Sex Chromosome Meiotic Drive in Hybrid Males of the Common Shrew (*Sorex araneus*)*

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Patterns of sex chromosome segregation in six homozygous males of the common shrew (*Sorex araneus* LINNAEUS, 1758) belonging to two chromosomal races, as well as in 16 interracial hybrids were studied. Based on their karyotypes the hybrids can be subdivided into two groups: (a) complex heterozygotes, which form meiotic quadrivalents in chain and chain + ring configurations, and (b) complex heterozygotes, which form meiotic pentavalents in chain configurations. Random (1 : 1) segregation of sex chromosomes was found in homozygous as well as those heterozygous males which form meiotic complexes of four chromosomes. However, in some hybrids with meiotic pentavalents we observed a strong preferential segregation in favour of X chromosomes.

Key words: *Sorex araneus,* meiotic segregation, interracial hybrids, meiotic drive, segregation distortion.

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Enormous differences between karyotypic races of the common shrews, *Sorex araneus* LINNAEUS, 1758 result in a high level of heterozygosity often observed in wild populations (e.g. FEDYK & LENIEC 1987; FREDGA 1996). There are two types of heterozygotes in the common shrew (SEARLE 1993). In populations in which metacentrics as well as homologous acrocentrics coexist, simple Robertsonian (Rb) heterozygotes are observed, which form trivalent configurations during meiosis. This type of polymorphism with simple Rb heterozygotes occurs on the contact between a race which posses metacentric chromosomes and one with homologous acrocentrics (LUKÁČOVÁ *et al*. 1994). The second type of heterozygote is known as a complex Rb heterozygote. These occur in narrow hybrid zones between races characterised by different metacentrics with monobrachial homology. Complex Rb heterozygotes form ring or chain meiotic configurations, which consist of at least four elements (FEDYK *et al*. 1991; see SEARLE & WÓJCIK 1998 for review).

In simple Rb heterozygotes one should expect an equal segregation of one metacentric and two homologous acrocentric chromosomes. However, some empirical data suggests that segregation is distorted in favour of metacentric chromosomes. For example, SEARLE'S (1986a) analysis of chromosomes of the fetuses and weanlings, coming from wild pregnant females, suggested biased transmission of metacentrics. However, SEARLE'S assumption that there was no multiple paternity in the common shrew turned out to be erroneous (SEARLE 1990; TEGELSTRÖM *et al*. 1991), which weakened the evidence for unequal transmission of chromosomes. On the other hand, crosses of simple Rb heterozygotes with homozygotes reared under laboratory conditions (WYTTENBACH *et al*. 1998) unequivocally proved meiotic drive in favour of metacentric chromosomes.

To date, chromosome segregation of the complex Rb heterozygotes has not been studied. Likewise, a thorough examination of sex chromosome segregation in *Sorex araneus* are lacking. Most relevant results are those from the study of Rb polymorphism in the Białowieża population (FEDYK 1980), reporting the proportion of X- to Y_1Y_2-bearing metaphases of the second meiotic division (MII) in eleven homozygous shrews. The analysis of 78 MII spreads showed no significant

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deviation from 1 : 1 expectation. Also, the analysis of almost 200 MII spreads from six simple Rb heterozygotes and homozygotes showed that sex chromosome segregation was very close to 1 : 1 (SEARLE 1986b).

ZENZES (1987), who reviewed the studies on the karyotypes of human sperm pointed out that a reliable analysis of segregation of the sex chromosomes requires a large sample size of more than 200 male germ cells. Earlier studies on segregation of sex chromosomes in *Sorex araneus* do not meet this methodological requirement. We have therefore carried out the analysis based on adequate numbers of MII spreads of homozygous males of the common shrew, as well as of the two classes of com-

plex heterozygotes. In the present paper we tested the hypothesis that the presence of complex meiotic configurations distort segregation of sex chromosome in interracial hybrids of the common shrew.

Material and Methods

22 adult male common shrews were collected from following locations: Natać Wielka (coordinate 20º34′E, 53º31′N) – 17 individuals, Zgniłocha (20º34′E, 53º33′N) – 1 individual, Czarny Piec (20º36′E, 53º35′N) – 3 individuals, and Łyna (20º26′E, 53º27′N) – 1 individual. These four locations are distributed within the area where four chromosome races come into the contact: Łęgucki
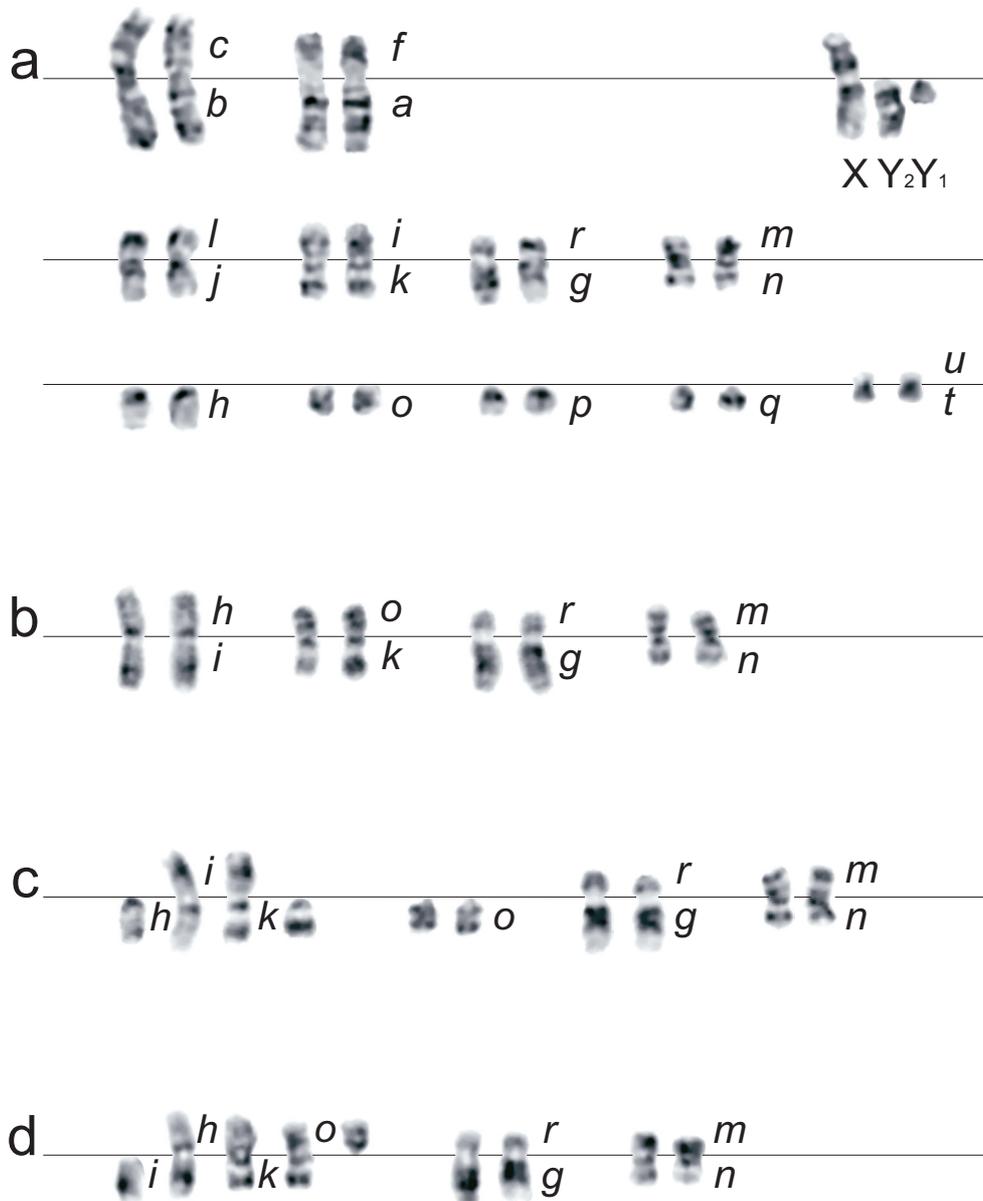

Fig. 1. G-banded karyotypes of selected individuals used in the study: full karyotype of the Popielno (Po) race [a], and partial karyotypes of Guzowy Młyn (Gu) race [b], Gu/Po hybrid which formed CIV complex during meiosis [c], and hybrid between Gu and Łg races [d] which formed CV complex.

Młyn race (Łg), Guzowy Młyn race (Gu), Popielno race (Po) and Drnholec race (Dn). The very coexistence of as many as four chromosome races in such a small area results in a very high frequency of hybrids forming complex configurations during meiosis. It is the only region in Poland, as well as in Europe, where it is possible to catch satisfactory numbers of complex heterozygotes. The shrews were collected during spring of 2002 and 2003.

Mitotic chromosomes were obtained from the spleen by standard methods (FEDYK 1980). G-banding of chromosomes was obtained by staining with Giemsa stain after treatment with trypsin, according to the SEABRIGHT (1971) method. Meiotic preparations were made by EVANS *et al*. (1964) method, as modified by SEARLE (1986b). In order to obtain sufficient numbers of cells in metaphase II stage (MII), the method was further modified by prolonged exposure to Colcemid. Six hours prior to killing the animals were intraperitoneally injected with 0.002 mg aqueous solution of Colcemid per g body mass. Meiotic preparations were made from the left testes. The right testes were preserved in Bouin fixative for later histological examination.

The karyotypes of shrews were determined on the basis of G-banding, which allows one to discriminate individual chromosome arms. According to the standard terminology for *S. araneus*, individual chromosome arms are labelled by lower case letters of the Latin alphabet (SEARLE *et al*. 1991).

Meiotic preparations were conventionally stained using Giemsa stain. In *S. araneus* it is easy to discriminate between MII spreads with an X chromosome and spreads with the Y_1 and Y_2 chromosomes. The X chromosome is almost as large as the two largest pairs of autosomes (*bc* and *af*). Thus MII spreads with an X chromosome contain 3 large metacentrics, whereas spreads with the Y_1 and Y_2 chromosomes contain only two large metacentrics (Fig. 2). In some cases one of the two arms of the X chromosome (the original X chromosome) is heteropycnotic (Fig. 2a), as shown earlier by SEARLE (1986b) and MERCER *et al*. (1991).

To test the reliability of our method of chromosome recognition the counts of MII for two males (Nos. 1 and 15 in Table 1) were scored independ-
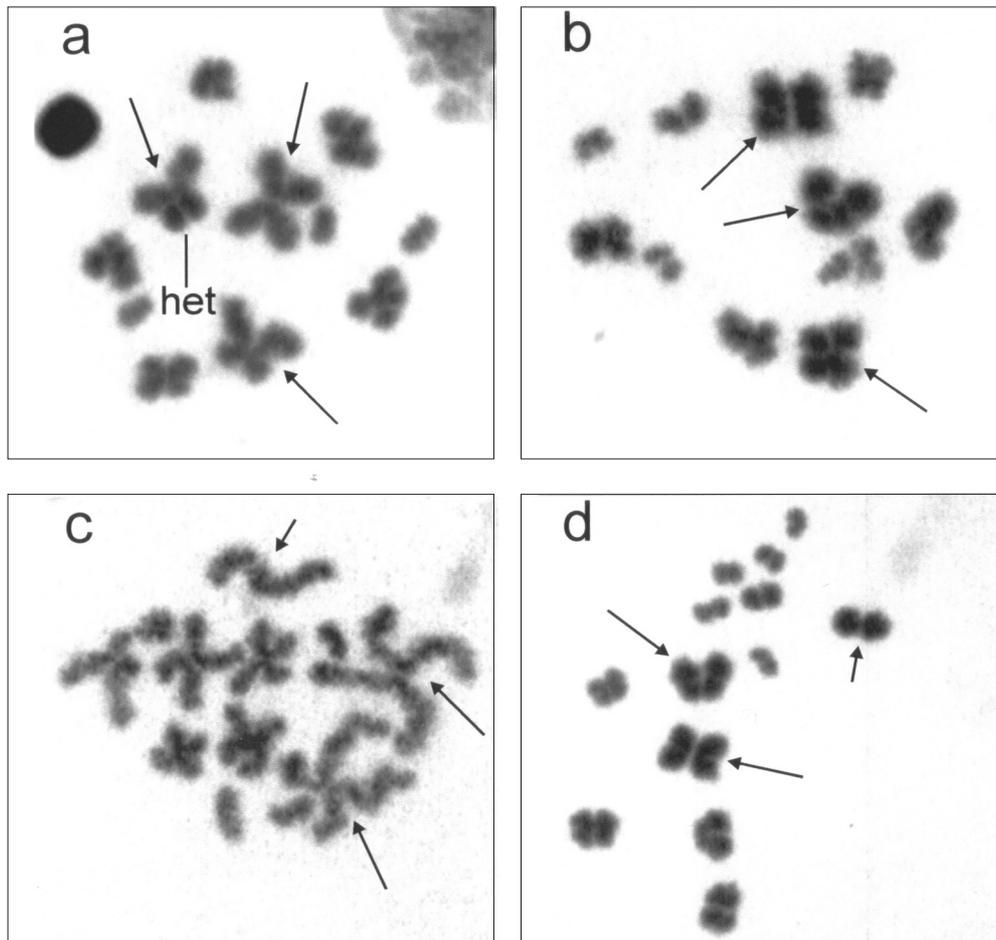

Fig. 2. Metaphase II (MII) spreads. X-bearing MII spreads with N = 11 [a] and N = 12 [b]. Y_1Y_2-bearing MII spreads with N = 12 [c] and N = 13 [d]. het – heteropycnotic arm of X chromosome (true X); big arrows – biggest metacentric chromosomes (*bc*, *af* and X); small arrows – Y_2 chromosomes.

ently by two observers (U. B. and S. F.). The tests showed that the data obtained by the two observers were homogenous within each individual; $\chi^2_{(1)}$ values were 0.243 (P>0.7) and 1.431 (P>0.2), respectively.

Results

Karyotypes of shrews examined

In *Sorex araneus* the invariant part of the karyotype consists of the sex chromosomes (XX in females; XY_1Y_2 in males) and four pairs of autosomes: *bc*, *af*, *jl* and *tu*. The remaining autosomal arms (*g, h, i, k, m, n, o, p, q, r*) form the variable part of the karyotype and either are fused, forming metacentric autosomes, or remain as uni-armed autosomes. Different arm combinations of the metacentrics are characteristic of chromosome races of the common shrew.

The karyotypes of the shrews examined are shown in Table 1. There were four shrews of the Po race (karyotype: 2N = 25, XY_1Y_2, *bc af, jl, ik, gr, mn, h, o, p, q, ut*; Fig. 1a). Two shrews belonged to the Gu race with 2N = 23, as indicated by the diagnostic chromosomes *hi, ko, gr, mn* (Fig. 1b). Two other races are also present in the study area: the Łg race – *hk, io, gr, mn*, and the Dn race – *hi, ko, gm, nr*. Although they were not represented in the sample of individuals studied, we found diagnostic chromosomes for those races in the karyotypes of hybrids.

The remaining 16 shrews were interracial hybrids. The most numerous class (n = 9) were hybrids between the Gu and Po races. Two Gu/Po hybrids had 25 chromosomes. At meiosis these hybrids form complexes of four chromosomes (CIV) in the configuration *h/hi/ik/k* (Fig. 1c). The remaining 7 Gu/Po hybrids had 24 chromosomes, which form CV complexes in the configuration *h/hi/ik/ko/o*. Four Gu/Łg hybrids with 24 chromosomes formed CV complexes in the configuration *i/ih/hk/ko/o* (Fig. 1d).

One shrew was a hybrid between the Dn and Po races, with 2N = 25. Diagnostic chromosomes for the Dn and Po races are expected to give rise of two independently segregating complexes. The first complex is a chain of four elements (CIV) in configuration *h/hi/ik/k*, the second one has form a ring of four elements (RIV) in the configuration *rg/gm/mn/nr*.

One individual shrew was a Gu/Dn hybrid with 24 chromosomes expected to form a CV complex with the configuration *g/gm/mn/nr/r*. Finally, one shrew was a Dn/Po hybrid (2N = 24). In this case

two meiotic complexes in the configurations *h/hi/ik/ko/o* (CV) and *rg/gm/mn/nr* (RIV) were expected (Table 1).

Meiotic segregation

In all homozygous shrews studied sex chromosomes segregated regularly. The number of MII cells bearing X- to Y_1Y_2 chromosomes showed only a slight deviation from 1 : 1 ratio (Table 1). On average, among 1075 MII spreads of homozygous shrews examined, the proportion of X to Y_1Y_2 spermatocytes was close to expectation (51% : 49%) (Table 1). The Gu and Po races formed a homogeneous sample. They did not differ significantly with respect to sex chromosome segregation ($\chi^2_{(1)} = 0.268$; P>0.6).

We also found random (1 : 1) segregation of sex chromosomes in CIV and CIV + RIV hybrids (Table 1; $\chi^2_{(1)} = 0.369$; P>0.5). However, in the case of hybrids forming a CV meiotic configuration, the interpretation of results is complicated due to significant differences between individuals. In only four out of 13 individuals was the proportion of X- to Y_1Y_2-bearing MII spreads in accordance with the 1 : 1 ratio. Those were two Gu/Po and two Gu/Łg hybrids (Table 1). In nine remaining CV hybrids we found preferential segregation in favour of the X chromosome. The most severe deviation from the 1 : 1 ratio was noted in individual 13 (a Gu/Łg hybrid) and in shrews 18, 19 and 20 (Gu/Po hybrids; Table 1). There is no heterogeneity between Gu/Łg and Gu/Po hybrids with respect to sex chromosome segregation ($\chi^2_{(1)} = 0.506$; P>0.5). Overall, segregation of sex chromosomes in hybrids forming autosomal pentavalents was biased in favour of the X chromosome. In 1650 out of all 2858 spreads scored the X was present, which was statistically highly significant ($\chi^2_{(1)}=68.357$; P<<0.001) (Table 1).

Analysis of diplotene/diakinesis spreads

Our finding that the occurrence of meiotic drive of the sex chromosomes was exclusively restricted to the hybrids forming meiotic pentavalents suggest that segregation disturbances are due to some sort of association between the chromosomes involved in CV complex and sex chromosomes (most likely Y_1). The aim of our analysis of diplotene/diakinesis spreads was therefore to look for such associations.

In homozygous males contacts between the sex trivalent and autosomal bivalents were restricted to sporadic cases, mostly large bivalents. In hybrids we did not observe any association between the sex trivalent and the chain of five chromo-

Table 1

Segregation of sex chromosomes in individuals with homozygous and heterozygous karyotypes

Karyotypic category	Shrew no.	Meiotic configuration	Variable part of karyotype	2N	Race affiliation	Counts of MII spreads with		Total number of scored spreads	$\chi^2_{(1)}$	Significance level
						X	Y_1Y_2			
Homozygotes	1	normal bivalents	*hi, ko, gr, mn, p, q*	23	Gu	65 (50.8%)	63 (49.2%)	128	0.031	P>0.8
	2	normal bivalents	*hi, ko, gr, mn, p, q*	23	Gu	73 (48.7%)	77 (51.3%)	150	0.107	P>0.7
	3	normal bivalents	*ki, gr, mn, h, o, p, q*	25	Po	75 (52.8%)	67 (47.2%)	142	0.451	P>0.5
	4	normal bivalents	*ki, gr, mn, h, o, p, q*	25	Po	126 (51.2%)	120 (48.8%)	246	0.146	P>0.7
	5	normal bivalents	*ki, gr, mn, h, o, p, q*	25	Po	126 (50.6%)	123 (49.4%)	249	0.036	P>0.8
	6	normal bivalents	*ki, gr, mn, h, o, p, q*	25	Po	83 (51.9%)	77 (48.1%)	160	0.225	P>0.6
	Totals					548 (51.0%)	527 (49.0%)	1075	0.410	P>0.5
	7	CIV	*h/hi/ik/k, gr, mn, o, p, q*	25	Gu/Po	94 (52.2%)	86 (47.8%)	180	0.355	P>0.5
	8	CIV	*h/hi/ik/k, gr, mn, o, p, q*	25	Gu/Po	97 (52.1%)	89 (47.9%)	186	0.344	P>0.5
	9	CIV + RIV	*h/hi/ik/k, rg/gm/mn/nr, o, p, q*	25	Dn/Po	95 (49.5%)	97 (50.5%)	192	0.021	P>0.8
	Totals					286 (51.3%)	272 (48.7%)	558	0.351	P>0.5
Complex heterozygotes	10	CV	*i/ih/hk/ko/o, gr, mn, p, q*	24	Gu/Lg	137 (48.4%)	146 (51.6%)	283	0.286	P>0.6
	11	CV	*i/ih/hk/ko/o, gr, mn, p, q*	24	Gu/Lg	42 (57.5%)	31 (42.5%)	73	1.657	P>0.1
	12	CV	*i/ih/hk/ko/o, gr, mn, p, q*	24	Gu/Lg	89 (59.3%)	61 (40.7%)	150	5.227	P<0.025
	13	CV	*i/ih/hk/ko/o, gr, mn, p, q*	24	Gu/Lg	163 (63.4%)	94 (36.6%)	257	18.525	P<<0.001
	14	CV	*h/hi/ik/ko/o, gr, mn, p, q*	24	Gu/Po	84 (58.3%)	60 (41.7%)	144	4.000	P<0.025
	15	CV	*h/hi/ik/ko/o, gr, mn, p, q*	24	Gu/Po	189 (55.6%)	151 (44.4%)	340	4.247	P<0.025
	16	CV	*h/hi/ik/ko/o, gr, mn, p, q*	24	Gu/Po	122 (55.5%)	98 (44.5%)	220	2.618	P>0.1
	17	CV	*h/hi/ik/ko/o, gr, mn, p, q*	24	Gu/Po	70 (53.8%)	60 (46.2%)	130	0.769	P>0.3
	18	CV	*h/hi/ik/ko/o, gr, mn, p, q*	24	Gu/Po	132 (60.5%)	86 (39.5%)	218	9.706	P<0.005
	19	CV	*h/hi/ik/ko/o, gr, mn, p, q*	24	Gu/Po	195 (59.3%)	134 (40.7%)	329	11.310	P<0.001
	20	CV	*h/hi/ik/ko/o, gr, mn, p, q*	24	Gu/Po	99 (64.3%)	55 (35.7%)	154	12.571	P<<0.001
	21	CV	*hi, ko, g/gm/mn/nr/r, p, q*	24	Gu/Dn	189 (56.9%)	143 (43.1%)	332	6.373	P<0.025
	22	CV + RIV	*h/hi/ik/ko/o, rg/gm/mn/nr, p, q*	24	Dn/Po	139 (61.0%)	89 (39.0%)	228	10.965	P<0.001
	Totals					1650 (57.7%)	1208 (42.3%)	2858	68.357	P<<0.001

somes. Occasionally connections between sex trivalents and rings of four elements were observed (Fig. 3c). Associations between the sex trivalent and large size bivalents (*af* or *bc* pair) were much more frequent. Some of the associations looked like the accidental contacts, arising during preparation (Fig. 3b), but genuine connections between the large bivalent and sex chromosomes were also observed (Fig. 3f). However, contacts between chains of five chromosomes and large size bivalents were most frequent (Fig. 3d, e).

Many of the atypical configurations among sex chromosomes (17.8%) were autosomal univalents attached to the sex chromosome trivalents (or even bits of autosomes, as very small pieces of chroma-

tin were also observed in some spreads, Fig. 3d, e, g). The sex chromosome trivalents with a hairpin-like bend on the genuine X-Y$_1$ segment were observed in the CV + RIV hybrid and in two CV hybrids. The chromosome bend occurred in half of the X chromosomes, and was of similar morphology (Fig. 3h, i). Regularity and repeatability of the bends suggest that they were not accidental arrangements of segments of sex trivalents.

The above observations prompted us to hypothesise that the association between sex trivalents and autosomal univalents affected distortion of sex chromosome segregation. We therefore analysed the incidence of univalence in the three karyotypic classes of shrews (Table 2). Generally, a low level
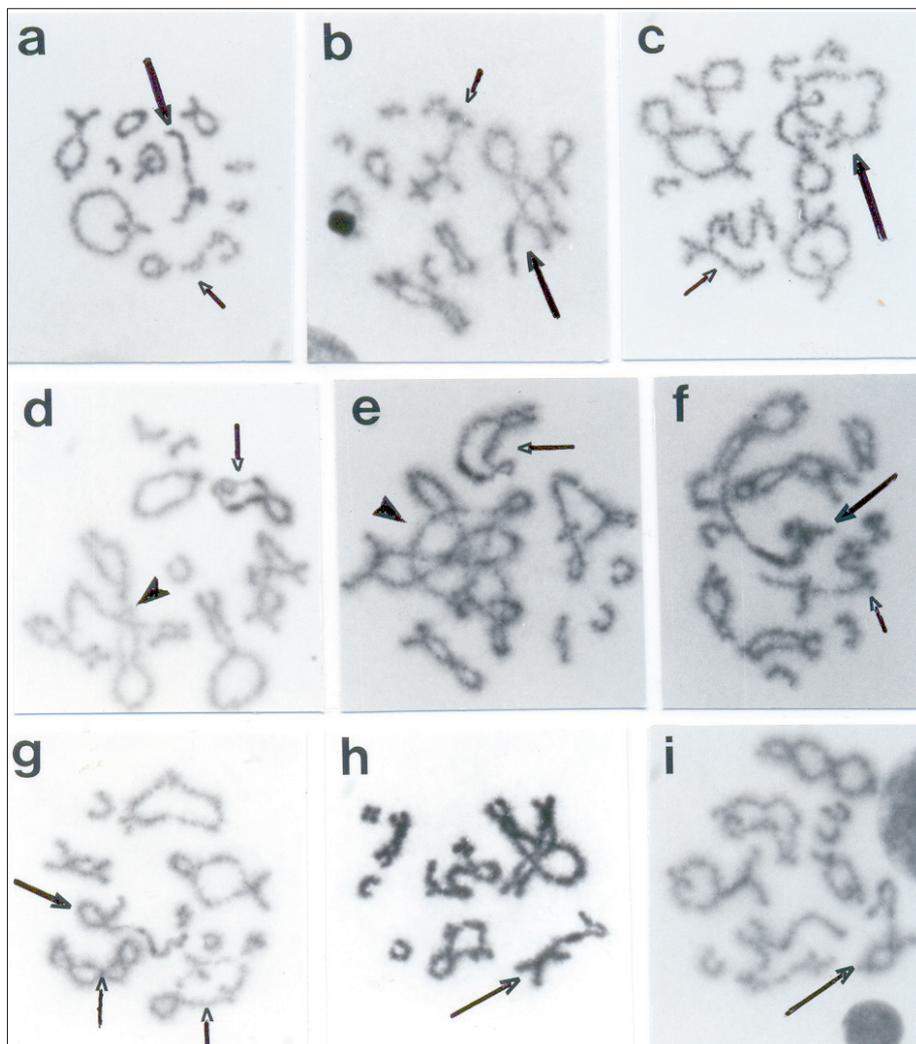

Fig. 3. Late diakinesis/MI spreads of hybrid shrews: a – Gu/Dn hybrid with *g/gm/mn/nr/r* chain (small arrow) and normal sex trivalent (big arrow); b – Gu/Po hybrid with *h/hi/ik/ko/o* complex (small arrow). Note contact between sex trivalent and big bivalent (big arrow); c – Dn/Po hybrid with CV (small arrow) and RIV (big arrow) complexes. Note the contact between sex trivalent and ring of four; d, e – Dn/Po hybrid with CV and RIV complexes. Arrows indicate atypical sex trivalent probably with univalent attached. Note connections between chains and biggest bivalents (arrowheads); f – Gu/Po hybrid with *h/hi/ik/ko/o* complex (small arrow) and sex trivalent associated with big size bivalent (big arrow); g – Dn/Po hybrid with CV and RIV complexes (small arrows) and sex trivalent with autosomal univalent attached (big arrow); h, i – Dn/Po hybrid with CV and RIV complexes. Note that the sex trivalents have hairpin–like bended genuine X-Y$_1$ segments (arrows).

Table 2

Incidence of univalence at diplotene/diakinesis in common shrew

Shrew no.	Meiotic configuration	No. of spreads	The origin of the observed univalent chromosomes			Connection between sex trivalent and univalent
			X/Y$_1$	Autosomal	Unknown	
1	bivalents	358	3	0	4	0
5	bivalents	167	1	0	0	0
	Subtotal	525	4 (0.76%)	0	4 (0.76%)	0
7	CIV	307	5	0	2	0
9	CIV+RIV	251	2	0	0	1
	Subtotal	558	7 (1.25%)	0	2 (0.36%)	1 (0.18%)
10	CV	203	2	1	2	0
12	CV	404	15	3	3	4
13	CV	219	4	1	2	1
15	CV	509	7	5	3	5
17	CV	248	2	2	0	3
22	CV+RIV	324	9	3	2	8
Subtotal		1907	39 (2.04%)	15 (0.79%)	12 (0.63%)	21 (1.10%)
Total		2990	50 (1.67%)	15 (0.50%)	18 (0.60%)	22 (0.74%)

of univalence was observed in spreads from late diplotene/diakinesis (maximum of 2.77%, including all univalents of unknown provenance). The most common was univalence of the Y$_1$ chromosome. It occurred in almost 1% of homozygotes; 1.25% of hybrids which form meiotic complexes of four elements, and in slightly over 2% of CV hybrids. The proportions of univalents of unknown origin was nearly equal in the three classes of shrews (average 0.6%), whereas autosomal univalents were observed exclusively in hybrids which form meiotic pentavalents (0.79%). One can suppose that, at least part (if not all) of the univalents originate from the chains, although the possibility of an origin from bivalents cannot be excluded. Also, the absolute majority (21 out of 22 scored) of the sex trivalent/univalent associations were observed in the class of CV hybrids (Table 2).

Discussion

To date, the data on segregation of sex chromosomes in *Sorex araneus* is very scanty. In the common shrews from the Białowieża population 78 MII spreads from 11 homozygotes were studied (FEDYK 1980). Sex chromosome segregation was very close to 1 : 1 (40 of X-bearing to 38 of Y$_1$Y$_2$-bearing cells). In England, 198 cells from 6 males were scored (SEARLE 1986b). Overall 102 were X-bearing and 96 were Y$_1$Y$_2$-bearing, also very close to a 1 : 1 proportion. Among those six shrews, there were homozygotes and simple Robertsonian heterozygotes, but there was no evidence

for heterogeneity in the ratio of X-bearing to Y$_1$Y$_2$-bearing MII spreads between the samples from different individuals ($\chi^2_{(5)} = 7.45$; P>0.05).

A survey of studies on human sperm karyotyping showed that a significant deviation from 1 : 1 ratio in sex chromosomes segregation can only be demonstrated in large samples of material (ZENZES 1987). Thus, one can conclude that the earlier studies in *S. araneus* give little basis for a credible evaluation of sex chromosome segregation. The main reason for this is the lack of proper techniques for obtaining sufficient number of MII cells. The application of original technique of EVANS *et al.* (1964), which gives satisfactory results in mice, gave insufficient results in shrews (see FEDYK 1980). Modifications introduced by SEARLE (1986b) slightly improved the technique, but still only small numbers of MII spreads were obtained. For example, MERCER *et al.* (1992) managed to analyse only 16 MII spreads from three hybrids, whereas MERCER *et al.* (1991) analysed in total 366 spreads from 20 homo- and heterozygous shrews. Furthermore, NARAIN & FREDGA (1997) failed to obtain any MII spreads. More MII spreads (2050, in total, coming from 27 examined shrews) were analysed in the area of hybridization between the Gu and Łg races (BANASZEK *et al.* 2002). Only with prolonged Colcemid treatment was it possible to obtain well over 100 MII spreads of sufficient quality from a single male of *S. araneus* (Table 1).

In this study we have shown that a considerable meiotic drive in favour of the X chromosomes acts exclusively in complex heterozygotes which form

chains of five autosomes in meiosis. The sex chromosome segregation ratios in homozygotes as well as in hybrids with CIV and CIV + RIV meiotic configurations differed insignificantly from 1 : 1, although an excess of X chromosome was also found (Table 1). It seems that the sex chromosome distortion in hybrids forming meiotic chain configurations and germ cell death has a common basis. An undisturbed course of spermatogenesis results in four times more round spermatids (sd) than primary spermatocytes (sc). Germ cell death can be studied by analysis of the sc/sd ratio. Although homozygotes and simple Rb heterozygotes are characterized by very similar ratios, simple Rb heterozygotes often have slightly lower germ cell death rates than homozygous shrews. The greatest germ cell losses were recorded in complex heterozygotes. Among them slightly higher losses were found in C- than R-hybrids (GARAGNA *et al.* 1989; NARAIN & FREDGA 1997, 1998; BANASZEK *et al.* 2000). These data confirm that the germ cell death depends on the degree of complication of meiotic configurations, although there is no evidence that in CVII hybrids the sc/sd ratio is markedly lower as compared with the hybrids carrying shorter meiotic chains (MERCER *et al.* 1992). Our results suggest that in CV hybrids the mortality of Y_1Y_2-bearing cells is higher than those carrying X chromosome.

There seems that at least two factors affect the magnitude of distortion of sex chromosome segregation, which result in an increased mortality of Y_1Y_2-bearing cells: (a) disturbances in pairing of chromosomes in chain configurations, and (b) interactions between sex chromosomes and chain configurations. The hypothesis concerning correlation between chromosomal abnormality during meiosis and male hybrid sterility has been tested by JOHANNISSON & WINKING (1994) in laboratory reared mice, carrying super-rings and super-chains of 15-18 chromosomes. The total length of unpaired segments of super-complexes was 18% and 32%, for the rings and chains, respectively. MIKLOS (1974) and BURGOYNE & BAKER (1984) suggested that the lack of saturation of pairing sites of meiotic chromosomes leads to impairment of spermatogenesis. Thus the results of JOHANNISSON & WINKING (1994) did not support this supposition. Even the occurrence of long segments of unpaired chromosomal axes in pachytene synaptonemal complexes does not arrest spermatogenesis: mice with super-rings manifested the normal course of germ cell maturation. On the other hand, JOHANNISSON and WINKING (1994) suggest that associations of meiotic super-chains with the proximal part of the X chromosomes, observed in more than 60% of pachytene spreads, may cause the impairment of spermatogenesis and male infertility. In most cases these associations were

formed by X chromosomes and unpaired acrocentrics from the extreme ends of the chains. On the other hand, it can be assumed that the closure of the chromosomes into the ring configuration prevent them associating with sex chromosomes.

It is also likely that the interference between sex chromosomes and CV complexes is the reason of distortion of segregation of the sex chromosomes in the common shrew. It is worth emphasising that, except of fairly short segments positioned very close to centromeres, the quadrivalents of both ring and chain configuration become completely paired in pachytene (NARAIN & FREDGA 1997, 1998). Thus, the associations between chains of four autosomes and sex chromosome trivalents should not form. To date the pachytene chromosomes in the CV shrew hybrids have not been studied. We can therefore only assume that some segments of the pentavalents may remain unpaired. This is supported by the exclusive occurrence of autosomal univalents in the hybrids which form meiotic chain pentavalents (Table 2), although no univalents coming from the complex configurations were found in the previous study, also concerning CV hybrids (BANASZEK *et al.* 2002). However, incomplete pairing of chains and univalence of the autosomes were observed in CVII hybrids of the common shrew (MERCER *et al.* 1992). We can therefore hypothesise that the distortion of sex chromosome segregation was due to interactions between the sex chromosomes and univalents coming from autosomal complexes, which were recorded almost exclusively in CV hybrids (Table 2). The interactions between the sex chromosomes and bits of chromosomes could also occur. NARAIN and FREDGA (1997) observed surprisingly high frequency (58%) of broken ring configurations. Unfortunately, they did not record any contacts between the sex chromosome and bits of autosomes.

The frequency of univalence (Table 2) is too low to serve as an explanation of such a high incidence of sex chromosome meiotic drive (Table 1). However, it appears that the observation of chromosomes in diplotene/diakinesis cells does not allow for a reliable evaluation of an incidence of univalence. This would require the observation of pachytene cells.

The derivation of hairpin-like bends, which were observed in three complex heterozygotes, is not clear. Morphological repeatability of the bend (Fig. 3h, i) suggests that the chromosomes were not arranged by chance. It would be interesting to know whether the bends resulted from a previous association between the sex and autosome meiotic complexes.

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