

<sup>6</sup> Metz, *Biol. Zentralb.*, **51**, 121 (1931); Metz and Schmuck, these PROCEEDINGS, **17**, 272 (1931).

<sup>7</sup> Metz, *Amer. Nat.*, **68**, 487 (1929).

<sup>8</sup> DuBois, these PROCEEDINGS, **18**, 352 (1932); *Jour. Morph.*, **54**, 161 (1932); *Zeits. f. Zelf. u. mik. Anat.*, **19**, 395 (1933).

<sup>9</sup> Metz and Schmuck, *Genetics*, **16**, 225 (1931).

<sup>10</sup> Metz and Schmuck, these PROCEEDINGS, **15**, 863 (1929); *Ibid.*, **15**, 867 (1929); Metz, *Quart. Rev. Biol.*, **6**, 306 (1931).

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ON THE OCCURRENCE OF TRANSLOCATIONS AND  
AUTOSOMAL NON-DISJUNCTION IN *DROSOPHILA*  
*MELANOGASTER*

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Recent findings on different plants indicate that the presence of extra chromosomes in an organism facilitates the occurrence of exchanges of non-homologous chromosomal parts. It seemed desirable to test if such exchanges occur also in heteroploid *Drosophila melanogaster* both from the point of the validity of the generalization of the findings as well as for the possibility of finding a method to obtain non-homologous exchanges in non-radiated flies. Triploid *Drosophilae* were chosen for this investigation. Translocations within one chromosomal pair as well as between non-homologous chromosomes were to be expected if the findings on plants would hold true for *Drosophila*. However, as a first part of the investigation, only the possibility of translocations between non-homologous chromosomes was tested.

The outcome was fully negative: None of the more than 900 haploid gametes coming from triploid females contained a translocation between the first, second or third chromosomes (the fourth chromosome was—on account of its comparatively small size—expected to be of less importance than the others and its fate therefore not followed). The result can be explained as due to the fact that the frequency of translocations between non-homologous chromosomes in triploid *Drosophilae* is very low. If one considers the fact, however, that the production of a haploid egg from triploid females, which contains the two non-homologous chromosomes that underwent a possible interchange, is only one of different possibilities during meiosis, the number of 900 gametes tested might still have been too low. Certainly the method used has proved to be of no value for obtaining translocations.

A brief record of the data, which constitute not only the basis for the

above considerations, but are also the most extensive on the possibility of translocations of the kind in question in non-radiated diploid males, follows below. Furthermore, some new facts about chromosome distribution during reduction in special types of males and in triploid females came to light, showing the occurrence of autosomal non-disjunction.

Triploid females were mated to males carrying in different chromosomes the dominant characters Curly (wing; Cy, II), Plum (eye; Pm, II), Stubble (bristles; Sb; III) and Hairless (H; III):

$$3N \text{ ♀} \times \frac{\text{Cy}}{\text{Pm}} \frac{\text{Sb C}}{\text{H}} \text{ ♂}.$$

Both Cy and Pm are associated with inversions which suppress practically all crossing-over between these two genes. Sb was also associated with a crossover suppressor (C), so that no crossing-over occurs between Sb and H. Some of the triploid females contained different recessive genes in the X-chromosome. Possibly some also contained H in single dose, as appeared later.

TABLE 1

$$\begin{array}{r} 3N \text{ ♀} \times \frac{\text{Cy}}{\text{Pm}} \frac{\text{Sb C}}{\text{H}} \text{ ♂} \\ +^{\text{Cy}} \quad +^{\text{Sb}} \\ \frac{\quad}{+^{\text{Pm}}} \quad \frac{\quad}{+^{\text{H}}} \text{ ♀ ♀} \times F_1 \text{ ♂} \end{array}$$

Types of $F_1$ -♂♂	Cy Sb	Cy H	Pm Sb	Pm H	Total
Number of each type tested (fertile)	229	219	228	227	903

The male offspring of this cross consisted of four different regular classes in about equal numbers in regard to the four dominant autosomal genes: Cy Sb, Cy H, Pm Sb and Pm H. A total of 1172 such males

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were mated individually to females carrying the wild type alleles of these dominant characters. 269 cultures were sterile (in large proportion due to unfavorable conditions in one batch), leaving 903 fertile matings. Had the P-males of these matings, being the  $F_1$  of the triploid cross, contained any translocation between two or three of the chromosomes I-III, then an apparent linkage between the characters carried by the chromosomes involved in the translocations (sex-Cy or Pm-Sb or H), would have appeared. The findings that free recombinations between all characters occurred in all 903 cultures is evidence that no translocation occurred either in the gametes from the 3N-female or in those of their diploid mates (table 1).

Besides the four regular classes eight other types of males appeared. They contained either none or both of the two dominant genes carried in the two chromosomes II or in the two chromosomes III of their father (table 2).

TABLE 2

Non-disjunction of II				Non-disjunction of III			
Both II from ♀ No II from ♂		Both II from ♂ No II from ♀		Both III from ♀ No III from ♂		Both III from ♂ No III from ♀	
$\frac{+}{+} \frac{Sb}{+}$	$\frac{+}{+} \frac{H}{+}$	$\frac{Pm}{Cy} \frac{Sb}{+}$	$\frac{Pm}{Cy} \frac{H}{+}$	$\frac{Pm}{+} \frac{+}{+}$	$\frac{Cy}{+} \frac{+}{+}$	$\frac{Pm}{+} \frac{Sb}{H}$	$\frac{Cy}{+} \frac{Sb}{+}$
5	1	6	1	1	1	4	1
6		7		2		5	

A test, carried out in each case, showed that the *two* mutant genes of one original pair were carried in different chromosomes in these exceptional males and were not, as a result of crossing-over in an earlier generation, carried together in one chromosome. This test was not possible in case *none* of the genes was present in the  $F_1$ -males, but the possibility of not otherwise detected crossing-over was very low. The fact that the  $P$ -males transmitted to these sons none or both of either their chromosomes II or III is best explained by the assumption of non-disjunction of these autosomes in the male. This non-disjunction must be comparatively frequent, considering, for example, the finding of 13 such cases for chromosome II among 903 gametes. This is especially clear if we consider that the appearance of the exceptional males is only possible when such non-disjunctive spermatozoa meet the right type of egg to give a viable male combination. For the spermatozoa which carry no chromosome II or III the chances of finding a favorable egg are good as a triploid female produces normally many eggs with two chromosomes II or III. For the spermatozoa with two chromosomes II or III, however, only eggs with no chromosome II or III will be fitted. Such eggs were not known to occur, but the fact that 7 exceptional  $F_1$ -males carrying both *Cy* and *Pm* in separate chromosomes II were found seems to indicate their occurrence.

It may be added that three of these males (in the  $\frac{Cy}{Pm} \frac{Sb}{+}$  class) carried also *Bar* (eye; B, I), which came from the 3N mother thus excluding any possibility of contamination. For the classes carrying both *Sb* and *H* the evidence is not quite as clear, as there was the possibility of *H* being present in some of the 3N-females, thus accounting for this class without the assumption of non-disjunction. The proportion in which the eight exceptional classes appeared are striking in different respects but should be tested by experiments especially designed for it before a discussion can be of value. Such experiments which will throw more light on the

new findings of non-disjunction in autosomes of triploid females and of males carrying inversions in their autosomes seem to be desirable. It should be noted that cases of autosomal non-disjunction in males which carry inversions have already been found by *Dobzhansky*<sup>2</sup> (1933) and by *J. Schultz* (unpublished). *Dobzhansky* and *Darlington* have observed cases of non-disjunction of autosomes cytologically in *Drosophila pseudo-obscura* (unpublished).

*Summary*.—1. No translocations between chromosomes I, II and III of *Drosophila melanogaster* were found in more than 900 eggs from triploid females and the equal number of spermatozoa from diploid males.

2. Non-disjunction of the autosomes in males, resulting in spermatozoa with two or none of a special pair of autosomes was frequent.

3. Triploid females frequently produced eggs which did not receive any of the chromosomes II or III.

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<sup>1</sup> Work done—as Fellow of the Rockefeller Foundation—at the Biological Laboratories of the California Institute of Technology, Pasadena, Cal.

<sup>2</sup> Dobzhansky, Th., *Zeitschr. ind. Abstgsl.*, **64**, 269–309 (1933).

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## UNISEXUAL MAIZE PLANTS AND THEIR RELATION TO DIOECISM IN OTHER ORGANISMS

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Dioecious plants occur naturally in at least 61 families scattered among some 48 orders of angiosperms in both monocotyledons and dicotyledons. With these unisexual plants there are often monoecious and hermaphroditic individuals in the same species. From the widespread distribution in the plant kingdom, it seems probable that various systems of partial and complete sex-separation have been developed. In 7 dioecious species of bryophytes and 51 dioecious species of angiosperms there are differences in the size, shape or number of chromosomes associated with the two sexes. In all but a few cases the female gametes are alike. In 33 dioecious species no allosomes have been found. Many hypothetical factors, both germinal and environmental have been postulated to account for the appearance of different sexes in the offspring from the same parents.

The occurrence of dioecious forms in a species that heretofore has not