A STRAIN OF MAIZE HOMOZYGOUS FOR SEGMENTAL INTERCHANGES INVOLVING BOTH ENDS OF THE P-BR CHROMOSOME[1,2]

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Semisterile-1 in maize involves an interchange of terminal segments between the *B-lg* and *P-br* chromosomes. The probable positions of the breaks in relation to several genes known to lie in the respective linkage groups concerned are depicted in figure 1.

The principal numerical data upon which the map is based are given in an earlier publication.[3] It has been established more recently that brown midrib (bm_2), which gives about 41 per cent crossing-over with semisterile-1, lies in the *P-br* chromosome some 40–50 units from *f* on the side remote from *P*.[4] Green striped (*gs*) gives about six per cent recombination with semisterile-1 in back-crosses and about 27 per cent with bm_2. While the confirmatory tests are not yet completed, the available evidence indicates that both *gs* and bm_2 are on the translocated piece of the *P-br* chromosome.

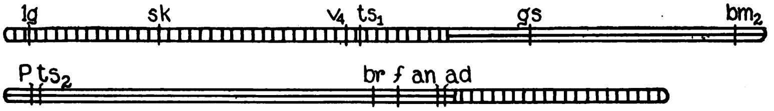

FIGURE 1

Chromosome map of the segmental interchange involved in semisterile-1. The exact positions of the ts_1, ts_2, *an* and *ad* are not yet worked out although they are known to be in the regions indicated.

Some doubt has arisen in regard to the validity of the respective percentages of crossing-over earlier reported for *an*, *ad* and semisterile-1.[3] The two supposedly semisterile *ad* segregates found have proved to breed as normals, as have three plants which were originally classified as semisterile *an*. It would appear that some extraneous factor was responsible for the aborted pollen found in these plants, and that crossing-over between the two respective genes and the point of break either does not occur at all or is substantially less than earlier given.

As Burnham[5] first reported, semisterile-1 plants show eight bivalents and a ring of four chromosomes at diakinesis. Semisterile-5 exhibits a similar configuration, the ring being attached, however, to the nucleole.[6] Semisteriles-1 and -5 in combination form a ring of six chromosomes and seven bivalents (Fig. 2). They consequently involve one chromosome in common.

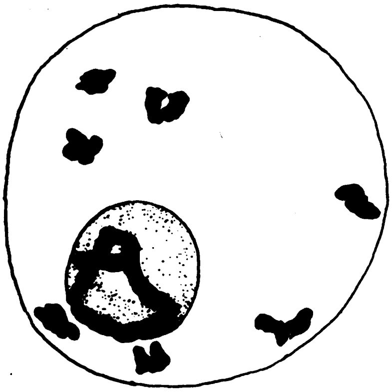

FIGURE 2

Ring of six chromosomes and seven bivalents in hybrids between semisteriles-1 and -5.

Linkage tests show that the chromosome common to the two semisteriles corresponds to the *P-br* group. Semisterile-5 and ts_2 give 24.0 per cent crossing-over. This value is based on counts of 254 Ts_2 plants in three back-cross progenies which showed 32.0, 9.75 and 27.3 per cent recombination, respectively. The position of the point of break in relation to *br* and *f* may be inferred from the data from a single progeny presented in table 1. The amounts of crossing-over shown are as follows: semisterile-5 and *f*, 16.0 per cent; semisterile-5 and *br*, 13.4 per cent; *br* and *f*, 2.7 per cent. A back-cross progeny of 100 plants segregating semisterile-5 and bm_2 gave 34.0 per cent recombination.

TABLE 1

DISTRIBUTION OF PLANTS FROM THE BACK-CROSS SEMISTERILE-5, *Br F.br f x* NORMAL, *br f*

SEMISTERILE				NORMAL				TOTAL
Br F	*Br f*	*br F*	*br f*	*Br F*	*Br f*	*br F*	*br f*	
32	1	0	4	6	0	1	31	75

The other chromosome involved in the semisterile-5 ring corresponds to the *Y-Pl* linkage group. The summarized data from six small progenies bearing on this relationship are presented in table 2.

TABLE 2

DISTRIBUTION OF PLANTS FROM BACKCROSSES OF THE TYPE, SEMISTERILE-5 *Y pl.-y Pl x* NORMAL, *y pl*

SEMISTERILE				NORMAL				TOTAL
Y Pl	*Y pl*	*y Pl*	*y pl*	*Y Pl*	*Y pl*	*y Pl*	*y pl*	
0	30	3	20	18	4	22	1	98

The amounts of crossing-over indicated are as follows: semisterile-5 and *Y*, 45.9 per cent; semisterile-5 and *Pl*, 8.2 per cent; *Y* and *Pl*, 39.8 per cent.

On the basis of the linkage data presented in summary form above the semisterile-5 segmental interchange may be mapped as in figure 3.

The *Y-Pl* chromosome is attached by its satellite end to the nucleole. The cytological evidence shows that it is the opposite end of this chromosome which is involved in the semisterile-5 segmental interchange. This fact together with the linkage data bearing on the relation of *Y* and *Pl* to the point of break demonstrates that the order in the chromosome is nucleole-*Y*-*Pl*-break. A revision is necessary of our earlier report[6] regarding the relative lengths of the chromosome segments involved in the semisterile-5 interchange. The error was one of statement rather than of observation, and we are indebted to Miss McClintock for calling it to our attention. In semisterile-5, according to our measurements of early prophase figures in pollen mother cells, approximately one-third of the satellite chromosome (*Y*-*Pl*) is interchanged with about two-thirds of the *P*-*br* chromosome. These relations are depicted in figure 4 which is intended to replace the corresponding figure in our earlier publication.[6]

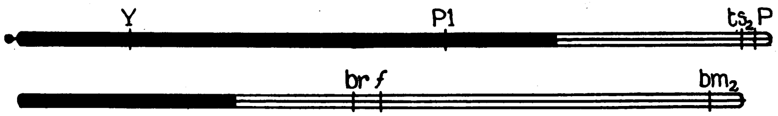

FIGURE 3

Chromosome map of the segmental interchange involved in semisterile-5.

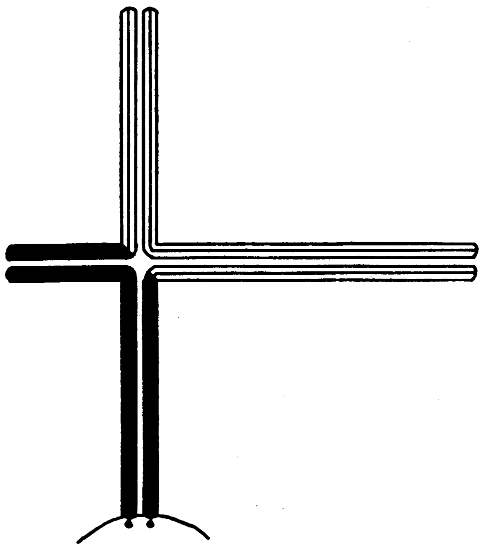

FIGURE 4

A diagrammatic representation of the cross-shaped figure found at early prophase in semisterile-5. The chromosome shown entirely in black and attached to the nucleole corresponds to the *Y*-*Pl* linkage group.

When semisteriles-1 and -5 are crossed, three kinds of offspring result, namely, normals with all sound pollen, semisteriles with 50 per cent of the pollen aborted and a third class in which only 15–25 per cent of the pollen is functional. The latter group of individuals is heterozygous for the two segmental interchanges and shows seven bivalents and a ring of six chromosomes at diakinesis (Fig. 2). Among the normal offspring of such double semisteriles selfed four classes of plants differing in the structure of their chromosomes are expected: (1) the standard type, which is designated *o*-normal; (2) two classes of *x*-normals, *x*-normal-1 and *x*-normal-5, homozygous, respectively, for the segmental interchanges characteristic of semisteriles-1 and -5; and (3) the double *x*-normal form (*x*-normal-1.5) homozygous for both segmental interchanges. These three groups should be distinguishable on the basis of their reactions in crosses to the *o*-normal or standard type. In such matings *o*-normals should give only normal offspring, the two kinds of *x*-normals should give semisteriles, and the double *x*-normal should yield plants with, presumably, a much lower percentage of functional pollen.

A test of this type has been completed on two fully fertile segregates from a self-pollinated hybrid between semisteriles-1 and -5 which produced 85 per cent aborted pollen. One of the plants in question was an *o*-normal, since, in crosses with the standard line, its offspring were fully fertile. The other plant proved to be a double *x*-normal (*x*-normal-1.5), giving hybrids with the standard line in which upward of three-quarters of the pollen grains were empty and shriveled. The offspring of the two fertile segregates selfed were all fully fertile.

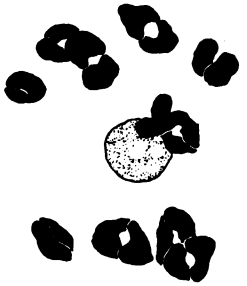

FIGURE 5

Diakinesis in a pollen mother cell of *x*-normal-1.5. Ten bivalent chromosomes are present in this type which is homozygous for two segmental interchanges involving opposite ends of the *P*-*br* chromosome.

Cytological examination of one plant in the progeny adjudged to be *x*-normal-1.5 revealed ten bivalent chromosomes as expected (Fig. 5). While forming ten pairs, such plants differ from standard maize in that the *P*-*br* chromosome is replaced by a composite one whose interstitial segment consists of the middle part of the *P*-*br* chromosome but whose respective ends correspond to parts of the normal *B*-*lg* and *Y*-*Pl* chromosomes, the latter being altered in a complementary way.

Hybrids between the *x*-normal-1.5 line and the *o*-normal type show a six-armed chromosome complex in the pollen mother cells at early prophase. Figure 6 is based on a preparation in which the relations of the parts in the interchanged chromosomes were particularly clear. The interchange group (shown in black) is attached to the nucleole by the satellite end of the *Y*-*Pl* chromosome. Two well-defined chiasmata are in evidence from each of which three arms extend. The upper chiasma in the figure corresponds to that in semisterile-5 which involves an interchange between the *Pl* end of the *Y*-*Pl* chromosome and the *P* end of the *P*-*br* chromosome. The lower chiasma is that characteristic of semisterile-1 in which the v_4 end of the *B*-*lg* chromosome is exchanged with the opposite (bm_2) end of the *P*-*br* chromosome. Between the two chiasmata lies an interstitial segment of the *P*-*br* chromosome corresponding to a map distance of roughly 25 units. The loci of the *br* and *f* genes are in this piece.

The plant from which the homozygous *x*-normal-1.5 stock was derived resulted from a cross between semisteriles-1 and -5. In this individual the two segmental interchanges were present consequently in repulsion phase.

In order that *x*-normal-1.5 gametes be formed by such a plant crossing-over must occur in the region between the semisterile-1 break in one interchanged *P-br* chromosome and the semisterile-5 break in the other interchanged *P-br* chromosome. Such a crossing-over, followed by distribution of alternate chromosomes in the ring to the same pole (and non-disjunction if crossing-over occurs in the four-stand stage), would give rise to *x*-normal-1.5 and *o*-normal nuclei (Fig. 7). It is a rather remarkable circumstance that the two fertile derivatives tested proved to be of these two particular complementary types; both must have resulted from combination between like crossover gametes of the two respective kinds.

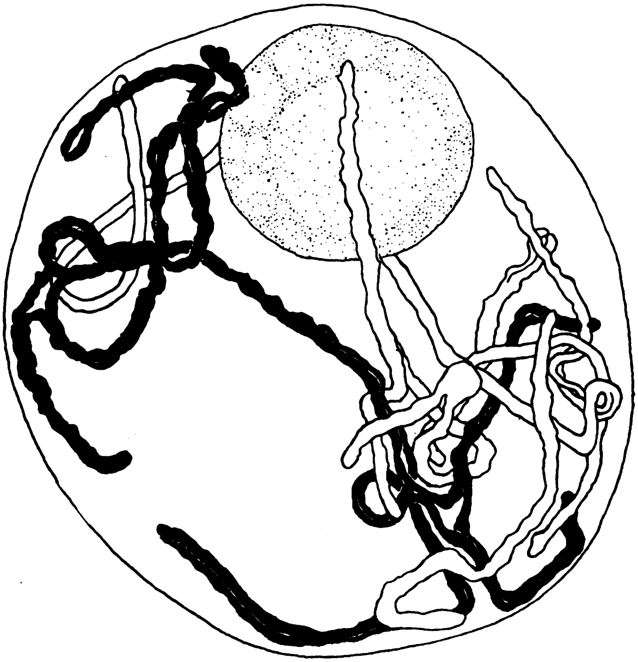

FIGURE 6

Early prophase stage in a hybrid between standard maize and the doubly interchanged type, *x*-normal-1.5 showing a six-armed complex and seven bivalent chromosomes.

As may be seen from figure 6, pairing of the chromosomes in the semisterile-1.5 complex is almost complete. In each of the six arms and the interstitial segment, corresponding parts lie in close association. In this case, therefore, as in semisteriles-1 and -5 considered earlier, there is definitive evidence that translocation in itself does not radically alter the ability of the chromosomes concerned to pair. Only at the chiasmata where the strands change partners does the relationship appear to become somewhat looser. On the basis of the cytological evidence alone one might well doubt with reference to these cases in maize whether the effect of segmental interchange on effective pairing extends beyond the chromosome parts immediately adjacent to the chiasmata. Data on crossing-over in these regions are needed. Until there is experimental evidence to support it Darlington's[7] *a priori* argument that the amount of pairing of corresponding parts of two chromosomes is lessened when the homology is not continued in adjoining segments is not to be taken too seriously.

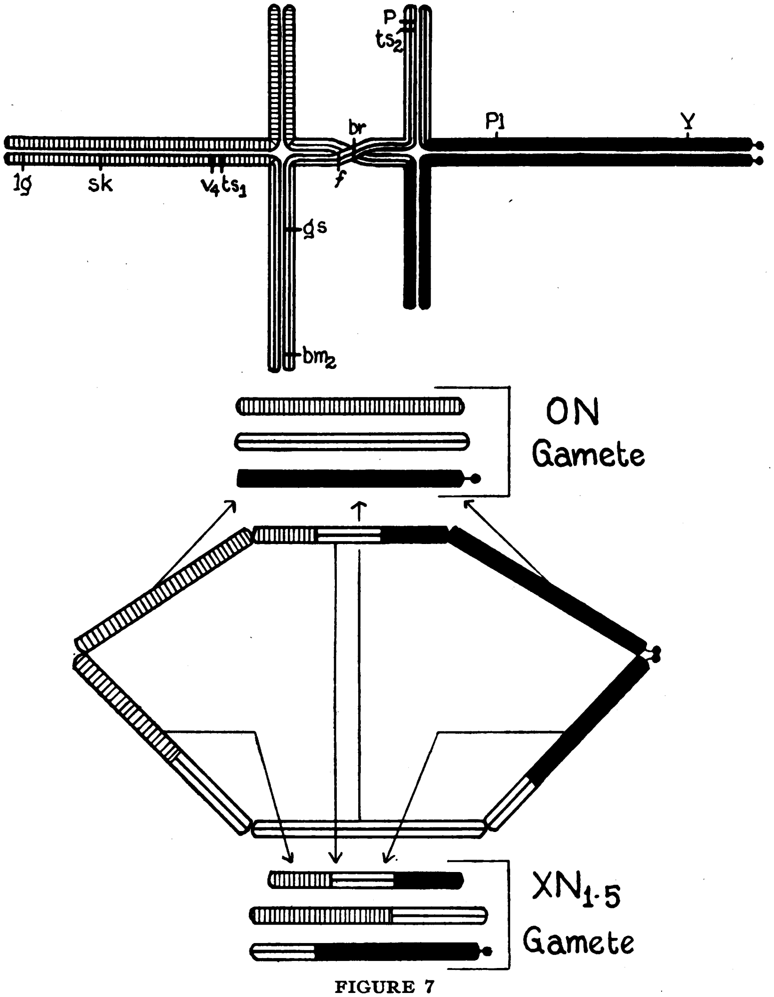

FIGURE 7

Diagrammatic representation of the origin of the *x*-normal-1.5 type through crossing-over in the interstitial segment of the ring of six chromosomes found in hybrids between semisteriles-1 and -5.

The estimated length of the interstitial segment in the doubly interchanged *P-br* chromosome, as stated above, is about 25 crossover units. It is not yet definitely known what the effect on amount of crossing-over is of the two structural changes in the region proximal to the two breaks. That crossing-over must occur rather freely in this segment, however, is indicated by the fact that of the two normal segregates from a semisterile-1.5 plant (repulsion phase) selfed both were crossover types. It would appear that in this case, therefore, crossing-over between corresponding parts is not confined to the arms of the interchanged chromosome complex.

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[2] The authors desire to express their appreciation for the assistance received from the Research Fund of the University of Wisconsin, the National Research Council and the Elizabeth Thompson Science Fund.

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CHROMOSOME RINGS IN MAIZE AND OENOTHERA[1,2]

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As Håkannson,[3] Darlington,[4] Cleland and Blakeslee,[5] and Emerson and Sturtevant[7] have shown, Belling's[8] hypothesis of segmental interchange affords a consistent explanation of the chromosome attachments in Oenothera. It is by no means clear, however, to what extent the other peculiarities in cytological and breeding behavior of this genus are thus accounted for. Renner's[9] extensive researches on the genetic interrelations of the Oenotheras demonstrate that not only do certain genes display anomalous linkages but also many characters which segregate freely in some crosses assort in stable groups in others. In the origin and integrity of the "complexes" of Renner lie the main problems which the Oenotheras present. Cleland[10] has established the fact that ring-formation is a characteristic feature of certain Oenothera species and, furthermore, that the chromosomes within the rings are distributed, for the most part, in a determinate