THE significance of chromosomal rearrangements of various kinds in the adaptive polymorphism of many animal and plant species depends to a large extent on their effects on crossing over. In Drosophila species, crossing over does not normally occur in the male, so that we are only concerned with the effects of rearrangements on crossing over in oogenesis. The evidence (Morgan, Bridges and Schultz 1930; Sturtevant and Beadle 1936; Steinberg 1936, 1937; Komai and Takaku 1940, 1942; Steinberg and Fraser 1944; Dobzhansky and Epling 1948; Schultz and Redfield 1951; Carson 1953) has been almost entirely genetic, cytological studies being technically too difficult in this material. Among the effects of heterozygosity for paracentric inversions in Drosophila the following are well-established; (1) almost complete suppression of effective crossing over within the limits of the inversion, due in part to elimination of crossover strands in the polar body nuclei, (2) suppression or drastic reduction of crossing over outside the inverted region, both proximally and distally, (3) an increase in the amount of crossing over in the other members of the chromosome complement (the “Schultz-Redfield effect”). Most of those who have studied these phenomena seem to consider that the second type of effect extends as far as the ends of the chromosome limbs, but Komai and Takaku (1940, 1942) have reported an actual increase of crossing over near the distal end of the Drosophila virilis X chromosome when two heterozygous inversions were present in the proximal region.

Highly complex systems of chromosomal polymorphism are now known in many species of grasshoppers, and more particularly in those belonging to the North American group Trimerotropi (see White 1954a, pp. 148–155 for a general review). The most characteristic type of rearrangement in this group has the effect of converting an acrocentric chromosome into a metacentric element. Such rearrangements are accordingly pericentric; whether they are actually inversions is still uncertain, but appears probable (a detailed study of the pachytene bivalents is needed to settle this point).

Rearrangements of this type are not confined to the group Trimerotropi. They occur, for example, in certain races or populations of the Australian grasshoppers Cryptobothrus chrysophorus and Austroicetes pusilla and in at least four species of the genus Moraba, which belongs to a different family of grasshopper-like insects (the Eumastacidae). As previously pointed out (White 1951) such rearrangements, when heterozygous, almost completely suppress chiasma formation in the segment between the two centromeres of the bivalent, so that hardly any chromatids with duplications and deficiencies are produced at meiosis, at any rate in the male. Thus the regions which are structurally heterozygous are genetically isolated and no gene-transfer can occur between them.
The present study represents an attempt to determine more precisely the general effects of these pericentric rearrangements on chiasma formation, and hence on genetic recombination, in the chromosome segments outside the limits of the rearrangement. Since in grasshoppers chiasmata are formed in both sexes it would be necessary to have data from both oogenesis and spermatogenesis in order to present a complete picture; but for technical reasons it is hardly practicable to carry out a cytological study on the oocytes and the investigation was accordingly limited to spermatogenesis.

MATERIALS AND METHODS

It was important for the present purpose to study chromosomes that could be recognized from cell to cell and from one individual to another. Out of several dozen cases of ‘heteromorphic’ chromosomes available for study, four were selected for detailed analysis, one in *Trimerotropis sparsa* (material from various localities in Utah and Nevada), two in *T. gracilis* (material from the Humboldt Range, Nevada) and one in *Moraba scurra* (material from Blundells, Australian Capital Territory). In addition, some studies on the effect of different numbers of heterozygous rearrangements on the amount of recombination in the entire chromosome complement were carried out on Californian material of *Trimerotropis suffusa*. All the material of *Trimerotropis* spp. was sectioned, but in the case of *Moraba scurra* both sections and squash preparations were employed.

The Sevier rearrangement in *Trimerotropis sparsa*

On a number of alkali flats in western Utah and eastern Nevada there live populations of *Trimerotropis sparsa* in which almost every individual has one or more chromosome pairs structurally heterozygous (White 1951). One rearrangement, in the largest chromosome, which is particularly recognizable, has been called Sevier. The Standard first chromosome is acrocentric, while the Sevier one is a metacentric with two rather unequal arms. The appearance of *St/St*, *St/Sev* and *Sev/Sev* bivalents with various numbers of chiasmata is shown in figure 1. It will be noted that the *St* chromosome usually shows a conspicuous constriction very close to its proximal end, which separates an ovoid satellite from the main body of the chromosome. It is uncertain whether this is actually the centromeric constriction, i.e. whether the satellite represents the second arm of the chromosome. Occasionally, the constriction and satellite are not visible, and whenever this is so the condition is constant throughout the individual (a bivalent in the middle of the top row in figure 1 is heterozygous for the absence of the satellite). Probably a minute rearrangement affecting the centromere region is present in some individuals in heterozygous or homozygous form. This rearrangement is, however, fairly uncommon in the populations studied and there is no reason to believe that its presence or absence affects the chiasma frequency of the bivalent. No constriction can be seen in the centromere region of the *Sev* chromosome at first metaphase.

The number of chiasmata in the first bivalent was counted in 14 *St/St*, 23 *St/Sev* and 9 *Sev/Sev* individuals (table 1), the total number of bivalents examined being 4168. Most of the individuals were collected at a locality approximately 5 miles SE of Cherry Creek, White Pine Co., Nevada, but a few of them came from Milford,
FIGURE 1.—The various appearances assumed by the largest bivalent of *T. sparsa*, according to whether it is heterozygous or homozygous for the Standard and Sevier sequences and according to the number of chiasmata in the distal and proximal regions.

**TABLE 1**

<table>
<thead>
<tr>
<th>Type of bivalent</th>
<th>Individuals number and location*</th>
<th>0 prox. dist.</th>
<th>0 prox. 2 dist.</th>
<th>0 prox. 3 dist.</th>
<th>1 prox. 0 dist.</th>
<th>1 prox. 1 dist.</th>
<th>1 prox. 2 dist.</th>
<th>2 prox. 0 dist.</th>
<th>2 prox. 1 dist.</th>
<th>Mean Prox.</th>
<th>Mean dist.</th>
<th>Total bivalents</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>St/St</em></td>
<td>14 CC</td>
<td>74</td>
<td>96</td>
<td>—</td>
<td>24</td>
<td>860</td>
<td>60</td>
<td>1</td>
<td>3</td>
<td>0.875</td>
<td>1.105</td>
<td>1118</td>
</tr>
<tr>
<td><em>St/Sev</em></td>
<td>16 CC + 4 M</td>
<td>1441</td>
<td>784</td>
<td>6</td>
<td>—</td>
<td>3</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>2234</td>
</tr>
<tr>
<td></td>
<td>3 B</td>
<td>309</td>
<td>9</td>
<td>—</td>
<td>—</td>
<td>25</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>343</td>
</tr>
<tr>
<td><em>Sev/Sev</em></td>
<td>8 CC + 1 M</td>
<td>54</td>
<td>35</td>
<td>—</td>
<td>3</td>
<td>326</td>
<td>55</td>
<td>—</td>
<td>—</td>
<td>0.798</td>
<td>1.108</td>
<td>473</td>
</tr>
</tbody>
</table>

* CC indicates a locality 5 miles S.E. of Cherry Creek, White Pine Co., Nevada; M indicates Milford, Utah; B indicates a locality near Beaver, Utah.

† Complete data on file at the GENETICS Editorial Office.

Utah and three individuals, which will be discussed separately, were collected at Beaver, Utah.

In table 1 the terms 'proximal' and 'distal' are used to designate the regions of the Standard chromosomes corresponding to the short and long limbs of the one carrying the Sevier rearrangement. There is, of course, no difficulty in deciding whether a
chiasma is in the ‘proximal’ or ‘distal’ segment of the $St/Sev$ or $Sev/Sev$ bivalent. In the case of an $St/St$ bivalent, however, there is nothing to mark the boundary between the two regions and the scoring of chiasmata as proximal or distal is less objective. Since, however, the great majority of the chiasmata lie clearly in one region or the other, only a small number lie so close to the boundary that any real doubt exists. A few errors of assignment have probably been included in the data, but these must have been far too few to affect the validity of the conclusions reached. A study of diplotene bivalents showed that there is no appreciable terminalization of chiasmata except in the case of ones very close to the chromosome ends.

Considerable heterogeneity between individuals was evident in the data. Thus in the case of $St/St$ individuals the chiasma frequency of the proximal region ranged from 0.640 to 0.970 and that of the distal region from 0.850 to 1.393. In the case of the $Sev/Sev$ individuals the corresponding ranges were from 0.489 to 1.000 and from 1.000 to 1.257. Such variation from one individual to another is characteristic of chiasma frequency data. It is shown, for example, in Montalentí’s (1947) Simulium data, in Callan and Montalentí’s (1947) data on various species of mosquitoes, and even in the grasshopper Bryodema tuberculatum with extreme chiasma localization (White 1954b). It is not known to what extent this variation results from genetic causes or is due to environmental influences (age may be an important factor).

In figure 2 the average chiasma frequencies of the proximal and distal regions of
St/St, St/Sev and Sev/Sev bivalents are shown (these frequencies are the means of the separate means of individuals). In calculating the means for the St/Sev bivalents the data for the three individuals from Beaver have been omitted, for reasons explained later. The analysis of variance (using the angle transformation) showed that there was no significant difference between the chiasma frequencies of the proximal segments in St/St and Sev/Sev bivalents, and the same is obviously true for the distal segments. However, St/Sev bivalents have a significantly higher chiasma frequency in the distal segment than either of the homozygous types. It will be seen that in St/Sev bivalents the chiasma frequency of the proximal region (except in the Beaver individuals) is virtually zero. Thus we may say that chiasma formation is almost completely suppressed within the structurally heterozygous region. But heterozygosity for a proximal rearrangement seems to actually increase the chiasma frequency of the regions beyond the rearrangement (from approximately 1.10 to 1.37).

Any chiasmata formed in the “prohibited” proximal region of St/Sev bivalents would lead to chromatids carrying duplications and deficiencies (White 1951). Such chiasmata, if they occurred, would be expected to cause partial sterility. In the Cherry Creek and Milford material only 3 such chiasmata (out of a total of 3033) were found. In the three individuals from Beaver the chiasma frequencies of the two regions of the heterozygous bivalent are quite different from those found in the Cherry Creek and Milford populations: there is a significant chiasma frequency in the proximal region between the two centromeres (0.07 as contrasted with <0.001 in the Cherry Creek and Milford heterozygotes) and the chiasma frequency in the distal region is much lower. Since these were the only individuals collected at Beaver, no homozygotes are available for comparison and the data on the three heterozygotes have accordingly been omitted from the comparison between the three types of bivalents. It is possible that the three individuals from Beaver are heterozygous for a rearrangement which is cytologically indistinguishable from Sevier but is in fact different.

The individuals from Beaver are interesting since they prove conclusively that chiasmata can be formed in the “prohibited” proximal region of bivalents heterozygous for pericentric rearrangements. Regardless of whether Sevier is a shift or an inversion, the 25 bivalents (out of 343) which formed chiasmata in the prohibited region would have produced 50 sperm chromosomes with duplications or deficiencies, out of a total of 1372, i.e. about 3.6%. Thus if heterozygosity for Sevier is maintained at a high level in the Beaver population it must either confer a heterotic advantage sufficient to compensate for this loss of fertility, or the loss in fertility must be in reality less than appears from the data.

The Humboldt rearrangement in Trimerotropis gracilis

At the south end of the Humboldt Range, Pershing Co., Nevada, in a sagebrush environment at approximately 6000 ft elevation there exists a population of Trimerotropis gracilis in which chromosomes 5, 6, 7, 8 and 9 are heteromorphic. The rearrangement in chromosome 6 only involves a minute region adjacent to the centromere, so that it is most difficult to identify. Chromosomes 7 and 8 are both trimorphic, i.e. the population contains two different metacentric types of each as well as the
EFFECT OF PERICENTRIC REARRANGEMENTS ON RECOMBINATION

<table>
<thead>
<tr>
<th>Type of bivalent</th>
<th>No. of individuals</th>
<th>0 prox. 1 dist.</th>
<th>0 prox. 2 dist.</th>
<th>1 prox. 0 dist.</th>
<th>1 prox. 1 dist.</th>
<th>Mean Prox.</th>
<th>Mean dist.</th>
<th>Total bivalents</th>
</tr>
</thead>
<tbody>
<tr>
<td>St/St</td>
<td>19</td>
<td>554</td>
<td>14</td>
<td>338</td>
<td>298</td>
<td>0.501</td>
<td>0.745</td>
<td>1204</td>
</tr>
<tr>
<td>St/Ht</td>
<td>10</td>
<td>612</td>
<td>3</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>1.005</td>
<td>615</td>
</tr>
</tbody>
</table>

* Complete data on file at the Genetics Editorial Office.

acrocentric one. Chromosome 5, on the other hand, is represented only by two easily distinguished types, one acrocentric and one with an almost median centromere. The former will be referred to as the Standard type, the rearrangement present in the latter being called Humboldt. The Standard 5th chromosome occurs in this population with a frequency of approximately 0.73, the frequency of Humboldt being about 0.27 (figures based on an analysis of 559 male individuals or 1118 chromosomes collected in 1949, 1950, 1951).

For the purposes of the present investigation the Humboldt rearrangement has one serious disadvantage, since bivalents homozygous for Humboldt are easily confused with bivalents 1, 2, 3 and 4 (all of which are invariably metacentric in this population, with the single exception of chromosome 4, in one individual, noted below). Thus it was only possible to compare the chiasma frequencies of the proximal and distal segments in St/St and St/Ht bivalents, those of the Ht/Ht bivalents being impossible to determine without serious errors.

The chiasma frequency data for 19 St/St and 10 St/Ht males are given in table 2. In the case of St/St bivalents there is hardly ever any difficulty in deciding whether a chiasma lies in the proximal or the distal section. As in the case of T. sparsa, there was a most striking heterogeneity in the data for St/St individuals. However, there can be no doubt that the mean chiasma frequency of the distal segment rises from about 0.74 in the St/St bivalent to slightly above 1.0 in the St/Ht one, the difference being highly significant.

Rearrangements in chromosome 7 of Trimerotropis gracilis

In a few instances, in the Trimerotropine grasshoppers, two different pericentric rearrangements have managed to establish themselves in the same chromosome, thus creating a ‘triad’ of gene sequences. This is so in the case of the 7th chromosome in the Humboldt Range population of T. gracilis, which is represented by an acrocentric type (Standard) a metacentric with markedly unequal arms (Oreana) and another metacentric with nearly equal arms (Rochester). The frequencies of these types during the years 1949 and 1950 were approximately: Standard—0.123; Oreana—0.563; Rochester—0.314 (based on an analysis of 446 individuals, i.e. 892 chromosomes).

In this case we have six types of bivalent to consider: St/St, St/Or, St/Roch, Or/Roch, Or/Or, and Roch/Roch. In the Or/Roch bivalent there are three regions in which chiasmata might, theoretically, be formed. We may call these the proximal, median and distal segments. In the St/Roch and Roch/Roch bivalents there is nothing
Chiasma frequency data on the rearrangements in chromosome 7 of *T. gracilis*

<table>
<thead>
<tr>
<th>Type of bivalent</th>
<th>No. of individuals</th>
<th>1 prox.</th>
<th>1 med.</th>
<th>1 dist.</th>
<th>1 dist. 1 prox.</th>
<th>Total bivalents</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>St/St</em></td>
<td>3</td>
<td>51</td>
<td>8</td>
<td>55</td>
<td>13</td>
<td>127</td>
</tr>
<tr>
<td><em>St/Or</em></td>
<td>5</td>
<td>-</td>
<td>13</td>
<td>237</td>
<td>-</td>
<td>250</td>
</tr>
<tr>
<td><em>St/Roch</em></td>
<td>5</td>
<td>-</td>
<td>-</td>
<td>250</td>
<td>-</td>
<td>250</td>
</tr>
<tr>
<td><em>Or/Roch</em></td>
<td>5</td>
<td>-</td>
<td>-</td>
<td>235</td>
<td>-</td>
<td>235</td>
</tr>
<tr>
<td><em>Or/Or</em></td>
<td>5</td>
<td>97</td>
<td>135</td>
<td>-</td>
<td>18</td>
<td>250</td>
</tr>
</tbody>
</table>

* Complete data on file at the GENETICS Editorial Office.

Chiasma frequency of *Roch/Roch* homozygotes

<table>
<thead>
<tr>
<th>Number of individuals</th>
<th>1 chiasma</th>
<th>2 chiasmata in same limb</th>
<th>1 chiasma in each limb</th>
<th>Total bivalents</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>254</td>
<td>4</td>
<td>8</td>
<td>266</td>
</tr>
</tbody>
</table>

* Complete data on file at the GENETICS Editorial Office.

to mark the boundary between the proximal and median segments, and in the *St/Or* and *Or/Or* bivalents there is nothing to mark the boundary between the median and distal segments; while in the *St/St* bivalents all three segments are arbitrary.

Chiasma frequency data for five different types of bivalents are given in table 3. In the case of the *Roch/Roch* bivalents there is no detectable difference in length between the two arms (one of which corresponds to the proximal + median segments, the other to the distal one); the data for this type of bivalent are accordingly given separately in table 4.

The general picture which emerges from these data on the chiasma frequencies of the various segments in the different kinds of bivalents is shown diagrammatically in figure 3 (it being assumed that the chiasma frequency of the two arms of the *Roch/Roch* bivalent is the same). It will be clear that the chiasma frequency of the proximal segment is zero in all the heterozygous combinations, and that the median segment also has a zero chiasma frequency in the *St/Roch* and *Or/Roch* bivalents. The chiasma frequency of the distal segment, which is <0.6 in the homozygous bivalents, rises to about 0.95 in *St/Or* and to 1.0 in *Or/Roch* and *St/Roch*.

Out of 250 *Or/Or* bivalents (table 3) 97 have a single chiasma in the short arm, 135 have a single one in the long arm and 18 have chiasmata in both arms. This indicates a chiasma frequency of 0.46 in the short arm and 0.61 in the long one. If there were no interference across the centromere, one would expect that 70.2 of the 250 bivalents would show chiasmata in both arms and 52.6 would lack a chiasma altogether. The data thus provide evidence of strong interference between the two arms of the bivalent.

An unusual type of rearrangement in *Trimerotropis gracilis*

A rearrangement which has several interesting properties was found in the heterozygous condition in a single individual in the Humboldt Range population of *T.*
EFFECT OF PERICENTRIC REARRANGEMENTS ON RECOMBINATION

**Figure 3.**—Diagram showing the chiasma frequencies of the various chromosomal regions in the different kinds of 7th bivalents in the Humboldt Range population of *T. gracilis*.

*gracilis* (out of 559 collected in 1949–1951). In this individual, chromosome 4, which is invariably metacentric in the other 558 individuals, is represented by an acrocentric and a metacentric. It was possible to analyse 124 first metaphases in the testis of this grasshopper. In 23 of them there was a 4th chromosome bivalent of the usual heterozygous type (i.e. with a single chiasma in the distal segment); in 74 there was a chiasma in the ‘short arm’ of the acrocentric; and in the remaining 27 cells the 4th chromosome was represented by two univalents (fig. 4). In no case were chiasmata simultaneously present in the short arm and the distal segment, so as to produce a ring-bivalent.

Several tentative conclusions may be drawn from these data. Assuming that univalents segregate at random, about 11% of the gametes of the individual in question must have lacked chromosome 4 or have carried it in duplicate. Haploidy or trisomy for such a large element is likely to be lethal or strongly deleterious, and in fact no individuals carrying 1 or 3 4th chromosomes have been encountered. Thus, on the assumption that the aneuploid sperms are functional, the fertility of this individual was probably only about 89% of normal, which is much more serious than the loss of fertility in the three individuals of *T. sparsa* from Beaver (estimated at 3.5%). It is unlikely that any increase in viability, due to heterosis, will be great enough to compensate for a loss of fertility amounting to 11%. Thus the acrocentric type of chromosome 4 must be at a selective disadvantage in the Humboldt Range.
FIGURE 4.—Three types of first metaphases met with in an individual of *T. gracilis* heterozygous for an unusual type of rearrangement in chromosome 4.

FIGURE 5.—The various forms assumed by the second largest chromosome in *Moraba scurra*, heterozygous and homozygous for the Standard and Blundell sequences, according to whether there is only a distal chiasma (1 D), only a proximal one (1 P) or a chiasma in both the distal and proximal regions (1 P, 1 D).

population. Since there is no evidence that it is transmitted to more gametes than the metacentric type, it could not be expected to persist at this locality. Its presence in a single individual may be due to its being a recent chromosomal mutation. More probably, it has reached the Humboldt Range locality by immigration from a colony.
EFFECT OF PERICENTRIC REARRANGEMENTS ON RECOMBINATION

TABLE 5

<table>
<thead>
<tr>
<th>Type of bivalent</th>
<th>No. of individuals</th>
<th>1 S.A.*</th>
<th>1 S.A.</th>
<th>0 prox. 1 dist.</th>
<th>1 prox. 0 dist.</th>
<th>1 prox. 1 dist.</th>
<th>Mean prox.</th>
<th>Mean dist.</th>
<th>Total bivalents</th>
</tr>
</thead>
<tbody>
<tr>
<td>St/St</td>
<td>4</td>
<td>—</td>
<td>—</td>
<td>112</td>
<td>97</td>
<td>491</td>
<td>0.811</td>
<td>0.841</td>
<td>700</td>
</tr>
<tr>
<td>St/Bl</td>
<td>4</td>
<td>—</td>
<td>—</td>
<td>800</td>
<td>—</td>
<td>—</td>
<td>0.000</td>
<td>1.000</td>
<td>800</td>
</tr>
<tr>
<td>Bl/Bl</td>
<td>7</td>
<td>3</td>
<td>1</td>
<td>278</td>
<td>421</td>
<td>497</td>
<td>0.762</td>
<td>0.630</td>
<td>1200</td>
</tr>
</tbody>
</table>

* S.A.—a chiasma in the minute short arm of an acrocentric chromosome.
† Complete data on file at the GENETICS Editorial Office.

where it is not deleterious, either because the metacentric type of 4th chromosome is absent or in which, for one reason or another, univalents are not produced in 4th chromosome heterozygotes. The presence of a supernumerary chromosome in 2 out of the 559 individuals of the Humboldt Range population examined may be additional evidence in favor of the view that some immigration has occurred (a beneficial supernumerary should be much commoner and a deleterious one would be expected to become extinct unless its presence was due to immigration from a locality in which it was not deleterious).

The fact that the heterozygous 4th chromosome bivalents form chiasmata either in the short arm or in the external segment (but not in both) is remarkable. If chiasma-formation in these two segments were independent we should expect approximately 13.7 of the 124 bivalents to possess chiasmata in both segments, whereas in fact none of them did so. Formally, the situation might be ascribed to strong chiasma interference. But a type of interference which extends over a long pericentric rearrangement is unprecedented, and it seems more likely that the mechanism of synopsis in this bivalent is peculiar in some way and permits pairing in either the short arm or the external segment but not in both regions of the same bivalent.

The Blundell rearrangement in Moraba scurra

A description of the cytology of this species will be published elsewhere, as part of a general account of the cyto-taxonomy of the genus Moraba and its relatives. For the present it will be sufficient to state that _M. scurra_ has 2n = 15 and that the Blundell rearrangement occurs in the second largest chromosome, which cannot be confused with any other member of the complement. There is some reason to believe that this element was originally metacentric and derived by fusion between two acrocentric chromosomes C and D which are separate in some other members of the genus. Thus we shall refer to the condition where both second chromosomes are acrocentric as _Bl/Bl_, individuals with two metacentric second chromosomes being regarded as homozygous Standard. The frequency of the metacentric (Standard) chromosome in the population studied is about 0.49, that of the Blundell chromosome being approximately 0.51 (based on a sample of 52 individuals, i.e. 104 chromosomes).

As shown in table 5 the chiasma frequency of the distal segment of the bivalent was always 1.0 in the _St/Bl_ heterozygotes, but averaged 0.84 and 0.63, with a range from 0.22 to 0.97 in the homozygotes. Thus, in spite of considerable heterogeneity among both classes of homozygotes, there is a highly significant increase in the
chiasma frequency of the distal segment in the heterozygotes, exactly as in the species of Trimerotropis. The chiasma frequency data for the proximal and distal segments of the second bivalent in the \(St/St\) individuals, like those for the Oreana homozygotes of \(T. gracilis\), provide evidence for interference across the centromere region.

**Chiasma frequency and structural heterozygosity in a population of Trimerotropis sujsusa**

In the examples discussed above, the reduction in the chiasma frequency of the various bivalents, caused by the structural heterozygosity, depends largely on the homozygous chiasma frequency. Thus the reduction was 0.57 for the Sevier rearrangement in the largest chromosome of \(T. sparsa\), in which the average chiasma frequency of homozygous bivalents was 1.94. In the heterozygous bivalents of \(T. gracilis\) (Humboldt rearrangement and the various sequences of chromosome 7) and in those of \(M. scurra\), the chiasma frequency in all cases was 1.00, the reduction being 0.24, 0.07 and 0.52. There are, in addition, in the Trimerotropine grasshoppers, many instances of small chromosomes with pericentric rearrangements, whose chiasma frequency is always 1.0 (i.e. in which structural heterozygosity causes no change in the chiasma frequency of the chromosome as a whole, although it undoubtedly affects the chiasma frequency of the various regions). In all cases where the chiasma frequency of the homozygous bivalent is greater than 1.0, it seems likely that structural heterozygosity causes a diminution in chiasma frequency. This diminution must be small in some cases, but may be greater than 0.5 in bivalents with high chiasma frequencies.

We may now inquire what the situation is in populations with much cytological polymorphism, i.e. with many multiple heterozygotes. In particular, we wish to know whether the reduction in chiasma frequency which occurs in heterozygous bivalents is compensated for, to any extent, by a rise in the chiasma frequency of the other members of the chromosome set, i.e. whether the "Schultz-Redfield effect" operates in these grasshoppers. In an attempt to answer this question the chiasma frequencies of 45 individuals of Trimerotropis sujsusa from a population inhabiting the vicinity of Truckee, California were determined. The number of structurally heterozygous bivalents in these individuals ranged from 0 to 6. In most cases the individual bivalents cannot be identified with certainty, so that only the total chiasma frequency of the chromosome complement could be ascertained (there are 11 autosomal bivalents in this species). In the absence of the Schultz-Redfield effect one would expect the total chiasma frequency to decline as the number of heterozygous bivalents increases. The extent of this decline would depend on the homozygous chiasma frequency of the bivalents which were heterozygous. Thus if all rearrangements were in bivalents whose homozygous chiasma frequency was 1.5 or greater, a decline in total chiasma frequency of at least 0.5 per heterozygous bivalent would be expected. However, the decline would be much less if rearrangements were above average frequency in "short" chromosomes. There is no reason for believing that in \(T. sujsusa\) rearrangements are more frequent in chromosomes with few chiasmata per bivalent. In the Truckee population (excluding chromosome 10—see table 6) the average total chiasma frequency of the 28 individuals with 0, 1 and 2 heterozygous
TABLE 6

Chiasma frequency per nucleus in 45 individuals of Trimerotropis suffusa from Truckee, California

<table>
<thead>
<tr>
<th>No. of bivalents heterozygous</th>
<th>No. of individuals studied†</th>
<th>Mean chiasma frequency of 11 bivalents</th>
<th>S.E. of mean†</th>
<th>M.S. (individuals)</th>
<th>M.S. (residual)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>3</td>
<td>14.2</td>
<td>±0.56</td>
<td>7.0**</td>
<td>0.98</td>
</tr>
<tr>
<td>1</td>
<td>12</td>
<td>14.4</td>
<td>±0.28</td>
<td>24.9**</td>
<td>0.88</td>
</tr>
<tr>
<td>2</td>
<td>13</td>
<td>14.6</td>
<td>±0.26</td>
<td>33.2**</td>
<td>0.94</td>
</tr>
<tr>
<td>3</td>
<td>10</td>
<td>14.2</td>
<td>±0.30</td>
<td>5.0**</td>
<td>0.86</td>
</tr>
<tr>
<td>4</td>
<td>6</td>
<td>13.9</td>
<td>±0.39</td>
<td>4.8**</td>
<td>0.64</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>13.8</td>
<td>±0.98</td>
<td>-</td>
<td>0.68</td>
</tr>
<tr>
<td>Total</td>
<td>45</td>
<td>14.3</td>
<td>±0.14</td>
<td>19.4**</td>
<td>0.86</td>
</tr>
</tbody>
</table>

* The small 10th bivalent is disregarded in this column, since its chiasma frequency is invariably 1.0, regardless of whether it is homozygous or heterozygous. Thus some individuals counted as having x bivalents heterozygous actually had x + 1.
† 20 cells scored in each individual.
‡ Estimated as $\sqrt{\frac{I}{n} + \frac{R}{20n}}$ where $I$ is the variance among individuals (estimated from the whole sample) and $R$ is the variance among cells in individuals.
** Significant at 1 percent level.

bivalents is 13.47. Assuming that chiasma frequency and rearrangement frequency are independent, one would expect a decline in total chiasma frequency of approximately 0.35 per heterozygous bivalent if the Schultz-Redfield effect were not operating.

On the other hand, if the Schultz-Redfield effect were operative, one would expect no decline in total chiasma frequency until a stage which we may term "interference saturation" is reached (i.e. beyond a certain point one would expect that the Schultz-Redfield effect would be unable to compensate for the loss of chiasmata due to increasing heterozygosity). The data obtained are set out in table 6. Analysis of variance shows that the differences in chiasma frequency between the six classes of individuals are not significant. (Mean square among heterozygous classes only 0.6 as large as that among individuals in classes.) Taking the whole of the data, the regression of chiasma frequency on number of heterozygous bivalents is $-0.13 \pm 0.14$. The negative sign of the regression is derived entirely from the 7 individuals in the last two classes (those with 4 and 5 heterozygous bivalents). It is possible that this is the level at which "interference saturation" is reached. Since we do not know just how much the chiasma frequency of the individual bivalents is decreased by structural heterozygosity, a rigorous proof that the Schultz-Redfield effect is operating is not possible. However, the data do very strongly suggest that it is operative, and in any case indicate that in a population with extreme structural hybridity there is little or no difference in chiasma frequency between the most heterozygous individuals and the structurally homozygous ones.

If we include chromosome 10, which is ignored in table 6, the mean heterozygosity of the Truckee population is 2.6 (i.e. each individual has, on the average, 2.6 structurally heterozygous bivalents). The eastern race of T. suffusa, which inhabits Colo-
rado and Wyoming, is much less heterozygous, a population from Archuleta Co., Colorado having a mean heterozygosity of 0.3. As shown in table 7, the chiasma frequency of the individuals in this population is significantly higher than in the Truckee population. There is also a higher variance in the number of chiasmata per cell in the Archuleta Co. individuals.

The data in table 6 do not suggest that the difference between the chiasma frequencies of these populations is determined by differences in heterozygosity. The increased chiasma frequency of the Colorado population seems more likely to result from decreased interference. The difference in variance among cells of individuals may reasonably be ascribed to the same cause, especially as there is no significant or important difference among residual variances of the classes of table 6. The excess chiasma frequency, over the 11 necessary for normal disjunction, is 4.8 in the Colorado population and 3.3 in the Truckee population. The ratio of the excess chiasmata is 1.45 and of variances 1.66. These ratios agree well within the sampling errors of such estimates, suggesting that both increased chiasma frequency and increased variance among cells are expressions of decreased interference.

Differences in total chiasma frequency among individuals of the Truckee population may be caused in part by the chiasma frequencies of those bivalents which are heterozygous for a rearrangement. However heterogeneity among individuals without heterozygous bivalents in this and also in the Colorado population may well reflect genetic variations. Differences between the populations are presumably largely genetic in origin. Therefore there seem to be reasonable grounds for believing that the degree of interference has different optima in different localities and that this character is subject to natural selection.

**DISCUSSION**

In such organisms as grasshoppers the chromosomes are only held together in bivalents after pachytene by the presence of chiasmata. If a chiasma is not formed, the two chromosomes will fall asunder and behave as univalents which will pass to the same anaphase pole at the first meiotic division in approximately 50% of cases. Thus in grasshoppers the only rearrangements which can be expected to survive are those which leave the chromosome with a chiasma frequency $\geq 1.0$ in all heterozygous and homozygous combinations, and in all genotypes which it may encounter in the population. The rearrangements which we can study in natural populations
are hence not a random sample, natural selection having eliminated any which reduced the chiasma frequency to a point where regularity of disjunction was adversely affected. The situation may be different in Drosophila where, as Cooper (1945) puts it, chiasmata are only a sufficient and not a necessary cause for normal segregation.

It is accordingly not surprising to find that the pericentric rearrangements of grasshoppers, when heterozygous, do actually increase the chiasma frequency of the distal region (although, in the case of the Sevier rearrangement the increase seems to be greater than is strictly necessary to ensure regular disjunction). The actual mechanism responsible for producing this increase is almost certainly the removal of the interference which in structurally homozygous bivalents is caused by the presence of chiasmata in the proximal region. The physical basis of chiasma interference is, of course, still unknown, but the phenomenon itself is probably found in all species that form chiasmata at meiosis (Haldane 1931; Callan 1949; Callan and Montalenti 1947; Montalenti 1947).

In general, we may regard chiasma interference as an adaptive property of genetic systems, since it permits each bivalent to form at least one chiasma, without the bivalents having an inordinately high chiasma frequency (if there were no chiasma interference and the numbers of chiasmata followed the Poisson distribution the mean would have to be over 5 per bivalent in order to ensure a negligible proportion of bivalents with 0 chiasmata). The existence of this interference has permitted certain pericentric rearrangements to establish themselves in grasshopper populations without causing frequent nondisjunction. But it was certainly present in the species long before the origin of the rearrangements.

The effects of structural rearrangements in grasshopper chromosomes on the chiasma frequency of the region outside the rearrangement appear at first sight very different from those found in the case of Drosophila by Dobzhansky and Epling (1948) and other workers. There can be no doubt that this difference is partly genuine. To some extent, however, it may reflect the respective disadvantages of the genetic and cytologic methods of analysis. Dobzhansky and Epling were only able to study crossovers in the genetically marked regions of the chromosome; it is at least conceivable that crossing over was actually increased beyond the marked region, as in the case of D. virilis, studied by Komai and Takaku. Conversely, in the present work, the data by no means exclude the possibility of a decrease in the chiasma frequency of the region immediately adjacent to the rearrangement—but if such a decrease exists it must be more than compensated for by an increased distad.

The data from the Truckee population of T. sujusa provide some evidence that the Schultz-Redfield effect is not confined to Drosophila. It is probable that the mechanism underlying the effect is a very general one, since Mather and Lamm (1935) demonstrated that in Secale and Vicia the variation in chiasma frequency among cells was less than that which would be expected on the basis of the distribution of chiasmata in bivalents in cells (assuming in the case of Secale that the various bivalents have the same chiasma frequency). These results suggested that a reduction in chiasma frequency in one bivalent was compensated by increased chiasmata in one or more other bivalents. In other words, there was a tendency for individual cells to have very similar numbers of total chiasmata. Rearrangements are unlikely to
have been important in the material studied by Mather and Lamm. Therefore a mechanism probably exists for damping variation in total cell chiasma frequency, whether such variation arises from structural heterozygosity or some other cause. (Using some recently popular terminology, one might state that the Schultz-Redfield effect is an expression of a "homeostatic" mechanism which maintains chiasma frequency close to some value which is presumably optimal for the population.)

**SUMMARY**

1. In three species of grasshoppers, pericentric rearrangements effectively suppress chiasma formation within the region heterozygous for the rearrangement.

2. The chiasma frequency of regions distal to the rearrangement is, however, increased by heterozygosity for pericentric rearrangements.

3. These results are interpreted in terms of chiasma-interference. In several instances it is shown that interference may extend across the centromere.

4. Presumably due to the operation of the "Schultz-Redfield" effect, in a population of grasshoppers containing from 0 to 6 structurally heterozygous bivalents per individual, the frequency of structural heterozygosity has little or no influence on total chiasma frequency.

**ACKNOWLEDGMENTS**

The material of *Trimerotropis sparsa*, *gracilis* and *suffusa* was collected with the aid of grants from the American Philosophical Society and the Research Institute of the University of Texas to the senior author. Dr. T. C. Hsu, Mr. Frederick L. Petersen and Mr. Homer W. Phillips helped to collect the material in the field. We are grateful to Dr. Marvin Wasserman, Dr. Frances E. Clayton and Mr. W. L. Evans, formerly graduate students at the University of Texas, for assistance in the preparation of the slides.

**LITERATURE CITED**


