RELATIONSHIP BETWEEN CROSSING-OVER AND CHIASMA FORMATION IN A TRANSLOCATION HETEROZYGOTE OF *ATRACTOMORPHA BEDELI* (ACRIDIDAE, ORTHOPTERA)

MASANOBU SANNOMIYA

Institute of Biology, Oita University, Oita, 870-11, Japan

SUMMARY

A male of *Atractomorpha bedeli* $(2n\male = 18 + X)$ was heterozygous for a complex translocation in which exchange involved three non-homologous chromosomes. Unaltered and altered chromosomes constituted special pairs each with proximal homologous segments (interstitial segments) and distal non-homologous segments. Two of such pairs were " heteromorphic " for unequal length of the distal non-homologous segments. Thus occurrence of a single crossing-over in the proximal segment resulted in equational AI separation for the distal inequality. A good conformity was found between formation of a chiasma in the proximal segment and equational AI separation for the distal inequality. Thus occurrence of a crossing-over corresponded to formation of a chiasma, supporting the view of the chiasmatype hypothesis.

1. INTRODUCTION

OBSERVATIONS of frequencies of chiasma(ta) and the types of AI separation, reductional and equational, in heteromorphic chromosome pairs of various sources have been used for showing relationship between crossing-over and chiasma formation in support for the view of the chiasmatype hypothesis (cf. John and Lewis, 1965; Whitehouse, 1973). Further evidence for the chiasmatype hypothesis has been presented by Noda (1967, 1974) in *Scilla scilloides*, Watanabe and Noda (1974) in *Allium thunbergii*, and Sannomiya (1968) in *Acrida lata*.

The purpose of the present paper is to show additional evidence for the chiasmatype hypothesis, use being made of a male *Atractomorpha bedeli* De Haan $(2n\male = 18 + X)$ which was heterozygous for a complex translocation. The male *A. bedeli* was found among 80 males collected in 1970 from a wild population at Okazyo-ato, Taketa-shi, Oitaken (cf. Sannomiya, 1973).

2. RESULTS AND DISCUSSION

In a total of 217 primary spermatocytes at metaphase, configurations of pairing of the chromosomes were $1_{VI} + 6_{II} + X$ (83 cells or 38·3 per cent; fig. 1), $1_{IV} + 7_{II} + X$ (including a heteromorphic bivalent, 100 cells or 46·1 per cent; fig. 2), $2_{III} + 6_{II} + X$ (2 cells or 0·9 per cent) and $9_{II} + X$ (including two heteromorphic bivalents, 32 cells or 14·7 per cent; fig. 3).

Analysis of the configurations at MI disclosed that the male was heterozygous for a complex translocation due to exchange of segments among three non-homologous chromosomes. Thus the three non-homologous chromosomes 1, 2, and 4 had given rise to 1^2, 2^4, and 4^1 (fig. 5A). Diagram of a possible pairing of the six chromosomes 1, 1^2, 2, 2^4, 4, and 4^1 at pachytene is shown in fig. 5B. Since the homologues change their partners at the point of exchange the multiple consists of six homologous parts, three of

proximal segments (interstitial segments) and three of distal segments. The proximal homologous segments of 1 and 1^2 chromosomes are designated as a; likewise, those of 2 and 2^4, b, and those of 4 and 4^1, c (fig. 5B). The distal homologous segments of 1^2 and 2 chromosomes are designated as d; likewise, those of 2^4 and 4, e, and those of 4^1 and 1, f (fig. 5B).
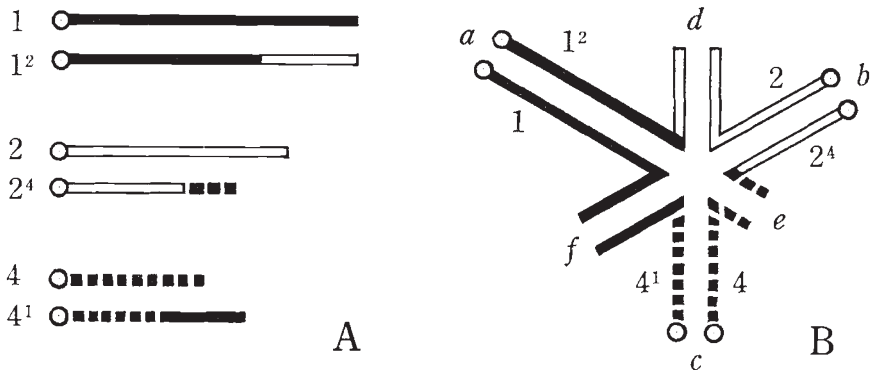

FIG. 5.—Diagrammatic representation of a complex translocation involving three non-homologous chromosomes. A. Unaltered and altered chromosomes in pairs. B. A possible pairing of the six chromosomes at pachytene.

Presence or absence of chiasma(ta) in each of the six homologous parts affects the pairing configuration of the six chromosomes at MI. In most of the cells at MI, a single chiasma was formed in each of the segments a, b, and c, and in a few cells two chiasmata in the segment a (table 1; figs. 1-3).

TABLE 1

Frequencies of chiasma(ta) in the interstitial segments at MI

Segment	No. of chiasma(ta)	No. of cells	(%)
a	0	1	(0·5)
	1	209	(96·2)
	2	7	(3·3)
b	1	217	(100·0)
c	0	1	(0·5)
	1	216	(99·5)

In addition to these proximal chiasmata, formation of a chiasma in the distal segments d, e, and f resulted in a ring of six at MI (8 cells) and without a chiasma in the segment e resulted in a chain of six (75 cells) (fig. 1; fig. 6). Lack of a chiasma in both the distal segments d and e, or in both e and f, resulted in $1_{IV} + 1_{II}$ instead of 1_{VI}, the bivalent being heteromorphic (fig. 2; fig. 6). Formation of a chiasma in the segments a, b, and c, but non-formation of a chiasma in the segments d, e, and f, resulted in 3_{II}, of which two were heteromorphic (fig. 3; fig. 6).

With a single crossing-over in the segment b, unequal distal segments of the pair 2 and 2^4 should give rise to equational AI separation (fig. 4; fig. 6). In the same manner, with a single crossing-over in the segment c unequal

distal segments of the pair 4 and 4^1 should give rise to equational AI separation (fig. 4; fig. 6). In fact, both the pairs were found to be separated equationally in all of 28 cells at AI. The result indicates that in almost all the primary spermatocytes a single crossing-over occurred in the segments b and c, respectively. A single chiasma in the segment b was found in 100 per cent of the cells and in the segment c it occurred in 99·5 per cent of the cells (table 1). Therefore, a good conformity is found between occurrence of a crossing-over and formation of a chiasma.

Occurrence of a crossing-over in the segment a should give rise to equational AI separation for the distal non-homologous segments of 1 and 1^2 chromosomes. However, equational AI separation of these chromosomes could not be distinguishable from reductional one because of equal lengths of the distal non-homologous segments (fig. 4; fig. 5; fig. 6).
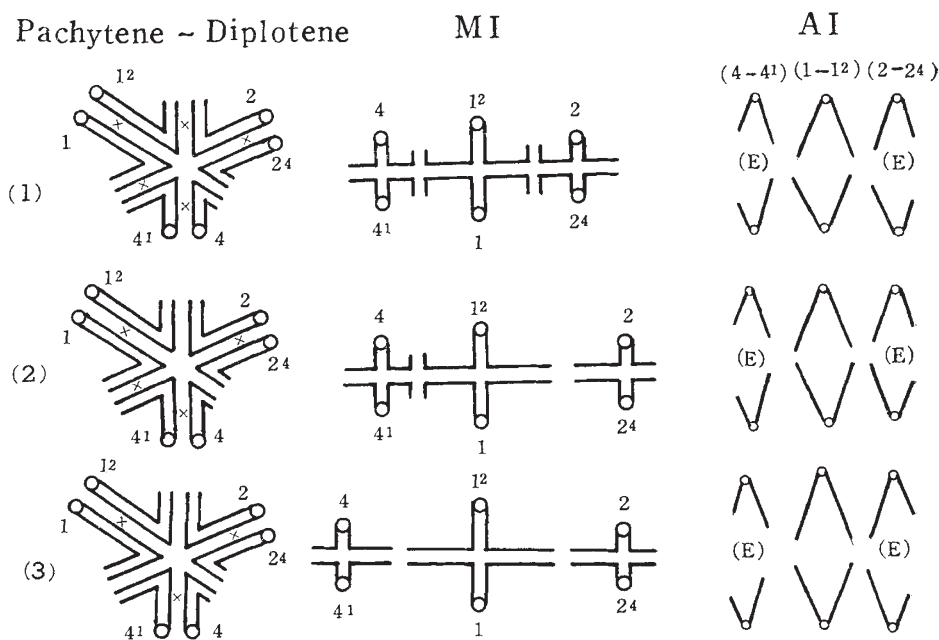

FIG. 6.—Schematic representation of relationship between occurrence of crossing-over, pairing configuration at MI, and separation of the chromosomes at AI in the translocation heterozygote. × indicates position of crossing-over. (1) A case of a chain of six chromosomes at MI (cf. fig. 1). (2) A case of $1_{IV} + 1_{II}$ at MI (cf. fig. 2). (3) 3_{II} at MI (cf. fig. 3).

Occurrence of a complex translocation involving as many as four non-homologous chromosomes has been reported in a male of *Keyacris (Moraba)* *scurra* and it has been presumed that the exchange of segments occurred in a sperm or in an ovum from which the male was derived (White, 1963). With no indication of mosaicism within the testis of the male of *Atractomorpha* *bedeli* mentioned above, the complex translocation is very likely to have occurred in a gamete.

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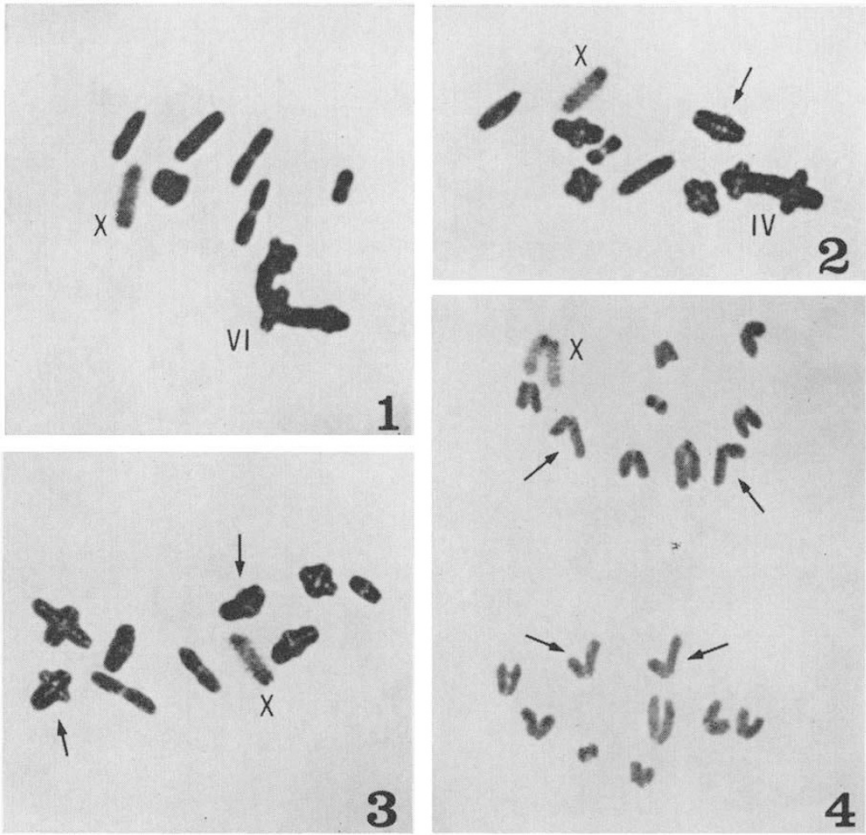
Figs. 1-4.—Metaphase and anaphase of primary spermatocytes of a male *A. bedeli* heterozygous for a complex translocation. (1) $1_{VI}+6_{II}+X$. (2) $1_{IV}+7_{II}+X$, with a heteromorphic bivalent (arrow). (3) $9_{II}+X$, with two heteromorphic bivalents (arrows). (4) Anaphase of a primary spermatocyte showing two pairs of half-bivalents separating equationally (arrows). × 1000.