A CYTOGENETIC DEMONSTRATION OF CROSSING-OVER BETWEEN X- AND Y-CHROMOSOMES IN THE MALE OF DROSOPHILA MELANOGASTER

By Curt Stern and Dorothy Doan

Department of Zoölogy, University of Rochester

Communicated September 25, 1936

It has been suggested[1] that the "attachments" and "reorganizations" involving the X- and Y-chromosomes in the male of *Drosophila melanogaster*[2] are due to crossing-over. This interpretation became strengthened through Kaufmann's discovery of interchanges between X- and Y-chromosomes as the cause of the "detachments" of attached X-chromosomes in $\overset{\frown}{XX}Y$ females.[3] Miss Philip added genetic data indicating double crossing-over in the male between the heterochromosomes.[4] No combined genetic and cytological data had been presented. Such work will be reported below. During the preparation of the manuscript a preliminary note containing similar evidence was published by Neuhaus.[5]

We have found cases of "detachment" in males similar to those investigated in females by Kaufmann. The "detachments" represented a separation of an X-chromosome and a small duplication, called Theta (θ), which originally were joined together at the fibre point.[6] It was possible that the detachment process consisted simply of a breaking-apart of the X- and θ-chromosomes. On the other hand, it seemed probable that the separation had resulted from crossing-over in the male between the $\overset{\frown}{X\theta}$-group and the Y-chromosome. In the latter case the detached X- and θ-chromosomes should possess complementary parts of the Y-chromosome attached to them. The purpose of this investigation was to decide between the above alternatives.

Methods.—In order to obtain detachments of the $\overset{\frown}{X\theta}$-group, males of the constitution $\overset{\frown}{X\theta}Y$ were mated to females with attached X-chromosomes. The X-chromosomes of the female were homozygous for yellow while that of the males contained yellow and singed-3. The θ-fragment possesses the normal allele of yellow plus some adjacent loci and the locus of bobbed with a part of the inert region of the X-chromosome. The $\overset{\frown}{X\theta}Y$ males accordingly were phenotypically not-yellow and singed. If crossing-over occurs in these males four different possibilities have to be considered (Fig. 1): (1) crossing-over between the X-chromosome and (*a*) either the long arm of the Y-chromosome ("Y^L") or (*b*) the short arm of the Y-chromosome ("Y^S"); (2) crossing-over between the θ-part and (*a*) either Y^L or (*b*) Y^S. The cross-over products from these processes are the chromosome groups $\widehat{XY^S}$, $\widehat{\theta Y^L}$, $\widehat{XY^L}$ and $\widehat{\theta Y^S}$. In the mating described F_1-males carrying "detachments" would contain an $\widehat{XY^S}$ or $\widehat{XY^L}$ group and would be yellow and singed in contrast to the majority of males which are non-yellow singed. F_1-females carrying detachments would contain a $\widehat{\theta Y^L}$ or $\widehat{\theta Y^S}$ group and would be non-yellow in contrast to the majority which are yellow.

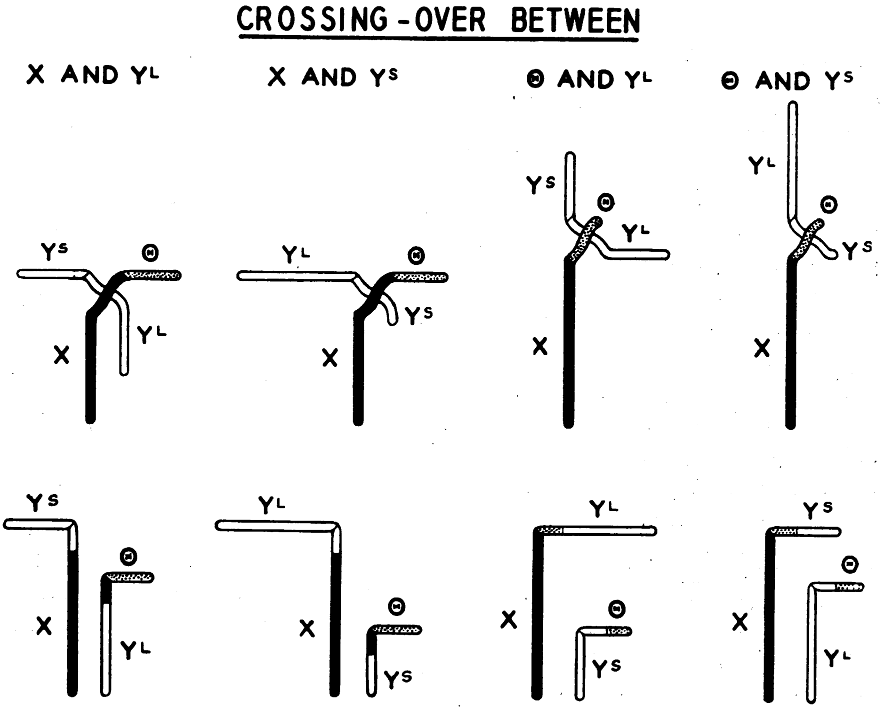

FIGURE 1

Possible modes of crossing-over between the heterochromosomes in $\widehat{X\theta Y}$ males
X-chromosome: black
Y-chromosome: empty
θ-chromosome: dotted

Exceptional F_1-classes are also expected as a result of crossing-over in the P-females between the attached X-chromosomes and the Y-chromosome. While the F_1-males resulting from such a process are readily distinguished by their yellow, not-singed phenotype from those produced in consequence of crossing-over in the P-males, the exceptional F_1-females derived from crossing-over in the P-females or P-males are phenotypically alike. However, they can be separated by progeny tests.

TABLE 1

$\overset{\frown}{XX}Y$ ♀ × $\overset{\frown}{X\theta}Y$ ♂

Experiment	No. of cultures	Total F_1	Detached X	Detached θ
1	20	1636	5	3
2	191	30627	4	5
Total	211	32263	9	8

Results.—Two series of cultures each of which contained 3 P-females and, in most cases, 3 P-males, yielded 1636 and 30627 F_1-flies (Table 1). Among these there were 17 individuals which resulted from "detachments" in the $\overset{\frown}{X\theta}Y$-males. Nine of these were F_1-males and eight F_1-females. Two more females, from experiment (2), may possibly have been of this type but complete sterility made it impossible to determine their origin in respect to detachment in the mother or father.

Of the 8 F_1-females, in 3 cases, from experiment (2), no analysis was possible. When these non-yellow females were mated to unrelated males they produced only yellow daughters and no sons. This result is understandable under the assumption that the non-yellow females had obtained an attached X-chromosome from their mothers and a detached θ-fragment from their fathers and that the $\overset{\frown}{XX}$-group during the reduction division segregated to the opposite pole from the θ-fragment. Thus all female offspring would be yellow and all male offspring would carry the θ-piece, besides their X-chromosome. As males carrying the θ-duplication are often of very low viability, their absence in the progenies of the three females is not surprising.

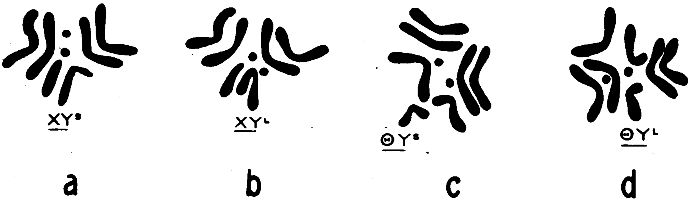

FIGURE 2

Oögonial figures showing the four different kinds of cross-over products. 2250 ×.

There remain 14 cases of detachments of the $\overset{\frown}{X\theta}$-group, namely, 9 detached X-chromosomes and 5 detached θ-fragments. Stocks containing them were established in order to carry out a genetic and cytological analysis.

The cytological investigation showed in all 14 cases the presence of a chromosome piece attached to the X- or θ-chromosome. Two stocks died out before the length of the attached piece had been determined accurately.

In the other 12 stocks it was found to be of a length which corresponded either to that of the long or to that of the short arm of the Y-chromosome. All four possible types of combinations of X- or θ-chromosome with Y^L- or Y^S-attachment were found (Table 2). The cytological determinations were made on the chromosomes of oögonial cells by means of temporary aceto-carmine slides. From all stocks tested at least five completely clear cytological figures were obtained. The diagnosis with respect to a Y^L- or Y^S-arm was made on the basis of length as measured by a comparison with X-chromosomes of the same cell. In the case of the detached θ-chromosomes a normal Y-chromosome in the same cell was also available for comparison.

TABLE 2

CONSTITUTION OF 12 DETACHMENTS OF THE $\overset{\frown}{X\theta}$-GROUP

$\overset{\frown}{XY}^S$	$\overset{\frown}{XY}^L$	$\overset{\frown}{\theta Y}^S$	$\overset{\frown}{\theta Y}^L$
3	5	3	1

Genetically the nature of the attached Y-chromosome arm was judged by fertility tests. By suitable crosses the $\overset{\frown}{XY}^{L \text{ or } S}$ and the $\overset{\frown}{\theta Y}^{L \text{ or } S}$ chromosomes were brought together with the Y''-chromosome so that males of the constitution $\overset{\frown}{XY}^{L \text{ or } S}\ Y''$ and $X\ \overset{\frown}{\theta Y}^{L \text{ or } S}\ Y''$ resulted. (Y'' is a Y-chromosome fragment which has to be supplemented by a Y^L-arm in order to make possible male fertility.) By testing the males of the above mentioned constitution in regard to fertility the presence of a Y^L or Y^S arm could be distinguished. Extensive tests of the 12 available detachments demonstrated fertility in 6 cases and sterility in the other 6 cases, pointing to equal numbers of Y^L- and Y^S-arms. In each detachment the results of cytological and genetic determinations were in agreement with each other.

Discussion.—The experiments demonstrate that crossing-over between the X- and Y-chromosomes occurs in the male of *Drosophila melanogaster.* The question might be asked which parts of the $\overset{\frown}{X\theta}$-group and the Y-chromosome cross-over with each other. It was seen (Fig. 1), that $\overset{\frown}{XY}^S$ and $\overset{\frown}{\theta Y}^L$ as well as $\overset{\frown}{XY}^L$ and $\overset{\frown}{\theta Y}^S$ groups result from crossing-over either of the Y^L-arm with the X- or θ-chromosome or of the Y^S arm with these chromosomes. The same configurations could also be expected from crossing-over of either arm of the Y-chromosome with the θ-duplication or of either arm of the Y-chromosome with the X-chromosome. The results obtained show that at least two of the four possible types of crossing-over occur. On the basis of Neuhaus' findings[7] regarding crossing-over between the X- and Y-chromosomes it is probable that the two processes in males involved mainly or exclusively the Y^S-arm and both the θ- and the X-chromosomes.

It is a striking fact that the cross-over individuals had a strong tendency to occur together in one and the same culture (Table 3). Furthermore, in the two cultures where a complete analysis of more than one cross-over was possible, only complementary cross-over products were obtained. In one case two detached X-chromosomes showed a Y^S- and one detached θ-chromosome a Y^L-attachment, while in the other case four detached X-chromosomes possessed a Y^L- and two detached θ-pieces showed a Y^S-attachment. The different cross-over products in these cultures may conceivably have arisen from independent events in more than one of the three P-males. On the other hand, it is quite probable that they are the result of crossing-over in one individual. If this latter is true, then either the crossing-over process occurred once at a spermatogonial division resulting in spermatocytes containing complementary cross-overs or there existed a tendency for all crossing-over in the spermatocytes of one individual to take place in the same manner. It is difficult to imagine a uniformity of method in different cells such as the second alternative demands. It seems more probable that crossing-over occurred in one way once in a spermatogonial cell.[8]

TABLE 3

No. of detachments per culture	0	1	2	4	8
No. of cultures	204	4	1	1	1

If crossing-over occurs at a spermatogonial stage, a calculation of the frequencies of crossing-over has to take account of the fact that probably all cross-overs from one P-male are results of one single process. As the frequency of the cross-over gametes depends upon the early or late spermatogonial stage in which crossing-over occurred, no special significance can be attached to calculations based on the total number of cross-over progeny. It is, however, a striking fact that the frequency of cross-overs varied so greatly in the two experiments reported in table 1.

Summary.—1. In males with X-chromosomes to which the duplication Theta (θ) was attached, separations of the X-chromosome and the θ-duplication were found.

2. Genetical and cytological tests on progeny of 14 different flies containing the separations showed that the disjoined pieces always contained an attachment of one arm of the Y-chromosome. The length of the attachment could not be determined in 2 cases. The remaining cases were represented by four "X-chromosome with Y^L-arm," three "X-chromosome with Y^S-arm," one "θ-chromosome with Y^L-arm," three "θ-chromosome with Y^S-arm."

3. At least two of four different cross-over processes occurred.

4. A consideration of the frequencies and kinds of cross-over products

obtained in individual cultures suggests that crossing-over can occur in spermatogonial divisions.

---

[1] Darlington, C. D., *Jour. Genetics*, **24**, 65–96 (1931).

[2] Stern, C., *Zeit. Abstgsl.*, **51**, 253–353 (1929); Stern, C., and Ogura, S., *Zeit. Abstgsl.*, **58**, 81–121 (1931).

[3] Kaufmann, B. P., *Proc. Nat. Acad. Sci.*, **19**, 830–838 (1933).

[4] Philip, U., *Jour. Genetics*, **31**, 341–352 (1935).

[5] Neuhaus, M. J., *Nature*, **137**, 996 (1936).

[6] The Theta-duplication had been provided kindly by Prof. H. J. Muller.

[7] Neuhaus, M. J., *Zeit. Abstgsl.*, **71**, 265–275 (1936); *Nature*, loc. cit.

[8] Data concerning spermatogonial crossing-over of autosomes have recently been presented by H. Friesen, *Bull. Biol. Med. Exp.* (*U. S. S. R.*), **1**, 262–263 (1936).

NUMBER OF THE ABELIAN GROUPS OF A GIVEN ORDER

By G. A. Miller

Department of Mathematics, University of Illinois

Communicated September 22, 1936

The identity is the only group of order 1 and this may be regarded as an abelian group even if the law of combination of its operators cannot present itself since there is only one operator in it. There is one and only one group of order 2 and there are two groups of order 4. It will be proved in what follows that these are the only three orders for which the number of abelian groups is as large as half the order of these groups. On the contrary, the number of non-abelian groups of a given order may exceed this order. The lowest order for which this is the case is 32. In fact, 44 of the 51 groups of this order are known to be non-abelian. An Indian mathematician, S. Ramannjan (1887–1920), found an asymptotic formula from which it follows that the number of the abelian groups of order p^{200}, p being a prime number, is nearly four million millions.

Since every abelian group whose order is not a power of some prime number is the direct product of its Sylow subgroups, the number of the abelian groups of order $g = p_1^{\alpha_1} p_2^{\alpha_2}, \ldots, p_\lambda^{\alpha_\lambda}$ ($p_1, p_2, \ldots, p_\lambda$ being distinct prime numbers) is equal to the product of the numbers of the abelian groups of order $p_1^{\alpha_1}, p_2^{\alpha_2}, \ldots, p_\lambda^{\alpha_\lambda}$, respectively. Since the number of the abelian groups of order p^m, p being a prime number, is independent of the value of p, we proceed to prove that the number of the abelian groups of order 2^m, $m > 2$, is less than 2^{m-1}.

To prove this fact it is desirable to bear in mind that the number of the abelian groups of order 2^m is equal to the number of ways in which m