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Inherited Preferential Segregation in Translocation Heterozygotes of the Mosquito, *Culex pipiens* L.

LEONORE DENNHÖFER

Institut für Entwicklungsphysiologie der Universität zu Köln, Köln (BRD)

Summary. The present paper deals with crossing experiments on translocation heterozygotes in the mosquito *Culex pipiens* L. It is shown that the ratio of euploid and aneuploid gametes is determined by two allelomorphs of one single inheritable factor. These experiments agree with our hypothesis that the ratio of segregation types in a translocation heterozygous organism (alternate and adjacent) is determined by a series of multiple alleles of a single mendelian factor.

Introduction

In meiosis of a translocation heterozygote, the ratio of euploid and aneuploid gametes is fundamentally determined by the ratio of alternate and adjacent segregation of the chromosomes involved in the interchange complex.

The literature reports individual animals and plants with complete fertility (*Periplaneta americana*: Lewis and John 1957; *Oenothera muricata*: Cleland 1926), 34% sterility (*Cochliomyia hominivorax*: La Chance et al. 1964; *Hordeum vulgare*: L. Smith 1941), 50% sterility (*Drosophila melanogaster*: Muller 1930; *Zea mays*: McClintock 1930), or 66% sterility (*Gesonula punctifrons*: Sarkar 1955; *Strelitzia augusta*: Simmonds 1954) when translocation heterozygous. These rates of sterility in gametes and grains agree with the orientation resp. segregation of meiotic chromosomes. If any directed segregation in a population is excluded, translocation heterozygotes should produce euploid and aneuploid gametes in the ratio of 2:4 causing 66% sterility. Hitherto there has been no extensive explanation for the different amounts of translocation sterility valid for all eukaryotic organisms. Only for special subjects, or even special translocations, some authors have tried to give an interpretation (see literature review in Dennhöfer 1974a).

Because the rates of sterility are always very similar, it is evident that the same mechanism of segregation is responsible for it. The results of crossing experiments with plants of different chromosome races (prime types) of *Datura* (Bergner et al. 1933) and strains of *Pisum* (Lamprecht 1939, 1954) are especially remarkable.

A previous paper (Dennhöfer 1974a) presents the hypothesis that the ratio of segregation types in an interchange complex is determined by one single mendelian factor. Assessing what is known about translocations both in animals and plants gives grounds for the hypothesis of a genetically determined regulation in meiosis against sterility due to translocations. The existence of a factor, called "sg", inherent in all organisms consisting of a series of multiple allelomorphs, is postulated. When homozygous in an individual, the allele sg^1 (without any positive regulation) causes 66% sterility, sg^2 causes 50% sterility, sg^3 causes 34% sterility and sg^4 causes complete fertility in translocation heterozygotes. The ratios of aneuploid gametes giving rise to sterility are correlated with constant rates of alternate and adjacent segregation: 2:4, 3:3, 4:2 or 6:0. In the heterozygous condition the allele causing a lower rate of sterility is always dominant to the other. The hypothesis can be summarized in a scheme (Dennhöfer 1974a):

allelomorphs	sg^1	$< sg^2$	$< sg^3$	$< sg^4$
relation between alternate and adjacent segregation	2:4	3:3	4:2	6:0
fertility in %	34	50	66	100
sterility in %	66	50	34	0

These percentages of sterility may be influenced a little by other conditions, such as crossing over in interstitial segments.

The present paper reports crossing experiments with translocation heterozygotes in the mosquito *Culex pipiens*, demonstrating that the ratio of euploid and aneuploid gametes is indeed controlled by alleles of a single inheritable factor.

Material

A translocation line, named T 3 Lo (1—3), was induced in males of *Culex pipiens* by X-rays.[1] Mitotic chromosomes and larval salivary gland chromosomes showed

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[1] I am much indebted to Mr. B. Patel, who induced and screened this line, for his kindness in giving it to me.

that the small chromosome 1 and the longest chromosome 3 were involved. The breakpoints were determined and mapped (Dennhöfer 1974b). Chromosome 1 carries the sex determinator M or m (Gilchrist and Haldane 1946, 1947; Dennhöfer 1974c). The translocation is almost completely linked with the male sex determinator M, consequently the aberration can only be found in males.

In different males of this line we observed different rates of sterility. None of the other translocation lines described by Dennhöfer (1974b) shows this. In single matings some translocation males gave rise to $50.1 \pm 2.6\%$ lethality both in embryos and larvae of the first instar, while others showed $35.3 \pm 2.7\%$ lethality. The lines show homogeneity with $p = 0.10 > p > = 0.05$ resp. $0.90 > p > 0.70$. These values can only be explained by assuming a ratio of 3:3 of alternate and adjacent segregation causing 50% sterility in the first case. The sterility of 35% in the other line is due to the ratio 4:2.

Experiment and Results

In order to prove the genetic regulation of segregation in translocation heterozygotes, we performed the following crosses.

Isolated virgin females of a London strain were mated with single males of the translocation line. We used females of an extremely inbred strain for this experiment. All rafts of the P-generation were controlled for lethality.

Only two rafts of the P-generation, showing about 34% sterility, were reared in different lines, A and B. The adults of these lines (F_1) were inbred, all rafts were collected and evaluated for lethality. One part of these rafts showed about 50% sterility, the other part only 34%. All larvae of the F_2-generation were reared.

The males of the F_2, all translocation heterozygous, were mated in single matings with normal virgin females in order to control the rate of sterility caused by these F_2-males. Males which produced 50% aneuploid gametes and those which produced only 34% aneuploid gametes were found in the ratio of exactly 9:7 (Tab. 1). The results of the rafts in the F_1 are given in Table 2; the results of the F_2 are given in brief in Table 3.

Discussion

These results can be explained by assuming that the males of the P-generation had the allelomorphs sg^2/sg^3, while the females of an extremely inbred strain were sg^2/sg^2 (Tab. 1). Consequently, the individuals of the F_1-generation should carry the genotypes sg^2/sg^2 (= 50% sterility) and sg^2/sg^3 (= 34% sterility). All genotypes of the F_1 have the same chance of mating:

1) $sg^2/sg^2 \times sg^2/sg^3$
2) $sg^3/sg^2 \times sg^2/sg^2$
3) $sg^2/sg^2 \times sg^2/sg^2$
4) $sg^3/sg^2 \times sg^3/sg^2$

These matings produce offspring of the following genotypes in the F_2 (only males could be considered because the translocation is almost completely linked with the male determinator M):

	34% sterility		*50% sterility*
1)	sg^2/sg^3		sg^2/sg^2
	sg^2/sg^3		sg^2/sg^2
2)	sg^3/sg^2		sg^2/sg^2
	sg^3/sg^2		sg^2/sg^2
3)	-----		sg^2/sg^2
	-----		sg^2/sg^2
	-----		sg^2/sg^2
	-----		sg^2/sg^2
4)	sg^3/sg^3		sg^2/sg^2
	sg^3/sg^2		-----
	sg^2/sg^3		-----
	7	:	9

The results of the F_1- and F_2-generations show that the factor is not linked with a chromosome involved in the translocation. The rates of sterility in the F_1- and F_2-males are exactly either 50% or 34%. There is no difference between males of the genotype sg^2/sg^3 and males of the genotype sg^3/sg^3, a fact agreeing with our hypothesis.

The chromosomal interchange in the line T 3 Lo (1—3) has happened between the small chromosome 1 and the large one 3 (Dennhöfer 1974b). The breakpoints are situated near the centromeres and the interstitial segments are very small. It is improbable that interstitial crossing over had occurred to influence the rate of euploid and aneuploid gametes.

We found no linkage of the special male-sterilities (50 or 35%) with the translocation itself. The factor sg must be located on the autosomal chromosome 2 not involved in the translocation.

Our hypothesis, affirming that different alleles of a single factor are responsible for the ratio of euploid and aneuploid gametes in a translocation heterozygote, is experimentally confirmed by the finding of two alleles. The alleles of the factor sg had no effect in individuals which were not translocation heterozygous. Only in the presence of such an aberration do the alleles determine the ratio of segregation types.

In our experiment the allele (sg^3) causing more viable offspring is dominant over the other (sg^2) causing less viable offspring of translocation heterozygous males. Probably this allele sg^3 is induced by irradiation. Surely it must be possible to induce the allele sg^4, causing complete fertility, by X-ray treatment or by isolation of a natural population of *Culex pipiens*. The screening test for translocations in this mosquito (Laven and Jost 1971) has only regard to the dominant sterility, not to genetical markers or cytological analyses. So the allelomorph sg^4 may not have been detected till now.

It would be very interesting to induce the factor sg^3 in other translocation lines, especially in those involving chromosome 2, in order to localise the mul-

Table 1. *Crossings and results of the experiment*

		A)		B)	
	P	♀ sg^2/sg^2 × ♂ sg^2/sg^2 (34% sterility)			
	F_1	sg^2/sg^2 (50% ster.)	sg^2/sg^3 (34% ster.)	sg^2/sg^2 (50% ster.)	sg^2/sg^3 (34% ster.)
result (No. of rafts):		8	6	15	14
expected ratio:		1:1		1:1	
	F_2	sg^2/sg^2	sg^2/sg^3 sg^3/sg^3	sg^2/sg^2	sg^2/sg^3 sg^3/sg^3
result (No. of rafts):		108	83	183	150
expected ratio:		9:7		9:7	
X^2-test:		0,00666		0,2267	
p:		0,90–0,95		0,50–0,70	

Table 2. *Results of the F_1-generation*

F_1	genotypes: sg^2/sg^2				genotypes: sg^2/sg^3 sg^3/sg^3			
	fertilized eggs	larvae in the second instar	dead embryos and larvae of the first instar	sterility in %	fertilized eggs	larvae in the second instar	dead embryos and larvae of the first instar	sterility in %
A)	69	37	32	46,4	84	50	34	40,4
	87	42	45	51,7	77	50	27	35,1
	109	50	59	54,1	92	54	38	41,3
	102	46	56	54,9	102	63	39	38,2
	87	40	47	54,0	81	47	34	41,9
	98	44	54	55,1	75	47	28	37,3
	119	57	62	52,1				
	86	42	44	51,2				
	757	358	399		511	311	200	
			= 52,7 ± 3,3%				= 39,1 ± 5,6%	
	homogeneity p = 0,97–0,95				homogeneity p = 0,95–0,90			
B)	105	55	50	47,6	89	56	33	37,1
	115	63	52	45,2	109	66	43	39,4
	104	54	50	48,1	101	62	39	38,6
	113	60	53	46,9	83	58	25	30,1
	99	44	55	55,5	104	73	31	29,8
	101	50	51	50,5	97	61	36	37,1
	121	65	56	46,3	101	61	40	39,6
	75	34	41	54,7	102	63	39	38,2
	110	54	56	50,9	117	72	45	38,4
	109	58	51	46,8	119	75	44	36,9
	111	44	67	60,4	91	53	38	41,7
	123	41	82	66,7	102	67	35	34,3
	99	47	52	52,5	127	77	50	39,4
	98	52	46	46,9	108	67	41	37,9
	97	53	44	45,4				
	1580	774	806		1450	911	539	
			= 51,0 ± 4,1%				= 37,2 ± 4,2%	
	homogeneity p = 0,05–0,025				homogeneity p = 0,95–0,90			

Table 3. *Results of the F_2-generation in short form*

	genotypes	number of rafts	fertilized eggs	larvae in the second instar	dead embryos and larvae of the first instar	sterility in %	contingency tests: p
A)	sg^2/sg^2	108	10906	5360	5546	50,9 ± 1,2	0,30–0,50
	sg^2/sg^3 sg^3/sg^3	83	8314	5211	3103	37,3 ± 1,4	0,90–0,95
B)	sg^2/sg^2	183	17729	8887	8842	49,9 ± 1,0	0,10–0,30
	sg^2/sg^3 sg^3/sg^3	150	15019	9202	5817	38,7 ± 1,1	0,70–0,90

tiple factor. Moreover, segregation types should be looked for in the interchance complex in the different lines, characterized by 50 or 34% sterility, in order to register the rates of alternate and adjacent orientation. This should confirm results in other subjects showing ratios of 3:3 or 4:2 between alternate and adjacent segregation. Jost and Laven (1971) only described translocation heterozygotes in *Culex pipiens* characterized by about 50% sterility. They concluded that these mosquitoes show a ratio of alternate and adjacent segregation in meiosis of about 1:1.

The results of the crossing experiment in *Culex pipiens* sustain our hypothesis that the segregation of chromosomes in an interchange complex is regulated by one single, mendelian factor. This factor can be changed into different allelomorphs by mutation. When heterozygous, the allele causing more viable gametes is always dominant over the other one.

This regulation for viable gametes is important in view of genetics for control or eradication of vectors. This genetical regulation or "resistance" against sterility due to translocations may be compared with mutations in insects susceptible to insecticides which produce individuals resistant to insecticides.

The investigations were done in the Department of Biology (21) of the Johannes Gutenberg-University in Mainz.

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Frau Dr. Leonore Dennhöfer
Institut für Entwicklungsphysiologie
der Universität zu Köln
Gyrhofstr. 17
D-5 Köln 41 (Germany/BRD)