CHIASMA STUDIES IN STRUCTURAL HYBRIDS. X.
FURTHER STUDIES IN ACrida lata1)

MASANOBU SANNOMIYA

Institute of Biology, Ooita University, Ooita

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A pair or pairs of heteromorphic chromosomes are of special importance for
cytogenetic analysis, for reductional and equational separations for the inequality are
distinguished at AI. Based on the chiasmatype hypothesis, frequencies of these two
types of AI separation are governed by crossing-over in the region of the chromosomes
concerned (cf. Mather 1935, Darlington 1937). Observations of frequencies of chiasmata
and the types of AI separation in heteromorphic chromosome pairs of various sources
have shown close relationship between crossing-over and chiasma formation, supporting
the view of the chiasmatype hypothesis (Brown and Zohary 1955, Jain and Basak 1963,
(1961) data also support the above view. The present state of the problem has been
reviewed by Brown and Zohary (l.c.) and by Whitehouse (1965). The purpose of the
present paper is to show additional evidence of a close relationship between crossing-over
and chiasma formation, and also to show no reduction of number of chiasmata from
diplotene to MI, use being made of structural heterozygotes of Acrida lata Motschulsky
(Orthoptera, Acrididae).

MATERIALS AND METHODS

Three males of Acrida lata Motschulsky were used: (1) A translocation heterozygote,
2n=22 X, caught at Goshi, Kumamoto Prefecture in 1963, (2) an individual, 2n=22 X
+1B, with a heteromorphic bivalent in primary spermatocytes, which was caught on the
campus of Ooita University in 1962, and (3) a heterozygote for a centric fusion, 2n=21
+X, caught on the campus of Kumamoto University in 1961. The testes were fixed in
the mixture recommended by Newcomer (1953) and the preparations of spermatocytes
were made employing the usual iron-acetocarmine squash method.

RESULTS AND DISCUSSION

Crossing-over and chiasma formation. In the translocation heterozygote the complex
of 4 chromosomes was found to pair in 1b (6.5 %), 1a + 1 (91.7 %), 21 (0.9 %), and 1 +
21 (0.9 %), 217 primary spermatocytes at MI being observed (Fig. 2). Analysis of the
configuration of the multiples indicated that a segmental interchange occurred between
chromosomes 3 and 9, giving rise to chromosome 39 and 91 (Figs. 1, 2, and 6). The

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homologous segments of 3 and 39 chromosomes constitute the interstitial segment a, and those of 9 and 93 constitute the interstitial segment b (Fig. 6).

At MI no chiasma was formed in the segment a; chromosome 39 was found to pair with chromosome 9 at the distal end (7.4%) or to be left unpaired (92.6%). No equational AI separation of the pair of 3 and 39 was found (Figs. 2–6). In the segment b, a single chiasma was formed at MI in 98.2% and no chiasma in 1.8% of the cells (Table 1;
Figs. 2 and 6). At AI the distal unequal segments of $9$ and $9^a$ were shown to be separated equationally in 96.1% and reductionally in 3.9% of the cells (Table 1). The above frequencies were obtained by summing up the direct observation at AI and the observations of MII and AII cells in which the resultants from equational and reductional separation at AI were distinguished (Table 1; Figs. 3-6). Thus, a good coincidence is found between frequencies of formation of a chiasma and equational AI separation, showing a close relationship between crossing-over and chiasma formation. Fig. 3 shows AI with $9$ and $9^a$ chromosomes separating equationally, chromosome 3 included in the upper group, and $3^a$ lagged, suggesting that chromosomes 3, 9, and $3^a$ paired in 1 and $3^a$ left unpaired at MI (cf. Fig. 2). Fig. 5 shows AII resulted from equational AI separation of $9$ from $9^a$ chromosome, in which the components of 3 and $3^a$ are missing, probably because of both the chromosomes being included into the other dyad cell.

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**Table 1.** Frequencies of chiasmata in the interstitial segment of $9$ and $9^a$ chromosomes and reductional (R) and equational (E) separations at AI for the distal inequality in the translocation heterozygote

<table>
<thead>
<tr>
<th>No. of Xma</th>
<th>No. of cells</th>
<th>AI separation</th>
<th>No. of cells</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Obs.</td>
<td>%</td>
<td>AI</td>
</tr>
<tr>
<td>0</td>
<td>4</td>
<td>1.8</td>
<td>R</td>
</tr>
<tr>
<td>1</td>
<td>213</td>
<td>98.2</td>
<td>E</td>
</tr>
<tr>
<td>Total</td>
<td>217</td>
<td>100.0</td>
<td>Total</td>
</tr>
</tbody>
</table>

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**Fig. 6.** Diagrammatic representation of a complex of 4 chromosomes (A), the pairing at pachytene (B), and reductional and equational separations (C) in the translocation heterozygote.

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**No reduction of number of chiasmata from diplote to MI.** (1) The individual with an heteromorphic bivalent: The heteromorphic bivalent was distinguished from the other 10 homomorphic bivalents in each of the primary spermatocytes (Figs. 7 and 8). The partner chromosomes of the heteromorphic bivalent were different from each other for a block of heterochromatin adjacent to the kinetochore (Fig. 8). From one to three chiasmata were found in the heteromorphic bivalent and the average numbers of chiasmata per bivalent were 1.80 at diplote and 1.77 at MI (Table 2).

(2) The heterozygote for a centric fusion: In this individual the pairing of chromosomes in the primary spermatocytes was invariably $1_f+9_f+X$ (Fig. 9). The trivalent was composed of a metacentric chromosome and two telocentrics. This indicates that two non-homologous telocentric chromosomes, 1 and 9, were 'fused' into a metacentric
The long arm of chromosome 1.9 and one of the telocentrics, 1, were paired by two to four chiasmata with average numbers of chiasmata 2.79 at diplotene and 2.73 at MI (Table 3; Figs. 9-12). The short arm of chromosome 1.9 and one of the telocentrics, 9, were paired by one or two chiasmata, with average numbers of chiasmata 1.01 at diplotene and 1.02 at MI (Table 3; Figs. 9-12).

Change in the number of chiasmata per cell or per bivalent may or may not be accompanied by the process of terminalisation of chiasma from diplotene to MI (cf. Darlington 1937). The results described above show that number of chiasmata is not reduced from diplotene to MI in the distinct chromosome pairs in *Acrida lata*. Because of the difficulty to distinguish strictly between the terminal chiasma and the interstitial one that is nearly terminal at MI, ‘terminalisation coefficient’ (cf. Darlington 1937) was not obtained in the present case.

Table 2. A comparison between frequencies of chiasmata at diplotene and MI in the heteromorphic bivalent

<table>
<thead>
<tr>
<th>No. of Xta</th>
<th>Diplotene</th>
<th>MI</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. of cells</td>
<td>%</td>
</tr>
<tr>
<td>1</td>
<td>15</td>
<td>21.43</td>
</tr>
<tr>
<td>2</td>
<td>54</td>
<td>77.14</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>1.43</td>
</tr>
<tr>
<td>Total</td>
<td>70</td>
<td>100.00</td>
</tr>
<tr>
<td>Average</td>
<td>1.80 Xta/cell</td>
<td></td>
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</table>

Table 3. A comparison between frequencies of chiasmata at diplotene and MI in the two arms of a trivalent in the centric fusion heterozygote

<table>
<thead>
<tr>
<th>No. of Xta</th>
<th>Diplotene</th>
<th>MI</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. of cells</td>
<td>%</td>
</tr>
<tr>
<td>Long arm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>45</td>
<td>26.47</td>
</tr>
<tr>
<td>3</td>
<td>116</td>
<td>68.24</td>
</tr>
<tr>
<td>4</td>
<td>9</td>
<td>5.29</td>
</tr>
<tr>
<td>Total</td>
<td>170</td>
<td>100.00</td>
</tr>
<tr>
<td>Average</td>
<td>2.79 Xta/cell</td>
<td></td>
</tr>
<tr>
<td>Short arm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>168</td>
<td>98.82</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>1.18</td>
</tr>
<tr>
<td>Total</td>
<td>170</td>
<td>100.00</td>
</tr>
<tr>
<td>Average</td>
<td>1.01 Xta/cell</td>
<td></td>
</tr>
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</table>
1. In 98.2% of the MI cells of a translocation heterozygote of Acrida lata, one chiasma was formed in one of the 'interstitial segment' and the distal unequal segments were separated equationally at AI in 96.1% of the cells. No chiasma was found at MI in the other interstitial segment and no equational AI separation of the distal unequal segments of this pair. The result indicates a close relationship between crossing-over and chiasma formation.

2. Frequencies of chiasmata at diplotene and MI were compared using a heteromorphic bivalent in which partner chromosomes were different for a block of heterochromatin and a special trivalent in a so-called centric fusion heterozygote, respectively, of Acrida lata. Chiasmata at these two stages were equally frequent, showing that in the present case no reduction in number of chiasmata was accompanied by the process of terminalisation from diplotene to MI.
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LITERATURE CITED


