A SPONTANEOUS SOMATIC EXCHANGE BETWEEN NON-HOMOLOGOUS CHROMOSOMES IN DROSOPHILA MELANOGASTER

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INTRODUCTION

THE first kind of exchange between chromosomes to be discovered in Drosophila was crossing over, a term which when used without qualification still stands for exchange between homologous chromatids at identical loci in the four strand stage of meiosis in the female.

Spontaneous somatic crossing over has subsequently been observed resulting from exchange between homologous chromosomes of cells of the soma in females and males, and also of gonial cells, that is of cells in all of which nuclear divisions are mitotic. The frequencies of all of these kinds of exchange is known to be affected by one or more of such agents as X-rays, temperature and the presence of Minute mutations.

Exchange between chromosomes at non-homologous loci may readily be induced by X-raying males or females either when mature or at different stages of development. The exchanges result in different kinds of aberrations; they may be interchromosomal translocations (between arms of different chromsomes) or intrachromosomal translocations (a), between different arms of the same chromosome, called "eucentric inversions" by CATCHESIDE (1938), (b), within one arm, that is inversions, or (c), transpositions which involve at least three breaks in one chromosome.

The nuclei in which observed translocations have been induced have been those of the germ track. Sperms, among mature and immature germ cells of both sexes, are most readily affected.

Spontaneous aberrations involving non-homologous loci are extremely rare in *D. melanogaster*. Pale translocation (BRIDGES 1923) arose without treatment and had its origin in germinal cells since it is transmitted. Similarly Translocation E (2; 3) (STURTEVANT and DOZBHANSKY 1930) almost certainly arose spontaneously.

Spontaneous translocations in the soma, due to exchange between chromosomes at non-homologous loci, may be still more rare. There has been some opportunity to detect them by a method suggested by STERN (1939). In flies heterozygous for an inversion or for a closed X chromosome, single crossing over leads to the formation of some nuclei of unbalanced constitution. STERN believes that some somatic cells containing unbal-

anced nuclei may survive in the soma and identifies them with very small patches found to contain often only one short, fine seta. He believes that if somatic non-homologous exchange occurred in flies of normal chromosome constitution, the altered constitution which results also from exchange in cells heterozygous for a translocation would be similarly detectable and would have been observed unless they occurred only with extremely low frequency. He also examined flies genetically marked in a manner that would certainly have disclosed recognizable spots if somatic non-homologous translocation had occurred with a frequency equal to that of somatic crossing over. But neither has this possible source of evidence yielded any results.

A very favorable opportunity for detection of spontaneous translocation in one kind of somatic tissue is afforded by all experiments involving the inspection of salivary glands. In the very numerous X-ray experiments that have been carried out, a spontaneous translocation in a cell destined to contribute to the salivary gland might have been detected in the glands of any larva whether it had developed from sperm affected or unaffected by the X-ray treatment. A larval gland in which such a spontaneous translocation had occurred would contain it in some of the nuclei. The larvae from affected sperm would contain, in addition, the induced translocation in all of their nuclei. No instance of a spontaneous somatic translocation in salivary glands seems to have been reported in the literature, but recently one has been found in a mutant stock of *Drosophila melanogaster*

NEW OBSERVATIONS

Salivary glands of stock B^{36j} were being examined for a possible visible alteration of the bands near the Bar locus which might be correlated with the slightly bar allele of *B*, as originally found in a y^2 male. No such change has so far been detected but the large autosomes of two (possibly three) cells of one gland show a translocation, T(2; 3)39b, not present in the other nuclei.

The exceptional nuclei are heterozygous for a reciprocal translocation between the right arm of the second chromosome and the right arm of the third (figure 1a, b). The breaks occur in regions 57B in the second and 98C in the third chromosome (following BRIDGES' system), points that are not far distant from the distal ends of the chromosomes. In both nuclei the unbroken chromosomes are synapsed with their fractional homologues at their distal ends. In one nucleus (figure 1a) the proximal fragmented 3R is synapsed with the normal 3R. The proximal fragmented 2R and the entire 2R remain unsynapsed for a long distance to the right of the break

and as far as they can be traced toward the chromocenter. In the other nucleus (figure 1b) the entire and the broken 2R are synapsed and the 3R chromsomes are largely unsynapsed.

In the same gland the other nuclei in which the chromosomes are sufficiently spread have been examined. In 11 nuclei the distal sections of 2R and 3R show clearly and are not in any way associated with each other. In 10 other nuclei either one or the other of the two distal ends of the two chromosomes in question is entirely free. Special study was made of the

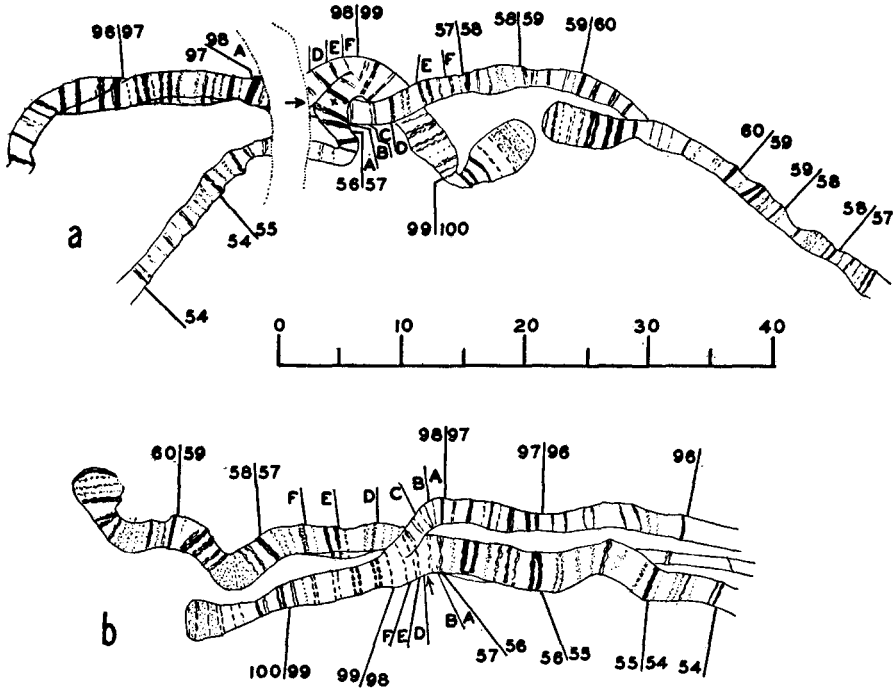

FIGURE 1.—Salivary chromosomes of two nuclei containing a somatic translocation, T(2; 3) 39b, between 2R and 3R. The region of one of the break-points is indicated by arrows. The scale (40 micra) indicates the magnification used in making the drawings.

more confused nuclei in which synapsis was not complete. In one of them two chromosomes are unsynapsed from a point near to the distal end of 2R, but the bands match in the haploid parts showing that there is no translocation with another chromosome. In two others haploid sections are not associated with a 2 to 3 translocation. One nucleus showing haploid strands has not been deciphered.

The observations are sufficient to show that a translocation occurred in the last or in a very late division in the nucleus of a somatic cell before the full number of cells of the salivary gland was attained.

DISCUSSION

The finding, in the soma, of a spontaneous occurrence of translocation, long known as a frequent kind of aberration induced in germ cells, leads to consideration of various effects on chromosomal behavior that have been obtained experimentally.

The extensive studies that have been made on the effects of external agents on interchange between chromosomes have shown that there are marked differences in the magnitude of effects of external agents on different kinds of exchange.

X-rays, high and sometimes low temperature and age, the presence of Minute mutations and sometimes the presence of the Y chromosome have been found to affect exchange between chromosomes at homologous loci in germ cells or somatic cells, usually causing increase in frequency of exchange especially near spindle fiber regions. Minutes have been found to increase somatic crossing over but when combined with high temperature there is a decrease (STERN and RENTSCHLER 1936). Induction by high temperature (WHITTINGHILL 1937) of exchanges between homologous chromosomes in the germ track of larval males produced no abnormal effect upon subsequent crossing over of the treated chromosome or viability of homozygotes, the usual properties of translocations. The same was found to be true of the majority of exchanges between homologous chromosomes obtained by PATTERSON and SUCHE (1934) from X-ray treatment of male larvae.

The order of magnitude of all of these several effects is not greater than that of temperature on chemical reactions. The processes affected, which include crossing over at meiosis, occur spontaneously with different but observable frequencies.

In addition to these effects X-rays cause random breaks, recoverable in translocations, which involve reattachment of broken ends at non-homologous loci.

Two results may be especially noted in connection with translocations or exchanges at non-homologous loci in *Drosophila melanogaster*. First, exchanges at non-homologous loci appear to be the least frequent of spontaneous exchanges, but they are the exchanges which are induced by X-rays, at least in germ cells, with high frequency increasing with the dosage. The rate of breakage may be so high that broken chromosomes recombined into viable combinations are present in as much as 40 percent of functional sperm (CATCHESIDE 1938; BAUER, DEMEREC and KAUFMANN 1938).

Second, in some X-ray experiments (MULLER 1925) interference was found to be but slightly, if at all, affected by the X-ray treatment, which

increased crossing over especially near the spindle fiber attachment. BAUER, DEMEREC and KAUFMANN point out that in contrast to the dependence of the position of one break upon the position of a second simultaneous break at crossing over, breaks induced by X-rays and found in translocations occur at random in euchromatic regions, that is the position of one break is independent of the position of another break in the same chromosome.

It appears then that X-rays may have two different, and both to some extent regionally differential, effects; they affect to a relatively slight extent (among other processes) the rate of crossing over, which is a natural ("spontaneous") process, depending on the properties and mechanism of the chromosomes and occurring regularly in all females; and X-rays also cause a high percentage of breaks in the chromosomes, many of which may be recovered in translocations but which are very rarely found in untreated material. The mode of reattachment of broken ends has not been solved even by recent critical experiments.

The possible importance of the telophase pattern of pairing of chromosomes in an understanding of aberrations was suggested by PAINTER (1934 and 1935). It has been emphasized also by DOBZHANSKY (1936) who found evidence from secondary spermatogonial nuclei of *Drosophila pseudoobscura* that if the telophase distribution is retained in young resting nuclei it must be more or less preserved during the entire interphase.

METZ (1916), from his extensive cytological studies of somatic, oogonial and spermatogonial cells of Drosophila and other Diptera, thought it highly probable that the chromosomes retain the telophase arrangement during the transformations in the resting nucleus.

MAKINO (1938) presents another kind of evidence in regard to the condition of the chromosomes in the resting stage. He has found that the definitive nuclei which are developed before larval stages, in *Drosophila virilis*, show in many tissues of the larva the same grouping of the haploid number of chromosomes that is found in salivary glands and Malphigian tubes. This involves close synapsis of homologues and attachment of one end of each of the chromosomes to a common center. He regards it as a condition of permanent resting stage. FROLOVA (1938) has made similar observations on various tissues of larvae of *melanogaster*, *virilis* and three other species of Drosophila.

If the telophase pattern persists through all stages of the nuclear cycle it is a comparatively constant factor in the origin of translocations.

In order to induce translocations in somatic cells contributing to the salivary glands, where rearrangements resulting from breaks might readily be observed, the embryo must be treated before the eighteenth hour of

development when the definitive number of cells of the salivary gland has been attained (POULSON 1937).

SUMMARY

An interchange of sections between the right arm of chromosome 2 and the right arm of chromosome 3 was found in two of the nuclei of a salivary gland of *Drosophila melanogaster*. Thus interchange between non-homologous chromosomes may, like mutation, elimination and regular and somatic crossing over, occur spontaneously in somatic nuclei of this species, though probably with relatively very low frequency.

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