

*THE BEHAVIOR IN SUCCESSIVE NUCLEAR DIVISIONS OF A  
CHROMOSOME BROKEN AT MEIOSIS*

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If a chromatid in maize is broken at a meiotic anaphase and if it enters a telophase nucleus, fusion between the two sister halves of this chromatid will result at the position of breakage.<sup>1</sup> Because of this fusion, the separation at a succeeding anaphase of the sister halves of this chromatid necessarily produces a bridge configuration. The pull on the chromatin of this bridge in the anaphase or telophase results in breakage and again a broken chromosome enters each telophase nucleus. The following questions immediately arise: Will this chromatid produce a bridge in the following mitotic anaphase by a similar fusion of sister halves at the position of the second break? Will this process continue indefinitely in each successive division or will the broken end of a chromosome eventually "heal" and continue through mitotic cycles without further fusions, bridges and breakages? It is stated in the previous publication that the evidence on this

point was conflicting. It is the purpose of this note to indicate the nature of this conflict. In brief, the evidence shows that the breakage–fusion–bridge–breakage cycle will continue, after an original meiotic break, in the endosperm, whether the broken chromosome is contributed by the male or by the female gamete. In contrast to the endosperm, healing of the broken end of the chromosome, i.e., discontinuance of the breakage–fusion–bridge–breakage cycle, occurs in the embryo.

The method previously used to demonstrate, cytologically, the fusion of broken ends of sister chromatids involved the use of an inversion. In all such cases the broken chromatid produced is deficient and would not be expected to survive regularly through ovules or to be transmitted by pollen grains. Hence, a test of the behavior of such a broken chromosome could not readily be obtained. Consequently, other methods have been used to obtain a broken chromosome with at least a complete set of genes.

The *first method* to be described involves the use of an x-ray induced rearrangement in chromosome 9. The morphology of a normal chromosome 9 is shown in *a*, figure 1. The short arm terminates in a large knob (stip-

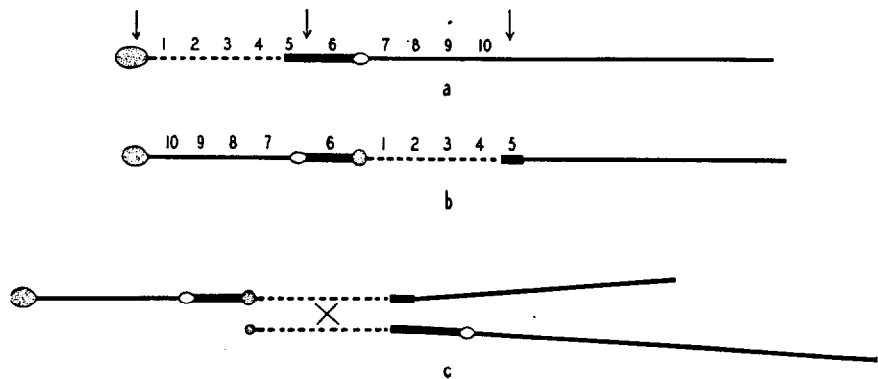


FIGURE 1

*a.* Diagram of a normal chromosome 9. The stippled region represents the large terminal knob, the dash line, the segment composed of small, loosely spaced chromomeres. The wide solid line represents the heavy, closely associated chromomeres adjacent to the spindle fibre attachment region which is represented as a clear bulge. The long arm is represented by a thin, solid line. The arrows point to the positions of the three breaks, followed by refusions, which produced the chromosome diagrammed in *b*. *c.* The association of homologous regions, 1 to 5, of a normal chromosome 9 with a very small knob and the rearranged chromosome 9 shown in *b*. The cross indicates a position of crossing-over to give rise to the dicentric chromosome shown in *a*, figures 3 and 4.

pled). (The presence of a knob is not necessary for the functioning of chromosome 9. Strains with no knob or knobs of intermediate sizes are known. The knob substance lengthens the chromosome at its end but does

not add necessary genic material.) The proximal one-third of the short arm (5 and 6, figure 1) adjacent to the spindle fibre region, is characterized by large, closely associated, deeply staining chromomeres, suggesting heterochromatin in appearance. The distal two-thirds of the short arm (dash lines, figure 1) is composed of small, widely spaced chromomeres. The x-ray induced rearrangement is shown in *b*, figure 1. The positions of breakage in the normal chromosome 9 which gave rise to this rearrangement are indicated by the arrows in *a*, figure 1. The terminal large knob has been broken into two unequal parts, the smaller part together with three-quarters of the short arm being inserted into the long arm, the other section being inverted. In plants possessing one normal chromosome 9 and one altered chromosome 9, homologous synaptic association of regions 1 to 5 (*c*, figure 1) followed by a crossover within this region, results in a chromatid with two spindle fibre attachment regions and a chromatid with no spindle fibre attachment region (*a*, figures 3 and 4). The composition of the chromatid with two spindle fibre regions should be noted. From right to left it is composed of a chromosome 9 complete as far as and including the small internal knob. This is followed by the conspicuous deeply staining region, 6, which joins the second spindle fibre attachment region. As the two spindle fibre regions pass to opposite poles at anaphase I, a break must occur between these two regions. Should it occur between the internal knob and the second fibre region (at position of arrow in *a*, figures 3 and 4) one of the two resulting chromatids will possess a full set of genes plus a short duplication composed of a part of region 6 extending beyond the small knob. This chromosome would be expected to be functional since no deficiency is present. The main factor to be emphasized is the presence in this chromosome of a broken end. It is the purpose of this paper to test the subsequent behavior of this broken end in the future nuclear cycles.

The genes *Yg*, *C*, *Sh* and *Wx* (*Yg*, normal green plant, *yg*, yellow-green plant; *C*, colored aleurone, *c*, colorless aleurone; *Sh*, normal endosperm development, *sh*, shrunken endosperm; *Wx*, normal starch in endosperm and pollen, staining blue with iodine, *wx*, waxy endosperm whose starch stains red with iodine) are located in the short arm of chromosome 9, the order being: knob-*Yg*-*C*-*Sh*-*Wx*-spindle fibre region.<sup>2</sup> The crossover distance between the genes are 19, 3 and 21, respectively.<sup>3</sup> All four genes are located in the translocated segment 1 to 5.<sup>4</sup> It should be emphasized that *Yg* is a plant character whereas *c*, *sh* and *wx* are endosperm characters. Plants possessing a normal chromosome 9 with the genes *Yg*-*C* (or *c*)-*sh*-*wx* and the altered chromosome 9 containing the dominants only, when crossed by *yg*-*c*-*sh*-*wx* or *Yg*-*c*-*sh*-*wx*, have given the results shown in table 1. The kernels have been divided into three main classes: I, full colored, non-variegated kernels; II, *c*-*sh*-*wx* kernels and III, kernels whose aleurone color is variegated for *C* and *c*. It will be noted that in the first

class, the non-variegated kernels, only 5 are detectable crossovers. Of the 41 in the variegated class, 38 are recognizable crossovers. The three that contain *Wx* are variegated for *Wx* and *wx* as well as *C* and *c*. The type of variegation is very specific. Colorless areas (*c*) of various sizes occur.

TABLE 1  
DISTRIBUTION OF ENDOSPERM CHARACTERS RESULTING FROM THE CROSS

♀	$\frac{C(\text{or } c)\text{-}sh\text{-}wx\text{-normal chromosome 9}}{C\text{-}Sh\text{-}Wx\text{-rearranged chromosome 9}}$	×	♂	$c\text{-}sh\text{-}wx\text{-normal chromosome 9}$	
I.	Non-variegated kernels:		<i>C Sh Wx</i>	<i>C Sh wx</i>	<i>C sh Wx</i>
			3185	4	1
II.	<i>c sh wx</i> kernels				
			3128		
III.	Variegated kernels:		<i>C-c (Sh-sh)* Wx-wx</i>	<i>C-c (Sh-sh)* wx</i>	<i>C-c sh wx</i>
			3	34	4

\* Variegation for *Sh* and *sh* cannot be readily detected.

Within these areas there are no colored (*C*) cells. The kernels that are likewise variegated for *Wx* and *wx* show a distinct relationship between patterns of the *C* and *c* and of the *Wx* and *wx* variegations. All the *C* spots are *Wx*. The *c* spots are of two types: (1) those that are totally *wx* and (2) those showing smaller areas of *wx* within a *c-Wx* spot. Just such variegation would be expected if the endosperms in these kernels had received chromosomes 9 with broken ends, the broken chromosomes carrying the dominant *C* or the dominants *C* and *Wx*, and if fusions of broken ends were occurring in successive nuclear divisions, i.e., continuance of the breakage-fusion-bridge-breakage cycle. It is only necessary to assume that the successive breaks are not always at the points of previous fusions. Since this is known to occur from direct cytological observations<sup>1</sup> and from observations of chromosomes which have undergone such successive breaks (see figures 3 and 4), it is a justifiable assumption. A chromosome 9 with a broken end and carrying *C* and *Wx* could result from a crossover (*c*, figure 1) between the translocation point to the right in the rearranged chromosome 9 and the gene *Wx*, followed by a break at anaphase I of the dicentric chromatid so produced (the chromatid recovered is that to the right of the arrow, *a*, figures 3 and 4). This broken chromosome should give *C-c* and *Wx-wx* variegation. If the crossover occurred between *Wx* and *C*, the chromosome with the broken end would contain the genes *C* and *wx*. A *wx* kernel with *C-c* variegation would result. In the case being described, variegation could result from fusions between the broken ends of two chromosomes 9 (the two contributed by the female parent) or between ends of sister halves of a chromosome. That the latter can occur will be evident

from the second case to be described. Figure 2 has been constructed to illustrate the method by which  $C-c$  and  $Wx-wx$  variegations are produced on the basis of fusion of broken ends of sister halves of a chromosome. If a broken chromosome with fused sister halves contains the genes  $C$  and  $Wx$  (left, figure 2) and if the break in the following anaphase occurs between

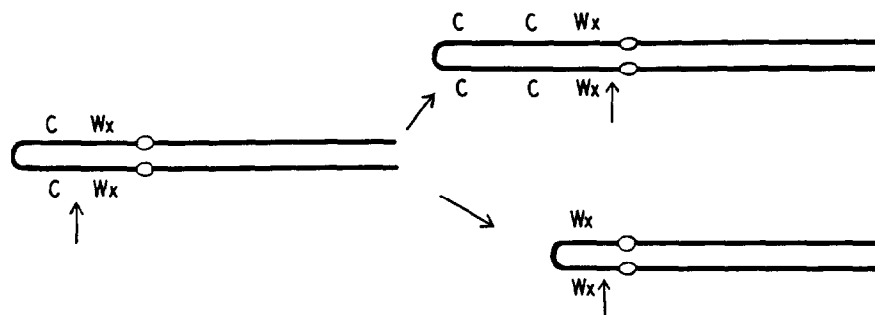


FIGURE 2

Diagram to illustrate the method by which variegation of the endosperm characters  $C$  and  $Wx$  can be produced. The figure to the left represents the two sister halves of a broken chromosome 9 fused at the position of a previous break. The chromosome carries the genes  $C$  and  $Wx$  in the order given. The spindle fibre attachment region is represented as a clear bulging region. Separation of the two halves in the following anaphase produces a bridge configuration. If breakage of the bridge occurs at the position of the arrow, a chromosome lacking  $C$  will enter one nucleus (lower right) and a chromosome duplicated for  $C$  will enter the sister nucleus (upper right). If fusions occur between the two split halves of each of these broken chromosomes, as represented in the diagrams, a bridge will form in the following anaphase. If breaks occur at the positions of the arrows,  $Wx$  will be deleted from one of the resulting nuclei in each case.

$Wx$  and  $C$  (arrow), the chromosome entering one nucleus will carry  $Wx$  and a duplication with  $C$  (upper right, figure 2). The chromosome entering the sister nucleus will have lost  $C$  but will possess  $Wx$  (lower right, figure 2). Through fusions of broken ends of the two sister halves of each of these chromosomes, in turn, an anaphase bridge will be produced in the following division. If the break occurs at the arrows in each case,  $Wx$  will be removed from the chromosome in one of the two daughter nuclei, respectively. On this basis, two types of spots are expected in a variegated kernel containing  $C$  and  $Wx$ : (1)  $c-wx$  spots and (2)  $c-Wx$  spots within which there are areas of  $wx$ . Since the size of the recessive spots range from large to very small, the breakage-fusion-bridge-breakage cycle must continue in successive nuclear divisions in the endosperm tissue.

From genetic data on normal chromosome 9, it is known that within the region 1 to 5, figure 1, single crossover chromatids are produced far more frequently than double crossover chromatids.<sup>3</sup> From the data in table 1,

it is strikingly evident that the majority of detectable crossovers are associated with variegated endosperm. Only 5 are not associated with variegation. It was therefore suspected that the 41 variegated kernels have obtained a chromosome with a broken end following a single crossover as diagrammed in *c*, figure 1, whereas the 5 non-variegated kernels have obtained a double crossover chromosome with a normal, non-broken end. The latter, therefore, should not show variegation. If the endosperm of a kernel possesses either a single crossover chromosome (with a broken end) or a double crossover chromosome (with a normal end), the embryo and plant tissues arising from such a kernel must possess either a broken chromosome or a normal chromosome respectively. If the crossover kernels, variegated and non-variegated, are sown, the plants arising from each should clearly show the expected type of chromosome in the meiotic pro-phases. The following will describe these results.

If the variegated kernels from the cross *Yg-C-sh-wx*-normal chromosome 9/*Yg-C-Sh-Wx*-altered chromosome 9 by *yg-c-sh-wx*-normal chromosome 9, possess a broken chromosome 9 introduced by the female parent, and if the breakage-fusion-bridge-breakage cycle involving broken ends of sister chromatids continues without healing of the broken ends, variegation for the *yg* character should be evident in the plants coming from these kernels. On the other hand, plants coming from the non-variegated kernels should show no variegation for *yg*. Sixty non-variegated kernels of the *C-Sh-Wx* class and 60 of the *c-sh-wx* class were sown. No evidence of *yg* appeared in the resulting individuals. The 12 *variegated* kernels from this cross gave rise to 6 *Yg* plants with no evidence of *yg* at any stage in the life of the plants, 5 *yg* plants and 1 *Yg* plant which showed a single *yg* streak on the first leaf but no other *yg* streaks throughout the life of the plant. The *yg* plants clearly indicated that a broken chromosome 9 was present, a break having occurred to the right of the internal knob, *a*, figures 3 and 4, deleting the *Yg* locus. Because the *Yg* plants did not show *Yg-yg* variegation it was assumed that although they possessed a chromosome 9 with a broken end, this broken end had healed in the embryo cells. Since the *Yg* locus is close to the right side of the small internal knob of the chromatid in *a*, figures 3 and 4, the *yg* plants should show no knob on the chromosome 9 contributed by the female parent whereas the *Yg* plants could possess the knob with or without an additional segment beyond the knob. Consequently, all 12 plants coming from the variegated kernels were examined at meiosis to obtain the constitution of the chromosome 9 contributed by the female parent. All 5 *yg* plants showed a deficiency in one chromosome 9, the knob being lost in all cases, an extensive deficiency of the short arm being present in two cases. Among the 7 *Yg* plants, the chromosome 9 contributed by the female parent was complete to and including the small knob, with or without, in the several plants, respectively, an extension of

chromatin beyond this small knob. Regardless of its composition, the broken chromosome 9 in all cells examined in any one plant was always exactly the same in appearance. In this particular cross, the plant tissues have corroborated both genetically (*yg* plants) and cytologically (all plants) the assumption of the presence of a broken chromosome 9, this assumption having been based upon the variegation exhibited in the endosperm of the kernels from which each plant arose.

Among the 26 examined plants coming from the variegated kernels of both crosses (by *Yg-c-sh-wx* or *yg-c-sh-wx*), 10 have shown a chromosome 9 terminating in the small knob, i.e., a complete chromosome 9. Seven have shown a deficient chromosome 9, either lacking the small knob or the knob plus an adjacent section of the short arm. In the remaining seven cases, the chromosome 9 was complete to and including the small knob but likewise possessed a section of chromatin extending beyond this knob. The composition of the chromatin extension in each case introduces important evidence not only for the presence of a broken chromosome 9 but also for the origin of this chromosome from a crossover diagrammed in *c*, figure 1, followed by a break at anaphase I in the dicentric chromatid. The extension always possessed a section of the easily identifiable chromatin of region 6, figure 1, clearly indicating the origin of this chromosome from one whose original composition was that of *a*, figures 3 and 4. A particularly interesting example of a recovered broken chromosome is shown in *c*, figure 3. The simplest method of diagramming the origin of this chromo-

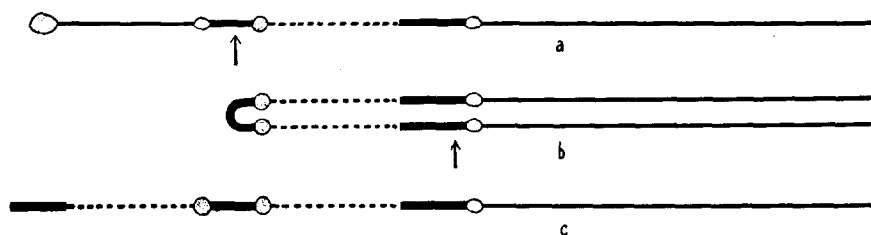


FIGURE 3

See text for description.

some is given in *a* and *b*, figure 3. In *a*, the dicentric chromatid is represented following a crossover as diagrammed in *c*, figure 1. The arrow points to the position of breakage, the portion to the right of the break being in the line of descent. Fusion occurred between the two sister halves of this chromosome as shown in *b*, figure 3. The arrow points to the position of the second break, the upper chromatid being recovered as shown in *c*, figure 3. That the breakage-fusion-bridge-breakage cycle involving sister chromatids must occur through several mitoses at least in the early

divisions (embryo sac ?) following the original break is evident from the composition of the recovered chromosome 9 in several of these cases. One example will be cited. The constitution of the chromosome 9 contributed by the female parent, as observed in the prophase of meiosis of this plant, is shown in *d*, figure 4. At least three breaks, followed by fusions of broken ends of sister halves of a chromosome are necessary to give rise to this chromosome. These are illustrated in *a*, *b* and *c*, figure 4. The arrow

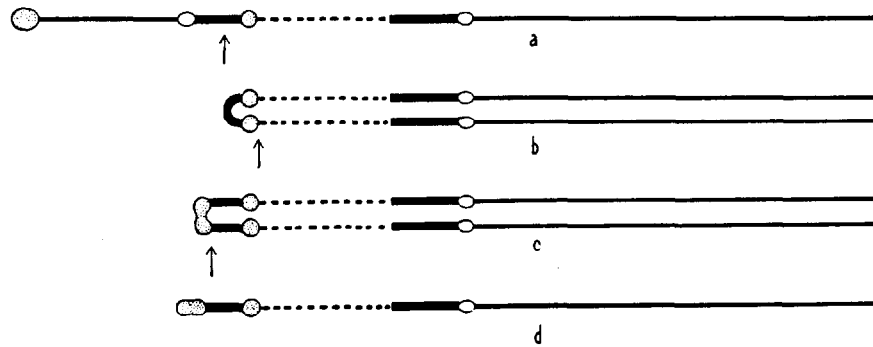


FIGURE 4

See text for description.

points to the position of the successive breaks, the upper chromatid in all cases being in the line of descent.

The composition of the chromosome 9 contributed by the female parent in these 26 cases has given abundant evidence of the presence in these plants of a broken chromosome 9 and has verified the assumed origin of such a broken chromosome.

If the variegated endosperm tissue is related to the presence of a broken chromosome arising after a single crossover, each of the 5 crossover kernels with no variegation (I, table 1) should possess an unbroken chromosome 9 which has arisen from a double crossover chromatid. Three of the 4 plants coming from the *C-Sh-wx* kernels were examined. All three possessed the rearranged chromosome (*b*, figure 1), obviously the result of a double crossover. The plant coming from the *C-sh-Wx* kernel contained a normal chromosome 9, likewise a double crossover. Thus, the evidence from the crossover kernels, variegated and non-variegated, is in complete accord with the prediction.

The *second method* involved the use of a chromosome 9 with a duplication of nearly all of the short arm attached to the end of the normal short arm. The order of the genes in the duplicated segment is inverted with respect to those in the normal short arm as in an attached-X chromosome of *Drosophila*. In plants containing a chromosome 9 with the duplication



and a normal chromosome 9, a number of types of 2-by-2 homologous associations at meiotic prophase can occur. Dicentric chromatids are produced by a crossover following the association of the duplicated segment with its homologous region in the normal chromosome 9, *a*, figure 5, resulting in a first division bridge or by a crossover as diagrammed in *b*, figure 5, following the association of the duplicated segment with its homologous region in the duplicated chromosome 9. The latter will result in a second division bridge. Counts of bridge configurations in *AI* and *AII* have given 13.8% (among 137 sporocytes) and 13.5% (among 74 sporocytes) respectively. It should be noted that the dicentric chromatid represents a completely duplicated chromosome attached at the end of the short arms, *c*, figure 5. Breakage at anaphase of such a chromatid can produce two

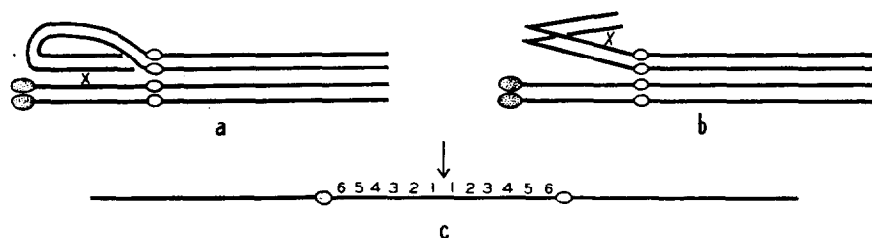


FIGURE 5

*a*. Diagram of a meiotic prophase association of a normal chromosome 9 and a chromosome 9 with a duplication of the short arm. The duplicated segment is homologously associated with the short arm of the normal chromosome 9. A crossover as indicated produces a chromatid composed of two attached chromosomes 9 as shown in *c*. This will produce a bridge configuration at anaphase *I*. *b*. Association of homologous regions within the duplicated chromosome 9. A crossover as indicated will give rise to the dicentric chromatid shown in *c* which will form a bridge configuration in anaphase *II*.

complete chromosomes 9 if the break occurs at the position of the arrow, or one chromosome with a duplication and one chromosome with a deficiency if the break occurs at any other position between the two spindle fibre regions. By this means, one can obtain a broken chromosome with at least a complete set of genes.

If such a broken chromosome carries dominant genes and if it is introduced through the pollen to plants carrying the recessive alleles, a continued breakage-fusion-bridge-breakage mechanism involving sister halves of a chromosome, should produce variegation in the endosperm tissues. When successive genes are lost, those distal to the spindle fibre region should be lost first followed by genes nearer to the spindle fibre region as illustrated in figure 2. When such variegated kernels are sown, the plants coming from them should show the presence of a broken chromosome 9 in the meiotic prophase configurations.

Plants carrying the duplicated chromosome 9 with the genes *I* and *Wx* in both the normal and the duplicated segment (*I*, inhibitor of color in the aleurone layer, *i*, color in aleurone layer, located at the same position as *C* in the crossover map) and a normal chromosome 9 with a large terminal knob on the short arm and carrying the recessive alleles, when crossed to plants with normal chromosomes 9 carrying *i wx*, have given the following results: 62 *I Wx*, 0 *I wx*, 29 *i Wx*, 765 *i wx* and 30 *I-i* variegated kernels.<sup>5</sup> Among the *I-i* variegated kernels 3 were totally *wx*. The remaining 27 were likewise variegated for *Wx* and *wx*, the pattern of variegation being similar to that of the previous case described (substitute *I* for *C* in figure 2). Cytological examination of plants coming from the *I Wx*, *i wx* and variegated kernels have been made to determine the nature of the chromosome 9 contributed by the pollen. All the plants coming from the

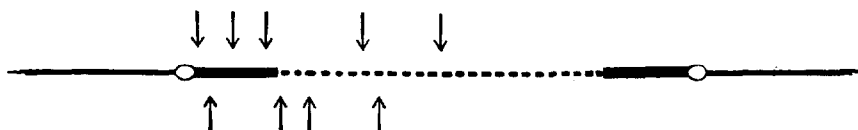


FIGURE 6

Diagram to illustrate types of recovered broken chromosomes in 16 plants arising from variegated kernels. Since small duplicated segments, as illustrated in figure 4, are not so readily detected in this material, the positions of breaks are referred to the original dicentric chromatid, *c*, figure 5. Only the middle section of the dicentric chromatid is represented. The chromatid recovered is the one to the right of the arrow in each case. In 8 cases, duplicated segments of various lengths, as shown by the arrows, were present in the recovered broken chromosome.

*I Wx*, non-variegated class contained either the normal duplicated chromosome 9 or a normal chromosome 9 with the large terminal knob resulting from a crossover which did not give rise to a dicentric chromatid (between the normal chromosome 9 and the normal short arm of the duplicated chromosome 9). All of the examined individuals derived from the *i wx* kernels contained a normal chromosome 9 with a large terminal knob. All the individuals coming from the variegated kernels have shown a broken chromosome 9. In each individual plant, the constitution of the broken chromosome 9 was the same in all of the cells examined. As has been shown in the previously described case, the broken end of chromosome 9 must heal in the very early embryo cells and remain healed throughout all later nuclear cycles. Examinations of anaphase configurations in root tips of these plants have shown no indication of bridge configurations, which agrees with similar observations made with the previously described case. The types of broken chromosomes 9 as determined by meiotic prophase examinations in plants arising from variegated kernels, are diagrammed in figure 6.

The reciprocal cross (plants heterozygous for the duplication carrying  $I Wx$  in the normal and the duplicated segment of the duplicated chromosome 9 and large knob,  $i wx$  in the normal chromosome 9 by plants carrying a normal chromosome 9 with  $i wx$ ) have given similar results. The types of kernels obtained with their ratios are as follows: 438  $I Wx$ , 0  $I wx$ , 23  $i wx$ , 445  $i wx$  and 17 kernels variegated for  $I-i$  and  $Wx-wx$ . Chromosome examinations in plants arising from the non-variegated and variegated kernels have given the expected results: non-broken and broken ends, respectively.

It is obvious that when the proper genic characters are used, the presence of individuals possessing a broken chromosome can be detected by the variegation produced in the endosperm. This variegation can appear when only one broken chromosome is present in the endosperm tissue. When  $Wx$  as well as  $I$  or  $C$  is present in the variegated kernels, the pattern of variegation for each accords with the interpretation of a breakage-fusion-bridge-breakage mechanism involving sister chromatids extending through successive nuclear cycles in the developing endosperm. It is at present unexplained why this mechanism does not continue in the embryo tissue. Here broken ends apparently heal and remain permanently healed. This is clearly demonstrated when the recovered broken chromosome has no duplication or deficiency, arrow to right, figure 6. These chromosomes behave in future generations as normal chromosomes 9, giving normal crossing-over and transmissions. No variegated kernels have appeared in progeny tests of 8 such cases. On the other hand, those broken chromosomes which have a newly derived duplicated segment, arrows to left of first, figure 6, are the source of new broken chromosomes by the same crossover mechanism as described for the original duplication. Extensive investigations with one derived duplication (the short duplication, second arrow from right, figure 6) and preliminary tests with all the others have repeated the original results. Non-variegated and variegated kernels are produced, the variegated kernels in all cases possessing newly broken chromosomes.

*In conclusion* it can be stated that in maize a bridge configuration at a meiotic anaphase results in the production of a broken chromosome. Fusion occurs at the position of breakage between the two sister halves of the broken chromosome. Because of this fusion a bridge configuration occurs in the following gametophyte division. This again results in a broken chromosome entering each telophase nucleus. Fusion likewise can occur between the broken ends of the sister halves of each of these chromosomes thus continuing the cycle of bridge-breakage-fusion-bridge. The variegation exhibited in the endosperm tissues of kernels carrying broken chromosomes indicates that this cycle can continue, apparently uninterrupted, in this tissue. In the embryo and plant tissues, however, the broken end

becomes healed. It remains permanently healed in future nuclear and plant generations regardless of the type of tissue in which it is present.

Limitation of space does not allow a full discussion or even mention of some interesting phases of these results. They will appear in a later publication.

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<sup>1</sup> McClintock, B., *Missouri Agr. Exp. Sta. Res. Bull.*, **290**, (1938).

<sup>2</sup> McClintock, B., *Proc. Nat. Acad. Sci.* **17**, 485-491 (1931); Creighton, H. B., *Ibid.*, **20**, 111-115 (1934); Burnham, C. R., *Am. Nat.*, **68**, 81-82 (1934), *Genetics*, **19**, 430-447 (1935).

<sup>3</sup> Emerson, R. A., Beadle, G. W., and Fraser, A. C., *Cornell Univ. Agr. Exp. Sta. Memoir*, **150**, (1935).

<sup>4</sup> Due to limitation of space, evidence for this will be presented elsewhere.

<sup>5</sup> The *I Wx* class is deficient in numbers since it comes from the infrequent crossovers between the normal short arm of the duplicated chromosome and the short arm of the normal chromosome or from the occasional transmission of the chromosome with the duplication carrying *I Wx*. A pollen grain carrying the duplication functions less successfully in competition with normal chromosome containing pollen grains.