* This investigation was supported by a research grant (USPHS C-1074-C4) from the National Cancer Institute of the National Institutes of Health, Public Health Service. The authors wish to express their indebtedness to Dr. L. C. Stevens for performing the ovarian transplantations described in this communication.

[1] H. Grüneberg, *The Genetics of the House Mouse* (2nd ed.; The Hague: Martinus Nijhoff, 1952); L. S. King and M. C. Meehan, "Spontaneous Demyelinating Diseases of Animals: A Study of Comparative Pathology," *Arch. Pathol.*, **46**, 567–598, 1948; P. J. Harman, "Genetically Controlled Demyelination in the Mammalian Central Nervous System," *Ann. N.Y. Acad. Sci.*, **50**, 546–550, 1954.

[2] R. D. Adams, D. Denny-Brown, and C. M. Pearson, *Diseases of Muscle* (New York: Paul B. Hoeber, Inc., 1954).

[3] G. G. Robertson, "Ovarian Transplantations in the House Mouse," *Proc. Soc. Exptl. Biol. Med.*, **44**, 302–304, 1940.

---

*RECOMBINATION INCREASE DUE TO HETEROLOGOUS INVERSIONS AND THE RELATION TO CYTOLOGICAL LENGTH**

BY HELEN REDFIELD

INSTITUTE FOR CANCER RESEARCH AND LANKENAU HOSPITAL RESEARCH INSTITUTE
PHILADELPHIA, PENNSYLVANIA

Communicated by L. C. Dunn, October 28, 1955

Various properties of the extreme left end of the X chromosome of *Drosophila melanogaster* make the region interesting for studies of the relationship of crossing over to chromatin. Among such properties is a disparity in the distances between loci as measured by the counting of bands in preparations of salivary gland chromosomes and the purely genetic distances given by linkage values. Thus the two short crossover intervals between *yellow* and *white* and between *white* and *split* are ordinarily equal; the standard linkage map gives them as 1.5 units each.[1] For comparison, the actual physical relations of these genes have been rather precisely defined by the cytological map of Bridges (1938); the number of bands from *yellow* to *white* (98) is approximately 20 times as great as the number (5) from *white* to *split*. One can, if he prefers, measure these distances in microns along the salivary gland chromosomes, but this is somewhat less objective, due to differential stretching. On Bridges' map,[2] however, the relative distances in this region remain in the same proportion no matter which cytological unit is used to measure separation, that is, banding or actual average distances along stretched chromosomes, and the disparity still holds—while the standard linkage values for the two subregions are 1:1, the cytological distances are as 20:1.

If the assumption is made that the structural relations are the same in the crossing-over chromosomes of the oöcytes as they are in the chromosomes of the somatic cells of the salivary gland, then it follows that there is 20 times as much crossing over per band in the *white-split* subregion as there is in the *yellow-white* subregion. (This is not meant to imply that crossing over necessarily occurs within the band.) The marked differential of 20 to 1 provides a convenient handle for experimentation, for, if the crossover values in the X can be changed by some agent external to it, then it can be determined whether the new values are approxi-

mately equal to each other or whether they become markedly unequal and are related (or are not related) to the difference in cytological length. In this connection it might be contended that crossing over is a direct function of length per se along the chromosomes and that the regional differences at the time of crossing over are not like those on the cytological map. Presumably there is less ground for believing that relative length as opposed to banding remains constant; of course, neither condition has been demonstrated. But however these matters eventuate, it is of interest to compare recombination changes in this region with the cytological map as it now stands.

The extreme left end of the X appears rather resistant to the usual agents which affect crossing over, such as temperature, X-rays, etc. However, the presence of heterozygous inversions in the autosomes has been shown greatly to increase recombination for the region. The presence of such heterologous inversions results in generalized increase in crossing over in noninverted pairs of the chromosome complement. These changes occur in a rather constant over-all pattern which displays some similarity to the pattern produced by other agents affecting crossing over (but there are differences). With heterologous inversions very large increases are shown near the centromere and typically also at free ends of the chromosome limbs; intermediate regions show increases, but these are less marked. (For a review see Schultz and Redfield.[3]) The problem of second-order differences has had little attention, but scattered bits of evidence, such as the exceptional decreases for the right end of III appearing in data of Steinberg and Fraser,[4] suggest that there is considerable variation within the pattern. It seemed desirable to set up a controlled experiment specifically to test the possible differential sensitivity, per unit of physical length, of the two small adjacent sections *yellow-white* and *white-split* to the booster effect on crossing over produced by simple inversions. The results have been presented in preliminary form elsewhere.[5]

Materials and Results.—Crossing over was measured in sister females of the composition *y* w^{51a}/*spl* of four types with respect to the inversions which they contained: those without inversions, those heterozygous for the left and right *Curly* inversions of II, those heterozygous for the left and right *Payne* inversions of III, and those simultaneously heterozygous for all four *Curly* and *Payne* inversions. The stocks used directly to derive the females, namely, *y* w^{51a}; *Cy*, sp^2/+ and *spl*; *Payne*, *Dfd ca*/+ (both continued by mating noninversion females by inversion males), were established from the highly inbred "p-1 Oregon-R" basic line of this laboratory; this made it reasonably certain that the chromosomes of tested females were alike except for the chromosomes containing the inversions. *White*^{51a} is a new occurrence of *white* which is phenotypically and cytologically indistinguishable from the original *white*. The structural picture of *white*^{51a} and the proper presence of the inversions were checked by the concurrent cytological study of Schultz and Hungerford[6] on inversion effects on patterns of pairing in salivary gland chromosomes of this same material.

All cultures and vials were kept at 25° C. Each virgin female from the early hatch of well-nourished parents was mated in a vial for one day with 10 tester males from y^2 *su-*w^a w^a *spl* stock (used instead of *y w spl* to insure proper fertilization of the non*yellow* females and to detect nondisjunction). She was then put with her males into a culture bottle, where she remained 5 days, and then was subcultured

for 5 days more. The number of such females per type varied from 13 for subcultures with *Curly* to 19 for the cultures with both *Curly* and *Payne*. Yields were good for all types; they varied from 205 per control female for subcultures to 237 per *Curly* female for first cultures.

The raw data and the crossover values with their differences are given in Table 1. The results are simple and consistent. It may be noted that crossing over without inversions is definitely below the expected standard value of 1.5 for each region, reaching only 0.4 and 0.5 for first cultures and 0.8 for both regions for subcultures. (Standard values are, of course, lumped values which presumably include data

TABLE 1

CROSSING OVER IN THE REGIONS *y-w*^{51a} AND *w*^{51a}*-spl* IN *y w*^{51a}*/spl* FEMALES WITH INVERSIONS INDICATED*

INVERSIONS	NONCROSSOVERS	SINGLE CROSSOVERS *y-w*^{51a}	SINGLE CROSSOVERS *w*^{51a}*-spl*	CROSSOVER VALUES *y-w*^{51a}	CROSSOVER VALUES *w*^{51a}*-spl*	DIFFERENCE
Age 2–6 days:						
None	2,119 + 2,101	17 + 5	6 + 11	0.5 ± 0.11	0.4 ± 0.10	0.1 ± 0.15
Cy	1,585 + 1,658	21 + 16	18 + 24	1.1 ± 0.18	1.3 ± 0.20	−0.2 ± 0.27
Payne	1,800 + 1,716	22 + 29	18 + 22	1.4 ± 0.20	1.1 ± 0.17	0.3 ± 0.26
Cy; Payne	1,932 + 2,079	61 + 66	41 + 63	3.0 ± 0.26	2.5 ± 0.24	0.5 ± 0.35
Age 7–11 days:						
None	1,841 + 1,785	16 + 15	11 + 20	0.8 ± 0.15	0.8 ± 0.15	0 ± 0.21
Cy†	1,462 + 1,508	19 + 24	18 + 26	1.4 ± 0.21	1.5 ± 0.21	0.1 ± 0.30
Payne	1,503 + 1,497	27 + 24	22 + 29	1.6 ± 0.23	1.6 ± 0.23	0 ± 0.33
Cy; Payne	1,970 + 2,057	79 + 81	61 + 60	3.7 ± 0.29	2.8 ± 0.25	0.9 ± 0.38

* In each pair of contrary classes the class with *yellow* is given first. Crossover percentages and the differences are given with their standard errors.

† Also one *y* F_1 male, presumably a double crossover, which proved sterile.

involving undetected heterologous inversions.) Within an age type, for these females lacking inversions, there is no statistically significant difference in crossing over between the two regions *y-w*^{51a} and *w*^{51a}*-spl*. In the females with *Curly* inversions, crossing over is significantly increased for both first and second cultures, the increase being approximately equal in each case for the two regions. Similar practically equal increases are produced in the presence of the *Payne* inversions. With both *Curly* and *Payne* inversions the increases are even more marked, but they still show no significant difference between the two regions. In no case for a given type is there a detectable difference between the increases for *y-w*^{51a} and *w*^{51a}*-spl*.

Just how great these changes are is shown in Table 2, which gives the ratios of crossing over in each region for each inversion type to crossing over without the inversions. Thus, with due regard to age of the mothers, the *Curly* and *Payne* inversions separately increase crossing over 2 to 3 times the value in the absence of

TABLE 2

INCREASES PRODUCED BY INVERSIONS EXPRESSED AS RATIOS OF CROSSING OVER IN *y w*^{51a}*/spl* FEMALES WITH INVERSIONS INDICATED TO CROSSING OVER OBTAINED IN SUCH FEMALES WITHOUT INVERSIONS

INVERSIONS	AGE 2–6 DAYS *y-w*^{51a}	AGE 2–6 DAYS *w*^{51a}*-spl*	AGE 7–11 DAYS *y-w*^{51a}	AGE 7–11 DAYS *w*^{51a}*-spl*
Cy	2.2 ± 0.52	3.3 ± 0.97	1.8 ± 0.43	1.9 ± 0.44
Payne	2.8 ± 0.73	2.8 ± 0.82	2.0 ± 0.47	2.0 ± 0.47
Cy; Payne	6.0 ± 1.42	6.3 ± 1.69	4.6 ± 0.93	3.5 ± 0.73

inversions; together, $3^1/_2$ to over 6 times. It is of some interest that the higher ratios appear in each case in the first cultures; the relatively greater inversion

effects are exhibited by females of age 2–6 days as compared with females of age 7–11 days. Of more significance for the present study is the fact that within these limits of the increases produced by the inversions (1.8–6.3 times), and for six different types with respect to age and inversions, there is no preceptible tendency for the increases to be greater in a region which would seem a priori to have 20 times the physical length available for accommodating them.

For the sake of the record, brief mention may be made of a later experiment, which was quite incomplete compared with the above but in which the same stocks were used (for another purpose) and which gave a result reasonably compatible with the results reported above. Counts were made for first cultures only (mothers of age 2–6 days) and for two types only, that is, for control females without inversions and for females with combined *Curly* and *Payne* inversions. The control crossover values (N = 1,557) were 0.51 ± 0.18 for *y-w*^{51a} and 0.45 ± 0.17 for *w*^{51a}-*spl*. In the presence of *Curly* and *Payne* inversions (N = 4,535), crossing over increased to 5.0 ± 0.32 and to 3.5 ± 0.27, respectively. It might seem that these values show somewhat different rates of increase for the two subregions, since the ratio produced by dividing the *Curly-Payne* value by the control value is 9.8 for *y-w*^{51a} and is 7.8 for *w*^{51a}-*spl*. However the difference, 2, between these ratios has a standard error of 4.6. The discrepancy is no doubt introduced, first, through the very low numbers in the control and, second, through the low magnitude of the control values. In any case the ratios as they stand are definitely more nearly equal than they are in the proportion of 20 to 1.

A few apparent exceptions exist, in other work on this region, to a definite equality of capacity to increase. Thus Lewis[7] in his study of the pseudoalleles of the *white* locus found that *yellow-apricot* crossing over for attached-X females was, in the presence of the inversions of *Curly* and *Ultrabithorax*^{130}, 6 times standard value, whereas *white-split* reached only 1.7 times standard value; no control without inversions was included here. Also, unpublished data of the present author, from females heterozygous for *apricot* and either *buff* or a new reversion of *buff* to wild type, gave increases with various inversions which in some cases were somewhat greater in the *yellow-white* subregion than in *white-split*. However, both these sets of experiments were designed for other measurements and are for a number of reasons not completely acceptable for the present comparisons. This is particularly true because of the lack of proper controls; it is common experience that *yellow-split* does not, in the complete absence of inversions, uniformly exhibit standard crossing over but may differ from stock to stock, and in certain stocks shows definite differences between *yellow-white* and *white-split*. Thus it seems likely that these cases would fall into line under more controlled experimental conditions.

However, it should be emphasized that the significant point is not the precise equality of the increases of the two subregions, which is approached in the present experiment. It is rather that such marked increases are possible in the *white-split* subsection which is relatively physically so minute, and especially that the increases here are of the same order of magnitude as those in the adjacent *yellow-white* subsection, which though still small, is structurally of a definitely higher order of magnitude. The difference between the subregions is in this respect a qualitative one. Per unit of length, *yellow-white* may be considered more nearly saturated in its ability to develop an increase than is *white-split*.

The data from Table 1 can be presented somewhat differently in terms of what Bridges[8] called "coefficients of crossing over," which provide a simple numerical measure of the differences between cytological and genetic distances. A region is said to have a coefficient of crossing over greater than 1, or a lesser 1, if it has, per unit of length, a greater, or a lesser, tendency to cross over than does the average unit of length of all the chromosomes taken together. Bridges was concerned primarily with the right distal tip of chromosome II, in which crossing over had been believed to be generally high, and indeed he found that the simple distances here were relatively much greater for the linkage map than for his cytological map. He was further interested in the fact that the high coefficient of crossing over for this region was independent of a similarly computed low coefficient of mutation, as defined in terms of the number of detected workable mutations per unit of length.

Such coefficients of crossing over making use of the whole chromosomal complement are not applicable in the present experiment, because of the presence of the inversions, but one can make use of modified coefficients which compare the two regions with the average, not of all the chromosomes, but of the whole X only in the same inversion type. For this the previous data of Redfield (reported briefly by Morgan, Redfield, and Morgan[9]) are employed which deal with the effects of the *Curly* and *Payne* inversions for the entire X in y^2 *cv v f/ec car bb* females. The measure of cytological length of the X is preferably not the length in microns which was used by Bridges but the number of bands; this, as noted above, is presumably a less subjective unit, since, while salivary gland chromosomes show marked differential stretching, their banding is constant (i.e., in the absence of deficiencies, etc.). Actually, the relative values attained by the coefficients are not, for the *y-w* and *w-spl* regions, particularly affected by the method of measuring the cytological distances. It may be recalled that the crossover values shown in Table 1 for mothers without inversions are definitely substandard; hence the coefficients given in Table 3 are undoubtedly consistently lower than would be expected under "standard" conditions; however, there is no obvious reason to suppose that this affects the comparison between the coefficients of the two regions within a type. Table 3

TABLE 3

EFFECTS OF INVERSIONS ON COEFFICIENTS OF CROSSING OVER OBTAINED BY COMPARING VALUES FROM *y* w^{51a}*/spl* FEMALES WITH THOSE FOR THE ENTIRE X FROM y^2 *cv v f/ec car bb* FEMALES*

INVERSIONS	COEFFICIENT		INVERSIONS	COEFFICIENT	
	y-w^{51a}	w^{51a}-*spl*		*y*-w^{51a}	w^{51a}-*sp*
None	0.11	1.87	*Payne*	0.18	3.08
Cy	.18	3.59	*Cy; Payne*	.29	4.19

* See text.

shows that, for mothers without inversions, crossing over per band is only 0.1 times as great in the *y*-w^{51a} region as it is per band in the X taken as a whole; with the *Curly* or *Payne* inversions taken separately, it is about 0.2 times as great; and with both *Curly* and *Payne* inversions, it is about 0.3 times as great. However, for the w^{51a}*-spl* region the corresponding values are roughly 2.0, 3.0, and over 4.0; thus the coefficients are, for each type, approximately between 15 and 20 times as great in the second region as in the first. Under the circumstances of use of data from two entirely different experiments, this is of course close to the 20-to-1 expectation.

The tangential question may arise whether the observed increases are due purely to the presence of the heterologous inversions or whether they depend also upon genic differences—in the present case dominants introduced in the inversion chromosomes, since the chromosomes of all females are otherwise the same. Certain anomalous results of Carson[10] in *D. robusta* and of Levine and Levine[11] in *D. pseudoobscura* have been assumed to depend upon genic differences superimposed upon inversion effects. However, in these two species the experiments are more difficult to interpret than are those in *D. melanogaster*, where special precautions can be taken with respect to the comparability of the females. And although one cannot now deny the possibility of minor genic influences, still the agreement in the nature of the results for many different inversions and for various regions of all major chromosomes indicates that, in the latter species at least, the inversions themselves are the primary influences responsible for the increases (see review by Schultz and Redfield[3]).

It should be noted further that the present results cannot easily be explained as the simple corollary of a selective disappearance of noncrossovers and other low-rank crossover strands or of nondisjunctional types (although such is undoubtedly involved in the changed weight of classes in some recombination data; see the work of Sturtevant and Beadle[12] and the recent paper of Cooper, Zimmering, and Krivshenko[13]). The increases produced by heterologous inversions seem rather to be dependent upon a real facilitation of exchange between homologues, for multiples of an extremely high rank and doubles within a very short region are found, and these particular classes do not appear under other circumstances. It is not just a matter of simple shift in the proportions of already existing classes. Thus in work not included in the present paper three tested doubles from three mothers have appeared in the *y-w-spl* region in the presence of *Curly* and *Payne*, or *Payne* and the left inversion only of *Curly;* and such doubles have not occurred in the absence of inversions. Also, there has been one tested quintuple for the second chromosome in the presence of *ClB* and *Payne* inversions (crosses mentioned by Morgan, Bridges, and Schultz[14]). Steinberg[15] reported one quintuple for the X with the use of *Curly* and *Payne*, and the tables of Steinberg and Fraser[4] show no less than six quintuples in III in the presence of various X-chromosome inversions. These seem to be the only reported quintuples for *D. melanogaster*.

The suggestion sometimes made of an explanation in terms of oögonial or other earlier crossing over may be mentioned, although there is no positive indication of such phenomena in these data with heterologous inversions. The increases held by Whittinghill[16] to be the result of this type of aberrant recombination are, so far as the evidence goes, restricted to the centromere region. If oögonial crossing over occurs at all under the circumstances of the present experiment, distal sections such as the *yellow-split* region used here are not expected to show increased recombination values under its influence..

Of considerable interest in connection with the increases produced by inversions is the cytological work of Schultz and Hungerford[6] (abstract) carried out simultaneously with, and on the same material as, the present crossing-over study. Their paper (presented at the 1952 meeting of the Genetics Society of America and kindly made available to me by the authors) compares the tendency to synapse of the homologous X chromosomes in the $y\ w^{51a}/spl$ females of the four inversion types.

Direct observations were made on the frequency, length, and position of asynaptic regions in the X chromosomes of salivary gland cells. Statistically significant differences were found, in the pattern of somatic synapsis, between females containing both *Curly* and *Payne* inversions and females without inversions; the former gave in their X chromosomes a greater proportion of short intercalary failures of synapsis. (For X chromosomes showing failures of pairing, 40 per cent of the failures were intercalary in females with *Curly* and *Payne*, as opposed to 17 per cent in females without inversions.) With the number of observations at hand it was not possible to establish a significant difference in this tendency for *Curly* and *Payne* taken separately. However, a further interchromosomal effect was definitely shown, in the presence of an extra set of autosomes, by the changed pairing of the two X chromosomes of intersexes (63 per cent intercalary versus the 17 per cent of the standard diploid). The cytological demonstration of the interchromosomal effects of the combined *Curly* and *Payne* inversions on the pattern of pairing of the X chromosomes has obvious possible bearing on increases in crossing over which are produced by interchromosomal effects on the X chromosomes by this same combination of inversions.

The specific mechanism responsible for the general pattern of interchromosomal effects cannot at this point be identified. It seems fairly clear that there is some relationship to such matters as the distribution of heterochromatin along the chromosome. The present results tell us a little about how the mechanism operates. They demonstrate in a controlled experiment, for a region of marked general increase, a constant difference in the capacity to react of very small adjacent subregions. One subregion which is 20 times the observed length of a second gives crossover increases which are equal to those of the second, and the increases produced remain equal for these two subregions for all the combinations of inversion and age types used. This suggests that the mechanism responsible for the increases in crossing over is distinct from the mechanism responsible for the local differences between linkage and cytological maps.

Summary.—Crossing over in the extreme left end of the X chromosomes in $y\ w^{51a}/spl$ females was measured for four inversion types: those without inversions, those heterozygous for the *Curly* inversions of II, those heterozygous for the *Payne* inversions of III, and those heterozygous for both *Curly* and *Payne* inversions. The inversion chromosomes taken separately increased crossing over 2 to 3 times the value without inversions; together, $3^1/_2$ to over 6 times; younger females giving the higher ratios. For each inversion type, crossover values for y-w^{51a} and for w^{51a}-*spl* were increased equally within the limits of error; this was true both of first cultures (age of mothers 2–6 days) and of subcultures (age of mothers 7–11 days). Since the cytological lengths of these two subregions are known to be as 20 to 1, there was a marked difference in the response of the subregions to the heterologous inversions with respect to the increase in recombination per unit of cytological length. Coefficients of crossing over for the subregions remained approximately in the ratio of 1 to 20. Thus the short distal *yellow-split* region, a region of marked general increase in the presence of the inversions, can still be separated into subregions acting in a constant relationship to one another as regards their capacity to increase per unit of length. The suggestion is made that the mechanism producing the increases is different from that which results in the discrepancies between linkage and cytological maps.

* This work was supported by a grant to Dr. Jack Schultz made by the American Cancer Society upon recommendation of the Committee on Growth of the National Research Council, and by an institutional grant of the American Cancer Society.

[1] C. B. Bridges and K. S. Brehme, "The Mutants of *Drosophila melanogaster*," *Carnegie Inst. Wash., Publ.*, No. 552, pp. 1–257, 1944.

[2] C. B. Bridges, "Cytological Maps for Chromosomes of *Drosophila melanogaster*," *J. Heredity*, Vol. 29 (suppl.), 1938.

[3] Jack Schultz and Helen Redfield, "Interchromosomal Effects on Crossing Over in *Drosophila*," *Cold Spring Harbor Symposia Quant. Biol.*, **16**, 175–197, 1951.

[4] A. G. Steinberg and F. C. Fraser, "Studies on the Effect of X-Chromosome Inversions on Crossing-over in the Third Chromosome of *Drosophila melanogaster*," *Genetics*, **29**, 83–103, 1944.

[5] Helen Redfield, "Effects of the Curly and Payne Inversions on Crossing Over in the Left End of the X Chromosome in *Drosophila melanogaster*," *Drosophila Information Service*, **26**, 118–119, 1952; "Crossing Over in the Left End of the X Chromosome of *Drosophila melanogaster* and Its Relation to Cytological Length," *Records Genet. Soc. Amer.*, **22**, 94, 1953.

[6] Jack Schultz and D. A. Hungerford, "Characteristics of Pairing in the Salivary Gland Chromosomes of *Drosophila melanogaster*," *Records Genet. Soc. Amer.*, **22**, 99, 1953.

[7] E. B. Lewis, "The Pseudoallelism of White and Apricot in *Drosophila melanogaster*," these PROCEEDINGS, **38**, 953–961, 1952.

[8] C. B. Bridges, "Correspondence between Linkage Maps and Salivary Chromosome Structure, as Illustrated in the Tip of Chromosome 2R of *Drosophila melanogaster*," *Cytologia, Fujii Jubilee Volume*, pp. 745–755, 1937.

[9] T. H. Morgan, Helen Redfield, and L. V. Morgan, "Maintenance of a *Drosophila* Stock Center, in Connection with Investigations on the Constitution of the Germinal Material in Relation to Heredity," *Carnegie Inst. Wash. Year Book*, **42**, 171–174, 1943.

[10] H. L. Carson, "The Effects of Inversions on Crossing Over in *Drosophila robusta*," *Genetics*, **38**, 168–186, 1953.

[11] R. P. Levine and E. E. Levine, "The Genotypic Control of Crossing Over in *Drosophila pseudoobscura*," *Genetics*, **39**, 677–691, 1954.

[12] A. H. Sturtevant and G. W. Beadle, "The Relations of Inversions in the X Chromosome of *Drosophila melanogaster* to Crossing-over and Disjunction," *Genetics*, **21**, 554–604, 1936.

[13] K. W. Cooper, S. Zimmering, and J. Krivshenko, "Interchromosomal Effects and Segregation," these PROCEEDINGS, **41**, 911–914, 1955.

[14] T. H. Morgan, C. B. Bridges, and Jack Schultz, "The Constitution of the Germinal Material in Relation to Heredity," *Carnegie Inst. Wash. Year Book*, **32**, 298–302, 1933.

[15] A. G. Steinberg, "The Effect of Autosomal Inversions on Crossing-over in the X-Chromosome of *Drosophila melanogaster*," *Genetics*, **21**, 615–624, 1936.

[16] M. Whittinghill, "Consequences of Crossing Over in Oögonial Cells," *Genetics*, **35**, 38–43, 1950; "Some Effects of Gamma Rays on Recombination and on Crossing Over in *Drosophila melanogaster*," *Genetics*, **36**, 332–355, 1951; "Crossover Variability and Induced Crossing Over," *J. Cellular Comp. Physiol.*, **45** (suppl. 2), 189–220, 1955.