

CHAPTER 4. INTERCHANGES

Behavior in pachytene stages. There are extensive non-homologous associations at meiotic prophase, as mentioned on Page 71. As stated by McClintock, 1941, "Secondary translocations involving the same two chromosomes have been recovered from such heterozygous plants. They are readily derived on the hypothesis of illegitimate crossing over in the regions associated non-homologously."

Orientations. The diagrams in Fig. 58 illustrate the zigzag (alternate) orientations which correspond to adjacent-1 and adjacent-2 orientations of the four chromosomes of the $\odot 4$ in an interchange heterozygote.

In three interchanges in cotton the four types have been shown to occur (Endrizzi, 1974). In all three the ratio of alternate-1:adjacent-1 was 1:1. In one of them alternate-2:adjacent-2 was also 1:1 but in at least one the latter ratio was 2:1. The ratio of alternate-1 plus adjacent-1:alternate-2 plus adjacent-2 was about 2:1 for each.

Analysis of segregation types in watermelon. In watermelon, association of the pollen in tetrads continues for a short time after the anthers dehisce. The frequencies of pollen tetrads with 0, 1, 2, 3, and 4 empty pollen grains were determined for 3 normal varieties and for heterozygotes for 3 different interchanges (Kihara and Shimotsuma, 1967). The results are summarized in the following tabulation:

Frequencies of 5 types of pollen tetrads in normal varieties* and 3 interchange heterozygotes.

Strains	Types of tetrads (no. of aborted spores)						% with 2 aborted (C.O.)	Ratio 0.4**	Pollen abortion	
	0	1	2	3	4	Total			Predicted	Obs.
MT-1	95	2	33	6	92	228	14.5	1.0:1	50.0	50.0
NT-1	66	2	145	8	25	246	58.9	2.6:1	42.3	43.0
FT-1	88	0	225	13	41	367	61.3	2.1:1	44.6	42.0
Miyako*	186	0	7	1	0	194				2.2
Asahi-Y*	135	1	8	2	0	146				3.8
Fumin*	116	2	11	3	0	132				6.3

** alternate:adjacent segregation

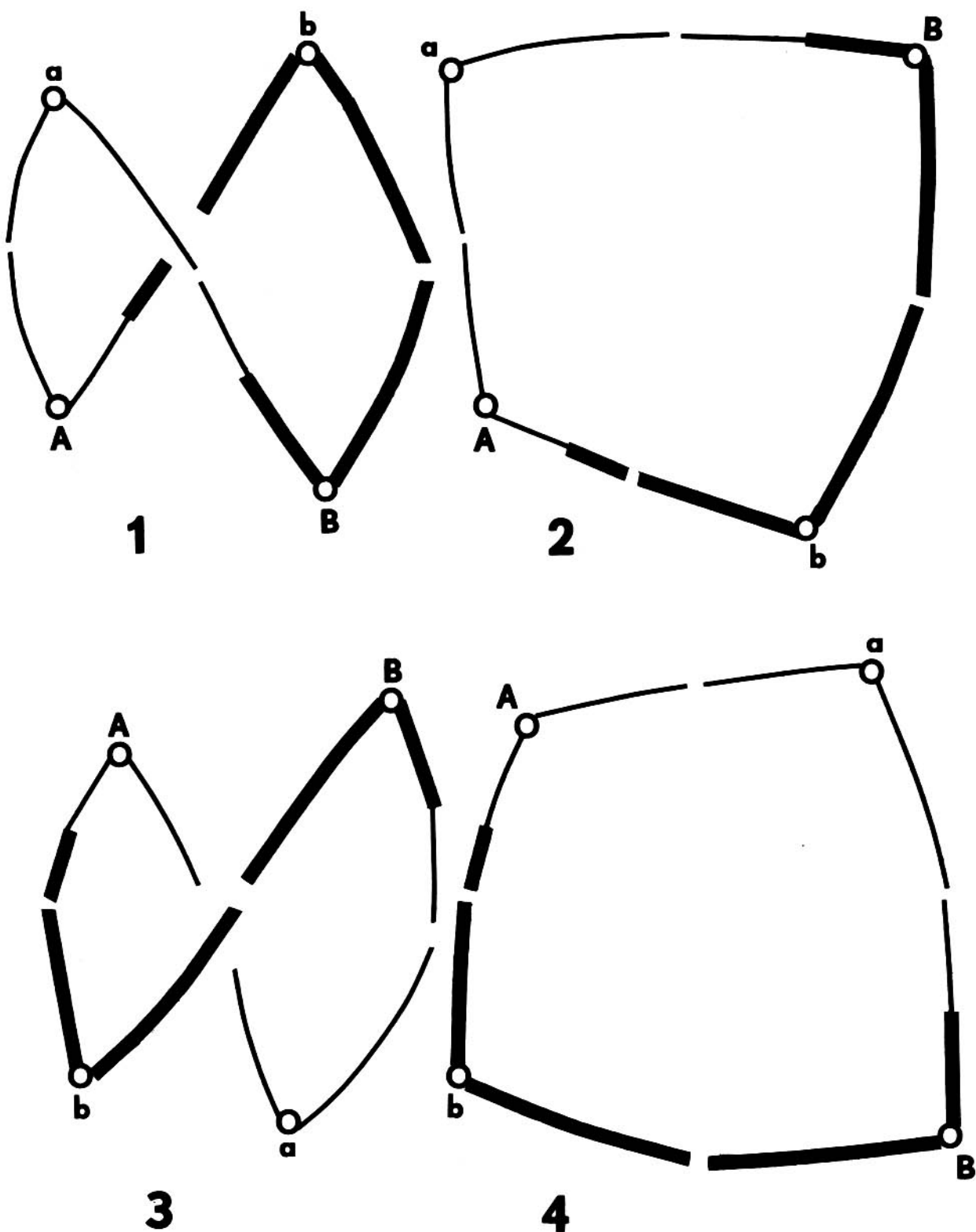


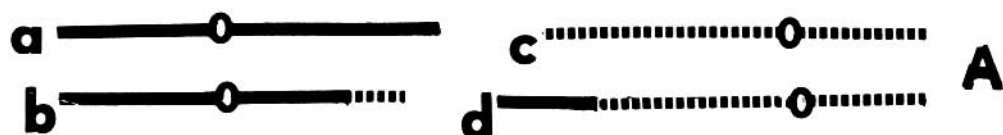
Fig. 58. Types of "zigzag" vs. "open" meiotic configurations in a ring of four chromosomes: 1 = alternate-1, 2 = adjacent-1, 3 = alternate-2, 4 = adjacent-2.

As in maize, when there is very little crossing over in the interstitial segments, as in MT-1, the ratio of alternate:adjacent segregations is 1:1. In the other two interchanges, the frequency of crossover tetrads (with 2 aborted) was very high. As they noted, adjacent-2 segregation was probably absent. My comment is that with such high frequencies of crossover tetrads, the ratios of 2.6:1 and 2.1:1 may not represent the ratio of alternate:adjacent segregation. It does account for the higher fertility. Following single crossovers in either interstitial segment, both alternate and adjacent-1 produce tetrads with 2 aborted spores.

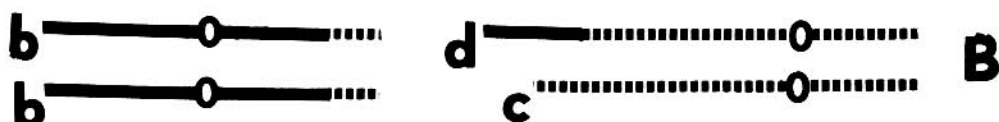
In *Collinsia heterophylla* ($2n = 14$), a species with chiasmata localized toward the ends, position of the interchange breakpoints and chiasma frequency are important in determining whether there is random or directed orientation. Random orientation was the rule for 18 colchicine-induced interchanges (Soriano, 1957). In these the interchange segments were short and the meiotic configurations often were "pairs" and chains rather than rings. In five radiation induced ones in those experiments and in 10 of 13 gamma-radiation induced ones (Zamon and Rai, 1973) there was directed orientation. In these the interchange segments were long, the breaks being in the non-chiasma-forming regions. The meiotic configurations were more often rings than chains. One of the 13 showed the random orientation and frequent chains and "pairs" characteristic of the colchicine-induced ones. Two others showed directed orientation and ring formation in X2 but random orientation and chain "pair" formation in X3. This change was accompanied by lower chiasma frequency. Here the two types of behavior are determined by chiasma position and frequency rather than directly by genetic factors.

Breeding behavior. The usual procedure in maize for establishing a line homozygous for an interchange is to self pollinate the heterozygote, select the fertile offspring, self them for increase and test cross them on a standard normal stock. The desired homozygote gives all semisterile progeny in the test cross.

This may not be sufficient in those interchange heterozygotes in which one of the Dp-Df chromosome combinations is functional through the female but not through the pollen (Patterson, unpublished). For example, if in the following interchange heterozygote:



the b + c combination is functional but only through the female, one of the types of fertile offspring from selfing will be:



Since only the b + d combination is functional through the pollen, its test cross on a normal female gives all interchange heterozygotes which are partially sterile, leading to the erroneous conclusion that the plant tested was an interchange homozygote. However, the self progeny of the plant shown above in B will include interchange homozygotes and also plants with the constitution shown above in B. If the latter are tested as the female parents in crosses with normal, there will be a ratio of 1 partially sterile:1 fertile among the offspring. This additional test will distinguish the true interchange homozygote from ones with the constitution shown in B.

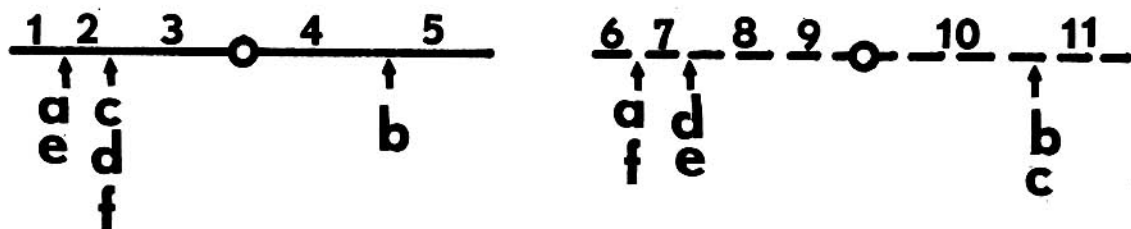
Induced interchanges - ultraviolet. Lines established from semisterile ears furnished by H. H. Kramer from a mutation program using ultra-violet treated pollen show the typical behavior of chromosomal interchanges, including a $\phi 4$ at meiosis and semisterility. Interchange homozygotes were established also.

Break positions and frequencies. An analysis of breakpoint frequency relative to length by Jancey and Walden (1972), using Longley's 1961 data on the maize interchanges shows an excess for certain chromosome arms and a deficiency for others. Also certain combinations were more frequent than others. Later they reported evidence for non-random reassociation frequencies; one involving segments within 5 μ of the centromere, the other within 5 μ of the telomeres (Jancey and Walden, 1973).

There is, however, a general relationship between chromosome length and break frequency (Burnham, 1978). Also see P. 94-95.

Pure breeding types with extra chromatin material

Intercrosses between stocks that involve the same two chromosomes. The kinds of meiotic configurations and their frequencies depend on the relative positions of the breakpoints in the parental interchanges, the lengths of the interchanged segments and also the lengths of the "between breakpoint" (B-B) segments. These also affect the degree of spore abortion in the intercrosses. The breakpoint positions in the two chromosomes for the a, b, c, d, e, and f interchanges are at the positions of the arrows:



from which the new interchange chromosomes can be derived. The $a \times b$ heterozygote is Type 1a (opposite arms), $a \times c$ is Type 1b (one arm the same), $e \times f$ is Type 2b (same arms, short-long \times long-short with reference to relative length of interchange segments), and $a \times d$ is Type 2a (same arms, short-short \times long-long). (See diagrams, p. 385.)

In Types 1a, 2a, and 2b the interchange chromosomes in one parent have the same combinations of ends as those in the other parent. As shown in Table 39, page 108, in these heterozygotes there is a high frequency of "pairs". There is one exception in Type 1a, the one with one break in chromosome 6 in the satellite. Here all were associations of four. The "pairs" in the other Type 1a intercrossoes are paired homologously only at the ends, the intercalary centromere-bearing regions in those "pairs" are non-homologous. In the one exception all were associations of four. In that cross, one of the interchange segments was a portion of the satellite. This is so short that pairing with its homologue occurs rarely if at all. If, instead, pairing initiation occurred in adjacent segments, this should be between the homologous centromere-bearing segments resulting in associations of 4 rather than "pairs".

In Type 1b, the combinations of chromosome ends in one parent are different from those in the other parent. Here, as shown in Table 39, most of the configurations were associations of four.

In intercross types 1a, 2a, and 1b, crossing over in both between-breaks segments can combine the two parental interchanges. Crossing over in both between breaks segments in 2b can produce an acentric ring fragment. Crossing over in one between breaks segment in 2b can produce a compound chromosome. Certain of the new combinations of parental interchange chromosomes have duplications with or without deficiencies. Low spore abortion can be used to screen for intercrossoes producing duplications and/or viable deficiencies (also see P. 107). For diagrams of the configurations at pachynema, and the expected behavior of such intercrossoes, together with data on meiotic configuration frequencies and spore abortion in intercrossoes among 24 T1-5 interchanges, see Burnham (1974). (See diagrams, p. 385).

Interchanges between normal and 'B' chromosomes. The 'B' chromosome in Fig. 32, page 104 should be shown with a short distal euchromatic tip. According to Ward (1973), this distal euchromatic tip controls non-disjunction of the B chromosome (d in the diagram) in the $b + d$ microspore.

Rhoades and Dempsey (1973) suggest that this same distal tip of the B suppresses replication of A chromosome knobs at the second microspore division, but two or more B's must be present in the microspore for suppression to occur.

Figs. 59, 60. Types of intercrosses between stocks of interchanges that involve the same two chromosomes. Upper row in each figure: breakage positions in the a, b, c, d, e, and f interchanges.

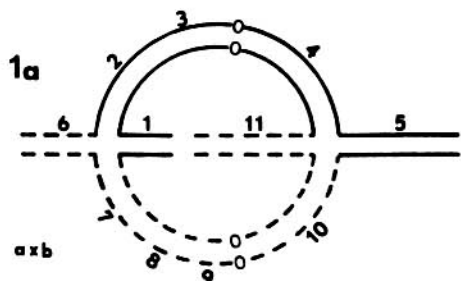
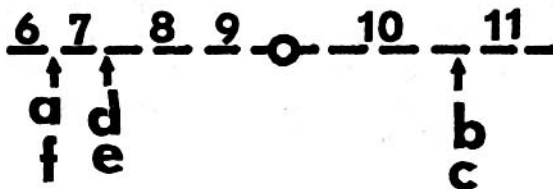
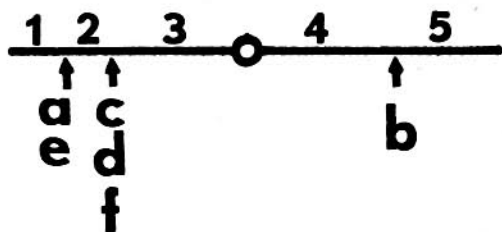


Fig. 59:

Type 1a intercross (opposite arms) = $\underline{a} \times \underline{b}$.

Type 1b intercross (one arm the same) = $\underline{a} \times \underline{c}$.

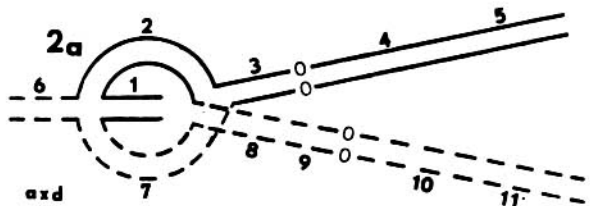
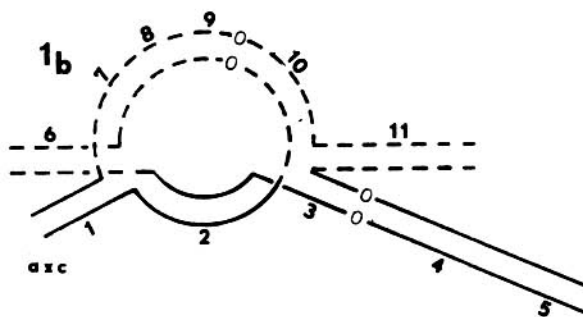


Fig. 60:

Type 2a intercross (both arms the same) = $\underline{a} \times \underline{d}$, interchange segments in \underline{a} : short + short; interchange segments in \underline{b} : long + long.

Type 2b intercross (both arms the same) = $\underline{e} \times \underline{f}$, interchange segments in \underline{e} : short + long; interchange segments in \underline{f} : long + short.

