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Chromosome pairing in altered constitutions and models of synapsis and crossing-over

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1. INTRODUCTION

Two alternative systems have been visualized for the distribution of genetic crossovers throughout the genome. Traditionally, crossing-over has been thought to be initiated by a relatively rare process (within completed synaptic configurations) which occurs with equal probability at all points along the genetic map. The proximity of two such events, however, must be somehow limited (interference). Pritchard (1960) suggested that the location of crossovers might be determined instead by the intimate pairing of short homologous segments in advance of the remainder of the genome. Crossing-over would then be restricted to these early pairing regions, which would in turn occur with equal probability at all points along the genetic map. Interference, in this case, might be an observable effect of pairing mechanics.

Pritchard proposed that if indeed the frequency of crossing-over is determined by the frequency of meeting (at the appropriate stage) of randomly mixing homologous segments, and if effective pairing is equally probable in all combinations, and other factors remain unchanged, the frequency of crossing-over should be tripled in cases where three homologues are available. Increases in crossover frequency have been observed with triplication (Darlington, 1934, 1941; Pritchard, 1960; Green, 1962). However, since it is unlikely that pairing in all combinations is equally probable or that other factors remain unchanged when a triplicating segment is added, critical tests of the hypothesis on this basis do not seem feasible. Dobzhansky (1934), Rhoades (1931) and others have found decreases in crossover frequency in regions present in triplicate.

Grell (1967) has reasoned that a two-thirds reduction in crossing-over in the presence of extra free fragments in *Drosophila* (which do not themselves participate in exchange) is evidence that total synapsis precedes crossing-over. This conclusion is based on the assumptions that, in the case of total synapsis before crossing-over, pairing would be 2-by-2 and random among the three homologues, and pairing of either normal homologue with a fragments would prevent its subsequent involvement in exchange. On the other hand, it is also assumed that in the case of the alternative model, extra fragments which do not participate in exchange would not pair with the normal homologues in such a way as to block crossing-over between them. The crucial questions here are why the extra fragments do not participate in exchange, and whether pairing and exchange could imply at least

two separable steps as readily if only short (effective) segments rather than whole chromosomes are involved. If so, Grell's evidence would not discriminate between the two models. It is also of interest that the very short free fragments of Grell's *Drosophila* experiments seem to compete for exchange pairing of the region they contain on an equal basis with whole chromosomes. This would suggest that completion of synapsis by zipping up from points of initial contact is at most of small importance as a preparation for crossing-over.

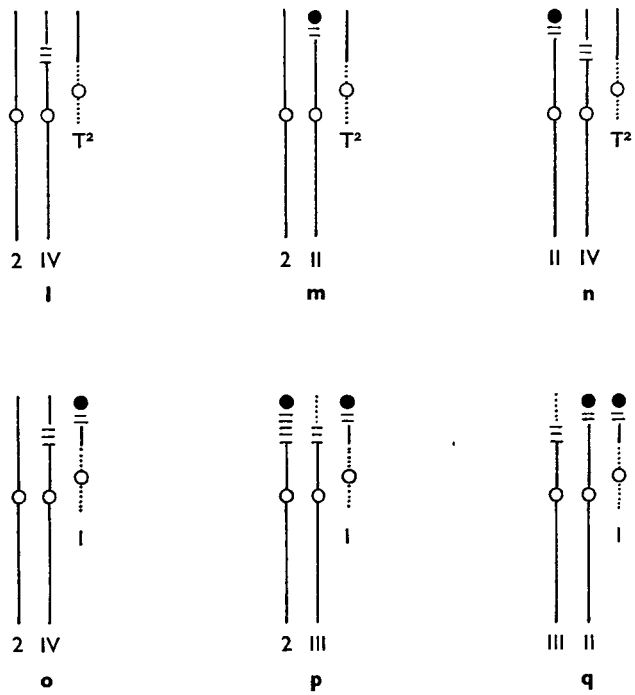

Fig. 1. Diagrammatic representation of the chromosomal constitutions of the new types (l–q) derived by combining primary and secondary maize–*Tripsacum* interchange chromosomes and normal maize chromosome 2. Types a–k are similarly diagrammed in an earlier paper (Maguire, 1965). Maize chromosome 2 is represented by a solid line, the *Tripsacum* chromosome by horizontal and vertical dashed lines. The different symbols for different parts of the *Tripsacum* chromosome serve only to distinguish the parts separated by the original interchange. Open circles indicate the approximate locations of centromeres. Roman numerals designate recovered derivatives of exchanges I–IV.

Evidence from maize (Maguire, 1965, 1966) has suggested that in two cases (a short paracentric inversion and certain maize–*Tripsacum* interchange trivalents) either the occurrence of at least one crossover is prerequisite to the pachytene pairing of certain regions (estimated to contain substantially less than 50 map units) or crossing-over must almost inevitably accompany their synapsis. In addition, in one of these studies (Maguire, 1965) frequency of metaphase pairing of rearranged segments seemed to be depressed by the presence of homologous

regions in triplicate. The magnitude of the effect was relatively insensitive to the length of the triplicated region, although pairing frequency increased with the extent of homology in the extra chromosome. It is the purpose of this paper to present and compare data from additional constitutions derived from crosses of the maize–*Tripsacum* interchanges described previously and from an additional secondary interchange.

2. MATERIALS AND METHODS

Newly derived chromosomal constitutions (**l** through **q**) are illustrated diagrammatically in Fig. 1. Types **a** through **k** as well as the derivation of exchanges I, II, and III have been described elsewhere (Maguire, 1965). Types **l**, **n** and **o** contain a new secondary interchange chromosome (exchange IV) whose derivation is illustrated in Fig. 2. Types **m**, **q** and **p** represent various combinations of the exchanges described previously.

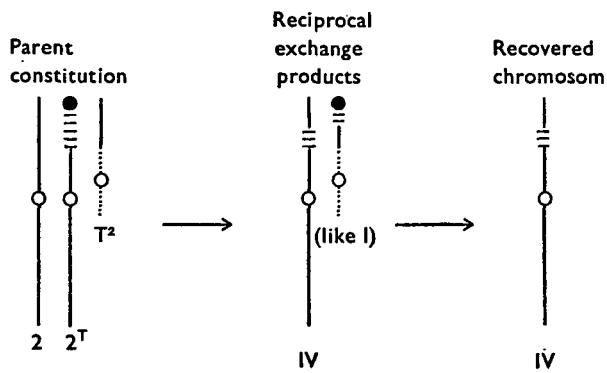

Fig. 2. Diagrammatic representation of the probable source of maize–*Tripsacum* secondary exchange IV. Exchanges I–III are similarly diagrammed in an earlier paper (Maguire, 1965). The various chromosomal regions are represented in the same way as in Fig. 1.

Metaphase I trivalent frequencies were observed in systematically scanned acetocarmine squash preparations of microsporocytes which had been fixed in a 3:1 alcohol–acetic acid mixture. Metaphase I trivalent frequencies found for the new constitutions are listed in Table 1.

3. RESULTS AND DISCUSSION

Type **n**, which is like type **c** in the extent of homology in the short chromosome (bearing the *Tripsacum* centromere), and in having parts present only in duplicate, also resembles type **c** in trivalent frequency. Similarly, type **o** resembles type **e**, type **p** resembles type **k** and type **q** resembles type **j**. As before, similarities in the extent of homology seem to override differences in the arrangement of *Tripsacum* segments and in the presence of the terminal knob. On the other hand types **l** and **m** differ markedly in trivalent frequency from types **g**, **h** and **i** although they are

similar in having parts present in triplicate as well as duplicate. It was reported in the earlier paper that depression of trivalent frequency in the presence of triplicated regions was similar in types **b**, **g**, **h** and **i** (which have the same extent of homology available in the short chromosome) in spite of the fact that the length

Table 1. *Metaphase trivalent frequencies of new constitutions*

Constitution	Plant no.	No. of cells	%	Average (%)
l	1	66/84	79	79
	2	119/151	79	
m	1	101/122	83	84
	2	111/134	83	
	3	114/136	85	
n	1	108/114	95	
o	1	85/167	51	
p	1	143/264	54	
q	1	173/188	92	92·5
	2	93/100	93	

Table 2. *Predicted trivalent frequencies for each constitution on basis of estimated extent of genetic map in the short chromosome which is duplicated and/or triplicated in the remainder of the complement*

(Estimates of genetic extent are based on correlations of genetic and cytological maps (Maguire, 1964, 1965). Genetic extents for types **l** and **n** are presented as ranges because the position of exchange IV is known only to be proximal to the *liguleless* (*lg*) locus and distal to the *glossy seedling* (*gl*) locus. An average of one crossover per 50 map units is assumed. Probabilities of exchange are summed for regions present in duplicate and triplicate.)

Constitution	Estimated map length in duplication	Estimated map length in triplication	Estimated metaphase trivalent probability	Observed average metaphase trivalent frequency
(a)	54	0	1·00	0·90
(b)	0	54	0·67	0·70
(c)	54	0	1·00	0·93
(d)	0	24	0·32	0·15
(e)	24	0	0·48	0·48
(f)	0	24	0·32	0·17
(g)	24	30	0·88	0·67
(h)	30	24	0·92	0·71
(i)	30	24	0·92	0·72
(j)	54	0	1·00	0·95
(k)	28	0	0·56	0·58
(l)	24–43	30–11	0·88–1·00	0·79
(m)	30	24	0·92	0·84
(n)	35–54	0	0·70–1·00	0·95
(o)	24	0	0·48	0·51
(p)	30	0	0·60	0·54
(q)	82	0	1·00	0·925

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of triplication in type **b** was approximately twice that in **g**, **h** and **i**. (Types **h** and **i** may have differed from each other in derivation only.)

In this light it is interesting to consider the expected trivalent frequencies of all types so far derived on the basis of random pairing of estimated genetic map lengths in duplicated and triplicated regions, if probability of exchange is shared where there are three homologous segments. These expectations are listed in Table 2, where probabilities are summed for regions present in duplicate and triplicate. Data from types where parts are present only in duplicate and from type **b** (where most extensive triplication exists) agree fairly well with expectation. Those with triplicated as well as duplicated regions, however, fall short of expectation in varying degrees. This variability seems unrelated to the terminal or intercalary position of the triplicated segment and thus to the exclusion of the short chromosome by 'zipping up' of the two longer chromosomes (which contain extensive regions of common homology external to the parts which have been interchanged with the *Tripsacum* chromosome). That greater similarities were seen between those in which the short chromosome was alike (**g** and **h** as compared to **l** and **m**) may be due to factors related directly to the length of the *Tripsacum* segment within it or to other genetic background factors. It is not known how map lengths compare in homologous regions of maize and *Tripsacum* chromosomes, but expected frequencies listed in Table 2 are based on an assumption of equivalence. Observations do not deviate greatly from predictions on this basis in constitutions **c**, **p** and **q**, but vary widely in **g**, **h** and **i**, the only constitutions with parts present in triplicate in which a portion of the pairing, for which map extent is estimated, involves *Tripsacum* homologues.

From a consideration of Table 2 it seems entirely possible that random effective pairing of short segments of the genetic map, however it is distributed among the chromosomes present, may be an underlying determinant of the trivalent frequencies observed. The random pairing expectation used, however, differs from that derived by Pritchard (1960), who conceived of a constant probability of crossing-over per meeting of homologues. Instead, the probability of a crossover for a given region is considered here to remain constant with the addition of an extra homologue, and to be shared among all homologues present. This is formally equivalent to the assumption that the probability of the meeting of any two where three are present is the same as where two are present. Such a condition could prevail if all homologues present become roughly aligned prior to meiotic prophase as proposed by Fabergé (1942) (unsaturated pairing). Evidence that homologues may pair in part or loosely through their length prior to the meiotic prophase has been reported (Feldman, 1966; Feldman, Mello-Sampayo & Sears, 1966; Maguire, 1967). Where more than two homologues are present, crossing-over can involve only two of them at any point. The factors which determine which two will actually be involved in any exchange may tend to randomize the distribution of exchanges among them (although circumstances may introduce various kinds of bias as well as distort map lengths).

Whether synaptinemal complex formation (see Roth, 1966) is completed (pachy-

tene stage) before crossover positions are fully determined is a question pertinent to the problem of the molecular mechanisms of crossing-over and interference. It is often suggested that the synaptinemal complex is a structure which enables crossing-over to occur, but it may be equally reasonable at present to propose that it is a mechanism for the prevention of excessive crossing-over and that it is normally first formed in regions adjacent to crossover positions (and possibly results in crossover interference). The seeming irrelevance to the distribution of chiasmata of the tendency of homologues to 'zip up' (once pairing is initiated) and tendencies for pachytene and metaphase pairing to have a 1:1 relationship in short regions (Maguire, 1965, 1966) seem to argue against the model which requires complete synapsis prior to crossover positioning.

Sved (1966) has suggested that synapsis may be initiated in higher plants by adjacent attachment of homologous telomeres to the nuclear membrane. This proposal is not supported by the evidence from maize reported here and previously (Maguire, 1965). On the contrary, it appears that the short chromosome pairs as readily in those cases where its only true homology to other chromosomes of the complement is intercalary as where it is terminal. If there exists an additional mechanism for initiation of intercalary pairing as efficient as that suggested by Sved for terminal pairing, to consider this supplementary scarcely seems justified. It should be emphasized that data cited by Sved as evidence for terminal initiation of synapsis fit models calling for initiation anywhere else equally well, where chiasmata are usually limited to one per arm (a common condition). The exceptions which do not fit his model tend to comprise those cases where more or fewer than one chiasma are found per arm.

SUMMARY

Metaphase trivalent frequencies from a number of new chromosomal constitutions (various combinations of maize chromosome 2–*Tripsacum* homeologue primary and secondary interchanges) are presented and compared to previous findings from similar material. It is suggested than an underlying direct relationship may exist between extent of gentic map present in duplicate and triplicate and expectation from a sharing of map probability of crossing-over among all homologues. Theoretical considerations are discussed.

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