THE CYTOGENETICS OF MAIZE

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Cytogenetics may be defined as the correlation of cytologically observed conditions with genetic data.

Although genetic studies with *Zea mays* began little more than twenty years ago and cytogenetic investigations are of much more recent date, an impressive amount of information has been accumulated concerning the heredity of the maize plant. No other plant has been studied from the cytogenetic point of view so intensively as has maize, and the purpose of this article is to present some of the more pertinent facts which have been discovered.

Genetic characters in maize show great diversity of effects but can be roughly classified into three groups on the basis of the type of tissue affected: (1) sporophytic characters ($2n$ tissue); (2) gametophytic characters ($1n$ tissue); and (3) endosperm and aleurone characters ($3n$ tissue).[1] A large majority of the known genes affect the sporophyte. Here are found a hundred or so genes for chlorophyll development alone; also genes for plant stature, plant color, modifications of male and female inflorescences, sterility, etc. Gametophytic genes are much fewer in number but among them are found genes for selective fertilization (due presumably to slower pollen tube growth or pollen germination), for pollen size, for ovule abortion and for type of carbohydrate in pollen grain and embryo sac. Endosperm and aleurone genes include those determining color and composition of endosperm and color of the aleurone layer. This classification of genes into those affecting the sporophyte, gametophyte and endosperm is an arbitrary one and does not imply that a given gene cannot affect more than one type of tissue. The waxy (*wx*) gene, for example, determines the nature of carbohydrate stored in both gametophytic and endosperm tissue.

Many genetic characters in maize represent some gross morphological modification in the normal structure of various parts of the plant. There are, however, some genes which affect chromosome behavior and cell division (5, 6, 7, 9, 10, 12). The asynaptic gene[2] (*as*), when present in a homozygous[3] condition, disturbs in some way the normal pairing of chromosomes in early prophase so that most of the chromosomes are present as univalents[2] at diakinesis[2] and metaphase.[2] The sticky gene (*st*), as its name implies, causes the chromosomes to stick together so that at metaphase I there is a clumped mass of chromatin rather than 10 independent bivalent pairs. The sticky gene apparently increases frequency of non-disjunction,[4] gene mutation and produces translocations,[5] deficiencies[6] and chromosome fragments. The polymitotic gene (*po*) causes the haploid nuclei in each spore of the quartet of spores, formed at the end of the second meiotic division, to undergo a series of division-like figures followed by cytokinesis in which the chromosomes are segregated to the two poles without splitting equationally (lengthwise). There are two variable sterile genes (va_1 va_2) which tend to prevent occurrence of cytokinesis[7] in meiotic divisions and which cause an apparent tendency of the chromosomes in the microspores to undergo a precocious division. The effects of these genes suggest that not only development of the plant as a whole proceeds under the influence of genes but that the chromosomes themselves, which carry the genes, are under genic control.

The number of mutant genes in maize is about 400, the great majority of them being recessive to the normal or usual condition.

The diploid[8] or somatic number of chromosomes in *Zea* is twenty. The monoploid or gametic number is ten. All of these chromosomes are morphologically distinguishable. The morphology has been studied both in somatic and meiotic divisions but study of the meiotic prophase has given far more information concerning the detailed morphology. In the meiotic prophase the chromosomes are long slender threads many times longer than at somatic metaphase, and the different chromosomes can be recognized by their relative lengths, the positions of the non-stainable spindle fiber[4] attachment regions and the presence of deep staining knobs in specific positions on certain of the chromosomes. The number of knobs varies in different stocks but when a particular knob is present it is a constant feature of that chromosome and is inherited with the same precision as a gene. One of the chromosomes is especially conspicuous because it possesses a satellite and is always found in association with the nucleolus.[9] A deep staining somewhat reticulate body adjacent to the nucleolus on this chromosome is responsible for the orderly organization of the nucleoli in the telophases[4] (48). The morphology of the ten chromosomes is shown diagrammatically in figure 1.

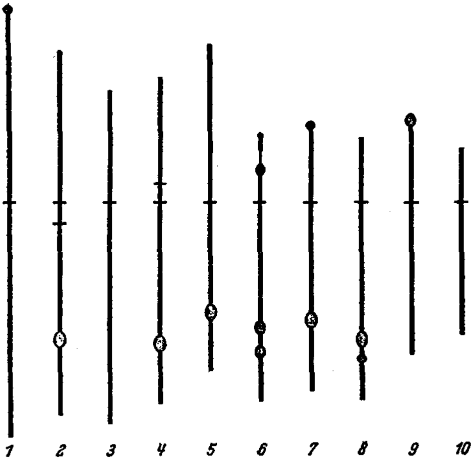

Fig. 1. Diagram of the ten chromosomes composing the monoploid complement of *Zea mays*. The positions of the spindle fiber attachment regions are indicated by cross lines. In chromosomes 2 and 4 two positions for this region have been found in the different cultures of maize. In chromosome 4 this difference in position has been correlated with an inversion. The positions of the knobs which are most likely to appear in the different cultures of maize are indicated. In any one culture a particular knob may or may not be present. (From McClintock, 1933.)

Since there are ten members of the monoploid[1] complement, all different in morphology, it is expected that the heritable characters in maize would fall into ten linkage groups which would show independence in inheritance with one another. Such is the case and figure 2 gives the ten linkage groups with the map distance (*i.e.*, cross-over value[10]) between the different linked genes. Only those genes whose approximate location in the genetic map is known are listed. About one half of the 400 known genes have been assigned to special linkage groups.

Not only has it been shown that the genetic characters in maize fall into ten linkage groups in correspondence with the number of chromosomes but each linkage group has been associated with a specific chromosome. The occurrence of a triploid[1] plant in 1925 (53, 42) was the starting point for the association of chromosomes and linkage groups. Theoretically the gametes produced by a triploid plant should have chromosome numbers ranging from ten

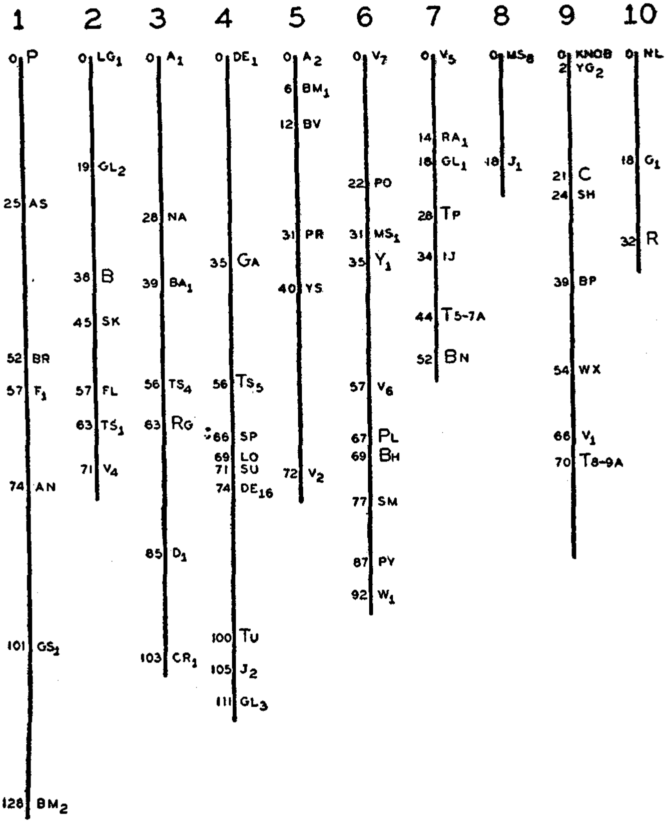

FIG. 2. The ten linkage groups in maize with the map distances (crossover values) between the different linked genes. The genes comprising linkage group 1 are carried in chromosome 1 (see figure 1), the genes in linkage group 2 are carried in chromosome 2, etc. The lengths of the genetic maps of the different linkage groups do not agree with the lengths of their associated chromosomes because certain linkage groups have been more extensively studied than others. Only those genes whose loci are known with approximate certainty are shown in the genetic maps.

to twenty and the cross of triploid with a diploid should give individuals with chromosome numbers ranging from twenty to thirty. Such was the case and from these individuals $2n + 1^{11}$ plants were isolated possessing different members of the set of 10 chromosomes as the extra chromosome. Cytological examination showed which member of the set of 10 was present in triplicate. These different trisomic[12] types were crossed with plants carrying genes in the ten linkage groups. F_1 $2n+1$ plants were either selfed or back-crossed to individuals homozygous for the recessive genes. When the progeny of the F_1 $2n+1$ individuals gave 3:1 and 1:1 ratios, respectively, normal diploid ratios, it was proof that the linkage group being tested was not associated with the trisomic chromosome under consideration. When, however, the progeny of the F_1 $2n+1$ individuals gave widely divergent ratios, or so-called trisomic ratios,[13] it was evidence that the particular linkage group being tested was associated with the particular trisomic being studied.

Six of the ten linkage groups, 2, 3, 5, 6, 7 and 10, were associated by this means with their respective chromosomes. Before studies with other groups were completed two new methods of associating linkage groups with particular chromosomes became available. The first method involved mutual translocations between non-homologous chromosomes. Through natural causes (13, 14, 15, 16, 19, 20, 21, 27, 57) or through X-ray treatment (2, 3, 4, 26, 28, 45, 48, 60, 62), breaks in chromosomes can be produced. If breaks occur simultaneously in each of two chromosomes, a 2-by-2 reunion of broken ends of one chromosome with those of the other chromosome may occur. In other words, a broken end of one chromosome can become attached to a broken end of the other chromosome and the remaining broken end of the first chromosome can become attached to the remaining broken end of the second chromosome. As a result of this mutual translocation, two chromosomes can be produced with new morphologies and new gene rearrangements.

In the meiotic prophase of a plant arising from fusion of a gamete possessing two normal chromosomes with one possessing these two interchanged chromosomes, the homologous associations of parts of these chromosomes produces a cross-shaped synaptic[2] configuration involving all four chromosomes. Thus through meiotic prophase studies, it is possible to determine not only which two chromosomes are involved but where the break occurred in each chromosome. It is obvious that such translocations of parts of chromosomes will involve transfer of blocks of genes. As a result, the linkage relationships of specific genes will be decidedly altered. The first case in which an interchange was serviceable in associating a chromosome with a linkage group involved a mutual translocation between chromosomes 1 and 2 (13, 14, 15). Genetic studies had indicated that genes of the two linkage groups *P–br* and *B–lg* (see figure 2) were involved. Cytological studies indicated that chromosomes 1 and 2 were concerned in the interchange. Since trisomic evidence had shown that genes of the *B–lg* linkage group were associated with chromosome 2 and that genes of the *P–br* linkage group were not associated with chromosome 2, it was an obvious conclusion that genes of the *P–br* linkage group were associated with chromosome 1. Eventually, through the efforts of Burnham, Brink, Anderson, Clokey, and others interchanges involving every member of the complement were obtained. Through this method chromosomes 1, 4 and 9 were associated with *P–br*, *su–Tu* and *c–sh–wx* linkage groups respectively and a definite check on previous trisomic determinations was afforded.

The second new method of associating chromosomes and linkage groups determined the final association, that of chromosome 8 with the j–ms_8 linkage group. When pollen containing the normal allelomorph of 'japonica' was X-rayed and placed on the silks of plants homozygous for the recessive gene, 'japonica' (*j*), occasional individuals resulted which showed the recessive character. Examination of the chromosomes of one of these plants at the mid-prophase of meiosis showed that there had been a loss of a portion of chromosome 8 brought in by the male parent. This indicated that the deficiency in chromosome 8 included the dominant allelomorph of 'japonica.' The loss of the dominant gene allowed the recessive allelomorph in the normal chromosome from the female parent to express itself. This method served to establish the final association between chromosomes and linkage groups (47).

THE LOCATION OF GENES WITHIN THE CHROMOSOME

Two of the methods which were useful in associating linkage groups with particular chromosomes, those involving translocations and deficiencies,[5] were further useful in determining the physical position of a particular gene locus within the chromosome which carries it. The theory to account for crossing-over had postulated a linear arrangement of the genes along the lengths of the chromosomes. The evidence obtained from combined cytological and genetic studies in *Drosophila* had given definite proof of this organization. If genes are distributed along the lengths of a chromosome, a break in a chromosome such as occurs in mutual translocation[5] should sever the gene string into two blocks. Just which genes each block would contain would depend upon where the break had occurred in the chromosome. In a mutual translocation, therefore, blocks of genes from the two chromosomes should be interchanged, the genes included in each block depending upon the position of the breaks in the two chromosomes involved in the interchange.

It is possible by studying synaptic configurations produced by the association of two normal with two interchanged chromosomes in a plant heterozygous for a mutual translocation to determine, in most cases, where the breaks occur in the two chromosomes involved in the interchange. Since the point of breakage is as useful as a gene in determining linkage relationships,[14] the order of known genes, within the chromosomes involved, from the point of breakage can be determined. As an example, the genes in a particular chromosome can be represented in their linear order as A B C D E F G as determined by genetic studies. Should a mutual translocation between this chromosome and another occur severing the chromosome between the genes C and D, the order of the genes with reference to the point of breakage would be in one interchanged chromosome, A–B–C–break, in the second interchanged chromosome, G–F–E–D–break. Cytological examination would reveal the position within the chromosome itself where the break had occurred but it would not indicate which block of genes was carried by each interchanged chromosome. If, however, a second translocation involving this chromosome with another were available which severed the gene string at another point, say between genes D and E, then gene D must lie between the point of breakage in the first translocation and that in the second, and the order of the genes within the chromosome with reference to the points of breakage is established. By combined cytogenetic study of many such translocations it is possible to determine with increasing precision the physical location of a gene within a chromosome. A large amount of this type of evidence has been accumulated within the past few years, some of which is published (44, 16, 45, 2, 19, 25, 28, 57, 56, 55, 59, 62, 63, 23, 24) and much of which is as yet unpublished but available to maize investigators.

A second means of determining positions of genes in the chromosomes is given by the deficiency method which was illustrated in the placing of the gene 'japonica' in chromosome 8. The piece deleted from the chromosome contributed by the male gamete may vary from a very small to a very large section in the different cases. The extent and position of the deletion is determined by the synaptic figures produced as the result of the association of the long normal chromosome contributed by the female with the shorter (deleted) chromosome contributed by the male. With more or less accuracy depending upon the deletion involved, the positions of several genes have been located within the several chromosomes (45, 47, 59, 28, 62).

Still a third method of determining location of genes within a chromosome is available in the study of fragment chromosomes. When such fragments are present in chromosome complements in addition to the normal diploid number twenty it is possible to determine by cytological observations the region of a particular chromosome with which the fragment is homologous (46 and Rhoades, unpublished). Genetic studies will determine which genes of a linkage group are included in the fragment and which are excluded. The smaller the fragment carrying known genes, the more accurate the determination of the physical positions of the genes within the chromosome from which the fragment arose.

It can be seen that our knowledge of the association of chromosomes with linkage groups and the positions of genes within the chromosomes has developed as a result of the fitting together and correlation of information obtained by the various investigators working with several different methods.

CYTOLOGICAL AND GENETICAL STUDIES ON CROSSING-OVER

The placing of genes in linkage groups and locating them on the chromosomes involves a study of the process called "crossing-over." The term "crossing-over" is used to denote the exchange of pieces or segments between homologous chromosomes. There are many facts which indicate that exchange of parts or segments occurs during the first meiotic prophase when the two homologous chromosomes are in intimate association. During the early stages of meiosis the chromosome derived from the paternal parent pairs with its homologue from the maternal parent. This association of the two homologues continues until disjunction[4] occurs during anaphase 1.[3] The phenomenon of crossing-over is effected at some time between synapsis and disjunction. The exact time at which crossing-over takes place is a controversial matter but it most probably occurs either at pachytene or diplotene. If we assume that the chromosome derived from the paternal parent carries genes *A* and *B* and that the maternal chromosome carries the recessive allelomorphs, *a* and *b*, we can illustrate the genetic phenomenon of crossing-over. If genes *A* and *B* are so situated in the chromosome that no crossing-over occurs between them there are only two gametic types possible, *i.e.*, *A* is always associated with *B* and *a* with *b*. If, however, crossing-over does occur so that *a* comes to lie in the same chromosome with *B* and *A* lies with *b*, two new chromosomes arise, namely, *aB* and*Ab*. These latter two types are called new combinations since the constitution of these chromosomes differs from those derived from the two parents. The gametic types *AB* and *ab* are called parental combinations since they are identical with the two chromosomes obtained from the parents. The amount of crossing-over between the linked genes is based upon the relative proportions of parental and new combinations. If ten per cent of the tested chromosomes from an F_1 heterozygote[15] are new combinations and 90 per cent are parental combinations then the cross-over value between *A* and *B* is ten per cent and on the genetic map they would be placed ten map units apart. It should be apparent from the above illustration that the linear locations of genes in the genetic maps of figure 2 are based on the amount of crossing-over between the different linked genes.

In the earlier days it was supposed that crossing-over between two paired chromosomes occurred before they had split equationally (lengthwise). *Drosophila* workers have shown, however, that each chromosome is split into two effective parts so that there are four strands (chromatids) present when crossing-over takes place. They were also able to show (1) that in diploids, at least, only two of the four strands at any one point were involved in an exchange of genes. These detailed studies on the mechanism of crossing-over were obtained genetically as it is impossible to study the early meiotic stages in *Drosophila*. Since, from each point of crossing-over there are two cross-over chromatids and two non-cross-over chromatids it follows that the number of points at which crossing-over occurs must be twice as great as the amount of recombination observed by genetic studies. That is, if genes *A* and *B* are 10 units apart on the genetic map there was a point of crossing-over between the two genes in twenty per cent of the sporocytes.[16] In *Zea,* as in *Drosophila,* it has been possible to demonstrate that chromosomes are split equationally at the time crossing-over takes place and that crossing-over occurs between chromatids; this demonstration has been made not only by genetical studies but also by direct cytological observation.

Genetic demonstration of chromatid[17] crossing-over rests on the following facts. When trisomic plants carrying two dominant and one recessive allelomorph are back-crossed there appear in the progeny some trisomic plants which carry the recessive gene in all three chromosomes. In order that an $n+1$ egg could receive two chromosomes both of which carry the recessive allelomorph, crossing-over must have occurred between chromatids and not between whole chromosomes. The frequency of these exceptional trisomic plants varies for different loci. The recessive gene, bm_1, never or rarely is found homozygous in a trisome from a cross of the above type, while v_2 trisomes are found with more than twice the frequency of *pr* trisomes. These different frequencies are intelligible if it is assumed that bm_1 lies closer to the insertion region than do *pr* and v_2 since the appearance of the exceptional trisomes is due to chromatid crossing-over between the locus of the gene in question and the insertion region. That bm_1 is situated in the short arm of chromosome 5 close to the insertion region with the *pr* locus in the long arm but some distance away from the insertion region and the v_2 locus beyond *pr* has been shown by cytogenetic studies with translocations, ring fragments, etc. These studies support the prediction based on the frequency of exceptional trisomes as to the relative positions of these three loci with respect to the insertion region (58 and Rhoades, unpublished).

Cytological proof of chromatid crossing-over was obtained in 4 ways but only two of them will be discussed here. Certain strains of maize have an inverted section in the short arm of chromosome 8. In plants heterozygous for the inversion[18] loop shaped configurations result at pachytene from the 2-by-2 alignment of the homologous loci within the inverted region. Crossing-over between two non-sister chromatids within the inversion gave at metaphase 1 one chromatid with two insertion regions, one fragment chromatid with no insertion region and two unmodified chromatids. When a second cross-over occurred in the inverted region between the other two chromatids there resulted at metaphase I two chromatids with two insertion regions each and two fragment chromatids with no insertion region (47).

A second cytological demonstration came from study of the position of the terminal knob on chromosome 9 when this chromosome had been involved in a reciprocal translocation[19] which gave a ring of four chromosomes at diakinesis. One chromosome 9 had a large knob on one end and a translocated piece on the other. The other chromosome 9 had a small knob and no translocated piece. The terminal knobs of the two chromosomes were associated end to end at diakinesis but it was observed in some sporocytes that one small-knobbed chromatid had exchanged partners with one large-knobbed chromatid. That the exchange took place between chromatids and not between whole chromosomes was shown by the synaptic relations of the entire translocation complex (30).

Although crossing-over has been defined as the exchange of parts or segments between homologous chromosomes it was not until 1931 that cytological corroboration of this genetically reasoned fact was demonstrated. It is true that the great mass of genetic data in such forms as *Drosophila* and *Zea* had led geneticists to the conclusion that such a physical exchange of segments must occur, but material suitable for the demonstration of a correlation between cytological and genetical crossing-over was lacking. Creighton and McClintock (29, 31) and Creighton (unpublished), utilizing a unique cytogenetic set-up in *Zea,* were able to show such a correlation. Stern (64) made a similar demonstration in *Drosophila.* Certain strains of maize have a large terminal knob on the short arm of chromosome 9 while other strains are knobless. This knob is inherited from generation to generation in the same manner as a gene. There also exists a reciprocal translocation between chromosomes 9 and 8 in which most of the long arm of chromosome 9 has been interchanged for a segment of the long arm of chromosome 8. The genes yg_2, *c* and *wx* lie in the region between the point of interchange in chromosome 9 and the terminal knob with yg_2 lying extremely close to the terminal knob. A plant heterozygous for the terminal knob, the genes yg_2, *c* and *wx,* and the reciprocal translocation, was crossed with a plant with no knob, homozygous for yg_2, *c* and *wx* and carrying unmodified chromosomes 9 and 8. The progeny from this cross were classified on the basis of genetic cross-overs and a cytological study of these plants was made at microsporogenesis[20] to see if the two heteromorphic points (the knob and the point of translocation) tended to be exchanged when a genetic cross-over in closely adjacent regions occurred. They found, for example, that when a genetic cross-over between yg_2 and *c* occurred the knob on the chromosome carrying yg_2 always was transferred to the other chromosome along with yg_2. A similar correlation was found for the other regions. Recently Brink and Cooper (19), using a different cytogenetic set-up in maize, reported data which substantiates this correlation of genetical and cytological crossing-over.

That there is a close correlation between crossing-over and end-to-end association at diakinesis has been shown by Beadle (11) in his studies on *Zea-Euchlaena* hybrids. In *Zea* the paired chromosomes are synapsed[1] throughout their lengths at pachytene[21] but at diakinesis[3] and metaphase I[3] the two chromosomes open out or fall apart so that they often are associated only at their two ends. This opening out of the two homologues begins at diplotene[21] and is completed by diakinesis. It is known in *Zea* (47) that chromosome segments which are non-homologously paired at pachytene fall apart in diplotene and this failure to remain associated is correlated with a lack of crossing-over. If, then, association at diakinesis is found only when genetic crossing-over occurs it would be expected that no end-to-end association at diakinesis would be found between two arms of homologous chromosomes in which no crossing-over occurred. When the maize chromosome was present with its teosinte[22] homologue, Beadle found that no crossing-over occurred in the short arm of chromosome 9 and that the ends of the two short arms never were associated at diakinesis. Although Beadle reported in his observations at pachytene that the two short arms were usually in close association Creighton (unpublished) found in comparable material that non-conjugation or irregular conjugation was common between the two short arms. Her observations suggest that some structural difference between the *Zea* and *Euchlana* chromosomes is responsible for the failure of crossing-over to take place.

Chiasmata are the places where exchanges of partners among the four chromatids have been observed cytologically. Genetic crossing-over may or may not occur at these places. Since, however, crossing-over has been shown to be related to post-diplotene association it would seem that chiasmata frequencies should also be related to post-diplotene association if there is any correlation between chiasmata and crossing-over. Beadle in his *Zea-Euchlaena* hybrids found that post-diplotene association was confined to a particular segment in which genetic crossing-over was known to occur and where chiasmata existed at diakinesis. Moreover, the frequency of chiasmata in this segment was roughly twice the amount of crossing-over. These data indicate some relationship between chiasmata formation and genetic crossing-over.

REARRANGEMENTS OF PARTS OF CHROMOSOMES

Brief mention has been made above of rearrangements of segments of chromosomes resulting from natural causes and from X-ray treatment. At this point an attempt will be made to describe the types of rearrangements which have been found and investigated. The evidence so far obtained suggests that most of these rearrangements can be explained by assuming that broken ends of chromosomes tend to unite 2-by-2. When, through natural causes or through X-ray treatment, a chromosome is broken at any one place, two broken ends are produced. If, simultaneously, the same chromosome at another position or another chromosome is broken, two more broken ends are produced. These broken ends then unite 2-by-2. The type of rearrangements obtained from such breaks and reunions will depend altogether upon which two broken ends reunite. It is altogether probable that the breaks and reunions in chromosomes occur between sections of chromosomes which are lying adjacent to one another at the time the breaks occur. The diagram in figure 3 will illustrate the categories of rearrangements expected on this assumption. In *a,* figure 3, a section of a chromosome is looped upon itself. If breaks occur in the chromosome at the position of the arrow to produce the condition shown in *b*, there could be three possible 2-by-2 unions of ends. If end 1 is united with end 4 and end 2 with end 3, no alterations would occur in the arrangement of parts of the chromosomes. If end 1 united with end 2 and end 3 with end 4, an *inversion* of a section of the chromosome would occur. If, however, end 1 united with end 3 and end 2 with end 4, two chromosomes would be formed. The union of end 1 and 3 would result in a rod-shaped chromosome with a

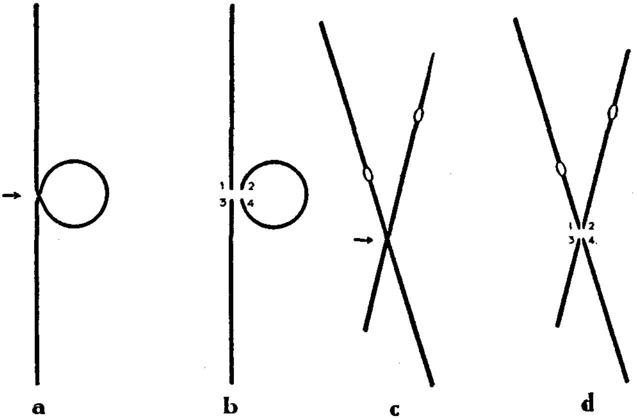

FIG. 3. Diagrammatic representation of origin of chromosomal rearrangements through the union of broken ends.

section *deleted.* The union of end 2 with end 4 would produce a *ring-shaped* chromosome, composed of a section of the normal chromosome. The evidence accumulated so far from studies of both plant and animal material has indicated that chromosomes which do not possess a spindle fiber[4] attachment region are incapable of functioning in the spindle figure and are, consequently, lost to future nuclear generations. Therefore, which chromosome will survive in future mitotic divisions and be visible to the investigator will depend upon which section retained the spindle fiber attachment region. If the spindle fiber attachment region is in the rod-shaped piece, the ring-shaped chromosome will be lost in the mitotic divisions and the rod-shaped chromosome will continue in future mitotic cycles as a deleted chromosome. If, however, the spindle fiber attachment region is in the ring-shaped section, the rod-shaped chromosome will be lost and the ring-shaped chromosome will survive in future mitotic cycles. Should breaks occur in two chromosomes at the position of overlapping, as at the arrow in *c,* figure 3, the four broken ends as in *d,* would be formed. In this case, also, three types of unions would be expected. Union of broken end 1 with 4 and 2 with 3 would produce no rearrangement. The union of broken end 1 with 3 and 2 with 4 would result in a *mutual translocation,* a segmental interchange, between these two chromosomes. The union of end 1 with 2 and 3 with 4 would result in a chromosome with two insertion regions and a chromosome with no insertion region. Examples of all of these chromosomal rearrangements have been found.

The linear organization of chromosomes makes it possible for breaks to sever specific elements of the chromosome into two parts. As a result of such breaks important information has been gained regarding specific regions of the chromosome. A break which severed the reticulate region of the satellited chromosome made it possible to prove that this element was responsible for the orderly development of the nucleolus[9] in the telophase.[3] Breaks in two cases which severed the spindle fiber attachment region of chromosome 5 revealed a feature of this structure not hitherto known (46). In the meiotic prophase, the spindle fiber attachment region appears as a relatively conspicuous, lightly staining region in the chromosome. In the two cases mentioned, breaks in chromosome 5 occurred as in *b*, figure 3, which involved the spindle fiber attachment region. A 2-by-2 reunion of the broken ends took place in such a way that a ring-shaped chromosome possessing a section of the spindle fiber attachment region and a rod-shaped chromosome possessing the remaining part of the spindle fiber attachment region were produced. Both sections of the broken spindle fiber attachment region were capable of functioning in the spindle figure and, consequently, both the rod-shaped and the ring-shaped chromosomes perpetuated themselves throughout the mitotic cycles. In the first case, the ring-shaped chromosome received only a relatively small section of the original spindle fiber attachment region whereas in the second case, the ring-shaped chromosome received a larger section of the original spindle fiber attachment region.

The implications which can be derived from the evidence produced by these two cases may be useful in explaining some hitherto puzzling cases. If sections of spindle fiber attachment regions are as equally capable of functioning as the original spindle fiber attachment region, it is possible that changes in chromosome numbers can occur with no necessary change in the genomic[23] complement. Just what part breakage of spindle fiber attachment regions and functioning of both sections has played in the building up of higher chromosome numbers in species and genera is not known but it is a factor which must be considered in any discussion of the evolution of chromosomes and of chromosome complements.

In describing the method by which translocations occur, emphasis was placed on the assumption that broken ends of chromosomes tend to unite. This is not, however, purely an assumption but finds substantial support in the mitotic behavior of ring-shaped chromosomes.

Detection of ring-shaped chromosomes has been facilitated by their striking mitotic behavior which results in the production of variegation (46 and McClintock, unpublished). In order to have the variegation appear it is necessary that the normal homologues of the ring-shaped chromosome carry recessive genes, the ring-shaped chromosome carrying the dominant allelomorphs. If the ring-shaped chromosome perpetuates itself throughout mitotic cycles in its original form, as do rod-shaped chromosomes, the plant should be totally dominant in appearance. However, ring-shaped chromosomes in maize do not perpetuate themselves unaltered through nuclear generations. Losses of sections of chromatin within the ring are continuously occurring. When the section lost includes the dominant gene, all cells arising from the cell which underwent the initial loss will lack the dominant gene in their nuclei. Therefore, expression of the recessive character carried by the normal rod-shaped chromosomes will appear in this tissue. Such behavior of ring-shaped chromosomes results in variegated plants, parts of the plant tissue showing the dominant character and other parts showing the recessive character. That the ring-shaped chromosomes actually undergo striking changes in size was readily apparent from an examination of the many microsporocytes[16] from a single anther whose nuclei are in the same stage of prophase development. Direct comparisons of ring size in these relatively closely related cells gave evidence of great differences in size and chromatin constitution, although blocks of related cells frequently had rings of similar size and constitution. It was not possible in these stages to obtain an idea as to how this change in size and constitution was occurring. Therefore, a study of somatic nuclear division was undertaken in an effort to determine the method and possible cause of this loss of sections of chromatin within the ring-shaped chromosome. Here the method by which the changes in size are produced became apparent. The cause of this phenomenon in ring-shaped chromosomes probably relates to the method by which a chromosome becomes split into two equal halves during mitosis. Whatever the method of splitting may be (a discussion of which will not be considered here), the end product does not always lead to two ring-shaped chromosomes lying adjacent to each other as if they had been split into two along one plane. Instead, especially with large rings, many anaphase figures reveal that the end product of the splitting process has produced two interlocking rings or one large double-sized ring with two spindle fiber attachment regions. In this latter case, the large single ring with the two spindle fiber attachment regions is built up from both split halves of the mother ring. On the simple hypothesis that the chromosome may start its splitting process at more than one place in the chromosome and that the planes of the splits so started do not correspond, it is relatively easy to see how such figures could be obtained. In both the interlocking rings and the double-sized rings, the pull on the chromosomes produced by the passage of the spindle fiber attachment regions to opposite poles introduces a strain on the chromosome which eventually leads to breakage. In the case of the double-sized ring with the two spindle fiber attachment regions, the chromosome does not always break in the middle but may break in several places, the parts adjacent to the spindle fiber attachment region at both poles passing into the telophase nuclei, the other parts being left in the cytoplasm. Obviously, then, the chromatin content and structural arrangement of the original ring has become altered. It might be expected that this mechanism would produce rod-shaped chromosomes. On the contrary, the broken ends thus produced apparently reunite to form rings. The presence of rings of various sizes in the root-tip nuclei and the microsporocytes and the fact that no rod-shaped chromosomes have been observed to have arisen from a ring-shaped chromosome make the conclusion inescapable that broken ends of chromosomes tend to reunite.

FACTORS AFFECTING MEIOTIC CHROMOSOME ASSOCIATION

Knowledge of the synaptic process in maize has been gained mainly as a result of studies of the association of chromosomes in complements which are unbalanced either numerically (monosomic, trisomic) or structurally (heterozygous for an inversion, a translocation). The main conclusions from these studies (22, 47) can be summarized as follows:

1. Homology is the main force which controls the attraction and

movement of homologous parts of chromosomes toward one another.

2. Association once started between homologous parts of two chromosomes tends to continue along the chromosome bringing successive regions into intimate association.

3. When three homologous chromosomes or sections of chromosomes are present in a nucleus, homologous associations take place only between two of the three homologous elements, *i.e.,* synaptic association is 2-by-2.

4. There is a tendency for all parts of all the chromosomes to be associated 2-by-2 at the meiotic prophase period whether or not the parts associated are homologous.

In ordinary diploids, factors 1, 2 and 4 all work in harmony to produce an intimate side-by-side association of homologous parts of homologous chromosomes. Each chromosome derived from the male gamete associates homologously throughout its length with its homologue derived from the female gamete resulting at the pachytene stage of meiosis in 10 double or bivalent chromosomes. In numerically and structurally unbalanced complements, these factors which in a diploid produce homologous associations of the chromosomes come into serious conflict. The nature of the conflict may best be illustrated by describing some of the synaptic configurations obtained from these plants.

In trisomic individuals the three homologous chromosomes must compete with one another in the production of 2-by-2 homologous associations (3, above). One of the chromosomes may be homologously associated with a section of a second and at another place homologously associated with a section of the third. In all cases, a section of one of the chromosomes, or even a whole chromosome, where 2 of the three chromosomes have synapsed completely throughout their lengths, does not have homologous regions with which to synapse. The tendency for 2-by-2 associations in the meiotic prophase (4, above) of maize frequently forces the unmated section in the first case, or the whole chromosome in the second case, into a 2-by-2 association within itself, *i.e.,* fold-backs occur bringing non-homologous parts of this chromosome into intimate association. There is no distinction as to where the folding occurs or as to which two parts become so associated.

Monosomic ($2n-1$) plants illustrate factor 4 exceptionally well.

In these cases one chromosome has no homologue with which to synapse. Although a few figures show the univalent unassociated throughout its length, most figures reveal one or more fold-backs at varying positions within the chromosome and involving from short to long sections of the chromosome.

Conflict resulting from the operation of factors 1 and 2 is strikingly illustrated in the configurations in plants heterozygous for deficiencies, translocations and inversions.

In plants heterozygous for an internal deficiency, the deficient chromosome is shorter than the normal chromosome by the extent of the deficiency. The association of the shorter chromosome with the longer chromosome necessitates the longer chromosome's buckling at some position to compensate for the deficiency within the shorter chromosome. If factor 1 operates solely in bringing parts of these two chromosomes together, the position of the buckle would be constant and would correspond exactly to the location of the deficiency within the shorter chromosome. Actually, in maize, there is a wide shifting in the position of the buckle from the theoretical expectancy based on homologous associations only. This shifting results from the operation of factor 2 working in conflict with factor 1. Two-by-two associations may start, for example, between homologous ends of these two chromosomes. Once commenced, this 2-by-2 association may travel along the chromosome, past the point of homology into the region of non-homology before meeting the 2-by-2 association travelling from the opposite direction, thus automatically shifting the position of the buckle from the region of the deletion. This results in a more or less extensive amount of intimate non-homologous association depending upon the degree of shift of the buckle from the theoretical expectancy on the basis of homologous associations only.

This same explanation also applies in interpreting variation in position of the center of the cross-shaped synaptic configuration resulting from association of the two normal chromosomes with the two interchanged chromosomes in plants heterozygous for a mutual translocation. Strictly homologous associations in such cases, *i.e.*, operation of factor 1, would produce cross-shaped configurations the centers of which would mark the position where the breaks had occurred in each of the two interchanged chromosomes. The operation of factor 2, however, results in some cases in a considerable shift in the position of the center of the cross. Any shift away from the theoretically expected center involves the association of non-homologous parts of chromosomes.

The conflict between factors 1 and 2 is rather interestingly illustrated in the synaptic configurations obtained from plants heterozygous for inversions. In order to bring about associations of homologous parts of the normal chromosome with those of the inverted chromosome, the chromosomes must undergo considerable movement within the nucleus. Factor 1, *i.e.*, the force of homology, controls this movement. If the inversion represents a relatively large section, the combined forces of homology within this region are sufficiently strong to insure a movement of the chromosome into a loop and the bringing together of homologous parts of these two chromosomes within the region of the inversion. As the relative size of the inversion becomes smaller, the combined effective forces of factor 1 in the region of the inversion likewise becomes smaller. In these cases, associations first initiated between regions outside of the inverted section tend to continue along the chromosome and even prevent loop formation within the region of the inversion. Thus the sporocytes of plants heterozygous for short inverted sections of a chromosome frequently show no synaptic evidence of the inversion, the two chromosomes being associated in the form of a rod. In these cases, the association in the region of the inversion is strictly non-homologous.

The consequences of such non-homologous associations as described above are several. Cytological studies have shown that sections of chromosomes which are associated non-homologously at pachytene usually separate from one another completely early in the diplotene stage without any obvious consequences arising from the former association. One would expect, therefore, that cross-over values in specific regions which are sometimes undergoing homologous and sometimes non-homologous associations in different sporocytes of the same plant would show marked reduction in cross-over values for the genes located in these regions. Burnham (23) and Stadler (63) have reported cases of reduction in crossing-over which can be directly related to non-homologous associations.

Although non-homologously associated parts of chromosomes usually are seen to separate completely from one another during the diplotene stage, the progeny from individuals in which non-homologous associations of a certain type are known to have occurred, give evidence that occasionally translocations occur between these parts which are non-homologously associated. In other words, new types of modified chromosomes occur in the progeny whose origin can be explained by translocations which have taken place between regions of chromosomes known to be non-homologously associated in the parent plant. In the progeny of trisomics, for example, rod-shaped chromosomes with deletions or ring-shaped chromosomes representing a section of one of the three homologous chromosomes of the trisomic, have appeared (Rhoades, unpublished; McClintock, unpublished). If one considers that the deleted rod-shaped chromosome and the deficiency ring-shaped chromosome arise from translocations occurring in fold-back univalents (see page 309) they are readily seen to be reciprocals of one another, the position of the spindle fiber region with reference to the points of translocation determining which chromosome, the ring or the rod, will survive. More direct evidence that translocations occur in regions non-homologously associated has recently been presented by Stadler (63). As stated above (page 310) the synaptic association of a normal chromosome with one possessing an internal deficiency produces a buckling in the normal chromosome to compensate for the loss of a segment in the deficient chromosome. The position of the buckle can vary over a considerable range of the chromosome. Since only one position of the buckle represents complete homologous associations, any shift from this position involves non-homologous associations. Since there are many such cases, there is ample opportunity for non-homologous parts to be associated. A translocation (or cross-over) occurring in this region would result in a short chromosome with a shifted deficient region and a chromosome of normal length but with a deleted and a duplicated section. By appropriate genetic means, Stadler has been able to detect such modified chromosomes.

ANEUPLOIDY AND EUPLOIDY

The normal somatic complement in maize, as has been stated above, is twenty chromosomes. There are, however, various modifications of this normal complement. Entire haploid sets of chromosomes may be added or subtracted to give a euploid series. The addition to the normal complement of one or more chromosomes, which may be either unchanged or modified in various ways, gives hyperploid types. Hypoploids are those strains in which a chromosome or part of a chromosome is missing. A plant may also be hyperploid for a section of one chromosome and hypoploid for a section of another.

The simpler types of hyperploids will be considered first. Strains of maize which have nine of the ten chromosomes in duplicate and the tenth in triplicate are called primary trisomes since the supernumerary chromosome is identical with its two homologues. Only eight of the ten possible primary trisomes in *Zea* have been isolated at the present time. The missing primary trisomes are for chromosomes 1 and 4. It has been possible to associate specific differences in the appearance of trisomic plants with the presence of certain chromosomes which are in triplicate. This is true of plants trisomic for chromosomes 2, 3, 5, 7, and 8. The primary trisomes in *Zea* are all, however, characterized by the fact that they are smaller and less vigorous than their disomic sibs.[24] The effect of an extra chromosome on the appearance of a plant was first shown by the work of Blakeslee *et al* on primary trisomes in *Datura* where the unbalance in the genic complement produced by the addition of an extra chromosome resulted in a changed appearance of the plant. There are twelve primary trisomes in *Datura* and as each of the twelve chromosomes contains a different packet of genes it might be expected that the primary trisomes would differ phenotypically[25] from one another. Such indeed is the case and the *Datura* workers can recognize the different primary trisomes by their characteristic appearances.

A secondary trisome differs from a primary in that the extra chromosome is not a replicate of one of the members of the monoploid set but has become modified so that its two arms are identical. Chromosome 5, for example, has an insertion region which is nearly median. We can represent the shorter arm by α and the longer arm by β. There are two secondary trisomes possible for chromosome 5. In one case the supernumerary chromosome is composed of two α arms, and in the other case it may be composed of two β arms. Only one secondary trisome has been found in maize. Cytological studies at pachytene in meiosis show that it was the α–α secondary (58). This secondary trisome differed markedly in appearance from its disomic sibs. It had in an accentuated degree certain of the characteristics which distinguish the primary trisome of chromosome 5. This accentuation of certain of the primary trisome characteristics is due to the fact that in the secondary the short arm of chromosome 5 is present in quadruplicate and the long arm in duplicate while in the primary trisome the short and long arms are both in triplicate. This piling up of genes of the short arm produces a different genic unbalance which is reflected by an exaggeration in the secondary of certain of the primary trisomic characters which presumably are conditioned by the genes in the short arm of chromosome 5.

A tertiary trisome is one in which the extra chromosome is composed of parts of two different members of the monoploid set. The numerous tertiary trisomes in maize have been derived from plants heterozygous for a reciprocal translocation in which a 3 to 1 distribution of the four members of the ring at anaphase 1 results in a functional eleven chromosome gamete.

These three types of $2n+1$ plants give, in addition to trisomic ratios for those genes which are included in the reduplicated sections, a range of synaptic configurations at diakinesis which is in accord with the theory that only homologous ends of chromosomes are associated at this stage.

Deficiencies. In another section of this paper the production of rod-shaped chromosomes with an internal deletion and ring-shaped chromosome fragments through translocation in univalent chromosomes has been discussed. Most of the deficiencies in *Zea* have been produced through the agency of X-rays.

Most of these X-ray induced deficiencies are incapable of being transmitted through either the eggs or pollen but a few of them are inherited through the eggs. These are called haplo-viable deficiencies. Stadler (62) who has obtained several such deficiencies reported one for chromosome 10 in which approximately one-third of the long arm including the locus of *R* was missing. Pollen from plants heterozygous for this deficiency was of two sizes. Those grains with the deficient chromosome were smaller than normal, only partially filled with starch and were incapable of sending forth a germ tube when placed on fresh silks while the other class of pollen containing the full genomic complement was normal in size, appearance and behavior. Female gametophytes with the deficient chromosome were also smaller. However, some of these gametophytes developed embryos as the result of fusion of the deficient nuclei of the female gametophyte with the nuclei of male gametophytes containing complete haploid sets of genes. Plants heterozygous for the deficient chromosome were also of reduced stature, presumably because of the chromosomal unbalance produced.

Failure of chromosomes with a deficiency to be transmitted through pollen when they may be carried through eggs is due to lack of competition between female gametophytes while deficient pollen must compete in a race down the long maize styles with normal pollen. Deficient pollen is often incapable of germinating. If it does, the rate of pollen tube growth might be slowed down sufficiently to mitigate any chance of achieving fertilization. It should be noted that in the case of deficiencies it is lack of chromatin essential for normal development which prevents functioning of the male gametophyte while in trisomic types it is the presence of duplicated chromatin which is responsible for failure of $n+1$ pollen to function. The underlying cause is the same in both cases, *i.e.*, the unbalance produced either by a deficiency or a duplication is too great a handicap for successful competition with normal pollen. It is entirely possible that a small deficiency, including no essential genes, could be transmitted through both pollen and eggs.

Burnham (21) found in his studies with a reciprocal translocation involving chromosome 1 and chromosome 6 that eggs having duplication for a considerable portion of chromosome 1 and deficient for the terminal chromomere[26] of the satellite of chromosome 6 were viable. Pollen of the same constitution was non-functional but was well filled with starch.

In the above discussion of supernumerary chromosomes only those types have been discussed in which the extra chromosome represents some modification of one or more members of the normal monoploid set of ten. There has been found, however, in certain strains of maize, especially Black Mexican sweet corn, a type of supernumerary chromosome which is totally unlike any members of the regular complement. It cannot be said, on the basis of its peculiar morphology, to have been derived from any one member of the monoploid set and its origin is unknown. This type of supernumerary has been called the *B*-type chromosome in contradistinction to members of the normal complement which Randolph (50) has designated as the *A*-type chromosome. The *B*-type has a distinctive morphology quite unlike any of the *A*-type chromosomes. It appears to be composed of genetically inert material and carries no known genes. The presence of one or many *B*-type chromosomes has no visible effect on the morphological character of the plant. Randolph has succeeded through successive crosses in accumulating more than twenty-five *B*-type chromosomes in a single plant in addition to the regular complement of twenty. In contrast with supernumeraries composed of *A*-type chromosomes the *B*-type is readily transmitted through both pollen and eggs.

The morphology of the *B*-type chromosome at pachytene and its synaptic behavior have been investigated by McClintock (47). In the meiotic prophase the *B*-type is slightly more than one-half the length of the shortest member of the normal complement. Its morphology at mid-prophase, beginning with the terminal insertion region, is as follows: (1) terminal spindle fiber attachment region, (2) pycnotic[27] region, (3) chromatic region composed of small but distinct chromomeres, (4) elongate pycnotic region with several definite constrictions, (5) bulging pycnotic region, (6) broken pycnotic region composed of four distinct parts. The greater part of the *B*-type at mid-prophase is composed of pycnotic material. As stated before, there is reason to believe that the *B*-type chromosome is genetically inert. That these two facts have some close relationship is suggested by Heitz's studies (37, 38) with *Drosophila* in which he shows that the pycnotic portions found in prophase chromosomes are genetically inert.

The *B*-type shows no synaptic affinity for any of the chromosomes composing the normal set. If a single *B*-type is present it behaves as a univalent but regions within it are often non-homologously paired at mid-prophase in meiosis. Synapsis occurs between *B*-type chromosomes if two or more are present in the same nucleus although non-homologous association is very common. McClintock found that in plants with two *B*-types there were more sporocytes with two univalent *B*-type chromosomes at diakinesis than there were in mid-prophase where the *B*-types were usually paired. This has been attributed to the complete separation of the two members of a *B*-type bivalent during diplotene and early diakinesis which occurs in some sporocytes. This precocious separation may be due to frequent occurrence of non-homologous association observed at pachytene and/or to partial failure of chiasma formation when homologous pairing does occur.

In the euploid series in maize the number of complete haploid sets of chromosomes ranges from one to eight. A haploid has one, a diploid two, a triploid three, a tetraploid four, and an octoploid eight complete sets of the ten chromosomes. Haploid and triploid maize plants occur spontaneously while tetraploids and octoploids have been produced (Randolph, 51) by the doubling and quadrupling of the chromosome number through the application of heat to young ears at the time of the first divisions of the zygote. Triploids can be obtained by crossing tetraploid with diploid maize but this cross is highly sterile and few seeds result. In contrast with hypo- and hyperploid maize where visible difference in the morphology of the plant often results from the chromosomal unbalance there is no striking external morphological difference between different euploid types except that the haploids are smaller and weaker plants. This is intelligible since the genic balance between the different chromosomes has not been altered as all loci are present in the same relative proportions throughout the euploid series. There is, however, a striking correlation between cell size and the number of times the haploid complement is replicated in the nucleus. Beginning with haploids, which have the smallest cells, there is a graded series ending with octoploids, which have the largest cells.

There has been, as yet, little genetic work with tetraploid maize as Randolph (52) found that, due to irregularities in chromosome distribution in meiosis, the offspring of tetraploids do not always have forty chromosomes.

Hybrids of Zea with Euchlaena and Tripsacum. There are two closely related genera, *Euchlaena* and *Tripsacum,* which have been successfully crossed with *Zea.* There are three annual strains of *Euchlaena mexicana,* each with a haploid complement of ten chromosomes. These three annual strains, referred to as the Chalco, Durango and Florida forms, cross readily with maize and the F_1 plants are fertile. The homology between the *Zea* and *Euchlaena* chromosomes must be very close since studies of these hybrids made by Emerson and Beadle (8, 35) show that the amount of crossing-over is essentially of the same order in all tested regions as in pure maize with the notable exception of the short arm of chromosome 9 in the Durango and Florida hybrids where no crossing-over occurred.

Tripsacum crosses much less readily with *Zea* than does *Euchlaena.* Both the diploid form ($2n = 36$) and the tetraploid form ($2n = 72$) of *Tripsacum dactyloides* have been successfully crossed with *Zea* by Mangelsdorf and Reeves (39, 40). The F_1 hybrids of *Zea* ($n = 10$) by the diploid *Tripsacum* ($n = 18$) had twenty-eight chromosomes while the hybrids of *Zea* with tetraploid *Tripsacum* ($n = 36$) have forty-six chromosomes. In the first case the chromosomes show no synaptic affinity and are present as 28 unpaired chromosomes in meiosis but in the second type the 36 *Tripsacum* chromosomes form 18 bivalents with 10 *Zea* chromosomes left as univalents. The F_1 of the diploid *Tripsacum* with *Zea* has a low degree of fertility on the female side but is completely male sterile. The F_1 of tetraploid *Tripsacum* is both female and male sterile. The hybrid, *Zea* by diploid *Tripsacum,* has been crossed with *Euchlaena* and a trigeneric hybrid containing chromosomes from *Zea, Tripsacum* and *Euchlaena* was obtained.

SUMMARY

The combined efforts of a group of people working in close unison and interchanging results and material previous to publication has contributed greatly to the rapid advance of maize in the field of genetics and cytology. The long generation cycle of maize coupled with the usual delays in publication would otherwise considerably delay progress with this plant. As a conclusion, we wish to summarize in a numerical manner some of the outstanding contributions that this cooperative study has produced.

A. *The relation of genes to chromosomes:*

1. The discovery of approximately 400 genes relating to a variety of life activities ranging from gross morphological changes to those affecting cell sap color, cell wall texture and color, chemical nature of starch, chlorophyll development, disease resistance, mitotic chromosomal behavior, meiotic chromosomal behavior, cytokinesis, pollen tube growth rates, aleurone color, etc.

2. The placement of many of these genes into 10 linkage groups corresponding to the 10 chromosomes comprising the haploid complement.
3. The association of each linkage group with a particular morphologically identifiable member of the chromosome complement.
4. The placement of specific genes at definite positions within the physical chromosome.

B. *Cytological proofs of genetic postulates:*
   1. Cytological proof of genetic crossing-over.
   2. Cytological and genetical proof of chromatid crossing-over.
   3. Cytological demonstration of the physical location within the chromosomes of reciprocal translocations, inversions and deletions.

C. *Cytological discoveries with genetic consequences:*
   1. The analysis of factors governing the meiotic association of chromosomes.
   2. The discovery that non-homologous parts of chromosomes can be intimately associated at the meiotic prophase period.
      a. The reduction in normal crossing-over resulting from this association.
      b. The production of occasional translocations resulting from this non-homologous association.
   3. Diakinesis associations of chromosomes are, for the most part, strictly homologous.
   4. Analysis of the importance of different sections of the chromosomes to viability of the gametophytes by means of haplo-viable and haplo-inviable deficiencies.
   5. The unique mitotic behavior of ring-shaped chromosomes resulting in genetic variegation.
   6. The discovery that both parts of a broken spindle fiber attachment region are capable of functioning in the spindle figure.
   7. The correlation of pycnotic chromatin with genetic inertness.

D. *Polyploidy and generic hybrids:*
   1. The artificial production of polyploidy by heat treatment.
   2. The cytological and genetical analysis of *Zea-Euchlaena* hybrids.
   3. The cytological analysis of *Zea-Tripsacum* hybrids.

EXPLANATORY NOTES BY THE EDITORS

1. For a description of these characters see 36. The bulky corn plant as ordinarily observed is the *sporophyte*; each of its cells contains two sets of 10 chromosomes each (constituting 2*n* or diploid tissue); each of these sets represents the descendants of a single set (1*n*, *haploid* or *monoploid* tissue) inherited from each parent. The haploid tissues contributing these single sets at fertilization are the male gametophyte (pollen tube) and the female gametophyte (embryo sac). These gametophytic tissues are produced by and constitute minute parts of each parent and their haploid nature arises through a reduction in the number of chromosomes they receive from the diploid parent.

Endosperm tissue has three sets of chromosomes in each cell (3*n* or *triploid* tissue). This condition arises by fusion of a nucleus from the pollen tube with two nuclei from the female gametophyte. The endosperm surrounds and nourishes the developing embryo; in cereals its outer layer constitutes the *aleurone* layer which contains protein material. Certain abnormal plants, arising in a variety of ways, may have three sets of chromosomes in every body cell and are then known as *triploids*.

2. *Synapsis* is the normal pairing of chromosomes preceding their distribution to daughter cells. *Asynapsis* is the failure of this pairing; they then appear as single chromosomes, *univalents*, rather than as *bivalents*. *Synapsis* and associated cytological phenomena appear during a type of cell-division known as *meiosis* during which a reduction occurs from diploid 2*n* to haploid 1*n* tissue. Initial stages of all nuclear divisions constitute the *prophase* and the last stage of a *meiotic prophase* is known as *diakinesis* which immediately precedes disappearance of the nuclear membrane. An intermediate stage of all nuclear divisions is the *metaphase*.

3. For every character of a sexually produced organism a *gene* or factor is ordinarily contributed by each parent. If each gene of such a pair is the same as the other, as red and red, the progeny is then *homozygous* for that character. If the two inherited factors are not alike, as red and white, the progeny is *heterozygous*. If only one of these two unlike factors is visibly expressed to the complete suppression of the other it is said to be *dominant* and the suppressed one is *recessive*. Each parent contributes one member of each pair of chromosomes in the progeny; the two chromosomes of each such pair are *homologous chromosomes*.

4. At metaphase of a meiotic (reduction) division, homologous chromosomes are ordinarily paired and then separate, each member going into a different daughter cell. This movement constitutes the *anaphase*. At *telophase* the daughter nuclei become organized into new cells. *Non-disjunction* is the failure of this separation and then both chromosomes move together. *Disjunction* or separation of the paired chromosomes is directed by the *spindle fibers*.

5. *Translocations* are changes in position of a segment of a chromosome to another part of the same or of a different chromosome (Darlington). *Mutual* or *reciprocal translocations* are interchanges of segments between

different chromosomes. *Deficiencies* are losses of a segment of a chromosome.

6. See page 314 for discussion of deficiencies.

7. *Cytokinesis* is the division of the extra-nuclear portion of the protoplast. It usually takes place immediately after nuclear division.

8. See page 312 for discussion of ploidy.

9. The *nucleolus* is a body in the nucleus which disappears during nuclear division. Its substance is most probably incorporated into the matrix of the chromosomes.

10. See page 299 for discussion of crossing-over.

11. This indicates that every body cell has the normal diploid ($2n$) number of chromosomes plus one extra chromosome.

12. See page 313 for discussion of trisomes.

13. This means that when corn plants with one extra chromosome ($2n+1$; F_1 because they were the first generation plants secured by crossing a triploid with a diploid) were self-pollinated, a certain character in the progeny appeared three times as often as its allelomorph. If, on the other hand, the plants were not self-pollinated but were back-crossed with other plants which showed the recessive character, then half of the progeny exhibited this recessive character and the other half the dominant one. A discussion of the types of ratios expected from trisomic inheritance would occupy more space than is considered pertinent to this review. Details can be obtained from 49, 56.

14. Genes, the units of heredity regarded as determinants of most characters, are borne on the chromosomes. Those on any one chromosome are said to be linked.

15. A *heterozygote* is the product of a fertilization which for one or more characters possesses opposing factors.

16. *Sporocyte* = spore mother-cell. *Microsporocyte* = pollen mother-cell.

17. A *chromatid* is one half of a longitudinally split chromosome which later becomes a daughter chromosome.

18. See page 311 for discussion of inversions.

19. See page 296 for discussion of translocations.

20. The production of microspores (pollen grains).

21. *Pachytene* is the double thread (and the stage at which it occurs) produced by pairing of chromosomes in the prophase of meiosis. It is followed by *diplotene* (Darlington).

22. *Teosinte* is the common name of *Euchlaena mexicana,* a Mexican grass regarded as the nearest living relative of maize which is unknown in the wild state.

23. A *genome* is an entire chromosome set inherited as a unit from one parent.

24. *Sibs* are sister plants.

25. *Phenotype* refers to the external appearance produced by the reaction of an organism of a given genotype with a given environment. *Genotype* is the kind or type of hereditary properties of an organism (Darlington).

26. *Chromomeres* are the smallest particles in the chromosome thread.
27. *Pycnosis* is chromatic matter of the nucleus contracted into a deeply staining homogeneous mass (Sharp).

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