THE COMPOUND X CHROMOSOMES IN DROSOPHILA

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Chromosomes formed by the union of homologous elements provide a situation in which somewhat more can be learned about the nature of the meiotic phenomena in Drosophila than may be deduced from a study of normal chromosomes. The classic example is, of course, the attached X chromosome; there are, however, five other types of compound X chromosomes theoretically realizable. All five are now known and have been studied to some extent. It is the purpose of this paper to describe the origin and synaptic properties of the newer compounds and to indicate the kinds of information that have come from a study of them.

Terminology

There are four ways in which two X chromosomes may be joined to give a compound with two ends. The centromere of the compound may be either median or terminal and, in each case, the two component chromosomes may be in reversed order with respect to each other or they may be arranged in tandem. A simple self-descriptive terminology is achieved if the compounds with median centromeres are referred to as metacentrics and those with terminal or subterminal centromeres as acrocentrics, and if these terms are preceded by tandem or reversed, depending on the relative order of the two components. The four possibilities are, then, the tandem metacentric, the tandem acrocentric, the reversed metacentric and the reversed acrocentric. It should be noted that the attached X chromosome is the reversed metacentric compound; the latter name is introduced here not to supplant the well established attached X designation, but to indicate the structural relation of the attached X to the other types.

Finally, there are two possible compounds in which the two X chromosomes are joined to form a continuous ring. Here also the two components may be in reversed or tandem order. The first is the reversed ring, the second, the tandem ring.

Origin of the Compound X Chromosomes

In principle, the detection of the different compounds is much the same. Females heterozygous for the two X chromosomes to be joined are mated to males carrying a sex-linked dominant, as, for instance, Bar. F1 female progeny are examined for the presence of Bar; those lacking it must have received both

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X chromosomes from the mother. Such exceptions are then tested to determine whether the two X's are free or whether they have been united.

The left column of figure 1 shows how, by simple crossing over in heterochromatic regions, most of these types might be synthesized. To indicate the relative order of the two chromosomes making up the compound, the letter p represents homologous regions at one end of the components, and the letter d the homologous regions at the opposite end. The nature of the attachments shown in figure 1 is obvious in most cases. The formation of the compound rings (lines 5 and 6) demands the union of the two free ends of a metacentric or acrocentric type. The tandem ring described below has been formed by a crossover between the distalmost heterochromatic region of the tandem acrocentric and a very short arm attached thereto specifically for the purpose of providing opportunity for an exchange to give this product. The reverse ring, on the other hand, might be formed (line 5) from an attached X provided with distal heterochromatin such that if pairing occurred in reverse order, as it might if the heterochromatic regions were derived from different sources, exchange would transform the attached X into a reversed ring. It was contemplated that it might be necessary to employ irradiation to effect this transformation, but before any attempt was made to produce this ring, it appeared spontaneously in a stock of the tandem ring, presumably by crossing over between the basal and interstitial heterochromatin in such a way as to invert one of the component chromosomes, in this particular case, the one in normal order.

The pairing relationships of these types are shown in the right column of figure 1. For simplicity the sister strands are omitted. The three reversed types pair by a simple foldback of the chromosome whereas the tandem types all pair spirally.

The attached X and the tandem metacentric (i.e., tandem attached) X chromosomes have received considerable attention previously and will not be considered in this work.

**THE REVERSED ACRONECTRIC COMPOUND X CHROMOSOME**

This chromosome type was first described by Muller (1943, 1944) and later by Valencia, Muller and Valencia (1949) and has been referred to by them as the double X chromosome. Its pairing properties are like those of an ordinary attached X chromosome (figure 1), the essential difference being its terminal centromere. The reversed acrocentrics derived by the above workers carried a heterozygous inversion, dl-49, which impairs the usefulness of these chromosomes for a study of crossing over.

Several new chromosomes of this type have been derived in a crossover experiment in which females heterozygous for In(1)sc8 and a normal chromosome, with sc cv v f as markers and with the long arm of the Y chromosome attached as an extra arm, were mated to y B males. Two F1 B non-yellow males appeared; they were interpreted as cases in which a crossover between the distal heterochromatin of In(1)sc8 and the proximal heterochromatin of
the normal X gave rise to a fragment carrying the small distal portion of the X not included in the sc\(^8\) inversion. An egg carrying such a crossover product, which would have the normal allele of yellow, when fertilized by an X-bearing sperm, would give rise to the B males. Because this was a crossover experiment in which only the male progeny were identifiable as crossover types, the female class had been disregarded, but the appearance of the B males led to
the examination of the progeny for matroclinous females, a class which might have the crossover product complementary to the fragments, i.e., a reversed acrocentric compound.

Of 8,906 F1 females examined, 9 were matroclinous, and of these, 4 were fertile and appeared to represent cases of attachment. Two of these were tested extensively, with the results given in table 1 in columns ND1 and ND9.

The consequences of exchange in this compound have previously been pointed out by Muller and co-workers. Single exchanges will produce no detectable effect if both strands involved are part of the same compound chromatid, but will produce second anaphase bridges when they come from different chromatids. Homozygosis in the progeny for mutants heterozygous in the mother is achieved only by double, or higher, exchange. When crossing over occurs freely, one expects a depressed number of female progeny, as well as a relatively infrequent occurrence of homozygosis. It is rather interesting to note that in both the above cases, mutants originally present in the normal chromosome appeared to be absent from the compound (f in ND1 and cvv f in ND9) and since the tests were made immediately after the recovery of the compound, it seems likely that the mutants were lost coincidently with its formation. Such a loss would require a double exchange, in addition to the single heterochromatic exchange furnishing the initial attachment; it should be considered, therefore, that the exchanges giving rise to the reversed acrocentric may be somewhat more complicated than the scheme presented above implies.

Additional information on the spontaneous origin of reversed acrocentrics has been collected by Mr. Larry Sandler of this department who has kindly consented to the inclusion of his data here. Of 15,575 female progeny from a cross of sc cv v f car/sc6 females x B males, 4 matroclinous exceptions were found. These proved to be simply nondisjunctural. However, a parallel cross using an X of normal sequence but with the long arm of the Y chromosome basally (sc cv v f : YL), gave 9,985 female progeny of which 13 were exceptional. Three of these were sterile or infertile, 5 were nondisjunctural and 5 had reversed acrocentric compound X chromosomes. This suggests that the presence, at the basal region, of material derived from the Y chromosome...
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facilitates the spontaneous occurrence of the kind of exchange necessary for the formation of this type. Of the five compounds, three were heterozygous for all the mutant alleles, one was homozygous for \textit{v} and \textit{f}, and another for \textit{f} only, the latter two paralleling the homozygosity for the wild type alleles characteristic of the first two analyzed. His results from tests of one of these newly derived reversed acrocentrics (ND18), heterozygous for \textit{cv}, \textit{v} and \textit{f}, are given in column 3 of table 1.

THE TANDEM ACROCENTRIC COMPOUND X CHROMOSOME

The tandem acrocentric compound was constructed in the manner indicated on line 4 of figure 1, i.e., by recovering the compound formed after attachment between the proximal heterochromatin of one chromosome and heterochromatin located distally in a second. The chromosome selected to provide the proximal heterochromatin was In(1)\textit{sc}^4 and the other, providing the distal heterochromatin was the X-Y chromosome. The X-Y chromosome is made up of an inverted X chromosome, with the short arm of the Y chromosome attached to the free end of the X and the long arm of the Y forming a second arm of the chromosome (LINDSLEY and NOVITSKI 1950).

Accordingly, females of the constitution \textit{y sc}^4 \textit{car m we}^a/In(1)\textit{dl-49}, \textit{y w lz}^a were mated to males carrying the X-Y chromosome. F\textsubscript{1} females heterozygous for the In(1)\textit{sc}^4 and X-Y chromosomes were irradiated and mated to B males and their progeny examined for non-Bar females. Of a total of 14,542 F\textsubscript{1} females counted, 10 were non-Bar, and of these nine were fertile. Further tests showed that six were simply nondisjunctional and three carried newly arisen compound X's. Two of them behaved like attached X's. The third, however, proved to be a tandem acrocentric compound X chromosome.

Reference to figure 2 and table 2 indicates the nature of the argument that this chromosome is, in fact, a tandem acrocentric compound. The large number of patroclinous males comes from the nullo-X eggs, which should amount to half of the total. The + females carry the compound X unaffected by exchange. The rest of the types are crossovers. It is interesting to note that a common single crossover product of the tandem acrocentric is a single chromosome. The region of the exchange responsible for the transformation of the tandem acrocentric into a single chromosome may be identified when the chromosome is recovered in an F\textsubscript{1} male, but cannot be identified when recovered in the female progeny since they carry the paternal X chromosome, which is marked only with Bar. The 110 heterozygous Bar females recovered in set 1 therefore represent single chromosomes recovered in the female sex compared to 119 recovered in the male. The total number of tandem acrocentrics recovered is only 16. Other types, occurring singly, and interpreted as a consequence of more complicated exchanges, are omitted from the table.

It was realized that the deficiency of the tandem acrocentric class in the progeny might result, in part at least, from a viability effect of an excessive amount of heterochromatin, since this compound would carry, adjacent to the centromere, the long arm of the Y chromosome and the basal heterochromatin
of the proximal component, an interstitial heterochromatic segment at the junction of the two components, and finally any heterochromatin present at the distal end of the In(1)sc4 chromosome. In addition, females with this chromosome would ordinarily have the Y chromosome of their father. Females carrying this chromosome were therefore mated to X-Y males in successive generations in order to remove the Y chromosome contributed by the father.

Figure 2.—Exchange in the tandem acrocentric compound heterozygous for car, m and w', showing the specific regions involved in the production of the various types of single chromosomes, the lower diagram illustrates the nature of the difference between the two distinct types of single exchanges.

The results from such females lacking a Y chromosome are given under set 2 in table 2.

The effectiveness of removing the Y chromosome is shown by the increase in the percentage of tandem acrocentric-bearing progeny recovered in the second set, 10.6%, as opposed to 4.1% in the first set. Confirmation of this is provided by a comparison of the numbers of male and female progeny carrying single chromosomes generated by crossing over. In set 1, they are recovered equally frequently (119 males: 110 females) but in set 2, where the females
are heterozygous for the X-Y chromosome, and consequently have the equiva-

cient of an extra Y chromosome, the ratio of males to females is 185:88. On
the basis of these results all subsequent experiments involving compound X
chromosomes have involved the use of the X-Y chromosome.

The inequality of the numbers of single and compound chromosomes recov-
ered merits comment. The higher frequency of single chromosomes might
appear to be a manifestation of the type of nonrandom disjunction which has
been found in certain cases where heteromorphic dyads are produced by cross-
ing over (Novitski 1951). However, it can easily be shown that, although
the configurations after crossing over are of the heteromorphic dyad type, the
data do not indicate any nonrandomness in this case. The argument may be
most simply stated in the following way. For each type of exchange producing
a single chromatid and leaving the compound intact, there should be another

<table>
<thead>
<tr>
<th>TABLE 2</th>
<th>The types of progeny produced by females with tandem acrocentric chromosomes heterozygous for the mutants w*, m and car, mated to sc51 BlnSw*d sc8 (Muller-5) males (set 1) and X-Y, v/f males (set 2).</th>
</tr>
</thead>
<tbody>
<tr>
<td>Set 1</td>
<td>Set 2</td>
</tr>
<tr>
<td>1. Patroclinous males</td>
<td>Muller-5</td>
</tr>
<tr>
<td>X-Y, v/f</td>
<td>...</td>
</tr>
<tr>
<td>2. a. Noncrossovers</td>
<td>+ ♀</td>
</tr>
<tr>
<td>b. Single crossovers in</td>
<td>mcar ♀</td>
</tr>
<tr>
<td>region A</td>
<td>car ♂</td>
</tr>
<tr>
<td>region B</td>
<td>+ ♂</td>
</tr>
<tr>
<td>region C</td>
<td>Total singles recovered in ♂♀</td>
</tr>
<tr>
<td>Singles in A, B or C recovered in ♂♀</td>
<td>B/+ ♀</td>
</tr>
<tr>
<td>c. Double crossovers in</td>
<td>m ♀</td>
</tr>
<tr>
<td>regions B and C</td>
<td></td>
</tr>
</tbody>
</table>

It should be noted that although only single exchanges are considered here, the net result
from double exchanges is equivalent to that from singles. Since the triple
chromosomes cannot be recovered, a correction must be made to account for
this class by doubling the number of tandem acrocentrics recovered (or by
halving the number of singles). On this basis, the best comparison of the fre-
quencies of the two types comes from set 2 and is given by the ratio of the
males carrying a single chromosome to double the number of females with a
tandem acrocentric, i.e., 185 to 164.

A more precise method of testing for the presence of nonrandomness involves
the derivation of a simple equation from the algebraic expressions for the
consequences of each type of exchange, which then expresses nonrandomness,
c, directly as a function of the frequencies of the observed classes. This had
been done previously for the tandem metacentric compound (Novitski 1951); the formula for the tandem acrocentric differs only in that two of the coefficients are changed:

\[ c = \frac{\text{Single chromosomes}}{(4 \times \text{Patroclinous})} + \frac{2 \times \text{tandem acrocentrics}}{\text{Single chromosomes}} + \text{C.F.} \]

where C.F. represents a correction factor dependent upon the relative frequencies of the tetrads of ranks 1 and 2, and upon \( c \) itself, but amounting to a few percent, at most.

When the best estimate available for determining these classes is substituted, a \( c \) value of 0.48 is obtained, which, after the addition of the small correction factor, brings \( c \) so close to 0.5 that there can be little doubt that nonrandomness does not appear to be operating here.

**THE TANDEM COMPOUND RING**

The tandem compound ring was formed in the manner indicated on line 6 of figure 1. In order to facilitate crossing over between the distalmost segment of the tandem acrocentric compound and the long arm of the Y chromosome which forms the short arm of this chromosome, the fragment from \( T(44)BB \) carrying the centromere of the X and the segment up to and including the Bar locus was added. A crossover attaching this basal piece of the translocation removes the normal allele of yellow found at the tip of the \( Y^p \) in the X-Y chromosome used in making up the tandem acrocentric. Many offspring of irradiated females carrying the tandem acrocentric and the \( B^s \) fragment were examined, and a small number were found which were simultaneously yellow and Bar; these proved to carry the desired attachments. Such a tandem acrocentric compound X chromosome now has an extensive homologous region at the base and at the tip, arranged in such an order as to produce a tandem ring, if crossing over should occur between them, an event which would be easily detectable since such a ring chromosome would lack the Bar locus. One such yellow non-Bar female appeared in the progeny of \( yB \) mothers; the presence of a large double sized ring was confirmed cytologically. All experiments have been performed with the progeny of this female.

The pairing configuration of this ring is illustrated in figure 3. Crossing over of nonsister chromatids can give rise to a number of different products, these are given in table 3. The designations of types of exchange in this table follow that shown in the figure.

The tandem ring chromosome as finally derived is homozygous for yellow and miniature. There are no heterozygous mutants present suitably located for making observations on frequencies of homozygosis, or relative frequencies of exchange in different regions of the chromosomes. The mutant allele \( w^a \) is heterozygous, but its position is so unfavorable from the standpoint of providing information that it has been disregarded. Instead, the number of single chromosomes produced is used as a measure of the frequency of exchange and a simple estimate of the total number of eggs with X chromosomes, or prod-
The essentially different types of exchange theoretically expected in the tandem compound ring configuration. A catalog of the consequences after exchange is found in table 3.

The first tests of females carrying the tandem ring, y m, X-Y v f B males produced the following types in the F1: 8224 v f B males; 1844 v f B/y m females; 2095 y m males and 735 y m females. There are several points about these data worth mentioning: (1) The discrepancy between the numbers of single rings recovered in females and males, 1844 to 2095; (2) the gross inequality between the number of single and double rings recovered, 3939 to 735, and (3) the much greater number of patroclinous males recovered than ring-bearing individuals.

The greater frequency of ring-bearing males than females may be interpreted as a depression of the female class because of the excess heterochromatin present on the X-Y chromosome as well as that present in duplicate adjacent to the centromere on the single ring, an effect analogous to that discussed in the section on the tandem acrocentric. For this reason, the appropriate figure for

TABLE 3

Expected consequences of exchange of ranks 0, 1 and 2 in the tandem ring chromosome. Certain types which represent duplicates of those given below are omitted when such omission does not lead to an error in calculating the frequencies of expectation of the distinctively different types.

<table>
<thead>
<tr>
<th>Rank</th>
<th>Crossovers involved</th>
<th>Relative frequency</th>
<th>Products after second anaphase division</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>None</td>
<td>$E_0$</td>
<td>Double ring + Double ring</td>
</tr>
<tr>
<td>1</td>
<td>A, B or E, C, D or F</td>
<td>$\frac{1}{2}E_1$</td>
<td>Single ring + acentric ring + Double ring</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Bridge</td>
</tr>
<tr>
<td>2</td>
<td>A + E, D + F, A + F, C + E, B + E, B + F, C + F, D + E</td>
<td>$\frac{1}{8}E_3$</td>
<td>Single ring + acentric rings + Single ring</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Bridge + acentric ring</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Bridge + acentric ring</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Bridge + acentric ring</td>
</tr>
</tbody>
</table>
the recovery of single rings will be arrived at by doubling the number of males carrying rings rather than by addition of the male and female classes.

From table 3, it is apparent that single and double exchanges are similar in that (assuming no chromatid interference) 25% of the products are single rings, 25% are double rings and 50% give rise to lethal zygotes. These lethal zygotes result from the formation of dicentrics or triple rings; the latter would be recoverable only in superfemales, a class which has not been seen. Since single rings are recovered in both sexes in the F1 irrespective of the type of sperm fertilizing the egg, and the compound rings only after fertilization of the egg by a nullo-X sperm, the total number of compound rings must be multiplied by a factor of two. The comparison is then 4190 single rings to 1470 compound rings. It should be noted that if the tandem ring were about 37% as viable as the single ring produced by it, the number of ring-bearing eggs accounted for (single rings + tandem rings + dicentrics = 4190 + 4190 + 2(4190) = 16,760) would be in good agreement with double the number of patroclinous males (2 \times 8224 = 16,448), which would suggest that no special assumptions need be made to account for the behavior of the tandem ring chromosome. It will be shown below, however, that there is reason to believe that the viability of the tandem ring may not be this low.

While most of the patroclinous males undoubtedly arise in the usual way, i.e., from the fertilization by X-bearing sperm of that half of the egg nuclei not receiving an X, it seemed conceivable that if certain types of second anaphase bridges persisted as bridges, a nullo-X egg might be formed by the exclusion of the bridge, or any breakage product of it, from the egg nucleus. This might happen for either of two reasons: (1) the bridges formed by crossing over in the tandem ring are unlike ordinary anaphase II bridges, in that two chromatids connect each centromere and (2) a new type of bridge could appear as a result of the intertwining of the ring chromatids. The distinction between the usual and the two new possible origins of nullo-X eggs is easily made by the simple addition of a genetically marked fragment which ordinarily disjoins from the compound X, for the nullo-X eggs formed in the usual way will carry the fragment whereas the latter two types will not.

The fragment used is that described by Novitski (1951) and designated as FR2. It is made up of the long arm of the Y chromosome and the distal uninvetred segment from In(1)sc8 carrying the normal allele of yellow. Accordingly, females of the constitution y m, tandem ring/FR2, y+ were mated to y B males. The progeny consisted of 2530 B males, 254 y B males, 766 y B/y m females, 913 y m males, 245 y m females and 3 m females. The last class is nondisjunctional, the egg nucleus having included within it both the ring and the fragment; the small size of this class testifies to the regular separation of these two chromosomes. Consequently we may regard the 2530 B males as coming from the usual nullo-X class and the 254 y B males as a new nullo-X type, probably produced in one or the other of the two ways postulated above.

The results can now be analyzed in much the same way as in the preceding
case. If we multiply the best figure for the occurrence of single rings by four, we arrive at a value of 3652, an unusually high value since four times the number of single rings recovered in the males should not exceed the number of patroclinous males (2530). It is clear that the discrepancy between the single rings and the double rings persists in this experiment.

THE REVERSED COMPOUND RING X CHROMOSOME

During the course of an experiment conducted by Mr. Stanley Zimmering of this department involving the tandem ring, a number of females being tested produced, not the usual array of types including single chromosomes, but only patroclinous daughters and patroclinous sons, that is, they behaved as though they carried ordinary attached X chromosomes. It was clear that the tandem ring chromosome had, in some way, stabilized itself, a condition that would have been selected for rather strongly in the stock cultures from which the females were taken.

Cytological examination revealed the nature of this stabilization. Prophases of larval neuroblasts showed that a double ring was still present and, in the salivary gland chromosomes, the two components could be seen to be arranged in reverse order, with the yellow ends of both components now located adjacent to the centromere. Cytologically, then, this chromosome satisfies the definition of the reversed compound ring and the genetic results agree with this determination.

While the reversed ring chromosome is of interest in its own right, one arising from the tandem ring is of particular interest since it throws some light on the question of the viability of the tandem ring, for the essential difference between the two lies, not in their gene content, but in the order of the components. Whether the two are identical genetically cannot, of course, be determined, since this would depend on the nature of the event leading to the transformation. It seems most likely that this change took place by, first, pairing of the interstitial heterochromatic segment located between the two components and the heterochromatin on one side or the other of the centromere and, second, the occurrence of an exchange in such a direction as to invert that component found in normal order (see fig. 4).

The consequences of exchange in the reversed ring chromosome parallel those in the reversed acrocentric X chromosome. No new recoverable chromosome types (like single chromosomes) are produced regularly, as they are in the tandem ring. In the absence of heterozygous mutants, exchanges can be considered to consist of two types: either they have no detectable effect, or they produce bridges, and, barring chromatid interference, these two types should occur equally frequently in tetrads of all ranks except, of course, zero. One should, therefore, observe a reduction in the number of reversed rings recovered, because of exchange and also because of any inviability inherent in the ring itself.

From a mating of females of the constitution double ring, \( y^m/FR2y^+ \) to \( X-Y, yB \) males, the \( F_1 \) consisted of 3951 \( B \) males, 391 \( yB \) males, 1443 \( y^m \)
females and 13 \( m \) females. The last class is nondisjunctual. If the total number of X eggs is taken as twice the number of fragment bearing males, \( (2 \times 3951 = 7902) \), then 2912 \( (= 2 \times 1456) \) of these are accounted for as double ring-bearing eggs, the doubling of the class being necessary since only that half of the ring-bearing eggs fertilized by nullo-X sperm are recoverable. But, except for the no exchange tetrads, there should be as many inviable zygotes from bridge formation as there are recoverable reversed rings. If all tetrads were to have at least one exchange, then the corrected figure for the number of reversed rings would be \( 2 \times 2912 \) or 5824. The figure for the viability of females carrying the reversed ring then becomes \( 5824/7902 \), or .74 of the \( B \) male class. On the other hand, if crossing over were completely suppressed in this configuration, the relative viability would then be \( 2912/7902 \) or .37. The frequency of exchange for this particular compound is not known, but unless it is basically different in its behavior from the other compound chromosomes,

![Diagram](image)

**Figure 4**.—The heterochromatic pairing relationships and crossover event that could convert the tandem ring into the reversed ring.

and particularly from the tandem ring from which it originated, it may be surmised that the viability value for the reversed ring is closer to the higher limit than the lower.

**DISCUSSION**

For each of the new compound X chromosomes described here, there is presented a set of presumably typical data which indicates a gross parallel between the theoretically expected behavior and the observed. In no case have the analyses been sufficiently detailed to determine whether there is complete agreement between the expectations based on the usual assumptions of crossover analyses and the observations; this is particularly true of the two compound rings since the observations were made without benefit of heterozygous loci, and it might be pointed out that a study of crossing over using chromosomes devoid of markers must leave some questions unanswered. For the tandem ring, the production of single rings is used as the measure of exchange.
But for the reversed ring, the only criterion of exchange is the depression of the female class in the progeny and this depression, unfortunately, is equally interpretable as a simple viability effect.

There are, nevertheless, several points that may be made on the basis of the data presented above. First, it is of interest to note that the tandem acrocentric compound described here does not behave in the anticipated way with respect to nonrandom disjunction. It had been shown previously (Novitski 1951) that the analysis of crossover data from experiments involving heteromorphic homologues leads to the conclusion that when a heteromorphic dyad is produced by crossing over, the smaller of the two chromatids is included in the functional egg nucleus of Drosophila more often than the larger. Since the tandem acrocentric also produces heteromorphic dyads after exchange, one might expect it to behave similarly. The results using this chromosome indicate that it does not. There appears to be no satisfactory explanation for this behavior of the tandem acrocentric at the present time. One possibility is that the presence of the long arm of the Y chromosome as an additional arm on both chromatids (see fig. 2) minimizes the relative difference between the two dissimilar chromatids.

The regular recovery of single ring chromosomes from the tandem ring with a frequency not far from expectation is of particular interest. Simultaneously with the production of single centric rings, acentric rings also may be formed and the evidence indicates that they must have little, if any, influence on the recoverability of the single centric rings. If crossing over were the consequence of a breakage of two nonsister chromatids, followed by an uncoiling and refusion of broken chromatids, the result would be an interlocked complex with the rings intertwined around each other. In the absence of any special faculty of the chromosomes to free themselves permanently from such interlocks (unlike the breakage of chromatids at the succeeding anaphase which would lead to interlocks in subsequent anaphases), the acentric fragments, as passive participants in such interlocks, might lead to an appreciable loss of the rings generated by crossing over. Since the data deny any appreciable loss of single centric rings, it seems reasonable to suggest that the mechanism of crossing over may be other than that described above.

In this connection, it should be pointed out that the genetic consequences of interlocking of ring chromatids after crossing over and the implications of the absence of a deficiency of rings with respect to theories of crossing over have been considered by others but that in previous work involving rings, all rings were centric, leaving open the possibility that interlocks formed in this way would simply break at anaphase, followed by a refusion of the broken chromatids to reconstitute normal rings. It was for the elucidation of this point that the tandem ring was synthesized.

**SUMMARY**

Two X chromosomes of *D. melanogaster* may be joined together in six structurally distinct ways. Four of the combinations have two free ends. When
the centromere is located medially, as it is in the attached X, the compound is referred to as a metacentric, and when the centromere is located terminally (or subterminally), it is called an acrocentric. In each case, the order of the two X chromosome components may be tandem or reversed (mirror image). Furthermore there are two compound rings, one with the two components in tandem and the other with the two components reversed with respect to each other. The six types of compounds are, then, the attached X (reversed metacentric), the tandem metacentric, the reversed acrocentric, the tandem acrocentric, the tandem ring and the reversed ring. The reversed types synapse by a simple foldback of the two components, whereas the tandem types synapse spirally. All the tandem compounds are unstable and produce single chromosomes by crossing over.

All six types are now known; data are presented indicating that the new types, the acrocentrics and the rings, behave in a way not inconsistent with the simple predictions based on the present knowledge of crossing over in Drosophila. The tandem ring produces single centric and single acentric chromosomes by crossing over. The absence of an appreciable deficiency of the single centric rings suggests that the centrics and acentrics are not ordinarily interlocked after crossing over, a condition which would have some bearing on theories of the mechanism of crossing over.

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LITERATURE CITED