

over in that arm. The short arm of chromosome 6 may be an exception. What happens to a crossover in the segment between the centromere and the break point will be answered in part a little later. Interchange heterozygotes differ greatly as to the relative frequencies of rings-of-four, chains-of-four and "pairs" at diakinesis (Table 17).

The data in Table 17 show there is a general relationship between the frequencies of the various configurations at diakinesis and the relative lengths of the interchanged segments. The shorter the segment the more likely is it to fail to pair with the homologous segment. For example, when both interchange segments are long most of the configurations are a  $\odot$  4 as in T8-9a. If one interchange segment is short, chains of four are frequent, as in T2-3a. In T1-6b, which forms only chains, one interchange piece is part of the satellite, a very short segment which has never been observed to pair with its homologue. If both interchange segments are short, "pairs" are frequent as in T5-9a and T3-6. For T5-9a, the probability of "pairing" failure is about .8. Data of this sort may be used to compare the pairing capabilities of distal segments of different chromosomes.

Interchanges in maize also show differences in degree of pollen abortion and in the appearance of the pollen which also is related in general to the lengths of the interchanged segments (Table 17). For example, the interchange heterozygotes that form mostly rings usually show about 50% of spore abortion, as in T1-6a. The excess in T8-9a (59% observed) has not been explained. This approaches the  $\frac{2}{3}$  sterility expected if the four chromosomes in the ring pass at random, two to each pole. Although 3-1 segregations will add to the sterility and in some interchanges may be as high as 10%, their frequency in T8-9a is too low to account for the excess sterility over 50% (Burnham 1948). In T2-3a, the deficiency for the short terminal segment of chromosome 2 resulted in pollen grains without starch. As expected, the effect of the deficiency differs, depending on the segment involved. For example, pollen grains with a deficiency for 0.22 of the long arm of 10 were filled with starch but smaller in size (Stadler 1935). In T5-9a, pollen abortion was about 50%, but the aborted grains were mostly smaller and only partly filled with starch. In T3-6 the visible pollen abortion was variable, and included pollen that was somewhat smaller than normal but with normal starch content as well as some that was partly filled. In T1-6b, only 25% pollen abortion was observed. Here there was no visible effect on the pollen of the deficiency for the short interchange segment of the satellite. This class of spores also carried a duplication which prevented functioning in the pollen. It did function in the ovules. The resulting plant was hyperploid for the distal 0.75 of the long arm of chromosome 1 and had certain distinctive morphological features, and in the original stock seemingly greater susceptibility to smut.

The relative frequencies of the different kinds of segregation would be expected to affect the percentage of pollen abortion.

### **Orientations at meiosis and the kinds of segregation**

#### *Direct Observations*

In maize, in the association of four chromosomes the orientation at metaphase I is either "open" or "zigzag" (i. e. adjacent or alternate) when the four centromeres are oriented toward the poles as shown in Fig. 21A, B and C. In barley, Tjio and Hagberg (1951) noted configurations in which two chromosomes opposite each other in the ring were not coorientated with reference to the poles and the equatorial plate (Fig. 21D).

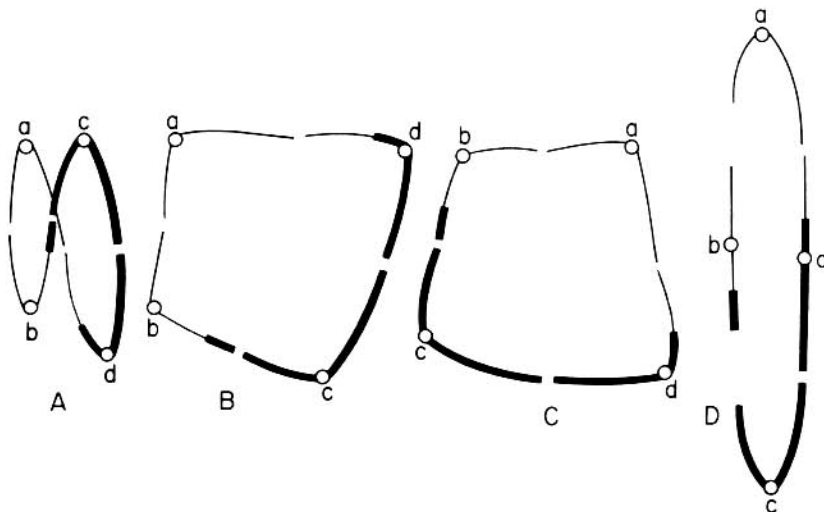


FIG. 21. The principal possible orientations of a ring of four chromosomes at metaphase I, assuming the poles are toward the upper and lower edges of the page. A = alternate, B = adjacent-1, C = adjacent-2, D = non-coorientation of the centromeres of two chromosomes in alternate positions in the ring.

In alternate and adjacent-1 segregations, homologous centromeres separate and pass to opposite poles. In adjacent-2 segregations, they pass to the same pole. The non-coorientated type may produce 3-1 segregations from the ring.

*A = alternate-1. Not shown is alternate-2, the zigzag orientation corresponding to adjacent-2.*

In mice a zigzag orientation in which adjacent chromosomes at the ends go to the same pole was observed occasionally by Koller and Auerbach (1941).

In alternate and adjacent-1 segregations, homologous centromeres pass to opposite poles, whereas in adjacent-2 segregation they pass to the same pole. If the three kinds of segregation occur, six kinds of spores (gametes in animals) are produced at the end of meiosis. In maize, if "pairs" are formed at diakinesis and metaphase, (both interchange segments short) they are probably a b and c d, never a c and b d. Hence the segregation from "pairs" is expected to be a+c/b+d or a+d/b+c, corresponding to the adjacent-1 and alternate segregations respectively from the ring of four.

The heterozygous interchanges in maize which form mostly rings are usually approximately 50% sterile, suggesting that the "open" and "zigzag" rings may be equally frequent. This might be expected if for each "open" type of orientation at metaphase I, there is an equal chance of alternate orientation. In other words adjacent chromosomes may orient with equal frequency toward the same or opposite poles.

The three kinds of segregation may be recognized at metaphase I if the chromosomes involved differ considerably in length. For example, the three types were observed in semisterile-5 (T1-6a) by Cooper and Brink (1931). An accurate count of their relative frequencies is difficult, because the "open" type is much more easily distinguished than the alternate one and hence the doubtful uncountable class may include more alternates. Experimental evidence which avoids this difficulty has been obtained from two sources in plants and one in Drosophila.

#### *Spore position in ascus*

In interchange heterozygotes in Neurospora crassa the frequencies of the different kinds of segregation were determined by noting the positions of aborted and normal spores in the asci (Singleton 1948).

*Spore quartet analysis in maize*

In maize, information has been obtained from interchanges involving chromosome 6 which carries the nucleolus organizer (McClintock, Unpublished, Burnham 1950). When nondisjunction occurs for chromosome 6 at meiosis, any spore receiving the extra chromosome has two nucleolar organizers and potentially two nucleoli (often fused into one), while any spore receiving no organizer has scattered small bodies of nucleolar material (referred to as a diffuse nucleolus). In the early prophases of division II of meiosis each chromatid pair appears to have nucleolar material associated with it (McClintock 1934). Only if a nucleolus organizer region is present will this material form a single nucleolus at later stages. The pachytene configuration and the various expectations from different segregations in an interchange in which the break was in the short arm of 6 are shown in Fig. 22A and B.

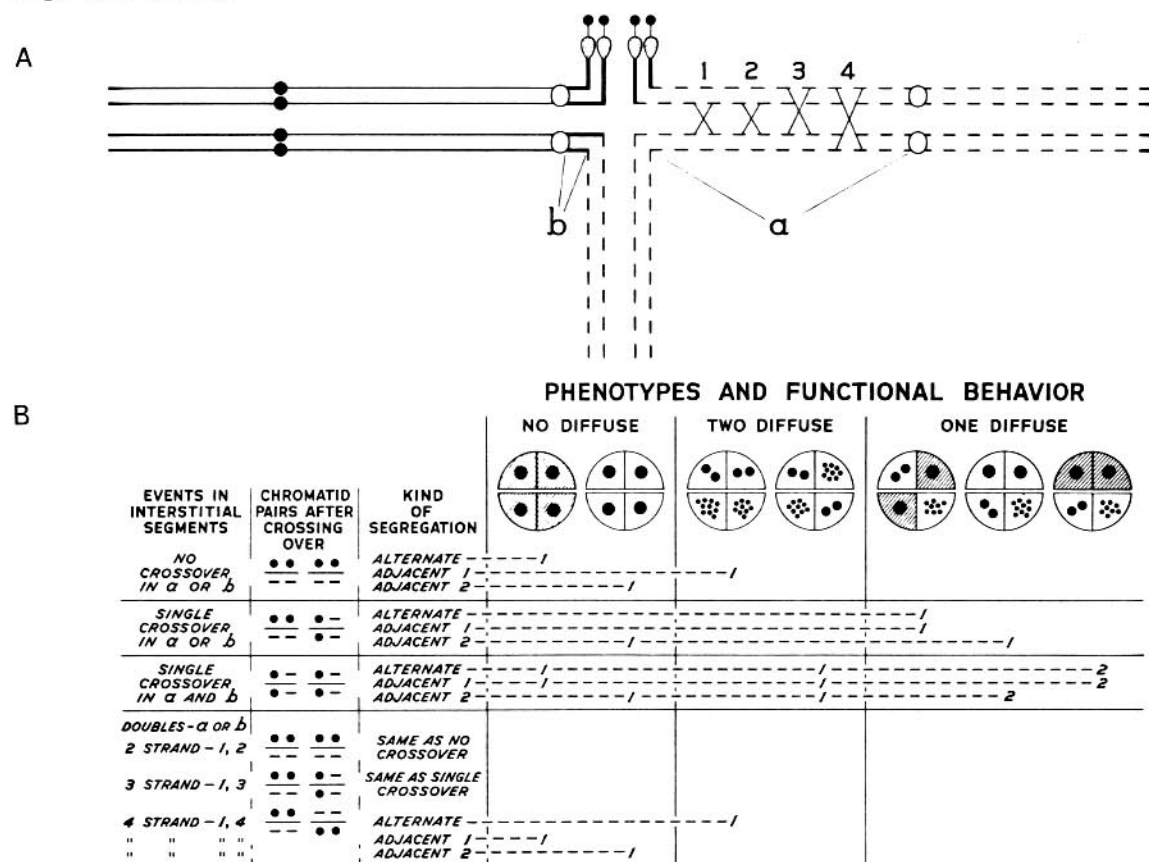


FIG. 22. Above. Diagram showing the pachytene configuration in a 5-6 interchange heterozygote in which the break in chromosome 6 was in the short arm; *a*, *b* = interstitial segments, between the centromere and the interchange points.

Below. Spore quartet types expected (1) from alternate, adjacent-1 and adjacent-2 segregations in meiocytes having no crossing over in an interstitial segment; and (2) from alternate and adjacent-1 segregations in meiocytes having a crossover in one of the interstitial segments, e.g., *b*. Non-disjunction of the chromosome bearing the nucleolus organizer region produces one type of cell which has two nucleoli and potentially two organizers and a second type of cell with no organizer in which the nucleolar material remains scattered or diffuse. (Burnham, 1950, Fig. 1 p. 447, Genetics 35).

**RESULTS EXPECTED IF NO CROSSING OVER OCCURS.** Reference to the pachytene diagram in Fig. 22A and to the tabulation below in Fig. 22B, shows that if adjacent-1 segregation occurs, and there has been no crossing over in an interstitial segment (between the centromere and the break point, regions marked *a* and *b* in the diagram), the

resultant spore quartet is the 2-diffuse type with all spores carrying a duplication and a deficiency. The four nucleolar organizers passed to one pole at Division I, leaving no organizers at the other pole. If alternate or adjacent-2 segregations occur, each of the four resultant spores has one nucleolus. Those from alternate segregation are normal, those from adjacent-2 are duplication + deficient and should abort. Since the microspores in the quartets remain together for a time, it is possible to count the various types and from the 2-diffuse quartet frequencies calculate a predicted percentage of pollen abortion. If the observed amount in the same plants is higher than the predicted, the excess should be a measure of the frequency of adjacent-2 segregation, thus separating the two types of non-diffuse quartets which cannot be distinguished under the microscope. This is true only if crossovers in interstitial segments had not occurred.

**RESULTS EXPECTED IF CROSSING OVER OCCURS:** Crossing over may occur in three kinds of segments: the interchanged ones, the non-interchanged chromosome arms distal to the centromeres, or the interstitial segments (between the centromeres and the break points). By referring to the pachytene diagram in Fig. 22A, note that crossing over in either the interchanged segments or in the non-interchanged arms merely exchanges blocks of genes without affecting the segment carrying the nucleolar organizer. Hence the resulting spore quartet types are not recognizably different, nor are the chromosome constitutions changed by the crossing over.

Crossing over in either interstitial segment, a or b leads to very different results (Fig. 22B). Single crossing over in one interstitial segment followed by alternate or adjacent-1 segregations produces a new quartet type recognizable under the microscope, since it has one spore with a diffuse nucleolus, one with two organizers and hence potentially two nucleoli and two spores with one organizer and one nucleolus. The two spores with one organizer are normal, the other two carry a deficiency and a duplication. This is referred to as a one-diffuse or "crossover-type quartet". The same crossover followed by adjacent-2 segregation would produce either a crossover type or a normal-appearing quartet, both with all spores deficient. Observations by McClintock of the plane of the first division in crossover quartets indicates that the chromosomes which cross over in an interstitial segment pass to opposite poles and hence adjacent-2 segregation is precluded. The crossover type quartet in which the four spores abort would not be expected. Another point to note is the fate of the crossover chromatids following a single crossover in one interstitial segment. If alternate segregation occurs, the two spores that received a crossover chromatid have a duplication and a deficiency and should abort. Hence those crossovers are not recovered. If adjacent-1 segregation occurs, the two normal spores receive the crossover chromatids. There are two important consequences of this relationship between crossing over and the type of segregation in species in which alternate segregation in the  $\odot$  4 is the rule: First, greatly reduced genetic recombination is expected in regions that include all or part of an interstitial segment, since the crossover chromatids pass to the abortive spores. Single crossovers may be recovered if adjacent-1 segregation occurs or if alternate segregation follows simultaneous crossing over in both interstitial segments. Second, normal fertility is expected only if the interstitial segments are short in terms of cytological crossing over. Sterility is expected when such crossing over occurs; even if the sole type of segregation is alternate. If every sporocyte crossed over, 50% spore abortion might be expected. In Datura, lines have been reported in which plants with a  $\odot$  4 have no pollen abortion; and others that have various degrees of abortion. Those with about 50% pollen abortion had what Blakeslee terms "necktie configurations". These regularly had a "figure of eight" with a crossover in an interstitial segment. As shown in Fig. 22, each crossover type quartet of spores should have two functional and two aborted spores, and hence 50% abortion.

The segregation described above following crossing over in interstitial segments was termed half-disjunction when it was first discussed by Sansome (1932). Its signifi-



cance had been recognized by Darlington (1931a) and was emphasized later (Lamm 1948, Hanson and Kramer 1949, and Burnham 1949a).

**OBSERVED RESULTS, SPORE QUARTET ANALYSIS.** In one experiment, interchanges with one break in the short arm of chromosome 6 were used. In one group of these interchanges, the interstitial segments were both short, in the other group the one in 6 was short, but the one in the other chromosome was long (Burnham 1949, 1950). In one of the interchanges, T5-6c, the break in chromosome 6 was in the short arm adjacent to the centromere, while in 5 it was distal to the subterminal knob. Hence this interchange has only one interstitial segment, that in 5 which includes .89 of the long arm. Also available was a stock of T5-6c in which a pericentric inversion, In5a, had been introduced by crossing over (McClintock, unpublished). It shifted the position of the centromere in chromosome 5 to a point adjacent to the subterminal knob. Since the short arm of 6 has densely staining chromomeres and the region distal to the subterminal knob in 5 has small chromomeres, the precise breakage points in T5-6c could be seen at pachytene. One break in the inversion appeared to be in the subterminal knob, and thus marked these two break points.

By crossing the T5-6c In5a stock with one homozygous only for In5a, plants were produced which were heterozygous for the interchange but homozygous for the In5a inversion and consequently homozygous for the new centromere position, much closer to the interchange point. Hence this belongs to the group of interchanges with both interstitial segments short whereas T5-6c without the inversion belongs to the group having at least one long interstitial segment. Based on a relative length of 100 for chromosome 10, the interstitial segment in chromosome 5 was 80 in  $\frac{T5-6c}{+}$  and 16 in  $\frac{T5-6c \text{ In5a}}{+ \text{ In5a}}$ . Note also that in these two heterozygotes, the lengths of the arms of the cross-shaped pachytene configurations as well as the axis lengths are expected to be the same.

Counts of the frequencies of the various spore quartet types and of aborted pollen in these two heterozygous stocks and in three other interchanges, two of them (T2-6a and 6-10b) with a short interstitial segment; and one (T4-6Li) with a long interstitial segment are shown in Table 18.

That the three heterozygous interchange lines in the upper portion of Table 18 do have short interstitial segments is shown by the low frequencies of crossover type quartets, 10.6, 1.0, and 5.3. At these low values, multiple crossovers within the segment should have been rare and not a problem in the analysis. All the other quartets were from meiocytes with no crossing over in an interstitial segment. For each of the three interchanges, there was an excess of observed over predicted pollen abortion. This was used as a measure of the frequency of no-diffuse quartets from adjacent-2 segregation. The remaining no-diffuse quartets are from alternate segregations. The segregation frequencies for the non-crossover quartets are in the last three columns of Table 18A.

For T2-6a, the ratio is close to 2 alternate: 1 adjacent-1: 1 adjacent-2. For  $\frac{T5-6c}{+}$  homozygous In5a, the percentage of alternate segregation is about 50%, but adjacent-2 segregation is considerably lower than adjacent-1. The reason for this will be found when segregation from chain configurations is considered. For T6-10b, the frequency of alternate segregation was 57.5, a highly significant excess over 50%. The percentage of pollen abortion was also considerably less than 50%. Certain interchanges in maize appear to show an excess of alternate segregations, others an excess of adjacents, as e.g. T8-9a (Table 17). There is no explanation at this time.

For the two interchange heterozygotes in Table 18B, the predicted pollen abortion was not greatly different from the observed indicating very little adjacent-2 segregation. In both, the percentages of "crossover type" quartets were about 63%. At these frequen-

**Table 18.** Spore quartet and pollen abortion data and the kinds of segregation in the non-crossover quartets for interchanges with short vs. interchanges with long interstitial segments (Burnham, 1950, from Tables 1, 2 and 3; pages 460, 462, and 464, Genetics 35). diff. = diffuse nucleoli.

Non-crossover P.M.C. in %									
alter-adj.- nate 1 2									
Pollen abortion									
Predict-* Difference ed(p) (o-p)									
% obs.(o)									
% c.o. type									
One diffuse, c.o.quart.									
Two diffuse									
No diffuse									
A. One short interstitial segment									
T5-6c In5a + In5a									
T2-6a/+									
T6-10b/+									
B. One long interstitial segment									
T5-6c/+									
T4-6Li/+									
no diff.** 55.1									
before- diff.** 44.9									
0.0									
2.7									
41.0									
2.7									
56.3									
49.8									
62.6									
62.8									
48.1									
49.3									
-1.2									
25.7									
25.9									
20.7									
22.2									
57.5									
19.1									
23.4									
48.4									
25.6									
26.0									
31.0									
17.2									
33.0									
50.2									
10.6									
759									
1,996									
4,434									

\* Predicted abortion is obtained as follows: no diffuse quartet = 4 viable; 2 diffuse = 4 aborted;  
one diffuse = 2 viable, 2 aborted spores.

\*\* Percentages of alternate and adjacent-1 segregation cannot be determined.

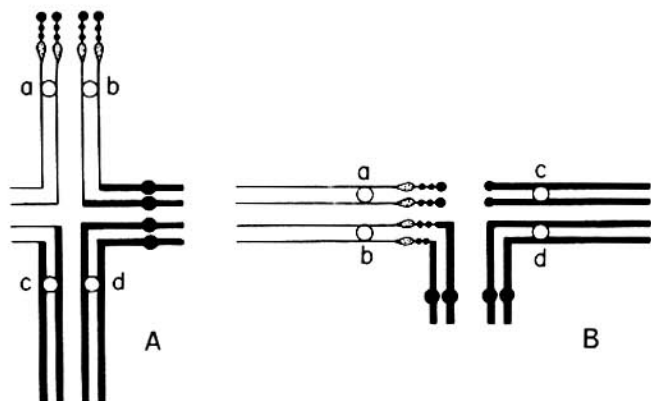


FIG. 23. Diagrams showing the pachytene configurations expected in a 5-6 interchange heterozygote (e.g., 5-6A), in which the break in 6 was in the long arm, and one in which the break in 6 was in the satellite (e.g., T5-6b). It is readily apparent that in both interchanges, adjacent-2 segregation is recognizable by the spore quartet type with diffuse nucleolar material in two of the four spores. Interchanges with one break in the satellite invariably formed chain configurations at diakinesis and metaphase I, and with few exceptions the only type of adjacent segregation was adjacent-1, in which the two chromosomes at the end of the chain passed to the same pole.

cies, multiple crossovers probably were frequent. As shown in Figure 22, the 3-strand doubles contribute to this class, whereas for the 4-strand doubles, alternate segregation results in the 2-diffuse quartet type, adjacent-1 segregation in the no-diffuse type; just the reverse of the results expected when there is no crossing over in the interstitial segments. To what extent multiple and non-crossovers contribute to the two classes of quartets is unknown, and hence the percentages of alternate: adjacent-1 segregation cannot be determined. The data suggest that the segregation in T4-6LI/+ is somewhat different from that in T5-6/+.

In interchanges in which the break in chromosome 6 was either in the long arm or in the satellite adjacent-2 segregation produces the 2-diffuse quartet type (Fig. 23 A and B). Hence its frequency can be determined by direct observation (Table 19). Crossing over

in interstitial segments does not produce a recognizable quartet and hence the frequency of this type of crossing over cannot be measured.

**Table 19.** Summary of data on frequencies of adjacent-2 segregations in plants heterozygous for interchanges involving chromosome 6, one group with the break in 6 in the long arm, the other with the break in the satellite. For each there are two subgroups, one with long and one with short interstitial segments (Burnham 1950 from Tables 5 and 6, pp. 469 and 471, Genetics 35).

A. Break in 6 in long arm	No. of different interchanges	Avg. % aborted pollen	Percent adjacent-2 seg.	
			Average	Range
Short interstitial segments	10	51.4	25.0	15.2-36.0
One or both interstitial segments long	8	48.3	3.6	0-9.8*
B. Break in 6 in satellite				
Short interstitial segment	2	23.1	0.48	-
One interstitial segment long	2	24.8	0.0	-

\* The one apparent exception with a higher percent was backcrossed to normal stocks, after which it showed low frequency.

For those with the break in 6 in the long arm (Table 19 Part A), a group of ten with short interstitial segments had an average value of 25.0% adjacent-2 segregation; as compared with an average of 3.6 for a group of eight with one or both interstitial segments long. Again, adjacent-2 segregation was about 25% when crossing over was probably low in the interstitial segments. Since pollen abortion was about 50% for them the ratio of alternate: adjacent-1: adjacent-2 segregation was probably about 2:1:1.

For those with the break in 6 in the satellite (Table 19, Part B), adjacent-2 segregations were lacking or rare in those with short interstitial segments as well as in those with long ones. The decreased sterility is a result of the failure of spores deficient for the segment of the satellite to abort. The configurations were invariably chains, since the association of four failed to hold together in the satellite arm. The segregation was probably 1 alternate:1 adjacent-1, the same as that expected in "pair" configurations in an interchange complex if homologous centromeres were paired. For interchanges that have one short interstitial segment and yet show a considerable proportion of chain configurations, there should be an excess of adjacent-1 over adjacent-2 segregations, since adjacent-2 segregation is not expected in chain configurations. For example, at diakinesis in  $\frac{T5-6c}{+} \frac{In\ 5a}{In\ 5a}$ , the combination with short interstitial segments; rings, chains and "pairs" occurred with frequencies of 52.6: 46.0: 1.4%, (Burnham 1950). If the segregation for the quartet types in the non-crossover meiocytes is assumed to be 1:1:0 for the chains and "pairs" and 2:1:1 for the rings; the expected percentages of alternate: adjacent-1: adjacent-2 segregation are 50:33:17, very close to the observed values of 49.7:31:19. Hence the deficiency of adjacent-2 segregations is traceable to the high frequency of chain configurations, for which adjacent-2 segregations are rare.

One question concerns the kinds of segregation that occur following single crossing over in an interstitial segment. Subsequent experiments in which the data from spore quartet analysis of  $\frac{T5-6c}{+} \frac{In\ 5a}{+}$  and  $\frac{T5-6c}{+} \frac{+}{In5a}$  were compared demonstrate that both alternate and adjacent-1 segregations occur following crossing over in the interstitial segment. The data were not adequate to determine if they were equally frequent (Burnham 1953). Although the above results were for interchanges in which chromosome 6 was one of those involved, there is no reason to think that they apply only to these interchanges.

Table 20 summarizes the observations.

**Table 20.** Summary of probable segregation types in maize interchanges.

Configuration	c.o. in interstitial segment	ratios of segregation types		
		alternate	adjacent-1	adjacent-2
1. ring	none	2	1	1
2. ring	yes	1*	1*	rare
3. chain	none	1**	1**	rare
4. chain	yes	1**	1**	rare

\* Probably 1:1 but no accurate measure; both occur in T5-6c.

\*\* These were not measured, but are considered probable.

The above behavior might be thought of as indicating that for every open configuration there is an equally frequent alternate one. These are the gross relationships. Certain interchanges in maize may deviate, as for example T8-9a with about 60% pollen abortion and T6-10b with about 43%.

Other plant species in which individuals with a  $\odot$  4 have about 50% sterility, suggesting a behavior similar to corn are: garden pea (Pisum sativum), Sansome 1932, 1950, Lamm, 1948, 1959; Sorghum versicolor, Garber, 1948; radish (Raphanus sativus), Maeda and Sasaki, 1934; soybean (Glycine hispida), Williams and Williams, 1938; and rice (Oryza sativa), Parthasarathy, 1938. For others, see the review by Burnham (1956).



**THEORETICAL AND OBSERVED RESULTS IN DROSOPHILA.** In *Drosophila melanogaster*, crosses between flies heterozygous for the same interchange have furnished evidence on the kinds of gametes formed and the frequencies. If a female gamete carrying a duplication and a deficiency (Dp-Df) is fertilized by one carrying the complementary Df-Dp a viable fly heterozygous for the interchange is produced. This occurs in *Drosophila* because deficient gametes are viable. The same type of adjacent segregation must occur in ♂ and ♀ if complementary Dp + Df gametes are to be available for fertilization. By proper selection of marker genes, the various kinds of segregations can be recognized phenotypically (Sturtevant and Dobzhansky 1930, Muller 1930, Dobzhansky and Sturtevant 1931, Dobzhansky 1933, Glass 1933, 1935, Pipkin 1940 and Brown 1940).

The theoretical pairing configuration in the parents of such a cross involving T (2;3 bw V<sub>4</sub>) and the marker genes used by Glass are shown in Fig. 24. The possible

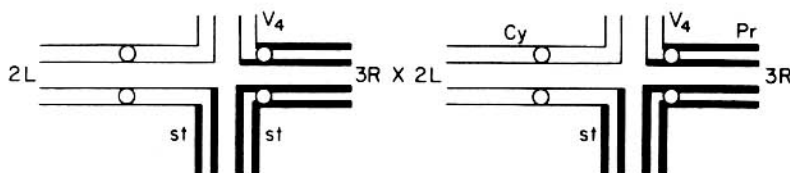


FIG. 24. Chromosomal and genetical constitutions in *Drosophila* crosses in which both parents in the cross were heterozygous for the same variegated V<sub>4</sub> interchange between chromosomes 2 and 3 (modified from Glass, 1935, Fig. 1, p. 8. Mo. Res. Bull. 231). The ♂ is shown on the right. The zygotes expected from the cross are shown in Table 21.

gamete types and the expected offspring are shown in Table 21.

**Table 21.** The gametes and phenotypes which might be expected from the cross of two individuals heterozygous for the same interchange and carrying the marker genes as indicated in the diagrams. Only the results of 2-2 chromosome segregation are shown. x = lethal in zygote, T = interchange, N = normal.

Kinds of ♀ gametes	Kinds of male gametes					
	alternate		adjacent-1		adjacent-2	
	Cy (N)	V <sub>4</sub> Pr st (T)	Cy V <sub>4</sub> Pr	st	Cy st	V <sub>4</sub> Pr
alternate st (N)	Cy (N)	V <sub>4</sub> Pr st (het.T)	x	x	x	x
st V <sub>4</sub> (T)	Cy V <sub>4</sub> (het.T.)	x(homo T.)	x	x	x	x
adjacent-1 V <sub>4</sub>	x	x	x	V <sub>4</sub>	x	x
st st	x	x	Cy V <sub>4</sub> Pr	st st	x	x
adjacent-2 st	x	x	x	x	x	V <sub>4</sub> Pr
st V <sub>4</sub>	x	x	x	x	V <sub>4</sub> Cy	x
					st st	

Note first in Table 21, that among the expected offspring formed by the union of normal gametes from alternate segregation there is a ratio of 2 interchange heterozygotes: 1 normal; since the homozygous interchange is lethal. Reference to Fig. 24 and Table 21 will show that the other four classes of offspring are expected from the union of gametes whose deficiencies and duplications complement each other to produce interchange heterozygotes.

The data obtained by Glass (1935) in the above experiment are summarized in Table 22.

**Table 22.** Progeny from T V4 st/st x T V4 st Pr/Cy C3Y ♂ (Glass, 1935, from Table 2, p. 9, Mo. Res. Bull. 231).

alternate				adjacent-1		adjacent-2	
V4/V4 st Pr homo.T.	Cy	V4 st Pr	Cy V4	Cy V4 st Pr	V4	V4 Pr	Cy V4 st
273	1900*	1789*	1700*	709	1242**	1	1

\* average = 1796

\*\* This and 1796 used as representative values for their classes.

Most of the flies homozygous for the interchange died. The relative numbers from alternate and adjacent-1 segregations are:

$\frac{1796}{1796 + 1242} : \frac{1242}{1796 + 1242}$  or 59%: 41%. If gametic frequencies are similar in ♂ and ♀, then the gametic frequencies should be:  $\sqrt{1796} : \sqrt{1242} = 42.4 : 35.24$  or 55% from alternate and 45% from adjacent-1 segregations. This method of calculation was used by Muller (1930) and also Glass (1935). The results for three of the ten T2-3, and two of the six T3-4 translocations will illustrate the general facts in relation to lengths of interstitial segments (Table 23).

**Table 23.** Chromosome segregation in representative 2-3 and 3-4 translocations in *Drosophila*. Observed phenotype frequencies are given in %; specially calculated ones are in parentheses.

Translocation heterozygote	Interstitial segments	% alternate	% adjacent-1	% adjacent-2	% flies hatched		Source
					het.TxN	Nxhet.	
2-3 bw V4	long, short	59 (55)*	41 (45)*	0+			Glass, 1935
2-3 A	short, short	84 (61)	7 (19)	9 (21)			Dobzhansky and Sturtevant, 1931
2-3 A <sub>1</sub>	short, short	81 (59)**	15 (25)**	4 (13)**	53(59)**	57(64)**	Pipkin, 1940
3-4 A27	short, short	94 (89)	6 (11)	0.1(0+)	64(73)	47(54)	Brown, 1940
3-4 A2	long, short	71 (78)	29 (22)	0.0(0+)	52(59)	48(55)	Brown, 1940

\* Values calculated on the assumption that segregation is similar in the ♂.

\*\* Corrected for observed egg hatch in control, both parents normal.

In general, the behavior in *Drosophila* is similar to that in maize. In ring configurations having short interstitial segments, and therefore little or no crossing over there, alternate, adjacent-1 and adjacent-2 segregations occur to produce six types of gametes as in T2-3A and T2-3A<sub>1</sub>. When at least one interstitial segment is long, the first four types of gametes are the most numerous; only an occasional one is from adjacent-2 segregation. The four types are the ones expected from alternate and adjacent-1 segregations in meiocytes with no crossing over. However, each meiocyte that has crossed over in the interstitial segment also produces these four types whether it is followed by alternate or by adjacent-1 segregation. An interchange with an interstitial segment long enough to have a crossover in all or most of its meiocytes would show a spurious ratio of 1 alternate: 1 adjacent-1 segregation in the ♀ in *Drosophila*. Matings between flies heterozygous

for such an interchange should reflect the actual alternate and adjacent-1 segregation frequencies in the  $\sigma'$ , but adjacent-2 segregation in the  $\sigma'$  could not be measured. If the three types in the  $\sigma'$  were in the ratio of 2:1:1, there would be an apparent excess of alternate over non-alternate segregations. The data obtained by Brown (1940) on egg hatch in reciprocal crosses with normals indicates the segregation may be different in the  $\sigma'$  for some translocations. An example is T3-4 A27 in Table 23. It is probable that T3-4 and T2-4 translocations regularly form chains. Adjacent-2 segregations are rare in 3-4 A27 which has short interstitial segments as well as in 3-4 A2 which has a long interstitial segment (Table 23). This is expected if homologous centromeres disjoin.

The actual frequencies of the types of segregation are somewhat in doubt because of the lack of knowledge about the behavior in the  $\sigma'$ . In the experiments of Dobzhansky (1933), Pipkin (1940), and Brown (1940) they have calculated the frequencies by considering the egg hatch data, and the phenotype frequencies from the heterozygous translocation x heterozygous translocation matings (Table 23). There appears to be an excess of alternate segregations over the total of the other types in the ring-formers with short interstitial segments, about 60:40 or 1.5:1. In the chain formers with short interstitial segments there is probably a much greater excess of alternate segregation, 3.5:1 or higher. It is of interest to note that the first translocations from x-ray treatment in *Drosophila* were described by Painter and Muller (1929) as having predominantly alternate segregation, a behavior comparable to that in *Oenothera*.

In mice, survival of Df-Dp gametes from interchange heterozygotes was found by Snell (1946). Matings between mice heterozygous for the same interchange produced offspring from both types of non-disjunctive segregation, i. e. adjacent-1 and adjacent-2, in tests of one interchange.

### Interchange heterozygotes with low sterility

A number of plant species have been reported in which a  $\odot 4$  may show low spore abortion, e. g. *Datura stramonium* (Blakeslee 1928), *Triticum monococcum* (Thompson and Hutcheson 1942, Yamashita 1947), *Hordeum vulgare* (Smith 1941, Burnham et al. 1953), *Lycopersicon esculentum* (Barton 1954) and *Oenothera* (Cleland 1929 and others).

**Table 24.** Summary of pollen abortion observed for interchanges with different configurations in *Datura stramonium*. (Bergner et al., 1933, based on Table 2, p. 112-113, Proc. Nat. Acad. Sci. 19).

Configurations at metaphase I	$\pm 50\%$	$\pm 25\%$	$\pm 15\%$	Fertile (Normal)	Total
$\odot 4$	0	9	2	17	28
$\infty 4$ (with a c.o.)	5	1		0	6
$\odot 4$ or zigzag	1	0		1	2
Tr 4*	6	2		2	10
$\odot 4$ or Tr 4	1				1
$\odot 6$	0	2	1	0	3
Tr 6	1				1
"II"	1				1
TOTALS	15	14	3	20	52

\* Described as being simple translocations (Tr) following radiation treatment, expected to form chains. Chains with a crossover were referred to by Blakeslee as "necktie" configurations.