 hybrids was also somewhat larger than that of C1+C2 hybrids (Table 3).

Table 3. Karyotypic categories found in the area of the Pasłęka and Drwęca Rivers. Gp – group of populations, R – recombinants. M, S, L – the Łęgucki Młyn, Stobnica and Laska races, respectively. * – the presence of homozygotes *nn*, *pp* in the populations polymorphic for *np*.

Gp	Population		Karyotypic categories						References	
	Name	Code numbers	M race	Hybrids			R	S race		L race
				C1	C1+C2	C2				
A	Ramoty	121	15	0	0	0	0	0	0	Fedyk 1995
	Worliny I, II	109, 110	16	2	0	0	0	0	0	Fedyk 1995
	Łęguty	100	16	3	0	0	0	0	0	Fedyk <i>et al.</i> 1991
	Podlejki	33	17	6	0	0	0	0	0	Fedyk <i>et al.</i> 1991
	Biesal	79	5	3	0	0	1	0	0	Fedyk 1995
	Gromel I, II, III	144, 145, 147	10	5	0	0	0	0	0	Szałaj 1994
	Unieszewo II	148	5	2	0	0	1	0	0	Szałaj 1994
	Pęglity	37	5	4	0	1	0	0	0	Fedyk <i>et al.</i> 1991
	Śródka	41	3	1	0	0	1	0	0	Fedyk <i>et al.</i> 1991
	Sarąg I, II	38, 39	4	4	1	0	2	0	0	Fedyk <i>et al.</i> 1991
	Gębiny	97	2	5	0	0	4	0	0	Fedyk 1995
	Miodówko	31	7	8	3	2	3	0	0	Fedyk 1995
	Guzowy Młyn I, II, III	16, 93, 96	2	8	1	3	2	0	0	Fedyk <i>et al.</i> 1991
	Mańki II, IV, VI	36, 88, 95	19	54	2	6	48	3	0	Fedyk <i>et al.</i> 1991
	Mycyny II	34	1	9	2	2	9	5(1*)	0	Fedyk <i>et al.</i> 1991
	Mycyny I, III	55, 104	2	5	6	7	9	4(3*)	0	Fedyk <i>et al.</i> 1991
	Mycyny IV	108	0	12	6	3	1	2	0	Fedyk 1995
	Jagielek	18	0	2	2	1	3	11(4*)	0	Fedyk <i>et al.</i> 1991
	Jemiółowo	102	0	0	0	0	0	12	0	Fedyk 1995
	Łutykowo	101	0	0	0	2	1	18	0	Fedyk 1995
Marózek	10	0	0	0	0	0	13	0	Fedyk and Leniec 1987	
B	Elgnówko II	87	0	1	1	2	0	3(1*)	0	Fedyk 1995
	Elgnówko I, III	85, 105	0	2	0	10	3	8(4*)	0	Fedyk 1995
	Tolejny	86	0	0	1	0	3	3	0	Fedyk 1995
	Świątajny I	30	0	0	1	0	2	14(2*)	0	Fedyk <i>et al.</i> 1991
	Świątajny II	103	0	0	0	0	1	9(2*)	0	Fedyk 1995

Individuals belonging to the Stobnica race were the most numerous karyological category in populations of group B (Table 3). Their frequencies were the highest in southernmost populations: 30 and 103, and were equal to 70.6% and 70.0%, respectively. C1 and C2 hybrids were only found in two populations: 85+105 and 87. Few C1+C2 hybrids were also trapped in three populations. However, the total number of C1 and C1+C2 hybrids found in the populations of group B was three times lower than that of recombinants.

Populations of group C were much diversified with respect to karyological categories found along north-south and east-west axes. Shrews belonging to the Stobnica race occurred exclusively in the southernmost populations: 111 and 137+139+142. This race is replaced with Laska race further north. However, in the populations situated on the western bank of Szelał Wielki Lake the percentage contribution of common shrews of the Laska race decreased at the cost of increase of frequency of the recombinants (Table 1, Fig. 1). Recombinants are the most numerous karyological category in group C. They occurred everywhere but southernmost population 111, whereas all shrews trapped in 165 were recombinants. The pattern of karyological diversification observed along the east-west axis was different. C1 hybrids were found only in the north-east, in the area where shrews belonging to the Łęgucki Młyn race were also trapped. On the other hand, C2 hybrids occurred in the western populations, in which the shrews belonging to the Laska race were also found (Table 1, Fig. 1).

Shrews with metacentric chromosomes *hi*, *ko*, *gm* and acrocentric chromosomes *n*, *p* (the Laska race) were found in all three groups of populations. However, in groups A and B they occurred sporadically and should be considered as the acrocentric morphs within the polymorphism of pair *np* (Table 3). Likewise, the shrews with karyotypes *hi*, *ko*, *gm* found in the populations 111 and 137+139+142 should be classified as acrocentric morphs, despite of the high frequency of their occurrence (Table 1). This is because of the presence of the pair *np*, which calls for their classification to the Stobnica race.

An increase of the mean frequency of acrocentrics *g*, *m*, *n*, observed between groups of populations A and B had no effect on the frequency of occurrence of C1+C2 hybrids. However, it reduced the frequency of recombinants (Table 3). In contrast, a conspicuous increase of the frequency of recombinants in group C

Table 4. Comparison of the frequencies of C1+C2 hybrids (HC1+C2) and recombinants (R) and the mean frequencies of acrocentrics *g*, *m*, *n* in population groups A, B, C.

Group of populations	Number of shrews	Frequencies of		Mean frequencies of acrocentrics <i>g</i> , <i>m</i> , <i>n</i>
		HC1+C2	R	
A	456	0.05	0.19	0.256
B	64	0.05	0.14	0.411
C	78	0.00	0.47	0.517

resulted in a complete disappearance of C1+C2 hybrids in the populations of this group. On the other hand, an increase of the frequency of acrocentrics between groups B and C was much smaller than that observed between groups A and B (Table 4).

Discussion

Investigations carried out in the transect running along the Pasłęka River and its tributaries revealed that there are three types of complex heterozygotes in the contact zone Stobnica/Łęgucki Młyn and that their contribution increased towards the centre of the zone (Table 3; group A) (Fedyk *et al.* 1991). Possible disadvantage of such hybrids has been emphasized as a likely selective force because of reduced fertility in karyotypic heterozygotes, caused by meiotic difficulties. For example, in *Mus musculus* carrying chain quadrivalents the proportion of nondisjunction at anaphase I reaches 25–50%. Moreover, lengthening of the chain by one element causes total sterility (Gropp *et al.* 1982). On the other hand, however, in individuals forming ring configurations the course of spermatogenesis is not significantly impaired, so their fertility is near-normal (Gropp *et al.* 1982). It is not known, whether these observations are relevant to the course of spermatogenesis in the complex heterozygotes of common shrews. To date, except few cases, spermatogenesis was only investigated in Robertsonian heterozygotes of the common shrews (Searle 1986b, Garagna *et al.* 1989, Mercer *et al.* 1991, Mercer *et al.* 1992). However, the analysis of genetic structure of a few well studied contact zones suggests that some of the meiotic configurations are direct targets of natural selection. For example, acrocentrics *i*, *o* are known to convert ring meiotic complexes into chain forms (Fedyk *et al.* 1991). Thus, outnumbering of chain complexes by ring ones and elimination of the acrocentrics *i*, *o* from the Stobnica/Łęgucki Młyn contact zone suggests that selection favours ring multivalents, but is against chain ones (Fedyk *et al.* 1991). This is corroborated by the results of studies on meiotic configurations in mice (Gropp and Winking 1981).

The strength of selection in the contact zones also depends on the size of meiotic configurations. In the area of Oxford and the Pasłęka transect, hybrids with shortened meiotic complexes are more common than those with chains of maximum length (Searle 1986a, 1990, Fedyk *et al.* 1991).

The structure of the contact zone can also be modified under the pressure of the selection. Two types of such modifications were described for hybrid zones of the common shrews. One of them is maximization of frequency of acrocentric chromosomes, which leads to minimization of the chance of production of hybrids, and therefore enhances fertility of hybrid populations (Searle 1986a). The contact zones characterized by high frequency of acrocentrics are also known as acrocentric buffer zones (Fedyk 1986, Halkka *et al.* 1987). Frequency of single-armed autosomes is moderate in the Stobnica/Łęgucki Młyn contact zone. The inability

of maximization of the frequency of acrocentrics is compensated by a maximization of the frequency of recombinants in this zone (Fedyk *et al.* 1991). Those recombinants are homozygotes, or simple Robertsonian heterozygotes, which fertility is probably equal to this of the shrews of pure races. Mercer *et al.* (1991) also showed that the frequencies of nondisjunction of chromosomes in anaphase I in simple Robertsonian heterozygotes and homozygotes of common shrews are similar. This therefore suggests that the maximization of the frequency of recombinants is the second mechanism facilitating gene flow through the contact zone. Fedyk *et al.* (1991) postulated that an increase of the frequency of recombinants in the Stobnica/Łęgucki Młyn contact zone occurs at the expense of reduction of the frequency of C1+C2 hybrids, which leads to a division of the contact zone into two zones, separated by the strip inhabited by recombinants. This is fully supported by the results presented here.

In the Drwęca River valley the clines of the frequency of metacentrics *gm* and *np* are more staggered than it was observed in the Pasłęka River region (Fedyk 1995). In population 111 the frequencies of *gm* and *np* metacentrics equal 0.55 and 0.22, respectively, and decrease down to zero northwards (Table 2). However, an earlier disappearance of the cline of autosome *np* causes a transition of the Stobnica race into the Laska race. The boundary between those two races partially overlaps. Shrews belonging to the Stobnica race may sporadically occur as far as in population 161, where a single individual with *gm/mn/np* complex was found.

A reduction of frequencies of *gm* and *np* metacentrics may theoretically cause two different modifications of the contact zone: (i) accumulation of acrocentrics and therefore, formation of the buffer zone, or (ii) extension of *gr* and *mn* clines (originating from the Łęgucki Młyn race), which in turn leads to the maximization of the frequency of recombinants. The latter mechanism operates in the contact zone under study. The frequencies of both acrocentrics and recombinants increase westward (Table 4). We also observed an increase of the frequency of acrocentrics coinciding with a decrease of the frequency of recombinants in the populations of group B (Table 4). We associate this with a composition of this group, which exclusively consists of the populations located in the southern part of the contact zone (Fig. 2b), in which the clines of the frequencies of *gr* and *mn* already disappear. On the other hand, in the Drwęca River valley recombinants excluded C1+C2 hybrids altogether (Table 4), whereas on the western shore of Lake Szelaż Wielki pure populations of recombinants (ie shrews of the Guzowy Młyn race) appeared (Table 1, Fig. 1).

The formation of recombinants in the Drużno/Łęgucki Młyn contact zone is a consequence of the introgression of *gr* and *mn* metacentrics to the area inhabited by the shrews of the Drużno race carrying *g*, *r*, *m*, *n* acrocentric chromosomes. This causes concentration of recombinants on the western side of the hybrid zone (Banaszek 1994).

In the Pasłęka River area, however, the maximization of the frequency of recombinants in the centre of the hybrid zone results from staggering of the clines

of metacentrics belonging to two, independently segregating meiotic complexes (Fedyk *et al.* 1991). As the centres of the clines moved away, the points of intersection of the clines also lowered. In other words, the separation of the peaks of the frequencies of the C1 and C2 hybrids causes a reduction of the frequency of C1+C2 hybrids. It seems therefore clear that a disappearance of the coincidence between clines is a modification enhancing fitness in hybrid populations (Barton and Hewitt 1981, Hatfield *et al.* 1992).

The clines of frequency of metacentrics *gm* and *np* are drawn aside, while clines *hi*, *ko*, *gr*, *mn* come nearer to the centre of the studied contact zone. As a consequence, the peak of frequency of recombinants arose in the centre of the contact zone, as observed in the Pasłęka River valley. Subsequent increase of the

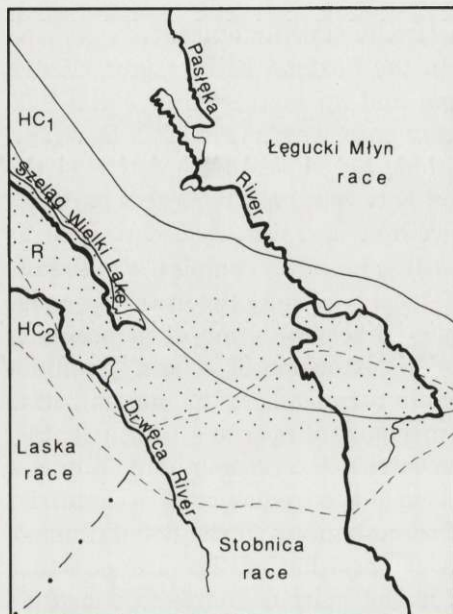


Fig. 3. The distribution of karyotypic categories of *Sorex araneus* in the contact zones Laska/Lęgucki Młyn and Stobnica/Lęgucki Młyn. Continuous line – C1 hybrids (HC₁), dotted line – C2 hybrids (HC₂), spotted area – recombinants (R).

frequency of recombinants and associated separation of the peaks of frequencies of C1 and C2 hybrids leads to a complete disappearance of the C1+C2 hybrids. This also leads to division of the hybrid zone into two zones (with C1 and C2 hybrids), separated by the strip of recombinants, as seen in the Drwęca River valley (Fig. 3)

One can presume, that environmental conditions facilitated maximization of the frequency of recombinants and formation of the two, separate hybrid zones. Populations of recombinants are limited by the Drwęca River from the west, and by Lake Szelaż Wielki from the east. These environmental barriers facilitate fixation of recombined karyotype.

Populations 141, 161 and 165 belong to the Guzowy Młyn race (Table 1, Fig. 1). Fedyk (1995) suggested that the range of that race presumably forms a narrow strip extending from the Družno/Łęgucki Młyn to the Stobnica/Łęgucki Młyn contact zones. This strip runs through the centres of the Laska/Łęgucki Młyn and the Stobnica/Łęgucki Młyn contact zones. On the other hand, in the area of disappearance of the cline *gm* (ie the area of transition of Laska race to Družno race) the recombinants should be moved from the centre of the zone to its western edge.

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References

- Banaszek A. 1994. The structure of the contact zone between the chromosomal races Družno and Łęgucki Młyn in the common shrew (*Sorex araneus*) in north-eastern Poland: preliminary results. *Folia Zoologica* 43 (Suppl. 1): 11–19.
- Barton N. H. and Hewitt G. M. 1981. Hybrid zones and speciation. [In: Evolution and speciation. Essays in honour of M. J. D. White. W. R. Atchley and D. S. Woodruff, eds]. Cambridge University Press, Cambridge: 109–145.
- Fedyk S. 1980. Chromosome polymorphism in a population of *Sorex araneus* L. at Białowieża. *Folia Biologica [Kraków]* 28: 83–120.
- Fedyk S. 1986. Genetic differentiation of Polish populations of *Sorex araneus* L. II. Possibilities of gene flow between chromosome races. *Bulletin of the Polish Academy of Sciences, Biological Sciences* 34: 161–171.
- Fedyk S. 1995. [Regional differentiation and hybrid zones between chromosomal races of *Sorex araneus* L. in north-eastern Poland]. *Dział Wydawnictw FUW, Białystok. Dissertationes Universitatis Varsoviensis* 439: 1–125. [In Polish]
- Fedyk S. and Leniec H. 1987. Genetic differentiation of Polish populations of *Sorex araneus* L. I. Variability of autosome arm combinations. *Folia Biologica [Kraków]* 35: 57–68.
- Fedyk S., Chętnicki W. and Banaszek A. 1991. Genetic differentiation of Polish populations of *Sorex araneus* L. III. Interchromosomal recombination in a hybrid zone. *Evolution* 45: 1384–1392.
- Garagna S., Zuccotti M., Searle J. B., Redi C. A. and Wilkinson P. J. 1989. Spermatogenesis in heterozygotes for Robertsonian chromosomal rearrangements from natural populations of the common shrew, *Sorex araneus*. *Journal of Reproduction and Fertility* 87: 431–438.
- Gropp A. and Winking H. 1981. Robertsonian translocation: cytology, meiosis, segregation patterns and biological consequences of heterozygosity. *Symposia of Zoological Society in London* 47: 141–181.
- Gropp A., Winking H. and Redi C. 1982. Consequences of Robertsonian heterozygosity: segregational impairment of fertility versus male-limited sterility. [In: Genetic control of gamete production and function. P. G. Crosignani, B. L. Rubin, and M. Fraccaro, eds]. *Serono Clinical Colloquium on Reproduction, Academic Press, Grune and Stratton* 3: 115–134.
- Halkka L., Söderlund V., Skarén U. and Heikkilä J. 1987. Chromosomal polymorphism and racial evolution of *Sorex araneus* L. in Finland. *Hereditas* 106: 257–275.
- Hatfield T., Barton N. and Searle J. B. 1992. A model of hybrid zones between two chromosomal races of the common shrew (*Sorex araneus*). *Evolution* 46: 1129–1145.

- Hausser J., Fedyk S., Fredga K., Searle J. B., Volobuev V., Wójcik J. M. and Zima J. (ISACC) 1994. Definition and nomenclature of the chromosome races of *S. araneus*. *Folia Zoologica* 43 (Suppl. 1): 1–9.
- Mercer S. J., Searle J. B. and Wallace B. M. N. 1991. Meiotic studies of karyotypically homozygous and heterozygous male common shrews. *Mémoires de la Société Vaudoise des Sciences Naturelles* 19: 33–43.
- Mercer S. J., Wallace B. M. N. and Searle J. B. 1992. Male common shrew (*Sorex araneus*) with long meiotic chain configuration can be fertile: implications for chromosomal models of speciation. *Cytogenetics and Cell Genetics* 60: 68–73.
- Ratkiewicz M., Banaszek A. and Łobodzińska J. 1994. Isoenzyme variation in the common shrew (*Sorex araneus*) from the hybrid zone between the chromosomal races Družno and Łęgucki Młyn: preliminary results. *Folia Zoologica* 43 (Suppl. 1): 21–28.
- Seabright M. 1971. A rapid banding technique for human chromosomes. *Lancet* 2: 971–972.
- Searle J. B. 1986a. Factors responsible for a karyotypic polymorphism in the common shrew, *Sorex araneus*. *Proceedings of Royal Society of London* 229: 277–298.
- Searle J. B. 1986b. Meiotic studies of Robertsonian heterozygotes from natural populations of the common shrew, *Sorex araneus* L. *Cytogenetics and Cell Genetics* 41: 154–162.
- Searle J. B. 1990. A cytogenetical analysis of reproduction in common shrews (*Sorex araneus*) from a karyotypic hybrid zone. *Hereditas* 113: 121–132.
- Szałaj K. A. 1994. [The course and width of contact zone between chromosomal races of common shrew (*Sorex araneus*) in the vicinity of Olsztynek town]. M Sc thesis, FUW, Białystok. [In Polish]
- Wójcik J. M. 1993. Chromosome races of the common shrew *Sorex araneus* in Poland: a model of karyotype evolution. *Acta Theriologica* 38: 315–338.

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