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Meiotic studies of karyotypically homozygous and heterozygous male common shrews[1]

BY

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Summary.–MERCER S.J., SEARLE J.B. and WALLACE B.M.N., 1991. Meiotic studies of karyotypically homozygous and heterozygous male common shrews. *In*: J. HAUSSER, ed. The cytogenetics of the *Sorex araneus* group and related topicsProceedings of the ISACC's Second International Meeting. *Mém. Soc. vaud. Sc. nat. 19.1*: 33-43.

Over a number of years, we have studied meiosis in male Robertsonian homozygotes and heterozygotes from the vicinity of the hybrid zone between the Oxford and Hermitage karyotypic races of common shrew in southern England. For the heterozygotes, most of the data derive from "simple" heterozygotes which form trivalents at prophase/metaphase I, but some data are also available for "complex" heterozygotes which form chains composed of more than three elements. Our general conclusion is that meiosis proceeds in a remarkably orderly fashion in Robertsonian heterozygotes.

At pachytene in simple Robertsonian heterozygotes, the three chromosomes which form the trivalent pair intimately along their length. Only rarely do the centromeric regions of the acrocentrics pair non-homologously to form a side arm. (By contrast, in the house mouse, such side arms are normal in Robertsonian heterozygotes.)

At diakinesis/metaphase I, regular trivalents can be observed in simple Robertsonian heterozygotes and quadrivalents in double Robertsonian heterozygotes with monobrachial homology. As at pachytene, univalence is unusual.

Chromosome counts at metaphase II indicate that anaphase I nondisjunction frequencies in male simple Robertsonian heterozygotes are no higher than those of Robertsonian homozygotes. Anaphase I nondisjunction leads to a reduction in fitness through production of aneuploid gametes and consequently aneuploid zygotes which are usually inviable. Clearly, male simple Robertsonian heterozygotes are not greatly unfit compared to homozygotes from this cause.

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Résumé.–MERCER S.J., SEARLE J.B. et WALLACE B.M.N., 1991. Etude de la méiose chez des mâles de la musaraigne carrelet à caryotypes homozygotes et hétérozygotes. *In*: J. HAUSSER, dir. The cytogenetics of the *Sorex araneus* group and related topics.Proceedings of the ISACC's Second International Meeting. *Mém. Soc. vaud. Sc. nat. 19.1*: 33-43.

Depuis plusieurs années nous avons étudié la méiose chez des mâles homozygotes et hétérozygotes Robertsoniens provenant du voisinage de la zone d'hybridation entre les races chromosomiques Oxford et Hermitage de la musaraigne carrelet dans le sud de l'Angleterre. En ce qui concerne les hétérozygotes, la plupart des données proviennent d' hétérozygotes "simples" qui forment des trivalents à la prophase/ métaphase I, mais nous avons également obtenu quelques données d'hétérozygotes "complexes" chez lesquels se forment des chaines de plus de trois éléments. Notre conclusion générale est que la méiose procède de façon remarquablement ordonnée chez les hétérozygotes robertsoniens.

Au pachytène, chez les hétérozygotes robertsoniens simples, les trois chromosomes qui forment le trivalent s'apparient étroitement sur toute leur longueur. La région centromérique des acrocentriques ne s'apparie qu'exceptionnellement de façon non homologue pour former un bras latéral. (Par contraste, ces bras latéraux sont la règle chez les hétérozygotes robertsoniens de la souris domestique).

A la diacinèse/métaphase I, des trivalents réguliers peuvent être observés chez les hétérozygotes robertsoniens simples, et des quadrivalents chez les doubles hétérozygotes avec homologie monobrachiale. Comme au pachytène, l'univalence est exceptionnelle.

Les comptages de chromosomes à la métaphase II indiquent que, durant l'anaphase I, la fréquence de non-disjonctions chez les mâles hétérozygotes robertsoniens simples n'est pas plus élevée que chez les homozygotes. Cette non-disjonction réduirait la valeur adaptative de l'individu par production de gamètes aneuploïdes, et par suite de zygotes aneuploïdes en général non viables. Il est donc clair que les mâles hétérozygotes robertsoniens simples ne sont pas désavantagés de façon marquée par rapport aux homozygotes, du moins pour cette raison.

INTRODUCTION

Throughout the range of the common shrew, the species is subdivided on the basis of karyotype as a result of many different Robertsonian fusion mutations. Populations frequently differ in their diploid number and in their complement of metacentric chromosomes, although the *Nombre Fondamental* (NF) remains the same. In Britain, three chromosomal groupings are recognised (SEARLE 1984) and designated as "karyotypic races", each possessing a different combination of Robertsonian fusion products specific to that race. In addition to these race-specific metacentrics, polymorphism for other fusions may give rise to local racial variants.

In southern Britain, the interface between the Oxford and Hermitage karyotypic races forms a complex hybrid zone and region of karyotypic polymorphism approximately 100 km wide (SEARLE 1986a), running from the Thames estuary eastwards to the Severn river valley. Within the vicinity of this zone, a large number of karyotypes may be found, with combinations of

the metacentric *ko*, specific to the Hermitage race, and *kq* and *no*, specific to the Oxford race (nomenclature of HALKKA *et al.* 1974, modified by FREDGA and NAWRIN 1977). In addition, the local variant of the Oxford race possesses the metacentric *pr*, and the acrocentrics *n*, *q*, *p* and *r* are present on the Hermitage side. The zone is further complicated by the presence of the acrocentrics *k* and *o*.

Two different types of Robertsonian heterozygote are recognised. The "simple heterozygote" possesses one metacentric and two acrocentric homologues for one or more arm combinations. Synapsis during prophase I of meiosis is expected to result in the formation of a trivalent for each heterozygous arm combination. In some cases, however, an animal may possess two or more metacentrics that share only one arm in common (for example *ko* and *kq*), a monobrachial homology. In such a situation, synapsis is expected to result in the formation of a multivalent of four or more elements during prophase I of meiosis, and this type of individual is termed a "complex heterozygote". It should be noted that the common shrew has an XX/XY_1Y_2 sex chromosome constitution, and thus males are expected to form a "sex trivalent" at prophase I of meiosis in addition to any autosomal multivalents.

Several studies of Robertsonian heterozygotes in mouse and man indicate that heterozygosity impairs fertility (CHANDLEY 1984, GROPP and WINKING 1981) and several mechanisms have been suggested to explain this. Firstly, the accuracy of homologous synapsis during meiotic prophase I is thought to affect the number of germ cells surviving to produce gametes, and this germ cell death may reduce fertility and gonad size. Secondly, nondisjunction at anaphase I may be increased and lead to the formation of unbalanced gametes, and postzygotic loss.

Although the mechanism is in debate, it would appear that in mammals a relationship exists between the degree of aberration at the time of pachytene pairing of homologues and the extent of germ cell death. Two mechanisms have been proposed to explain this relationship. The first is that association between unpaired regions of a heteromorphic autosomal configuration and the sex bivalent in the male (or in the case of the common shrew, the sex trivalent) interferes with the obligatory inactivation of the X chromosome and results in germ cell death and sterility or subfertility (FOREJT and GREGOROVA 1977). Whilst a good case can be made for this in many instances, it cannot explain subfertility in cases where no such association is observed, and is completely inapplicable to the female, where more germ cell death may also occur in karyotypic heterozygotes than in homozygotes (MITTWOCH *et al.* 1981).

The observation that unpaired regions are found at pachytene in heterozygotes for chromosomal rearrangements gives rise to the second mechanism. MIKLOS (1974) proposed the existence of sites scattered throughout the chromosomes, which must be saturated through homologous pairing. Failure to do so will initiate a mechanism resulting in death of the cell. The time taken for cell death to occur would be proportional to the number of unsaturated sites, thus explaining the differences observed in

severity and timing in similar chromosomal rearrangements. This mechanism has the advantage over that of FOREJT in that it is equally applicable to both sexes. BURGOYNE and BAKER (1984) further discuss the applicability of the MIKLOS model. The fact remains that in mammals, chromosomal rearrangements generally have more severe consequences for males than for females in respect to germ cell death, and it would therefore seem reasonable to assume that both the FOREJT and the MIKLOS models operate in many cases. In the male shrew, we should therefore look both for an association between autosomal multivalents and the sex trivalent, and also for accuracy of pairing within the multivalent.

The pattern of chromosome pairing at pachytene may also be relevant to the incidence of anaphase I nondisjunction in Robertsonian heterozygous common shrews. Thus, any minor inappropriate gene expression due to incomplete pairing, rather than being cell lethal, could result in disruption of the segregation process. Also, univalence at the pachytene stage (again, if not cell lethal due to inappropriate gene expression) could lead to random segregation at anaphase I. Alternatively, errors may not arise until orientation on the spindle, with autosomal multivalents more prone to malorientation than a bivalent, merely because the spindle is better adapted to handle bivalents, but not the rarer multivalent configurations.

The current study combines the data from a number of recent studies of homozygotes and the different classes of heterozygote. It aims to help determine the extent of disruption of fertility in heterozygotes, and to help understand the evolution of the Oxford–Hermitage hybrid zone.

MATERIAL AND METHODS

All animals studied were males collected from the vicinity of the Oxford–Hermitage hybrid zone south of Oxford, England, with the exception of two individuals born in captivity from a wild caught pregnant mother, and subsequently matured under conditions of long photoperiod (S.J. MERCER and J.B. SEARLE, in preparation). All animals were killed by cervical dislocation, and mitotic karyotypes were prepared from bone marrow using the method of SEARLE (1986a). These preparations were subsequently G-banded using a combined Trypsin/ASG method (SEABRIGHT 1972, SUMNER *et al.* 1971, SEARLE 1986a), and karyotyped under oil immersion.

Air-dried preparations of testis were made by the method of EVANS *et al.* (1964), as modified by SEARLE (1986b). Anomalies were scored at diakinesis/metaphase I and anaphase I nondisjunction was estimated from metaphase II counts. Spreads were analysed at a magnification of 400X, with verification under oil at 1000X.

Pachytene data were gathered from surface spread material (WALLACE and SEARLE 1990), silver stained and examined under the light microscope.

RESULTS

Pachytene

WALLACE and SEARLE (1990) gathered data of 252 pachytene spreads from ten animals, and conclude that the pairing process at pachytene is orderly both in homozygotes and simple heterozygotes. No complex heterozygotes were available for study.

General features of the pachytene cell were examined, and the locations of four nucleolar organising regions determined (Fig. 1). These were located distally on the arms *o*, *q*, *t*, and *u*, in accordance with silver staining (OLERT and SCHMID 1978, HALKKA and SÖDERLUND 1987), and the location of secondary constrictions (SEARLE 1983), in the mitotic karyotype. Although centromeres were frequently not visible, bivalents were identified on the basis of total length. The sex trivalent paired "straight through" with no discernible side arm, and no visible distinction between the autosomal and gonosomal arms (Fig. 1). The unpaired region of the sex trivalent was frequently distinguishable, due to a hooked or wavy appearance, and the presence of excrescences (Fig. 1).

In simple heterozygotes, the autosomal trivalent at pachytene was found to pair "straight through" in the majority of cases, with side arms being present in only 36% of trivalents. In some of these (7% of trivalents) the arms were unpaired, with a minority (1% of trivalents) in the rare *trans* configuration (MOSES *et al.* 1979). Other abnormalities were also rare; association between autosomal trivalents and the sex trivalent was estimated at between 2.8 and 7.5%. Univalence was estimated as only 4.4%, and no difference was detectable in this frequency between homozygous and heterozygous animals.

Diakinesis/Metaphase I

SEARLE (1986b) presents data on diakinesis metaphase I for a total of 40 animals (16 Robertsonian homozygotes, 21 simple and 3 complex heterozygotes). A mean of 22.8 chiasmata were visible per spread, with some indication of differences in chiasma number between chromosomal race as well as between homozygotes and heterozygotes. The number of chiasmata per bivalent appears to positively correlate with length, with those arms commonly involved in Robertsonian fusions (*g* to *r*) tending to have one chiasma each, thus acrocentric bivalents usually have one chiasma.

The sex trivalent is clearly visible at this stage (Fig. 1), with the Y_1 and one arm of the X (the "true-X" segment) often distinctly heteropycnotic. The Y_1 appears to be terminally attached, and the attachment is scored as a single chiasma, with between one and three chiasmata joining the X and the Y_2.

Chain trivalents and quadrivalents respectively were observed in the simple and complex heterozygotes examined. These multivalents usually averaged one chiasma per chromosome arm, in either a distal or interstitial position.

The incidence of univalence scored at diakinesis/metaphase I may be calculated for homozygotes and for both categories of heterozygotes (table 1), and the sum total univalence is found to be 4.5%. Although the frequency for simple heterozygotes (6.6%) is higher than that for homozygotes (2.5%), univalence in the complex heterozygotes is very low (0.7%), possibly due to the small sample of animals available for study. Much of the univalence in simple heterozygotes can be accounted for by separation of the X and Y_1 chromosomes.

Comparison between the degree of univalence in single, double, and triple simple Robertsonian heterozygotes (*i.e.* individuals heterozygous for 1, 2, and 3 arm combinations with no complications of monobrachial homology) also indicates that the rise in univalence correlates with the number of trivalents present in the cell (table 2). Again, the increased univalence is primarily due to the presence of a univalent Y_1.

Table 1.–Univalence at diakinesis/metaphase I in individuals of different karyotype.

	No. Animals	No. Spreads	Univalence			
			X/Y_1	chain	other	unknown
Homozygote[1]	16	800	15	-	4	1
Simple Het.	21	1050	32	21	5	11
Complex Het.	3	150	1	0	0	0

[1]Includes six individuals not collected from the Oxford - Hermitage karyotypic hybrid zone.

Table 2.–Univalence in single, double, and triple simple heterozygotes at diakinesis/ metaphase I.

	No. Animals	No. Spreads	Univalence			
			X/Y_1	trivalent	other	total
Single	9	450	2.2-2.9%	1.6-2.2%	0.4-1.1%	4.9%
Double	5	250	4.4-5.2%	1.6-2.4%	0.4-1.2%	7.2%
Triple	2	100	4.0%	3.0%	0.0%	7.0%

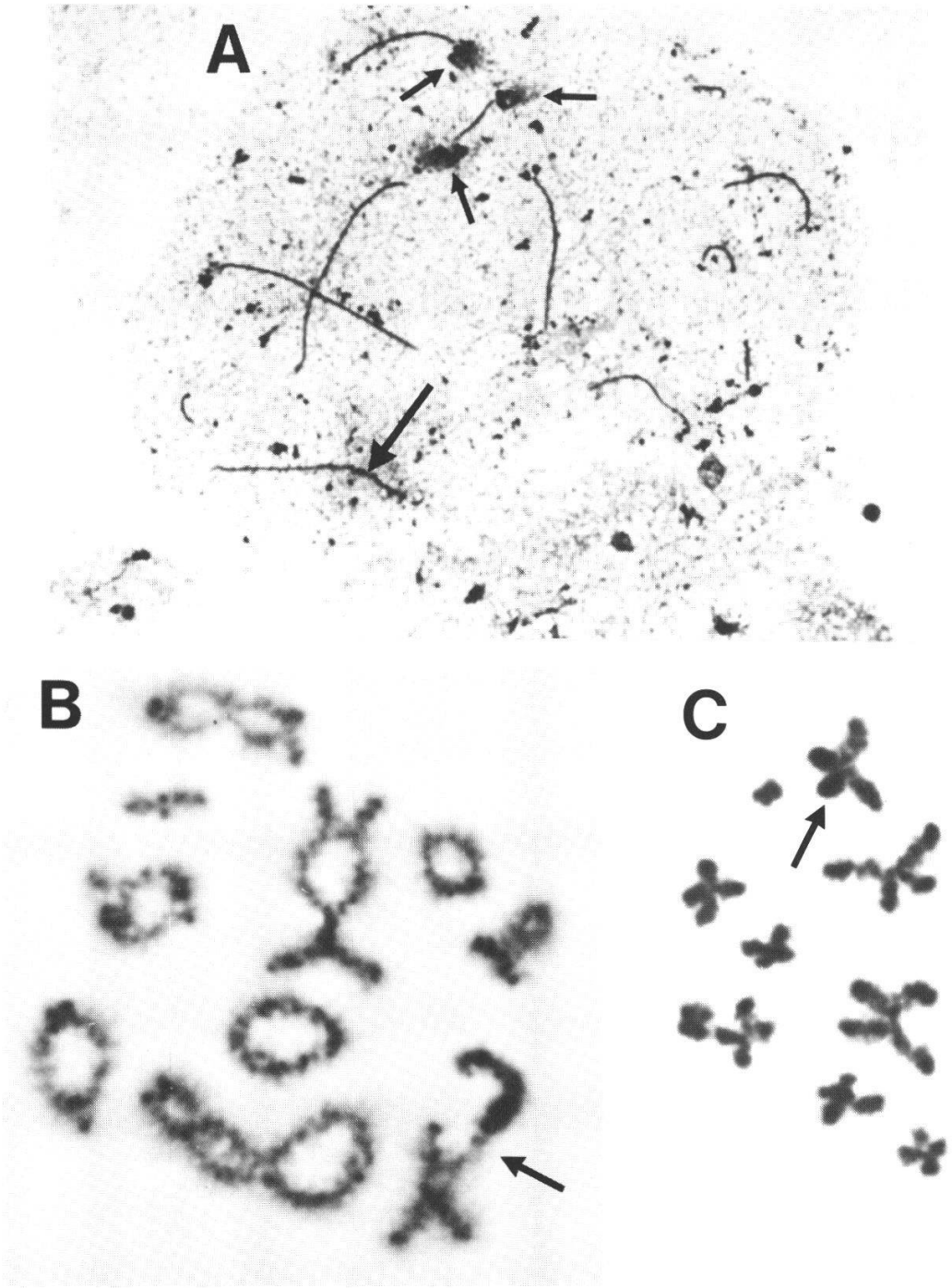

Figure 1. a.–Pachytene spread of a Hermitage race individual (2n=25, homozygous metacentric for arm combinations *jl* and *ko*, homozygous acrocentric for arms *n*, *p*, *q* and *r*) after silver staining. Note nucleolar material associated with chromosome arms *t*, *u* and *o* (short arrows), and excrescences around the unpaired region of the sex trivalent (long arrow).

b.–Diakinesis spread of an Aberdeen race individual (2n=21, homozygous metacentric for arm combinations *jl*, *ko*, *np* and *qr*). Note sex trivalent (arrow).

c.–Metaphase II spread of an Oxford race individual in which arm combinations *jl*, *kq*, *no* and *pr* are all present in fully metacentric form. The X chromosome is marked by an arrow.

Metaphase II

At metaphase II, all elements appear diffuse, with chromatids frequently separated. One arm of the X (the "true X" segment) or the Y_1 frequently appears heteropycnotic in X or Y bearing spreads respectively (Fig. 1). Anaphase I nondisjunction rates can be calculated from the incidence of hyperploidy (table 3).

With a total dataset of 20 animals and 366 metaphase spreads, the incidence of nondisjunction is calculated as 2.3% for homozygotes, 2.1% for single simple Robertsonian heterozygotes, and 0% for double simple heterozygotes. Therefore heterozygosity causes no detectable elevation in the rate of anaphase I nondisjunction in these animals.

Table 3.–Chromosomal counts at metaphase II in individuals of different karyotype.

	No. Animals	No. Spreads	No. Elements					Nondisjunction
			<18	18	19	20	21	
Homozygotes[1]	8	88	0	2	13	72	1	2.3%
Single simple heterozygotes[2]	9	189	0	6	19	162	2	2.1%
Double simple heterozygotes[3]	3	89	1	2	3	83	0	0%

[1] Includes one animal bred in captivity (A2111), and one animal from the Aberdeen race (2121). The complete dataset for homozygotes, given in the form (n=18, 19, 20, 21) is: 2092 (0, 0, 3, 0) 2093 (0, 1, 11, 0) 2094 (0, 0, 10, 0) A2111 (2, 3, 2, 0) 2121 (0, 2, 11, 0) 2395 (0, 0, 3, 0) 2417 (0, 0, 1, 0) 2420 (0, 7, 31, 1).

[2] Includes one animal from the Hermitage race, two from the Aberdeen race (one bred in captivity), and three Oxford race animals not from the region of the Oxford - Hermitage hybrid zone. In addition to the data of Searle (1986b) new data are: 2065 (0, 2, 2, 0) 2076 (1, 5, 21, 1) 2077 (1, 0, 16, 0) 2091 (1, 1, 16, 0) B2118 (0, 0, 1, 0).

[3] Data of Searle (1986b), plus 2079 (1, 2, 9, 0).

DISCUSSION

It is clear that although substantial variation was found between individual common shrews, meiosis in homozygous and simple heterozygous males is orderly, with only a very low level of irregularity. Pairing at pachytene appears to be precise, with nonhomologous pairing and the formation of side arms rare (side arms are very small if present). Association between the sex trivalent and autosomal trivalents was uncommon, and can probably be

explained as random orientation of synaptonemal complexes during preparation. The incidence of univalence at pachytene is very low, and agrees closely with the overall level observed at diakinesis/metaphase I.

At diakinesis/metaphase I, however, there is an indication that Y_1 univalence, albeit rare, increases with heterozygosity. Given this general regularity in chromosome behaviour in male simple heterozygotes, it is not surprising that they show no increase in anaphase I nondisjunction over homozygotes. Nor is there any substantial increase in the incidence of germ cell death (GARAGNA *et al.* 1989, WALLACE *et al.* in press), as may be predicted from both the FOREJT and MIKLOS models.

For the complex heterozygous males from the Oxford–Hermitage hybrid zone, only diakinesis/metaphase I data are available. The individuals examined formed chain quadrivalents with little irregularity. GARAGNA *et al.* (1989) found that spermatogenesis proceeds reasonably well in these individuals, although there appear to be indications of a greater degree of germ cell death than in male homozygotes or simple heterozygotes. The same may be said for male laboratory-bred hybrids between the Oxford and Aberdeen karyotypic races (MERCER, WALLACE and SEARLE in preparation), which formed a regular chain VII configuration at prophase I (*r - rp - pn - no - ok - kq - q*). In these individuals, abnormalities were observed at pachytene and there may be a higher frequency of anaphase I nondisjunction than in homozygous or simple heterozygous males.

It has been assumed that the maintenance of the Oxford–Hermitage hybrid zone, and other karyotypic hybrid zones like it, is due to some mechanism of heterozygous disadvantage. In the case of a zone separating two races of shrew differing in Robertsonian metacentrics, the assumption is that the unfitness of the heterozygotes is attributable to meiotic irregularity arising from Robertsonian heterozygosity. If this is true, then our data suggest that hybrid unfitness must either be attributed to heterozygous females (but see SEARLE 1990), or complex heterozygous males. There is no evidence that males that are simple Robertsonian heterozygotes suffer reduced fitness relative to homozygotes.

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NOTE IN PROOF

Common shrews that are karyotypic homozygotes and simple Robertsonian heterozygotes have recently been studied at pachytene under the electron microscope (FREDGA and ASHLEY 1990, BORODIN 1991), affording greater resolution than we could obtain at the light microscopic level. These EM studies show that instead of end-to-end pairing between the X and Y_1 chromosomes, as we suggested (see WALLACE and SEARLE 1990), the Y_1 chromosome becomes paired with the X along its whole length. We have now been able to see the same phenomenon under the light microscope (B.M.N. Wallace personal observation).

BORODIN (1991) examined autosomal trivalents in simple Robertsonian heterozygotes and notes that these configurations are fully paired throughout pachytene; this accords well with our results (see WALLACE and SEARLE 1990). However BORODIN (1991) found that the pachytene trivalents in Siberian shrews have a substantial side-arm due to extensive non-homologous pairing between the centromeric regions of the acrocentrics. This contrasts strongly with trivalents in British shrews which usually have no side-arms (see WALLACE and SEARLE 1990). It is most interesting that there should be such differences in morphology of the trivalent between Robertsonian heterozygotes from different geographical regions (and different inter-racial hybrid zones).

We are most grateful to Karl Fredga and Pavel Borodin for discussing these issues.

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