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Meiotic Disjunction and Embryonic Lethality in Sex-linked Double-translocation Heterozygous Males of the Onion Fly, *Hylemya antiqua* (Meigen)

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Summary. The frequencies of disjunction types in double-translocation heterozygous males ($2^6 2^Y 6^2 6XY^2$) in *Hylemya antiqua* have been established in MII cells and eggs of testcrosses.

Several disjunction types occurred but four predominated. A correlation was found between the frequencies of the disjunction types and the relative position of the centromeres. The frequency of numerical non-disjunction (NND) was 4%. Differences in frequency of NND between sex-linked and autosomal translocations of *H. antiqua* are discussed. A good correspondence between the frequencies of unbalanced karyotypes, and embryonic and larval mortality was found. The total genetic load which can be induced by the T14/T61 males is estimated to be 60-65%. Some duplication/deficiency karyotypes appeared to be viable in pupal and even adult stages. In $2^6 2^6 2^Y 6^2 6^2 X$ males a regular coorientation between 2^Y and X was observed, in spite of non-homologous centromeres and a complicated synapsis of 2^Y. Application possibilities of the present material for genetic control of *H. antiqua* are discussed.

Key words: *Hylemya antiqua* – Double-translocation heterozygotes – Disjunction types – Genetic control

Introduction

In several insect species double-translocation heterozygotes have been produced for genetic insect control purposes (reviewed by Robinson 1976; Cochran and Ross 1977; Petersen et al. 1977; Suguna et al. 1977; Terwedow et al. 1977). Attention has been paid mainly to the genetic load which can be induced. However, the current knowledge about meiotic disjunction of such complex translocation multivalents is limited. Difficulties in discriminating the separate chromosomes and inaccessibility of some insect species for cytogenetic investigations are the main reasons. In the onion fly (*Hylemya antiqua*) the frequencies of the disjunction types of translocation multivalents can be estimated by metaphase II classifications or by analysing eggs (embryos) of testcrosses (van Heemert 1974 a, b). An advantage of eggs is that somatic pairing makes it possible to discriminate, in many cases, between translocated and standard chromosomes of about equal length.

The present paper deals with the segregation types of double-translocation heterozygous T14/T61 males. These males were obtained by crossing females homozygous for an autosomal translocation (T14/T14) with males heterozygous for a Y-linked translocation (T61/+). The normal chromosomal complement of *H. antiqua* comprises 5 autosomal pairs and sex determination is either XX(♀)/XY_1(♂) or XX(♀)/XXY_2(♂) (Vosselman 1978). The breakpoints of the Y-linked translocation T61 are located in the short arm of autosome 2 and in the long arm of the acrocentric Y_1 chromosome (Fig. 1), both in the vicinity of the centromere (van Heemert and Vosselman 1980). Chromosome Y_1 will be further indicated as Y and the translocated Y_1 chromosome as Y^2. In MI cells of the T61/+ males a chain-of-four with X and Y^2 in terminal positions was generally observed. This was attributed to an earlier disjoining of the centromeric regions of X and Y^2. Since the segregation of the translocation multivalent was predominately alternate, the fertility of the T61/+ translocation heterozygotes was hardly reduced. Translocation T14 concerns a rearrangement between the long arms of the autosomes 2 and 6, with proximally located breakpoints. The orientation of the translocation multivalent (ring quadrivalents) in T14/+ heterozygous males was alternate or adjacent I, in a ratio of 7:3. Other orientations were not observed. Individuals homozygous for translocation T14 showed normal fertility (Vosselman 1980).

Recently Baker et al. (1978), Curtis (1978) and Sea-

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wright et al. (1978) have emphasized the significance of genetic sexing systems for genetic insect control. In *H. antiqua* it will also be attempted to develop such a sexing system in order to reduce costs of mass rearing for the sterile insect release method (van Heemert and Vosselman 1980). In this report it will be demonstrated, that the double-translocation heterozygous males T14/T61 are potentially suitable for the development of a genetic sexing system.

Materials and Methods

Translocations T14 and T61 have previously been induced in sperm by irradiation with X-rays and fast neutrons respectively, in both cases with a dose of 0.2 Gy (200 rad). By crossing T14-homozygous females ($2^6 2^6 6^2 6^2$ XX) with T61-heterozygous males ($2\ 2^Y\ 6\ 6XY^2$) a male offspring consisting of exclusively double-heterozygotes T14/T61 ($2^6 2^Y 6^2 6$ XY^2) and some duplication/deficiency karyotypes were obtained. Since in both translocations chromosome 2 is involved and males are achiasmate, the only balanced gametes which are formed by the double-heterozygotes are $2^6 6^2$ X and 2^Y 6 Y^2. Consequently a 'pure breeding' stock of T14-homozygous females and T14/T61 double-heterozygous males could be produced by crossing the double-heterozygous males with the T14-homozygous females. The flies with duplication/deficiency karyotypes did not reproduce. The rearing methods and the cytological techniques used for larvae and adults were reported earlier (Vosselman 1978). Egg-hatch reduction was determined after incubation of the eggs at 25°C for three days. The dead embryos could be recognized by a brown colour. Unfertilized eggs (white colour) have been excluded from the egg-hatch calculations. For the karyotype analysis of embryos, eggs of 14-20 hours incubation at 20°C were used. After careful removal of the chorion and the vitelline membrane in a drop of 2% lacto acetic orcein (LAO), the embryo was divided into small pieces, stained for 15-45 minutes in this drop and subsequently squashed in 45% acetic acid. Photographs were made with a Zeiss photomicroscope on an Agfa-Ortho 25 professional film (12 DIN).

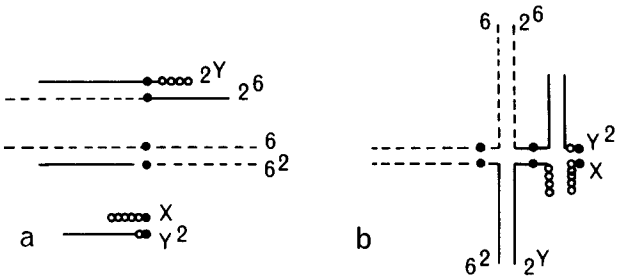

Fig. 1a. Chromosomes involved in translocation complex of double-heterozygous $2^6 2^Y 6^2$ 6 X Y^2 males. b Pairing-configuration, diagrammatic

Table 1. Karyotype frequencies in MII cells and in eggs of testcrosses of double-heterozygous $2^6 2^Y 6^2 6$ XY^2 males of *H. antiqua*. Only the male- derived chromosomes are given for eggs. A discrimination between 6 and 6^2 was not always possible

Eggs							MII	Total (MII + eggs)	
Chromosome	Chr. 6^2	Disjunction type	Chr. 6	Disjunction type	Chr. 6^2 or 6	Total	Chr. 6^2 or 6	Number	%
2^6 X	22[b]	Ia	5	Ib[a]	5	32	66	98	26.6
2^Y Y^2	7	Ib	20[b]	Ia	6	33	57	90	24.5
2^6 2^Y	15[b]	IIa	10[b]	IIb	5	30	51	81	22.0
X Y^2	9	IIb	6	IIa	3	18	55	73	19.8
2^Y X	3	IIIa	0	IIIb	0	3	3	6	1.6
2^6 Y^2	0[c]	IIIb	0	IIIa	0	0	5	5	1.4
2^6 X Y^2	1[b]		0		0	1	2	3	0.8
2^Y	0		0		0	0	6	6	1.6
2^6 2^Y Y^2	0[c]		0[c]		0	0	1	1	0.3
X	0		1		0	1	2	3	0.8
2^6 2^Y X	0[c]		0[c]		0	0	2	2	0.5
Y^2	0		0		0	0	0	0	0.0
Total	57		42		19	118	250	368	99.9

[a] Code for disjunction types of Figure 3
[b] Viable in larval and adult stage
[c] Probably viable in larval and adult stage, but not observed in these stages

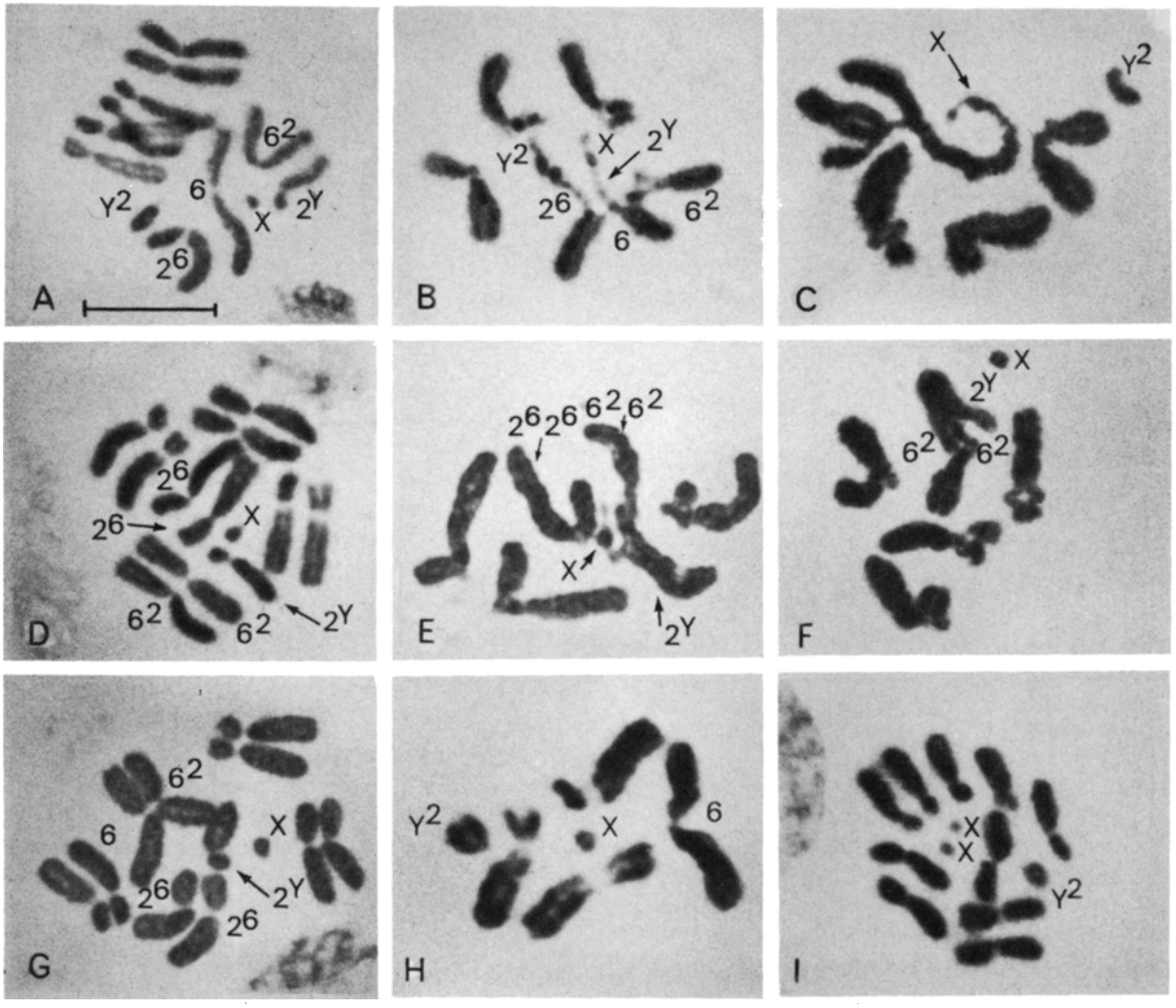

Fig. 2A-I. Karyotypes of *H. antiqua.* **A-C**: double-heterozygous $2^6\,2^Y6^2\,6$ X Y^2 males. **A** – spermatogonial metaphase; **B** – prometaphase/metaphase I; **C** – prometaphase/metaphase I, Y^2 apart from multivalent. **D-F**: duplication/deficiency $2^6\,2^6\,2^Y6^2\,6^2$ X males; **D** – spermatogonial metaphase; **E** – prometaphase/metaphase I; **F** – prometaphase/metaphase I, X apart from multivalent[a]. **G** – spermatogonial metaphase of duplication/deficiency $2^6\,2^6\,2^Y6^2$ 6 X male; **H** – M II cell of male, 6 XY^2; **I** – spermatogonial metaphase of duplication/deficiency $2^6\,2^6\,6^2\,6^2$ X X Y^2 female. Bar represents 10 μm.

[a] **E, F**: note normal double pairing in 2^6 and 6^2 but triple pairing in 2^Y, cf. Fig. 4.

Results

Disjunction Types of the Double-heterozygotes

In Figure 1 the chromosomes involved in the translocation complex of the double-heterozygous males are diagrammatically represented. Figure 2A shows a spermatogonial metaphase. In the first meiotic metaphase a chain-of-six with X and Y^2 in terminal positions (Fig. 2B) is generally observed but occassionally a chain-of-five and an univalent is seen (Fig. 2C).

In metaphase II cells of the double-heterozygous $2^6 2^Y 6^2$ 6 XY^2 males it was often not certain whether chromosome 6^2 or 6 was present, therefore no discrimination was made between these chromosomes in Table 1. The other four chromosomes involved in the translocation complex could easily be discriminated. Eggs (young embryos) were in general better classifiable, due both to the presence of somatic pairing and because many cells per embryo could be scored. However, a discrimination between 6^2 and 6 was not always possible, although it was easier than in MII cells (Table 1). About 50% of the MII cells and embryos correspond to the disjunction types Ia and Ib (Table 1, Fig. 3). Disjunction type Ia, producing the balanced gametes $2^6 6^2$ X and 2^Y 6 Y^2, occurred most frequently. The ratio of Ia to Ib in eggs was 42 (22 + 20) :

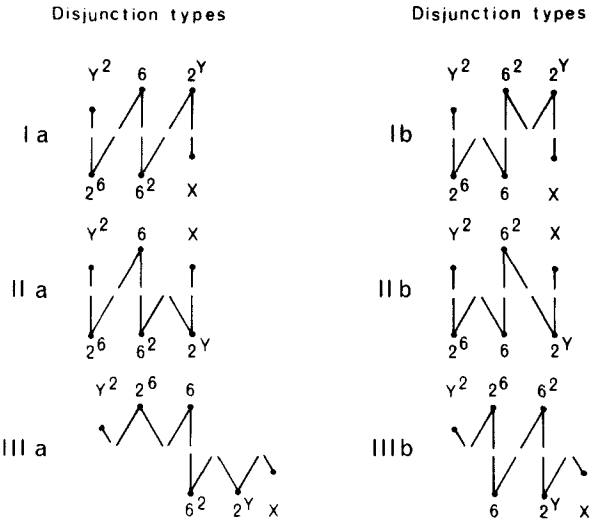

Fig. 3. Disjunction types of the chain-hexavalent of double-heterozygous $2^6 2^Y 6^2$ 6 X Y^2 males of *H. antiqua*, assuming co-orientation between 6^2 and 6 and excluding numerical non-disjunction (see text)

12 (7 + 5) (Table 1) and in MII cells, as far as a discrimination between 6 and 6^2 was possible, about 2 : 1 to 3 : 1 (not indicated in Table 1). Disjunction types IIa and IIb, corresponding to 41.8% of the MII cells and eggs scored, seem to occur in about equal frequencies. Types IIIa and IIIb were found in a frequency of 3%, but probably IIIa does not occur at all. All six disjunction types (Ia to IIIb) are the consequence of a 3 – 3 segregation and a coorientation between 6^2 and 6 and included together 96% of the MII's and eggs. The remaining 4% includes all cases of a 2 – 4 segregation, but with a coorientation between 6 and 6^2 as well.

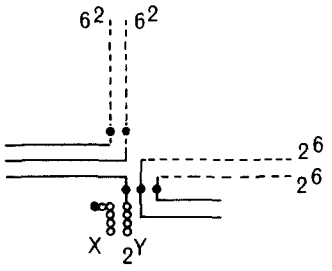

Fig. 4. Pairing-configuration, diagrammatically, in duplication/deficiency $2^6 2^6 2^Y 6^2 6^2$ X males

Viability of Unbalanced Karyotypes and Disjunction in Duplication/Deficiency $2^6 2^6 2^Y 6^2 6^2$ X Males

Not all unbalanced karyotypes died in the embryonic stage; some of them even reached the adult stage (Table 2). The duplication/deficiency karyotypes $2^6 2^6 2^Y 6^2 6^2$ X (Fig. 2D-F) and $2^6 2^6 2^Y 6^2$ 6 X (Fig. 2G), corresponding to the gametes $2^6 2^Y 6^2$ and $2^6 2^Y$ 6 (Table 2), both have a male phenotype. Because the translocation breakpoint in chromosme Y is in the vicinity of the centromere, the greatest part of Y is present in these individuals. The duplicated chromosome segments in $2^6 2^6 2^Y 6^2 6^2$ X are the long arm and centromeric region of 2 (Fig. 4) and in $2^6 2^6 2^Y 6^2$ 6 X almost the entire long arm of 6 and the centromeric region of 2. From Tables 1 and 2 it can be derived that a significant decrease in the relative frequency of these two duplication/deficiency karyotypes from embryonic to adult stage existed. This has to be attributed to a lower viability. in larval and pupal stage, manifested also by a very small body size. Indications were obtained that the viability of $2^6 2^6 2^Y 6^2$ 6 X individuals was more reduced than of $2^6 2^6 2^Y 6^2 6^2$ X. Another duplication/

Table 2. Karyotype frequencies (larvae and adults) in testcrosses of double-heterozygous $2^6 2^Y 6^2 6$ X Y^2 males of *H. antiqua*. The male-derived chromosomes are only given. In larvae a discrimination between 6 and 6^2 was not always possible. Cf. Table 1

Chromosome	Larvae							Adults			
	Chr. 6^2	Disjunction type	Chr. 6	Disjunction type	Chr. 6^2 or 6	Total	%	Chr. 6^2	Chr. 6	Total	%
2^6 X	47	Ia[a]	b	Ib[a]	–	47	40.9	44	b	44	37.9
2^Y Y^2	b	Ib	41	Ia	–	41	35.7	b	60	60	51.7
2^6 2^Y	15	IIa	7	IIb	4	26	22.6	8	3	11	9.5
X Y^2	b	IIb	b	IIa	–	–	–	b	b	–	–
2^6 X Y^2	1		b		–	1	0.9	1	b	1	0.9
Total	63		48		4	115	100.1	53	63	116	100.0

[a] Code for disjunction types of Figure 3; [b] Lethal in late embryonic stages

Table 3. MII scores in duplication/deficiency $2^6 2^6 2^Y 6^2 6^2$ X males

MII type	Number
$2^6 6^2 2^Y$	103
$2^6 6^2$ X	99
$2^6 6^2$	2
$2^6 6^2$ X Y^2	1

deficiency karyotype $2^6 2^6 6^2 6^2$ XXY^2 (Fig. 2I) appeared to be viable in the adult stage; its phenotype was female.

In six $2^6 2^6 2^Y 6^2 6^2$ X males metaphase II cells could be analysed (Table 3). In spite of non-homologous centromeres an almost perfect coorientation between 2^Y and X was found.

Fertility Reduction of the Double-heterozygotes

The percentage of dead embryos (brown eggs) in testcrosses of the double-heterozygous males was 39.5 (3846 eggs, unfertilized eggs excluded). This corresponds rather well with the data from the cytological analyses of MII cells and eggs. The majority of embryonic mortality was caused by the gametes: 6^2 XY^2 and 6 XY^2 (half of the gametes from disjunction types IIa and b), 2^6 6 X and $2^Y 6^2 Y^2$ (disjunction type Ib). The frequencies of these gametes can be derived from the combined data of MII cells and eggs (Table 1). Assuming the ratio of the disjunction type Ia to Ib to be about 3 : 1 (see above), the total frequency of these four gametes is estimated to be 34% ($\frac{1}{2} \times 41.8 + \frac{1}{4} \times 51.1$). Other karyotypes dying in embryonic stage all occurred in low numbers and the total frequency of these is estimated to be 3-5% (Table 1). The total genetic load induced by the double-heterozygous males is 20-25% higher because the majority of $2^6 2^6 2^Y 6^2 6^2$ X and $2^6 2^6 2^Y 6^2$ 6 X individuals and some other unbalanced karyotypes died either as larvae or as pupae; the surviving ones did not reproduce.

Discussion

Disjunction Types of the Double-heterozygotes

From the MII and egg scores (Table 1) it can be concluded that mainly a 3 – 3 segregation occurred and that chromosomes 6 and 6^2 always cooriented. In that case six different disjunction types can be distinguished (Fig. 3). Sybenga (1975) has emphasized that the position of a centromere in respect to its neighbours is an important factor for its stability (probability for reorientation). Also, in the present case a correlation exists between the frequencies of the six disjunction types given in Fig. 3 and the relative positions of the centromeres. The position of a centromere in respect to its neighbours is indicated with cis when oriented to the same pole and with trans when oriented to the other pole. Disjunction types IIIa and IIIb, observed together with a frequency of only 3%, have to be considered as unstable because in IIIa X, Y^2, 2^6 and 2^Y and in IIIb X and Y^2 do not have a neighbouring centromere in a trans-position (no counterforce for the pull exerted by the spindle fibres). In the remaining four disjunction types X and Y^2 always have a trans-position with respect to their (single) neighbour. The other four centromeres have two neighbours and are positioned as follows: in Ia all in trans-trans, in IIa and IIb two in trans-trans and two in cis-trans and in Ib all in cis-trans. Assuming that a trans-trans position is more stable than cis-trans, it may be expected that Ia was the most, and Ib the least, frequently observed disjunction type and that IIa and IIb occurred in intermediate frequencies.

The frequency of numerical non-disjunction (NND) among the 250 MII cells and 118 eggs analysed amounted to 4%, about the same value as was found in 2 2^Y 6 6 X Y^2 (T61/+) males (van Heemert and Vosselman 1980). For two X-linked translocations, one between X and 3 (van Heemert 1974a) and one between X and 4 (Vosselman, unpublished), the level of NND scored in heterozygous males was 2% and 15% respectively. In contrast, in males heterozygous for autosomal translocations NND has very rarely been observed, although five different translocations, including T14, were studied (Vosselman in prep.). In females, which, in contrast to males, are chiasmate, slightly different results were found which will be discussed elsewhere. It is suggested that the difference in NND between autosomal and sex-linked translocations scored in males is a consequence of an earlier disjoining of the sex chromosomes (translocated or non-translocated) from the multivalent. When this is followed by reorientation of either the multivalent or the univalent, NND can be the result. The early separation of the sex chromosomes from the multivalent can probably be attributed to the acrocentric (telocentric) nature of the sex chromosomes; the connection with the multivalent rests on only one short chromosome arm. In contrast, all autosomes have two bound arms (Fig. 2).

In *Culex pipiens* high frequencies of NND were reported by Jost and Laven (1971) for translocations involving chromosome 1. Lack of chiasmata and earlier terminalisation of chiasmata in chromosome 1 was considered to be the reason. For T70H/+ males in the mouse de Boer (1976) found high numbers (34-50%) of trivalent plus univalent configurations, but only 4-9% of the MII cells were aneuploid. Non-random segregation of the univalent was given as explanation for this discrepancy.

Viability of Unbalanced Karyotypes and Disjunction in Duplication Deficiency $2^6 2^6 2^Y 6^2 6^2$ X Males

In *H. antiqua* duplication/deficiency karyotypes produced by translocations are mostly lethal in the embryonic stage, but some can survive to the larval stage (Robinson and van Heemert 1975).

Individuals with a duplication for half the long arm of chromosome 3 showed a reduced viability but some stayed alive into the adult stage (van Heemert 1974a, b). On the contrary sex chromosome aneuploidy has in general no impact on the viability of the adults (van Heemert 1974a, b; Vosselman 1978). In the present case all three duplication/deficiency karyotypes $2^6 2^6 2^Y 6^2 6^2$ X, $2^6 2^6 2^Y 6^2$ 6 X and $2^6 2^6 6^2 6^2$ XXY^2 which were (partially) viable in the adult stage, had only a deficiency for a part of the Y-chromosome. The duplicated segments concerned different chromosomes. In *Aedes aegypti* (Ved Brat 1974) and in *Glossina austeni* (Curtis et al. 1972) viable duplication/deficiency karyotypes have been reported as well.

As $2^6 2^6 2^Y 6^2 6^2$ X and $2^6 2^6 2^Y 6^2$ 6 X were males and $2^6 2^6 6^2 6^2$ XXY^2 was a female, it is obvious that the male determining gene(s) is (are) located on the large segment of the Y-chromosome, translocated to the 2^Y-chromosome.

An interesting observation was the regular coorientation between 2^Y and X in $2^6 2^6 2^Y 6^2 6^2$ X males (Table 3). As is shown in Figure 4, the greatest part of the long arm of 2^Y is homologous with 6^2, most of the short arm is homologous with X and the centromeric region with 2^6. Considering the rather complicated synapsis of 2^Y (Fig. 2 E), at first sight the regular coorientation between 2^Y and X was surprising. However, on further consideration there seems to be a reasonable explanation, assuming firstly that 2^6 and 6^2 will both preferentially orient on their fully homologous pairing partners and secondly that the most stable orientation will be achieved when 2^Y and X coorientate. In that case for both 2^Y and X there is a counterbalance to the force of the pulling spindle fibres, which is essential for a stable orientation (Sybenga 1975). It is apparent that homology of centromeres is not necessary for a regular coorientation, as has also been suggested e.g. by John and Lewis (1965) and Douglas (1968).

Application Possibilities for Genetic Control

A pure breeding stock which is permanently reduced in fertility can be obtained by crossing T14-homozygous ($2^6 2^6 6^2 6^2$ XX) females with double-heterozygous ($2^6 2^Y 6^2 6$ XY^2) males. However, the applicability of this for genetic insect control is limited, as it seems impossible to replace a target population completely by these karyotypes. When this condition is not fulfilled or when immigration occurs, it is inevitable that the double-heterozygous males, as a consequence of their fertility reduction, will disappear from the population.

Conditional lethality, when determined by a locus on one of the chromosomes involved in a Y-autosome translocation, can be exploited for genetic sexing (elimination of females). Since in a stock consisting of T14-homozygous ($2^6 2^6 6^2 6^2$ XX) females and T14/T61 double-heterozygous ($2^6 2^Y 6^2 6$ XY^2) males, chromosome 6 is also inherited in a strictly holandric way and in males recombination is absent, loci on this chromosome 6 as well as on 2^Y and Y^2 can be used for this purpose. This is of interest because a locus for alcohol dehydrogenase has been localized on chromosome 6 (van Heemert and Witteveen-Pillen 1980). When a suitable alcohol dehydrogenase-null mutant can be induced in *H. antiqua*, it should be possible to produce a pure breeding stock of alcohol-positive (Adh$^+$ Adh°) T14/T61 males and susceptible (Adh° Adh°) T14-homozygous females. In *Drosophila melanogaster* several alcohol dehydrogenase-null mutants have been induced (Gerace and Sofer 1972) and Robinson and van Heemert (1980 pers. comm.) have recently developed a genetic sexing system in these species involving such a mutant.

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