Chromosome races of the common shrew *Sorex araneus* in Poland: a model of karyotype evolution

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Five distinct chromosome races of the common shrew *Sorex araneus* Linnaeus, 1758 including different metacentrics with monobrachial homology have been found in Poland. Their karyotypes include polymorphic arm combinations, and chromosomal forms differing in numbers of acrocentrics can be distinguished among them. The relationship between Polish and other European races of the common shrew has been examined by phylogenetic analysis using parsimony. Five phylogenetic groups of the common shrew, two of them consist only of one race, can be recognized in Europe. The Polish races belong to two groups: the West European and East European phylogenetic groups. A model of chromosomal evolution in the common shrew consisting of two components, an allopatric one and a parapatric or stasipatric one, has been proposed. This model is based on the distribution of different races and different metacentrics in karyotypes of shrews in Poland and in central Europe.

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Introduction

Intraspecific chromosome variation due to the presence or absence of Robertsonian rearrangement is commonly observed in mammals. The variation may involve either centric fusions (Robertsonian translocations) or centric fissions (dissociations). Robertsonian variation is observed both within populations (polymorphism) and between populations (polytypy).

The common shrew *Sorex araneus* Linnaeus, 1758 is one of the most variable species of mammals with respect to its chromosomes. An unusually extensive Robertsonian variability has been found in this species. It is assumed that the main mutations involved in karyotypic variation in the common shrew are centric fusions (Searle 1984, Wójcik and Searle 1988, Volobouev and Catzeflis 1989, Zima 1991).

Numerous karyotypic races have been described all over the extensive range of the common shrew (Halkka *et al.* 1974, 1987, Fredga and Nawrin 1977, Král *et al.* 1981, Searle 1984, 1988a, b, Wójcik and Fedyk 1985, Zima and Král 1985, Fedyk 1986, Hausser *et al.* 1986, 1991, Wójcik 1986, 1989, Fedyk and Leniec 1987, Fredga 1987, Zima *et al.* 1988, Aniskin and Lukianova 1989, Brünner 1991). Some

of these races have been found in Poland (Fedyk 1980, 1986, Wójcik 1986, 1989, Fedyk and Leniec 1987). The complex situation of Polish races needs to be clarified. In 1984 a phylogeny was presented which was based on a cladistic analysis of the chromosome races that had been described at that time (Searle 1984). Because of much new data a reevaluation of the relationship of European races of the common shrew is now necessary.

The differences in karyotypes that have been found between closely related species have had some believe that chromosome mutations play a special role in the formation of new species (White 1968, 1978a, b, Bush *et al.* 1977, Capanna 1982, Baker and Bickham 1986). Many descriptive models of chromosome evolution have been proposed to explain the increase and spread of chromosome mutations in populations (White 1968, 1978a, Bickham and Baker 1979, King 1981, Shaw 1981, Capanna 1982, Baker and Bickham 1986, Moritz 1986). A review of the assumptions and predictions of these models has revealed difficulties in applying them to natural situations (Sites and Moritz 1987). Nevertheless, I believe that *S. araneus*, being one of the best chromosomally characterized species, can be used to test these models of chromosomal evolution with empirical data. A recent review following this approach came to the conclusion that "there is (...) no evidence from the common shrew which indicates that simple chromosome mutations play a special role in speciation" (Bengtsson and Frykman 1990). In contrast to this negative conclusion, Zima (1991) has suggested that chromosome changes play a role in speciation processes in *S. araneus*, and that the speciation represents a response to increased information entropy caused by accumulated karyotypic variation. I believe that data from the common shrew support a model of chromosomal evolution based mainly on the assumptions of the White' stasipatric model (White 1968, 1978a, b).

Thus, the specific aims of the present study can be summarized as follows: (1) a comprehensive description of chromosome races of *S. araneus* from Poland, (2) a new review of the phylogeny of the European chromosome races of *S. araneus*, (3) presentation of a model of the chromosomal evolution in *S. araneus*.

Material and methods

A total of 150 common shrews from 29 localities in Poland were karyotyped (Table 1 and Fig. 1). Samples were collected from 1984 to 1990. Data is also included for 195 individuals from 7 localities, the details of which have been published elsewhere (Wójcik and Fedyk 1985, Wójcik 1986, Wójcik 1991).

In all cases direct air-dried chromosome preparations were made from spleen or bone marrow by a standard method (Ford 1966). The preparations were stained conventionally with Giemsa and G-banded as described previously (Wójcik 1986). The nomenclature of chromosome arms follows that of Halkka *et al.* (1974) as clarified by Fredga and Nawrin (1977) and revised by Searle *et al.* (1991). Each substantional chromosome arm is described by a letter of the alphabet with *a* as the largest arm.

Table 1. Karyotypes of *Sorex araneus* from different localities in Poland. Sample No 1 data from Wójcik (1991); sample Nos 11, 12, 15, 16 and 19 data from Wójcik (1986); sample No 13 data from Wójcik and Fedyk (1985), and Wójcik (1986). 2na – diploid autosome number. * – Karyotypes in terms of the variable chromosome arms *g* to *r*. Chromosomes not necessarily listed in order of size. Metacentrics are indicated in format *xy*, acrocentrics in format *x,y*, polymorphic arm combinations in format *x/y*, and metacentrics with monobrachial homology and homologous arms in format *xz/yz/x/y* (see: Searle *et al.* 1991).

No, locality	Geographic coordinates	*n* inds	2na	Karyotype*
1. Białowieża	52°42'N, 23°55'E	166	20 – 22	*j/l, ik, g/r, hn, m/p, o, q*
2. Antonowo	52°45'N, 22°10'E	7	20	*jl, ik, gr, hn, mp, o, q*
3. Długosiodło	52°46'N, 21°37'E	4	20	*jl, ik, gr, hn, mp, o, q*
4. Żebrak	52°04'N, 22°08'E	5	20	*jl, ik, gr, hn, mp, o, q*
5. Adamów	51°45'N, 22°17'E	4	20	*jl, ik, gr, hn, mp, o, q*
6. Radoryż Kośc.	51°49'N, 22°08'E	2	20	*jl, ik, gr, hn, mp, o, q*
7. Józefów	51°49'N, 22°23'E	5	20 – 21	*j/l, ik, gr, hn, mp, o, q*
8. Puławy	51°24'N, 21°57'E	4	20 – 22	*j/l, ik, gr, h/n, mp, o, q*
9. Krasnystaw	50°58'N, 23°12'E	3	20 – 22	*jl, ik, g/r, hn, m/p, o, q*
10. Zwierzyniec	50°36'N, 23°00'E	3	23 – 26	*jl, i/k, gm/gr/mp/m/p/r, h/n, o, q*
11. Popielno	53°45'N , 21°37'E	6	21 – 23	*jl, ik, gr, h/q, m/n, o, p*
12. Łęgucki Młyn	53°47'N, 20°08'E	1	21	*jl, hk, g/r, io, mn, p, q*
13. Krzewsk	54°05'N, 19°28'E	9	25 – 26	*jl, hi, k/o, g, m, n, p, q, r*
14. Śliwice	53°42'N, 18°10'E	4	22 – 25	*jl, hi, g/m, k/o, n, p, q, r*
15. Laska	53°55'N, 17°34'E	1	24	*jl, hi, g/m, k/o, n, p, q, r*
16. Słupsk	54°29'N, 17°02'E	5	25 – 26	*jl, hi, g/m, k, n, o, p, q, r*
17. Drawsko Pom.	53°32'N, 15°50'E	3	23 – 25	*jl, hi, gm, k/o, n, p, q, r*
18. Bolków	53°34'N, 14°23'E	9	24	*jl, hi, gm, k, n, o, p, q, r*
19. Stobnica	52°42'N, 16°36'E	7	20 – 22	*jl, hi, gm, ko, n/p, q, r*
20. Dziekanów Leśny	52°21'N, 20°50'E	3	20 – 21	*jl, hi, gm, ko, n/p, q, r*
21. Pułtusk	52°42'N, 21°05'E	7	20 – 21	*j/l, hi, gm, ko, np, q, r*
22. Kołodziąż	52°00'N, 21°55'E	4	20	*jl, hi, gm, ko, np, q, r*
23. Wilczyska	51°51'N, 21°53'E	3	20	*jl, hi, gm, ko, np, q, r*
24. Wilga	51°51'N, 21°24'E	2	20	*jl, hi, gm, ko, np, q, r*
25. Chełmno	52°07'N, 18°45'E	4	22	*jl, hi, gm, ko, n, p, q, r*
26. Wola Kopcowa	50°52'N, 20°43'E	18	23 – 24	*jl, hi, gm, k/o, n, p, q, r*
27. Szczucin	50°19'N, 21°05'E	5	23 – 24	*jl, hi, gm, k/o, n, p, q, r*
28. Chomranice	49°41'N, 20°33'E	3	24	*jl, hi, gm, k, n, o, p, q, r*
29. Gocieradów	50°52'N, 22°00'E	7	24	*jl, hi, gm, k, n, o, p, q, r*
30. Głogów Młp.	50°09'N, 21°58'E	10	24	*jl, hi, gm, k, n, o, p, q, r*
31. Krasne	50°15'N, 22°43'E	5	24	*jl, hi, gm, k, n, o, p, q, r*
32. Milicz	51°32'N, 17°18'E	4	21 – 22	*jl, hi, gm, ko, n/r, q, r*
33. Rogów	51°49'N, 19°53'E	6	20 – 22	*jl, hi, gm, ko, n/r, p, q*
34. Bogdanów	51°21'N, 19°33'E	6	20 – 22	*jl, hi, gm, ko, n/r, p, q*
35. Stanisławice	49°59'N, 20°24'E	4	23 – 24	*jl, hi, gm, k/o, n/r, p, q*
36. Malczyce	51°14'N, 16°30'E	6	20	*jl, hi, gm, ko, nr, p, q*

The description of the chromosome races of the common shrew in Poland was made according to the preliminary suggestions of the International *Sorex araneus* Cytogenetics Committee (Searle *et al.* 1991). Data used for description of the races came from Wójcik and Fedyk (1985), Wójcik (1986), Fedyk (1987), Fedyk and Leniec (1987), and the present study.

Fig. 1. The distribution of studied populations (black circles) and approximate ranges of five races of *Sorex araneus* in Poland. White circles indicate data from Fedyk and Leniec (1987), shaded circle – data from Wójcik and Fedyk (1985). See Table 1 for locality names.

The PAUP computer program (Phylogenetic Analysis Using Parsimony), version 2.4, Swofford (1985) was used in phylogenetic reconstruction to reveal the most parsimonious phylogenetic trees of the 24 known European races of the common shrew. A strict consensus tree was constructed using the CONTREE computer program (Swofford 1985).

The Polish chromosome races

The karyotypes of all shrews examined included arm combinations of autosomes *af, bc, jl* and *tu*, while chromosome arms *g-r* may be present as part of a variety of metacentrics or as acrocentrics (Fig. 2a –f). The sex chromosomes, XX for females and XY_1Y_2 for males were invariant.

Descriptions of karyotypes of Polish races of *S. araneus* races include only those chromosomes among the arms *g* to *r* that are known to be variable in Poland (Table 1). All races have the arm combination *jl*, that shows low-level polymorphism. Data collected so far allow to distinguish five chromosome races in Poland characterized by different metacentrics (Table 2). Previous names for races are retained (Wójcik 1986, 1989), excluding the name "Drużno race" (Wójcik and Fedyk 1985). It is suggested that the Drużno race be included within the Stobnica race. The name "Drużno race" was earlier used for a population of shrews near Lake

Drużno in northern Poland (Fig. 1; site 13). It is also proposed that a name of each race is the name of description locality, rather than a Roman numeral used by Fedyk (1986) and Fedyk and Leniec (1987). In the following account of each race, reference is given to the first published description of G-banded karyotype.

The Białowieża race (Fredga and Nawrin 1977) occurs widely in eastern Poland (Fig. 1). It is characterized by the arm combinations *ik, gr, hn,* and *mp* (Table 2). The arm combination *ik* always occurs as metacentrics and the chromosome arms *o* and *q* as acrocentrics (Fig. 2a). Due to Robertsonian polymorphism, four arm combinations *jl, gr, hn,* and *mp* are polymorphic in particular localities, and the diploid autosome number 2na varies from 20 to 24 (Fedyk 1980, Wójcik and Fedyk 1985, Fedyk 1986, Fedyk and Leniec 1987, Wójcik 1991, present paper). This race corresponds to "race VII" (named by Fedyk 1986).

The Popielno race (Wójcik 1986) occurs locally in northeastern Poland (Fig. 1). It includes the metacentrics *ik, gr, hq* and *mn,* and the acrocentrics *o* and *p* (Table 2). The arm combination *gr* always exists as metacentrics, *ik* shows low-level polymorphism in some populations, while race-specific arm combinations *hq* and *mn* show widescale polymorphism (Fedyk 1986, Wójcik 1986, Fedyk and Leniec 1987). Chromosome arms *o* and *p* always occur as acrocentrics (Fig. 2B). 2na = 21 – 24. This race corresponds to "race VI" of Fedyk (1986).

The Łęgucki Młyn race (Wójcik 1986) occurs locally in northeastern Poland (Fig. 1). The race is characterized by metacentrics *hk* and *io;* arm combinations *gr* and *mn* occurring also in the Popielno race, and chromosomes *p* and *q* as acrocentrics (Table 2 and Fig. 2c). This race has a very variable karyotype (2na = 21 – 26). The arm combinations *gr, io* and *mn* are polymorphic and two subdivisions are recognized within this race: the first one characterized by the metacentric *io* and the second one with the acrocentrics *i* and *o* (Wójcik 1986, Fedyk and Leniec 1987, Fedyk 1987). These two forms correspond to "race IV" and "race V" of Fedyk (1986) respectively.

The Stobnica race (Wójcik 1986) occurs widely in central, western, northern, and southeastern Poland (Fig. 1). All karyotypes belonging to the Stobnica race have metacentrics *hi* and chromosomes *q* and *r* as acrocentrics. The chromosome arms *g,k,m,n,p,* and *o* may exist as biarmed (*gm, ko,* and *np*) or uniarmed chromosomes or polymorphic arm combinations (Table 2). The population with 2na = 20 in central Poland, polymorphic populations northwards and southwards, and population with 2na = 24 in southeastern Poland can be found; and three widespread forms are recognized in this race (Table 2).

Karyotypes characterized by metacentrics *gm* and *ko* (Fig. 2d) and polymorphic arm combination *n/p* occur in central and western Poland (Wójcik 1986, Fedyk and Leniec 1987, present paper). 2na = 20 – 22. This form corresponds to the Drużno race (Wójcik and Fedyk 1985) and "race II" of Fedyk (1986).

In karyotypes from northern and northwestern Poland the arms *g* and *m* were found as the biarmed chromosomes *gm,* or as uniarmed chromosomes, or in a polymorphic state. The arms *k* and *o* exist in a polymorphic state or as uniarmed
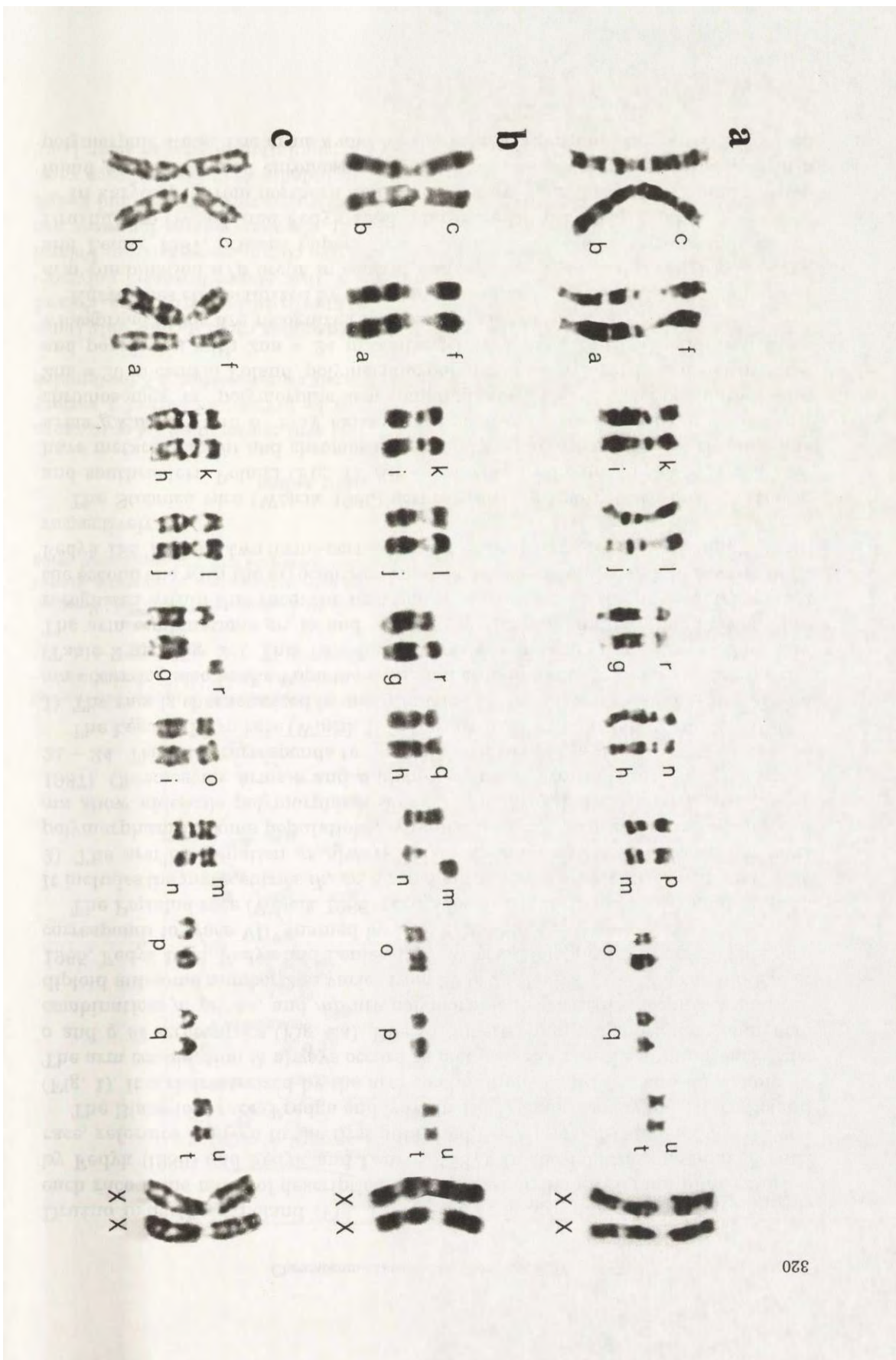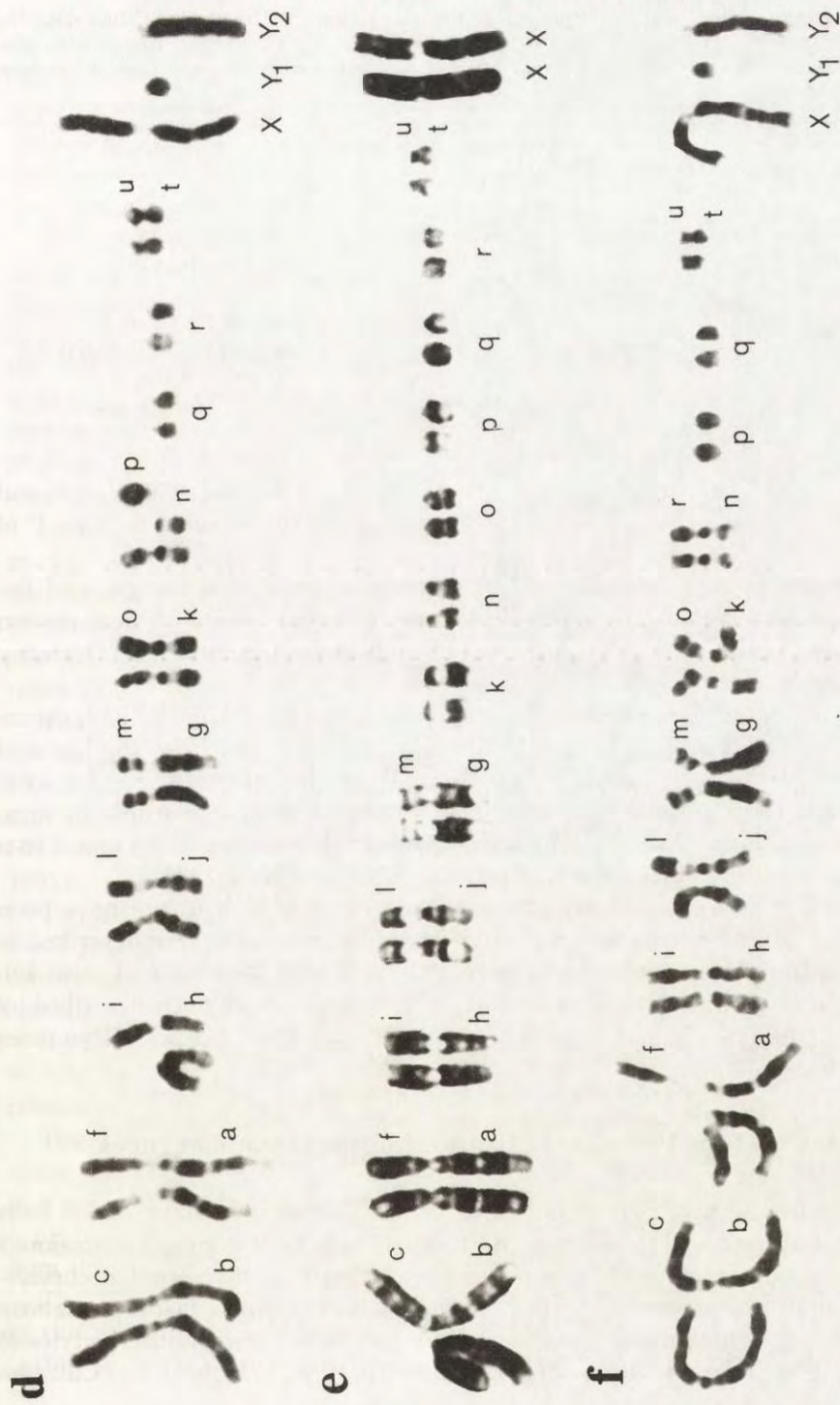
Fig. 2a – f. The karyotypes of different races of *Sorex araneus* in Poland: (a) homozygous female (2n = 22) from the Białowieża race; (b) heterozygous female (2n = 23) from the Popielno race; (c) heterozygous female (2n = 23) from the Łęgucki Młyn race; (d) heterozygous male (2n = 24) from Dziekanów (the Stobnica race, central type); (e) homozygous female (2n = 26) from Chomranice (the Stobnica race, southern type); (f) homozygous male (2n = 23) from Malczyce (the Drnholec race).

Table 2. Chromosome races of *Sorex araneus* in Poland. Based on already published data (for references see text) and data from this study. [*] – Karyotypes in terms of the variable chromosome arms *g* to *r*. The format *xy/x,y* indicates that two forms are found: biarmed and uniarmed chromosome forms. For more explanation see Table 1.

Name of race	Distribution in Poland	Karyotype[*]
1. "Białowieża"	E	*ik, g/r, h/n, m/p, o, q*
2. "Popielno"	NE	*ik, gr, h/q, m/n, o, p*
3. "Łęgucki Młyn"	NE	*kh, g/r, io/i,o, m/n, p, q*
4. "Stobnica":		
– central form	C & W	*hi, gm, ko, n/p, q, r*
– northern form (= "Drużno" race)	N	*hi, gm/g,m, ko/k,o, n, p, q, r*
– southern form	SE	*hi, gm, k, n, o, p, q, r*
5. "Drnholec" (= "Malczyce")	S & SW	*hi, gm, k/o, n/r, p, q*

chromosomes, and the arms *n* and *p* are acrocentric (Wójcik 1986, Fedyk and Leniec 1987, present paper). 2na = 22 – 26. This form corresponds to "race I" of Fedyk (1986).

Karyotypes that are characterized by the biarmed chromosome *gm* and the uniarmed chromosomes *k*, *n*, *o*, and *p* with 2na = 24 occur widely in southeastern Poland (Table 1 and Fig. 2e). This form corresponds to the Ulm race from Germany (Olert and Schmid 1978).

The Drnholec race (Zima and Král 1985) (= Malczyce race; Wójcik 1989) occurs in southern and southwestern Poland (Fig. 1). In this race the following biarmed chromosomes can be recognized: *hi*, *gm*, *ko*, and *nr*; chromosomes *p* and *q* exist as acrocentrics (Fig. 2f). Arm combinations *ko* and *nr* are polymorphic in some populations and 2na = 20 – 24. The karyotype of this race was also found in a geographically nearby part of Czech Republic (Zima and Král 1985).

Hybrid zones between different chromosome races of *S. araneus* have been found in eastern and northeastern Poland. Hybrid karyotypes were described in a population from Zwierzyniec in eastern Poland (Table 1 and Fig. 1; site 10). Different hybrid and interracial recombinant karyotypes have been described by Fedyk *et al.* (1991) in a hybrid zone between the Stobnica and Łęgucki Młyn races in northeastern Poland.

Relationships between Polish and other European races

Twenty four different karyotypic races of common shrews have so far been described in Europe and 3 from Western Siberia (Table 3). It is generally assumed that the ancestral karyotype of the common shrew consisted of acrocentric chromosomes and that all metacentrics were formed by Robertsonian fusion mutations (Searle 1984). This hypothesis is supported by comparisons with other species of *Sorex* (Meylan and Hausser 1973, Wójcik and Searle 1988, Volobouev and Catzeflis

1989). An alternative hypothesis is that the observed metacentrics were formed either by Robertsonian fusions of acrocentrics, or by whole-arm reciprocal translocations between different metacentrics (Halkka *at al.* 1987). The first hypothesis is more parsimonious and was assumed by Searle (1984) when constructing a phylogeny of the 12 chromosome races known at that time on the basis of a cladistic analysis. Searle (1984) has recognized four distinct phylogenetic groups: the Valais race, West European, East European and Siberian phylogenetic groups.

New phylogenetic trees for the 24 known European races are presented in this paper (Fig. 3a – c). For simplicity, each race is denoted by a letter of the alphabet. The letters A–L are allocated to the same 12 races as in the analysis presented by Searle (1984). Races that have been more recently described are designated by the letters M–S, sometimes with a numerical subscript in case of races karyotypically and geographically related (Table 3). This nomenclature is only intended for clarity in the present analysis, not as a permanent coding for these races. The phylogenetic reconstruction was only made for the European races; three Siberian races (H, D and E in Searle 1984) are not included in the analysis.

It is assumed that the acrocentric condition is ancestral and all metacentrics are formed by Robertsonian fusion mutations. The 35 Robertsonian fusions among the arms *g-r* found in European races are used in the phylogenetic analysis (Table 3). Each fusion hypothesis is represented by a character with two character states: one state in case of races that have the fusion, and the other one in the case of races that lack the fusion.

The International *Sorex araneus* Cytogenetics Committee has suggested that the karyotypes of the Finnish races described by Halkka *et al.* (1974, 1987) should be revised according to the nomenclature of Fredga and Nawrin (1977). This means that the arm "*m*" of Halkka *et al.* is labelled by the letter "*o*" and the arm "*o*" of Halkka *et al.* is labelled by the letter "*m*" (for more explanation see Searle *et al.* 1991).

Two fully resolved trees of equal length are selected from the 50 most parsimonious phylogenetic trees produced by the PAUP analyses (Fig. 3a, b). The strict consensus tree produced by the CONTREE program presents the information common to a set of all 50 equally parsimonious trees (Fig. 3c).

From the trees it is possible to distinguish five phylogenetic groups, two of which consist only of one race. Races that show the closest phylogenetic relationship are, in general, geographicaly related.

The Acrocentric race (or form) (S) corresponds to the primitive karyotype because the arms *g* to *r* are in an acrocentric state, except the arms *j* and *l* that are in a polymorphic state. The Valais race (L) with the metacentrics *gi, hj, kn,* and *lo* probably arose in Italy (Hausser *et al.* 1986, 1991) and may have been isolated from the other European races of *S. araneus* for a long period.

The West European phylogenetic group (WEPG) (Searle 1984) is characterized by the arm combination *hi* and *gm* (clade $ABFIJKMNOO_1PP_1$), and the concept of this group is supported by recent data (Table 3 and Fig. 3). Races belonging to

Table 3. Known chromosome races of *Sorex araneus*. The letters (A-S) refer designation of races for benefit of the present analysis only (see text and Fig. 3). * – Karyotypes in terms of the variable chromosome arms; the maximum number of observed metacentrics is shown (for details see references). Karyotypes recognized by international committee are in parentheses (see: Searle *et al*. 1991). For more explanation see Table 1 and text.

Known range Used name	Karyotype*	References
1	2	3
(A) Scotland, W Wales, SW England "Aberdeen"	*jl, hi, gm, ko, np, qr*	Searle 1984, 1988a
(I) England, S Scotland, Denmark "Oxford"	*jl, hi, gm, kq, no, pr*	Searle 1984, 1988a, Fredga 1987
(F) S England, Wales, S Sweden "Hermitage"	*jl, hi, gm, ko, pr, n, q*	Searle 1984, 1988a
(J) C Sweden "Stugun"	*jl, hi, gm, kp, nr, oq*	Fredga and Nawrin 1977
(M) C Sweden "Hällefors"	*jl, hi, gm, ko, nr, pq*	Fredga 1982, 1987
(B) S Sweden "Åkarp"	*jl, hi, gm, ko, nq, pr*	Fredga and Nawrin 1977, Fredga 1982
(K) Central Europe "Ulm"	*jl, hi, gm, k, n, o, p, q, r*	Dulić 1978, Olert and Schmid 1978, Zima and Král 1985, present paper
(N) N Switzerland, S Germany "Vaud"	*jl, hi, gm, kr, no, p, q*	Hausser *et al*. 1986, Brünner 1991
(O) Russia near Moscow "Cernogolovka"	*jl, hi, gm, kr, no, pq*	Aniskin and Lukianova 1989
(O₁) Russia near Moscow	*jl, hi, gm, kp, no, qr*	Ivanitskaya 1985
(P) C and W Poland "Stobnica"	*jl, hi, gm, ko, np, q, r*	Wójcik 1986, Fedyk and Leniec 1987, present paper
(P1) SW Poland, N & E Czechland "Drnholec" (= "Malczyce")	*jl, hi, gm, ko, nr, p, q*	Zima and Král 1985, present paper
(C) E Poland "Białowieża"	*jl, ik, gr, hn, mp, o, q*	Fredga and Nawrin 1977, Fedyk 1980, Wójcik 1991
(C1) NE Poland "Popielno"	*jl, ik, gr, hq, mn, o, p*	Wójcik 1986, Fedyk and Leniec 1987
(R) NE Poland "Łęgucki Młyn"	*jl, hk, gr, io, mn, p, q*	Wójcik 1986, Fedyk and Leniec 1987
(G) N Sweden "Abisko"	*jl, ip, hn, gm, kq, or*	Fredga and Nawrin 1977, Fredga 1982
(G₁) N Finland "Kuusijoki"(= "Race I")	*jl, ip, hn, gm, kq, or* (*jl, ip, hn, go, kq, mr*)	Halkka *et al*. 1974, 1987
(G₂) E Finland "Race II"	*jl, ip, hn, gm, kr, oq* (*jl, ip, hn, go, kr, mq*)	Halkka *et al*. 1987
(G₃) SE Finland "Race III"	*jl, ip, hk, gq, mo, nr*	Halkka *et al*. 1987
(G₄) S Finland "Race IV"	*jl, ip, hn, gq, ko, mr* (*jl, ip, hn, gq, km, or*)	Halkka *et al*. 1987

Table 3 – concluded.

1	2	3
(G5) W Finland "Race V"	jl, ip, hn, mr, oq, g,k (*jl, ip, hn, or, mq, g, k*)	Halkka *et al.* 1987
(G6) SW Finland "Race VI"	*jl, ip, g, h, k, m, n, o, q, r*	Halkka *et al.* 1987
(H) Russia, W Siberia "Novosibirsk"	*jl, ik, hn, go, mp, qr*	Aniskin and Volobouev 1980, Kral *et al.* 1981
(D) Russia, W Siberia "Chaldejevo"	*jl, gk, hi, mn, op, qr*	Aniskin and Volobouev 1980, Král *et al.* 1981
(E) Russia, W Siberia "Ermakovskoe"	*jl, gk, ho, iq, mn, pr*	Aniskin and Volobouev 1981
(S) SE France "Acrocentric"	*jl, g, h, i, k, m, n, o, p, q, r*	Hausser *et al.* 1991
(L) S Switzerland "Valais"	*hj, gi, lo, kn, m, p, q, r*	Hausser *et al.* 1986, 1991

the West European phylogenetic group are geographically related (excluding two races (O and O1) found near Moscow); they have been found in southern, central and western Europe, and in Scandinavia (Table 3 and Fig. 4). More sampling is needed to answer the question whether the range of this phylogenetic group extends across the Ukraine and the European part of Russia. Two Polish races, the Stobnica (P) and Drnholec (P1), are included in the West European phylogenetic group. Because they carry the fusion *ko* they are close to the Aberdeen (A) and Hermitage (F) races from Britain, and the Åkarp (B) and Hällefors (M) races from Sweden in the phylogenetic tree (Fig. 3). However, these races are at present not geographically related, and it can be suggested that the common occurrence of the fusion *ko* in these races is the consequence of independent fusion, rather than common ancestry.

Since the publication of Searle's phylogeny (Searle 1984), several new chromosome races have been described in eastern Poland and in Finland (Wójcik 1986, 1989, Halkka *et al.* 1987, Fedyk and Leniec 1987, Fedyk 1987). As the relationships between these races has become more complex, a new view on the concept of the East European phylogenetic group (EEPG) (Searle 1984) is now necessary. It is proposed that three races from eastern and northeastern Poland (the Białowieża, Popielno and Łęgucki Młyn races), characterized by the arm combination *gr* (clade CC1R), belong to the East European phylogenetic group (Figs 3 and 4).

It is also suggested that seven races from Scandinavia (clade GG1G2G3G4G5G6), characterized by the arm combination *ip*, belong to another phylogenetic group (Zima *et al.* 1988), and I refer to them as the "North European phylogenetic group" (NEPG) (Figs 3 and 4).

It is not easy to explain the relationships between the races from eastern Poland and from Finland because of lack of data from Belarus, Lithuania, Latvia and
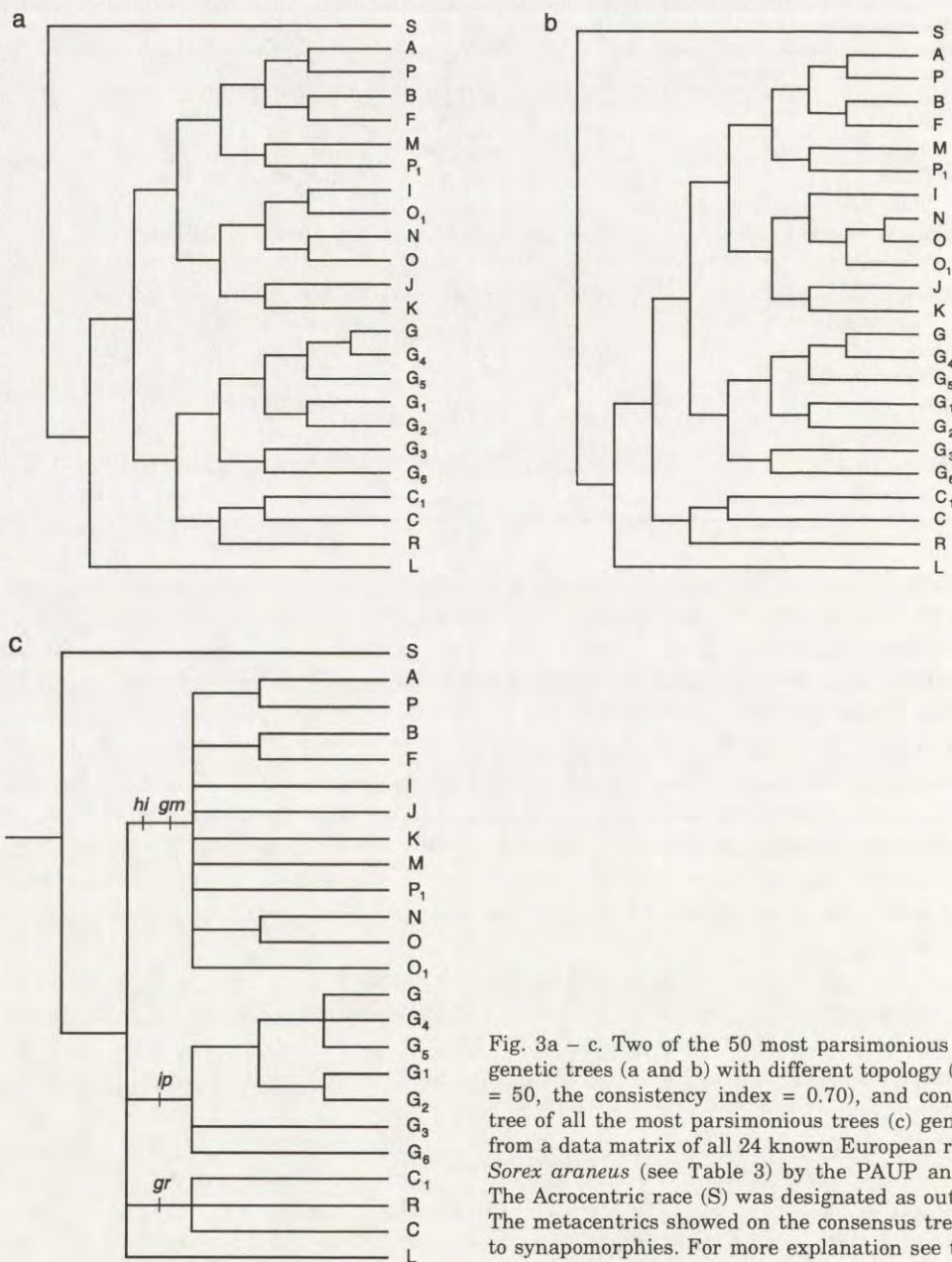
Fig. 3a – c. Two of the 50 most parsimonious phylogenetic trees (a and b) with different topology (length = 50, the consistency index = 0.70), and consensus tree of all the most parsimonious trees (c) generated from a data matrix of all 24 known European races of *Sorex araneus* (see Table 3) by the PAUP analyses. The Acrocentric race (S) was designated as outgroup. The metacentrics showed on the consensus tree refer to synapomorphies. For more explanation see text.

Estonia. The Białowieża race (C) from eastern Poland and four local races from Finland (G₁, G₂, G₄, and G₅) include the arm combination *hn*. The Łęgucki Młyn race (R) from northeastern Poland and one race (G₃) from southeastern Finland
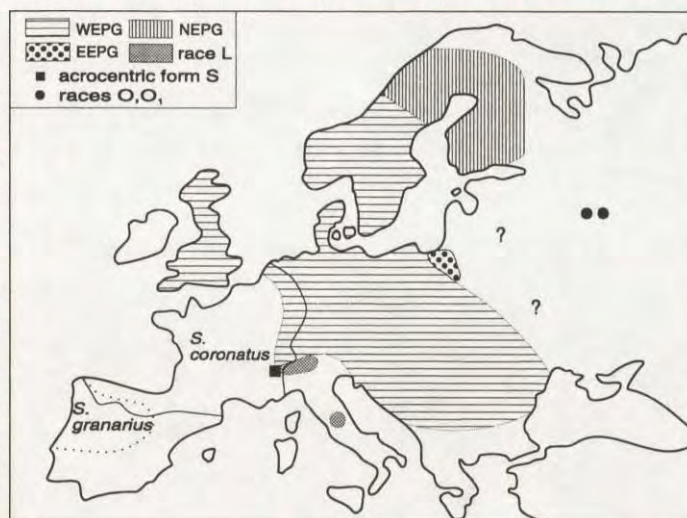
Fig. 4. The distribution of different phylogenetic groups and some local races of *Sorex araneus* (see Table 3) in Europe. Continuous line denotes approximate range of *S. coronatus* and dotted line range of *S. granarius*.

are characterized by the fusion *hk* (Table 3). Two alternative hypothesis may explain the common occurrence of these fusions in the Polish and Finnish races: common ancestry or independent fusion. Nevertheless, the phylogenetic analysis indicates that it is more parsimonious to put the Polish races into one phylogenetic group and the Finnish races into another (Fig. 3).

Model of chromosomal evolution in the common shrew

It is suggested that the distribution of *S. araneus* was restricted to refugia in the southern part of Europe during the most recent glacial maximum which occurred 20,000 to 15,000 b.p. (see Searle 1984: Fig. 7). Searle (1984) proposed that the West European phylogenetic group and perhaps also the East European phylogenetic group were formed within refugia in southeastern Europe during that period, and then (15,000 to 7,000 b.p.) spread north through Europe. The territory of Poland may have been recolonized by *S. araneus* during that time.

From our current understanding of the distribution of different karyotypes of *S. araneus*, it can be suggested that the fusion *hi* (the West European phylogenetic group), the fusion *gr* (the East European phylogenetic group), and perhaps also the fusion *ip* (the North European phylogenetic group) may have been formed allopatrically somewhere in southern or southeastern Europe during the last glacial maximum. It is also proposed that a number of metacentrics that are characteristic for races belonging to each particular phylogenetic group may have
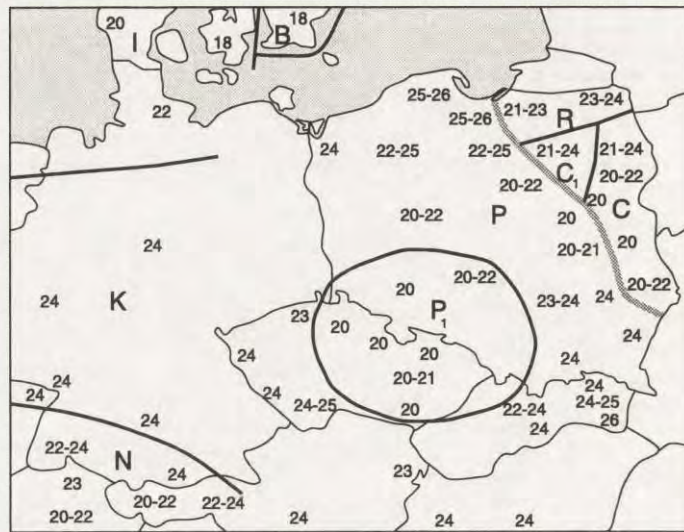
Fig. 5. Approximate ranges of different races of *Sorex araneus* in central Europe. Diploid autosome numbers (2na) found in different races are shown. Continuous lines indicate ranges of the Białowieża (C), Popielno (C₁), and Łęgucki Młyn (R) races; centre of range of the Drnholec (P₁) race; and predicted ranges of the Vaud (N), Oxford (I), and Åkarp (B) races. Thick dotted line denotes the secondary contact zone between the East and West European phylogenetic groups. Based on data from Zima and Král (1985), Fredga (1987), Brünner (1991), and the present paper.

arisen within the species' range during expansion through Europe, according to the White' stasipatric model (White 1968, 1978a, b).

A model of chromosomal evolution in the common shrew consisting of two components, an allopatric one and a parapatric or stasipatric one, will now be proposed. This model is based on the distribution of different races and different metacentrics in karyotypes of shrews in Poland and in central Europe as presented in Fig. 5.

It can be assumed that the ancestral karyotype of the West European phylogenetic group included the metacentric hi and jl (within the arms g–r), and the uniarmed chromosomes g, k, m, n, o, p, q, and r. The ancestral karyotype of the East European phylogenetic group might have included the metacentric gr and jl, and the uniarmed chromosomes h, i, k, m, n, o, p, and q. It is suggested that shrews possessing these karyotypes populated the area of Poland from south-western and eastern directions respectively with the amelioration of climate during the early post-glacial period (Fig. 6a).

The origin of the Stobnica and Drnholec races of the West European phylogenetic group may be explained in the stasipatric mode. The fusion gm is postulated to have arisen somewhere in southern or central Europe within the range of the fusion hi, and to have extended its range until it coincided with that of the fusion hi (Fig. 6a – c). Because of a very wide distribution of the fusion gm in southern, central and western Europe it seems that shrews possessing this fusion

recolonized Poland as soon as shrews with the fusion *hi* had come. The range of the fusions *hi* and *gm* may have spread northeast until they came into contact with the East European phylogenetic group in eastern Poland and the secondary contact zone was formed there.

The fusion *ko* is postulated to have arisen somewhere in western Europe within the range of the fusions *hi* and *gm*, and to have extended its range through southwestern Poland until it coalesced with that of the fusions *hi* and *gm* in eastern Poland (Fig. 6a – c).

Eventually, two different fusions *np* and *nr* may have established themselves at different points within the range of the fusions *hi*, *gm*, and *ko*, and extended their ranges, giving rise to two populations. It seems highly probable that the fusion *np* arose somewhere in western or central Poland and spread from there forming the karyotype with a maximum number of metacentrics for the Stobnica race (Fig. 6a – c). The fusion *nr* that is characteristic for the Drnholec race may have arisen in southwestern Poland or on the territory of Czech Republic and extended its range over a considerable area (Fig. 6b, c). The Stobnica and Drnholec races are very close in respect to karyotypes and there is no presumable barrier for gene flow between them.

Around the periphery of each new increasing fusion area a moving polymorphism or a hybrid zone ("tension zone") would have developed in which heterozygotes would have occurred (Key 1968, White 1968, 1978a, b). Such polymorphic areas have been found in Poland and in different parts of central Europe (Fig. 5).

It is an essential assumption of the stasipatric model that it should always be possible to recognize between the "derived" form and the "parent" form. Derived forms are expected to occupy central or interior areas and ancestral forms peripheral or external ones (White 1978a, b). Such distribution of derived and ancestral types is observed in Poland and central Europe (Fig. 5). The Ulm race, with the fusions *hi* and *gm* (2na = 24), described in West Germany (Olert and Schmid 1978) corresponds to the ancestral form of the Stobnica and Drnholec races.

The origin of the Białowieża, Popielno, and Łęgucki Młyn races belonging to the East European phylogenetic group can also be explained by the stasipatric model.

Initially, the area of eastern and northeastern Poland may have been populated by shrews with karyotypes that included the arm combination *gr* (Fig. 6a). Three different fusions *ik*, *hk*, and *mn* may have established themselves at different points within the range of the fusion *gr* (somewhere in eastern Europe) and extended their ranges until they met each other in northeastern Poland. Because of metacentrics with monobrachial homology, the primary hybrid zone may have been formed between populations including the fusions *ik* and *hk*. It is suggested that the fusion *mn* was able to introgress into those two populations and considerable sympatric areas developed there (Fig. 6b). It is supposed that some of the chromosomal rearrangements may have introgressed more or less freely across the contact zone between different forms (see Key 1968). In the proposed model,
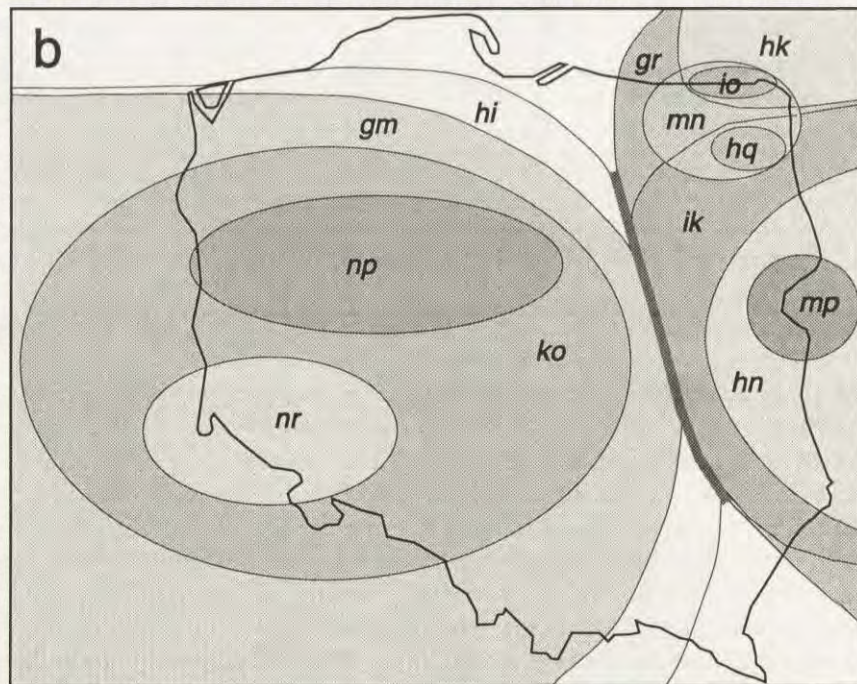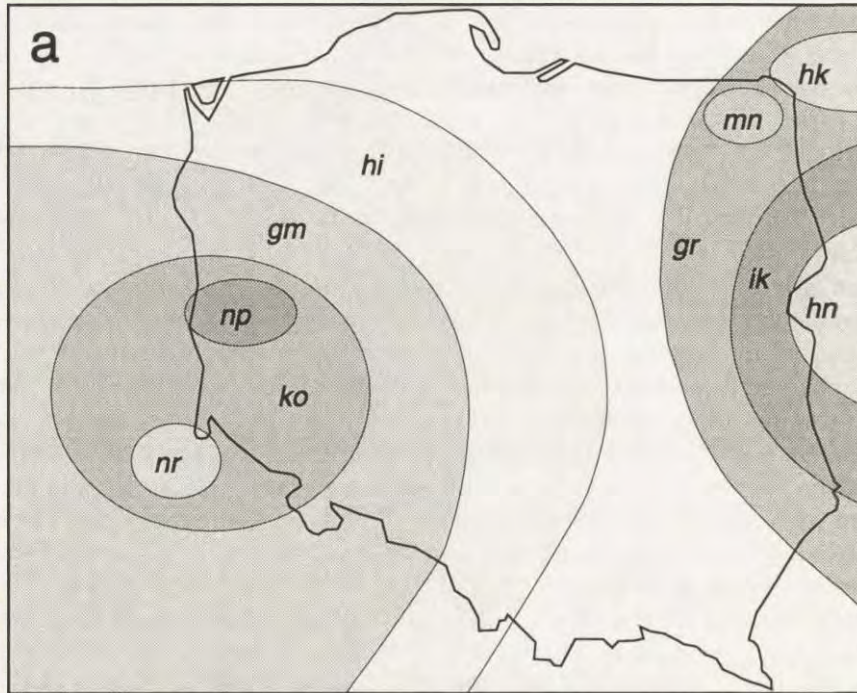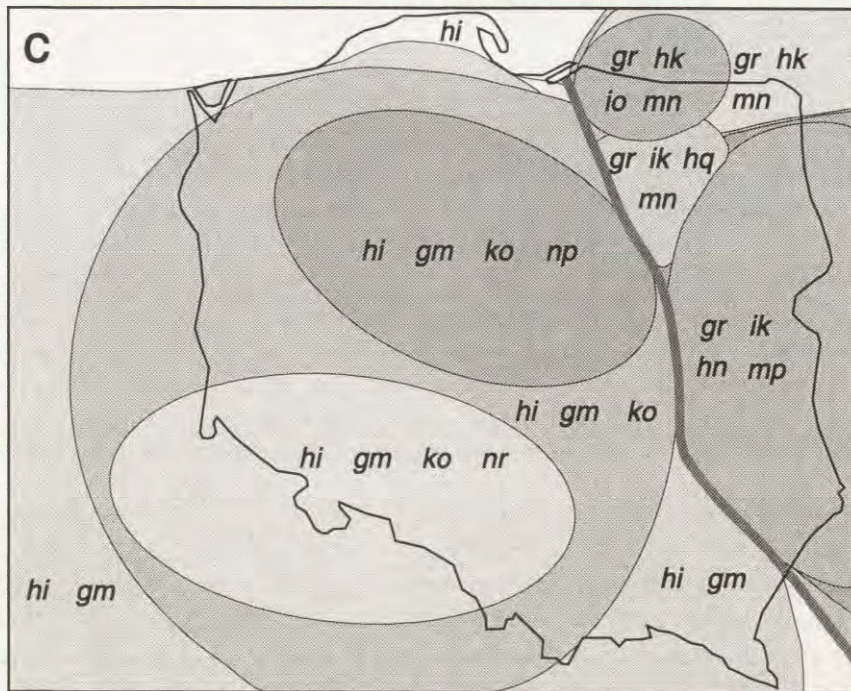
Fig 6a – c. Proposed model of the origin of Polish chromosome races of *Sorex araneus*. The hypothesized manner of range expansion of different fusions (a and b) and proposed approximate distribution of different karyotypes based on known data (c) are shown. Thick dotted line denotes the secondary contact zone between the East and West European phylogenetic groups. For explanation see text.

it was assumed that the fusion *mn* introgressed into the "derived" Białowieża and Łęgucki Młyn races until it met other fusions that included the arms *m* or *n*.

The fusion *hn* may have established itself somewhere within the range of the fusions *gr* and *ik*, and the fusion *mp* established itself somewhere within the area occupied by the fusions *gr*, *ik*, and *hn*, giving the karyotype of the Białowieża race. All these fusions may have extended their ranges until they coalesced and came into contact with populations which included other fusions (Fig. 6a – c).

The fusion *hq* that is characteristic for the Popielno race may have established itself somewhere within the area occupied by the fusions *gr*, *ik* and *mn*, and may have spread locally in northeastern Poland until it met populations including different metacentrics with monobrachial homology (Fig. 6b, c).

The fusion *io* is postulated to have arisen somewhere within the range of the fusions *gr*, *hk* and *mn*, and to extend its range in northeastern Poland and probably north outside of Poland, giving rise to the Łęgucki Młyn race (Fig. 6b, c).

All three races (the Białowieża, Popielno and Łęgucki Młyn races) may have came into contact between each other, and primary contact zones were formed in

northeastern Poland. There was presumable gene flow through these contact zones because of high frequencies of acrocentrics observed in neighboring populations of these races (Fedyk 1986, 1987). On the other hand, these three races may have came into contact with the Stobnica race belonging to the West European phylogenetic group and the secondary contact zone was formed in eastern and northeastern Poland (Fig. 5).

Wójcik (1986) assumed that the metacentrics *hk* and *io* in the Łęgucki Młyn race may have arisen as a result of a single whole-arm reciprocal translocation between the metacentrics *hi* and *ko* which are characteristic for the Stobnica race. However, reciprocal translocations occur very rarely because they cause heterozygote semisterility (White 1973, Lande 1979). It is, thus, more plausible to assume that the arm combinations *hk* and *io* were formed by independent Robertsonian fusions, rather than by a single whole-arm reciprocal translocation.

Fedyk (1987) suggested that Polish races may have been formed according to the stasipatric model, and the metacentrics *hk*, *io* and *mn* which are characteristic of the Łęgucki Młyn race could have arisen as a result of hybridization between races of the West European and East European phylogenetic groups. Fedyk's hypothesis on the origin of local fusions in northeastern Poland can be summarized as follows: Shrews differing in one or two metacentrics with monobrachial homology in a heterozygous state came into contact in northeastern Poland. Because of only slight disturbances in meiosis of hybrids a large sympatric zone was formed, where shrews with the metacentrics *hi*, *ko* and *np* (the Stobnica race), and with *ik* and *mp* (the Białowieża race) coexisted with each other. The close relation of centromeres of the arms *h* and *k*, *i* and *o*, *m* and *n* in three types of quadrivalents in the meiosis of hybrids made it possible to form the fusions *hk*, *io* and *mn* between these acrocentrics.

However, it seems that the above hypothesis is not plausible for several reasons. Firstly, it cannot be expected that such a large sympatric area could have been formed, even if populations differing only in two pairs of metacentrics with monobrachial homology came into contact. A narrow hybrid zone would be rather expected to form, as in the case of British races (the Oxford and Hermitage races) that differ from each other in two pairs of metacentrics with monobrachial homology (Searle 1986a). The hybrid zone would act against developing such a large sympatric area. Secondly, because the fusions *gm* and *gr* came into contact probably earlier than the fusions *np* and *mp* (Fig. 6a), the fusion *mr* would have been expected to arise, rather than the fusion *mn* according to Fedyk's hypothesis. Finally, if the metacentric *hk* had a hybrid origin it would be very difficult to explain its a wide distribution, presumably from northeastern Poland to southern Finland (Halkka *et al*. 1987).

Other explanations of the origin of different races in this species have been proposed. Searle (1986a) studied a hybrid zone between the Oxford and Hermitage races in Britain and concluded that it is not readily possible to choose between allopatric or stasipatric models to explain the origin of British races. Searle and

Wilkinson (1987) proposed that peripheral distribution of the Aberdeen race is attributed to subsequent partial displacement by other races. Eventually, Searle (1988a) suggested two possible hypothesis: either the Aberdeen, Hermitage and Oxford races colonized Britain as closely successive waves of invasion (the "closely successive waves model"), or the races colonized Britain independently as distinct temporally-separated pulses, and further range changes occured due to the separation of Britain (the "pulse model").

Halkka *et al.* (1987) presented a hypothesis on the chromosomal evolution of 4 local Finnish races of *S. araneus*. This was done through a series of whole-arm reciprocal translocations from a common ancestor karyotype during migration into Finland in the postglacial period from eastern Europe. A fifth one is postulated to be a hybrid race or to have arisen as a result of a new fusion. A sixth one, including all acrocentric chromosomes in a variable part of karyotype, is proposed to represent the extreme of the enrichment of acrocentrics.

Fedyk *et al.* (1991) suggested that interchromosomal recombinants in a hybrid zone between different chromosome races of *S. araneus* may form a new race. Zima (1991) stated that the permanent trend toward lowering 2na numbers observed in *S. araneus* can be considered as adaptive tool inhibiting an undesirable rise of information entropy. Then, he suggested that "karyotype changes do play a role in divergence processes in *S. araneus*, and that the speciation represents a response to increased information entropy caused by accumulated karyotypic variation".

Capanna (1991) compared speciation models for *Mus domesticus* and *S. araneus*; when refusing the stasipatric model of White for *M. domesticus* (see also Capanna 1982), he stated that "the mode of speciation of *Sorex araneus* could be considered more stasipatric than the *Mus domesticus* one".

General remarks

Some mechanisms are necessary to enable a new Robertsonian fusion to become fixed in a population. White (1978b) suggested that genetic drift, meiotic drive, selective advantage of the new homokaryotype, and inbreeding may separately or in combination lead to the fixation of new chromosomal rearrangement in a population. Lande (1979) postulated that the initial fixation of chromosomal rearrangements can happen only by genetic drift in a small inbred deme, because they are selected against when in the minority, but favored when in the majority. It is also suggested that once established in a deme they can spread in a homozygous form through a subdivided population by random local extinction and colonization (Lande 1979). Hedrick (1981) examined theoretically the different processes postulated by White (1978b), and concluded that meiotic drive alone, meiotic drive in combination with genetic drift, and inbreeding in combinations with, respectively, genetic drift and selective advantage of the new homokaryotype are potentially

important mechanisms which can lead to the fixation of the new chromosomal type in a population.

It is assumed that meiotic drive is likely to be the most important mechanism in the fixation of new chromosome rearrangements in shrews (Hausser *at al*. 1985, 1986, Zima 1991). Even a very low level of meiotic drive in favor of new Robertsonian fusions may play an important role in the fixation and spreading in populations of shrews.

It is often agreed that neither small demes nor intensive inbreeding are very likely in common shrews (see Hausser *at al*. 1985, Bengtsson and Frykman 1990), because of their strict territoriality and relatively high densities (Croin-Michielsen 1966, Nosek *et al*. 1972), and reproductive isolation of two successive generations (Pucek 1960). Nevertheless, this species inhabits the extensive Palearctic range (Corbet 1978), and it is possible that many of the populations in different parts of its range are relatively small and semi-isolated. There is strong evidence that in small semi-isolated and non-stable populations of shrews which exist on small islands in a lake in eastern Finland the "founder" effect and genetic drift play an important role (Hanski 1986, Hanski and Kuitunen 1986). These results support the supposition that conditions for chromosomal evolution are optimal on the fragmented border of a species' range (White 1978b), or during conditions of extinction/ colonization cycles (Lande 1979, 1985, King 1981, White 1982, Hedrick and Levin 1984).

It is hard to judge whether simple Robertsonian heterozygotes of shrews are at a fitness disadvantage in nature in comparison with homozygotes. Searle (1986b, 1988b) showed that very low anaphase I non-disjunction frequencies in simple Robertsonian heterozygotes of shrews existed: 0.8% in males and $1.0 - 2.5\%$ in females. Prenatal losses have been also recorded in female simple Robertsonian heterozygotes of shrews, and some of them were very likely due to anaphase I non-disjunction. However, numbers of ovulations were higher in these heterozygotes than in the homozygotes, and this could compensate for prenatal losses due to non-disjunction (Searle 1990). From our current understanding of this problem, it can be suggested that the fitness of individual Robertsonian fusion mutations in a heterozygous state is weak, rather than strongly underdominant, in the case of the common shrew. So, it cannot be expected that very strong selection against Robertsonian fusions in natural populations of shrews exists. There is indirect evidence that heterozygote advantage in different habitats may play an important role in maintenance of balanced chromosomal polymorphism in shrews (Wójcik 1991).

It is suggested that new chromosomal rearrangements may protect coadapted gene complexes ("area effect") from disruption by introgression from neighboring populations (White 1978a). According to the stasipatric model the genetic isolation of the populated area is progressively reinforced. It may be, thus, expected that evolutionary processes increase karyotypic differences between two populations of shrews. Bengtsson and Frykman (1990) examined the available data and

concluded that perhaps all karyotypic hybrid zones in shrews are penetrated by gene flow, and that secondary evolutionary process leads to a decrease of the isolation between the populations. Nevertheless, contrary to Bengtsson and Frykman's (1990) opinion is seems possible that Robertsonian fusions are in some cases sufficient to cut gene flow between chromosome races. Two races which differ from each other in 4 pairs of metacentrics with monobrachial homology (the Vaud and Valais races; see Table 3) came into contact in the Western Alps in Switzerland. So far, neither hybrids nor indirect evidence of hybridization between those races have been found (Hausser *et al*. 1991, Neet and Hausser 1991).

Chromosomal evolution in *S. araneus* that began perhaps during the last glaciation is still in progress. Karyotypic differentiation in the common shrew is certainly evolutionary and phylogeneticaly important, and may lead to the origin of a new species. The model of chromosomal evolution in *S. araneus* proposed in the present paper is based mainly on the assumptions of the stasipatric mode because the current distribution of different karyotypes is in strong support for it. It is conceivable that climatic and environmental conditions existed during the postglacial regression facilitated karyotypic evolution in, perhaps subdivided, populations of *S. araneus*.

Finally, I suggest that the model of chromosomal evolution presented in this paper, perhaps with some modifications, may explain the origin of most of the chromosome races of *S. araneus*. Further multidisciplinary population-level studies should bring not only more exact knowledge of the karyotypic evolution in this species, but also the basic features of chromosomal evolution in general.

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