Genet. Res., Camb. (1985), **45**, *pp.* 37–49
With 5 text-figures
Printed in Great Britain

Evidence on the nature and complexity of the mechanism of chiasma maintenance in maize

By MARJORIE P. MAGUIRE

Department of Zoology, University of Texas, Austin, Texas 78712, U.S.A.

(*Received 18 September 1984*)

SUMMARY

Inferences on the mechanism of chiasma maintenance can be drawn from study of the distribution and frequency of chiasma-like associations between bridges and fragments and between normal chromatids and fragments in meiotic material heterozygous for paracentric inversions. These bridges and fragments are the result of crossing over within the inverted region so that differing predictions for the associations are generated by the various models for chiasma maintenance mechanism. Results of such a study in material heterozygous for a large paracentric inversion in the long arm of chromosome 1 in maize are reported here. Findings are generally consistent with predictions of the 'generalized sister chromatid cohesiveness model', but are markedly at odds with the 'binder only at specific crossover sites model', and with the 'late effective doubling of telomeres model'. Some of the results do not conform quantitatively to predictions of the 'generalized sister chromatid cohesiveness model' for a linear relationship between potential extent of sister chromatid cohesiveness and frequency of maintained association, suggesting additional complexity.

1. INTRODUCTION

Normal disjunction of homologues at meiosis in many organisms seems to depend upon two preliminary, and probably separate (Maguire, 1978), major functions: (1) the occurrence of at least one crossover per bivalent to initiate chiasma formation, and (2) the maintenance of chiasmata until metaphase I, when homologues are actually directed to opposite poles. The fact that the crossover process by itself appears to be insufficient to provide for chiasma maintenance has been widely overlooked, although it was understood early (Darlington, 1932).

The mechanism of maintenance of crossover-initiated chiasmata has been discussed and reviewed elsewhere (Maguire, 1982). In brief, three differing models have been proposed: (1) a binder substance may be installed specifically only at crossover locations, and this serves to hold the chiasmata together between pachytene and anaphase I (Holm *et al.* 1981), (2) telomeres may not replicate, or at least become effectively double, before anaphase I, so that sister chromatids cannot separate terminally until this stage (Egel, 1979), and (3) there may be generalized sister chromatid cohesiveness during the interval between pachytene and anaphase I (Maguire, 1974). Of these ideas the one currently most favored seems to be that there is installation of binder substance specifically at crossover locations only.

Following the recognition that apparent chiasmate association can persist into anaphase I and even to prophase II, under special conditions where anaphase I movement does not disrupt them (Maguire, 1979), systems were sought where the predicted distribution of such associations at anaphase I would differ for the three proposed mechanisms of chiasma maintenance. It was realized that the behaviour of bridges and fragments in material heterozygous for a paracentric inversion could provide such a system. Since these bridges and fragments result from crossovers, and the fragments lack centromeres for autonomous anaphase movement, chiasmata and chiasma-like associations may be expected to persist into anaphase I in revealing ways. A comparative study of bridge and fragment behaviour in three differing paracentric inversion heterozygotes in maize was therefore performed (Maguire, 1982). This study involved two distal inversions of differing length in chromosome 1 of maize and a longer, more proximally located inversion in chromosome 4. Findings tended to support the 'generalized sister chromatid cohesiveness model'. The present work involves similar, but strategically more detailed, observations of a third distal inversion of chromosome 1 of still differing length, in an attempt to test further the inferences of the earlier work and to facilitate quantitative comparisons of behavior for differing portions of the same chromosome arm region (chromosome 1L).

2. RATIONALE

The expectations of bridge and fragment associations in accordance with each of the three models for chiasma maintenance can be discerned from perusal of the diagrams of Figs. 1–4. These diagrams are designed to indicate, for the various crossover classes, where bridges, fragments, loop dyads and normal dyads will be formed at anaphase I, as well as which segments share sister chromatid relationship. Effects of intertwining (where relevant) are also visible. Understanding of this paper may depend upon a thorough study of these diagrams. Most importantly, it can be seen from the diagrams that the three models generate certain expectations which differ substantially, and these are therefore considered diagnostic: (1) The association of a single bridge and fragment category is expected to arise from the most frequent crossover class if binding is installed specifically only at the location of crossovers (as a result of single crossovers in this region in this case) (Fig. 1); this category is expected to arise from three-strand double crossovers within the inversion if generalized sister chromatid cohesiveness prevails (Fig. 3), and in this case its frequency should be much lower, not exceeding approximately twice that of the total of the double bridge, two fragment categories; and importantly, this category is not expected to result at all from late functional doubling of telomeres. (2) The fragment produced at anaphase I (in the absence of a bridge) by three-strand double crossovers, with one crossover within the inversion and one proximal to it (Fig. 4), is expected, when it progresses to one of the poles at anaphase I, to progress most of the time to the same pole as the loop dyad, if binding is installed specifically only at the location of crossovers; but a fragment produced in this manner is expected to progress to the pole opposite the loop dyad (Fig. 4) if there is generalized sister chromatid cohesiveness, or if there is late functional doubling

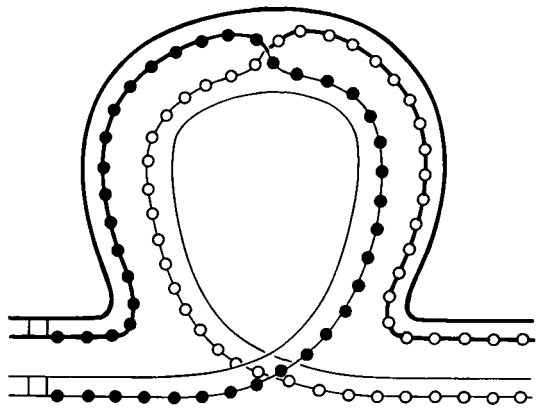

Fig. 1. Diagram of configuration expected at pachytene in a chromosome arm heterozygous for a paracentric inversion with a single crossover within the inversion. In this and the other diagrams the sister chromatids of one homologue are represented by heavy lines, while the sister chromatids of the other homologue are represented by light lines. X-shaped intersections represent crossovers, where there has been breakage and reunion between nonsister chromatids. Centromeres are represented by squares at the left in each homologue. An element destined to become a bridge or loop dyad when the centromeres move to opposite poles at anaphase I has been marked with closed circles; an element destined to become a fragment at anaphase I has been marked with open circles. From this figure, with a single crossover within the inversion, diagnostic features to be noted are that at anaphase I, a single bridge and fragment will be formed, and at first: (1) if there is binding only at the crossover location, the fragment will tend to be associated with the bridge at this location, (2) if there is late effective doubling of telomeres, the fragment will tend to be associated at one end with a normal chromatid moving to one pole and at the other end with a normal chromatid moving to the opposite pole, and (3) if there is generalized sister chromatid cohesiveness, the fragment will tend to be associated more extensively (distally to the crossover) with the normal chromatids moving to opposite poles.

of telomeres. Note that in these latter two cases, if the two crossovers follow events of twisting in the same and opposite directions equally frequently, in half the cells of this crossover class the fragment would be at first interlocked with the loop dyad (if there is generalized sister chromatid cohesiveness or late functional doubling of telomeres), so that disruption of the association of the fragment with at least one and perhaps both normal dyad chromatids would be expected to occur at anaphase I (in a manner similar to that of normal chiasma resolution). Thus the fragment could be left free in the central region of the anaphase I spindle (in this half of the cells of this class), unless the degree of association to the normal dyad chromatids differs substantially. (The frequency of meiocytes of this crossover class is most accurately calculated as twice the frequency of anaphase II cells with a bridge, produced by the loop dyad.)

In addition to the associations just mentioned, in the case of a single crossover within the inversion another instance of poleward migration of the fragment is predicted by one (and conceivably two) of these models. As noted above, the 'installation of binder specifically only at crossover location model' predicts that

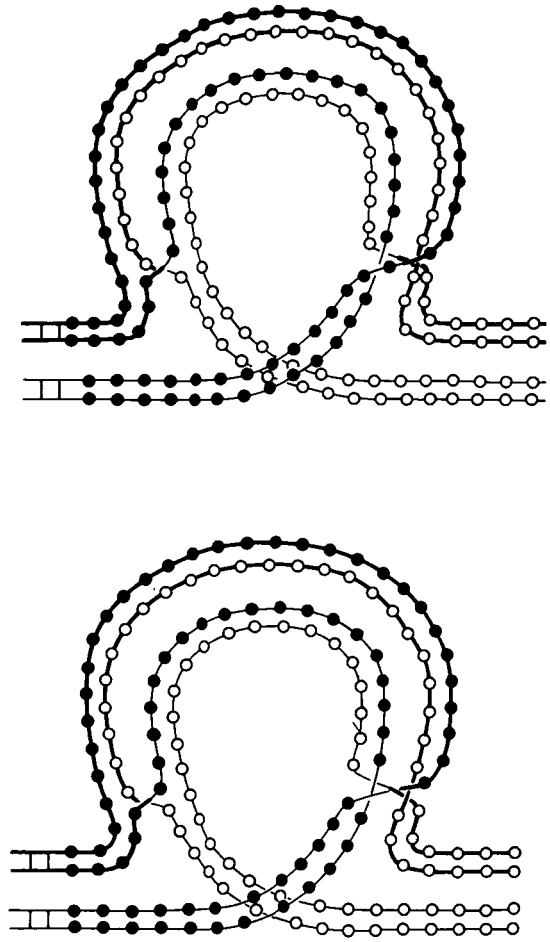

Fig. 2. Diagrams of configuration expected at pachytene in a chromosome arm heterozygous for a paracentric inversion with 4-strand double crossing-over within the inversion. Symbolism is as indicated in the Fig. 1 legend. Differences between the upper and lower diagrams represent differences with respect to the twists produced at the two crossovers as to whether they are in the same or opposite directions. It can be seen that at anaphase I there will be two bridges and two fragments, and at first (1) if there is binding only at crossover locations, a fragment will tend to be associated to each bridge at such a location, (2) if there is late effective doubling of telomeres, the two fragments will tend to be associated with each other at their ends, and if the two kinds of twists are equally frequent, half the time the fragment configuration will tend to encircle one bridge, and (3) if there is generalized sister chromatid cohesiveness, each fragment will tend to be associated with a bridge in the region between the two crossovers, and the two fragments will tend to be associated with each other in the regions proximal and distal to the two crossovers, and if the two kinds of twists are equally frequent, the fragment configuration will encircle a bridge half the time. This type of crossover class is the most rare, is not of critical importance to arguments presented here, and could probably be studied better in an organism with larger chromosomes.

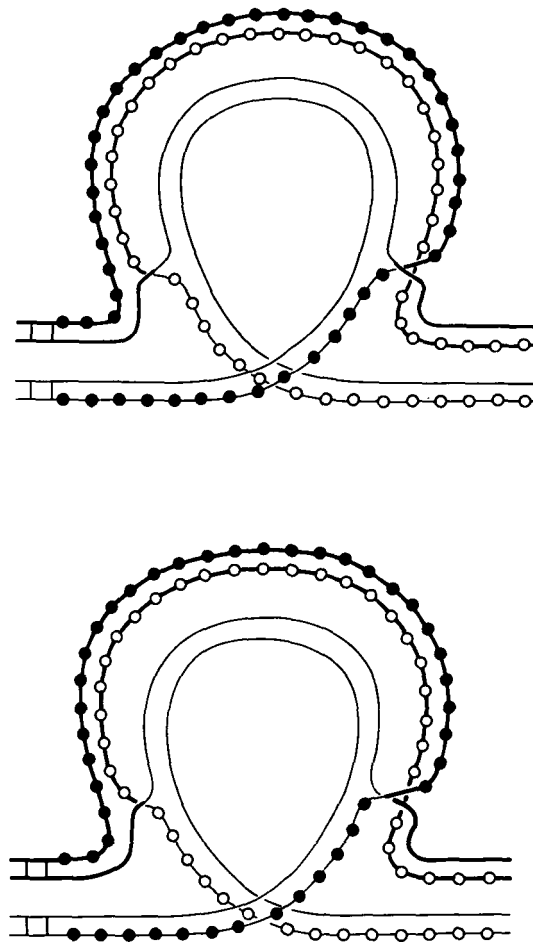

Fig. 3. Diagrams of configurations expected at pachytene in a chromosome arm heterozygous for a paracentric inversion with 3-strand double crossing over within the inversion. Symbolism is as indicated in the Fig. 1 legend. Differences between the upper and lower diagrams represent differences with respect to the twists produced at the two crossovers as to whether they are in the same or opposite directions. It can be seen that at anaphase I there will be one bridge and one fragment, and diagnostic features to be noted are that at first: (1) if there is binding only at crossover locations, the fragment will tend to be associated with a normal chromatid at one crossover, (and this normal chromatid with the bridge at the other crossover), (2) if there is late effective doubling of the telomeres, the fragment will tend to be associated at opposite ends with normal chromatids progressing to opposite poles and not at all with a bridge, and (3) if there is generalized sister chromatid cohesiveness, the fragment will tend to be associated with the bridge in the region between the two crossovers (and at opposite ends with the normal chromatids progressing to opposite poles). An especially persistent, clear example of association between a fragment and a telophase I bridge remnant is shown in Fig. 5(*c*).

https://doi.org/10.1017/S0016672300021947 Published online by Cambridge University Press

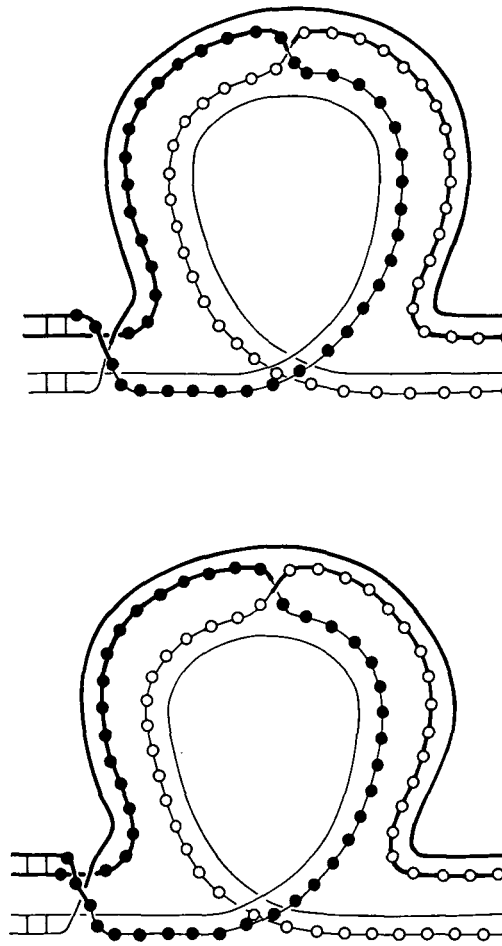

Fig. 4. Diagrams of configuration expected at pachytene in a chromosome arm heterozygous for a paracentric inversion with 3-strand double crossing over, with one crossover within the inversion and one proximal to it. Symbolism is as indicated in the Fig. 1 legend. Differences between the upper and lower diagrams represent differences with respect to the twists produced at the two crossovers as to whether they are in the same or opposite directions. It can be seen that at anaphase I there will be a loop dyad and a fragment, and diagnostic features to be noted are that at first: (1) if there is binding only at crossover locations, the fragment will tend to be associated to the loop dyad at the position of the crossover within the inversion, (2) if there is a late effective doubling of telomeres, the fragment will tend to be associated at each end to a chromatid of the normal dyad, and if the two kinds of twists are equally frequent, the fragment and the loop dyad will be interlocked half the time, and (3) if there is generalized sister chromatid cohesiveness, the fragment will tend to be associated with each of the normal dyad chromatids, with the extent to each one determined by the position of the crossover within the inversion, and if the two kinds of twists are equally frequent, the fragment and the loop dyad will be interlocked half the time. Note that the loop dyad is destined to produce a bridge at anaphase II.

the fragment will be associated with the bridge in this case. The other two models predict that in cells of this crossover class the fragment will be associated with both normal chromatids, which proceed to opposite poles at anaphase I, so that chiasma-like resolution of association would be expected. To the extent that binding of the fragment to one normal chromatid is stronger than to the other, the fragment might be expected to be carried poleward by the stronger association, generally producing an anaphase I cell with a bridge but no fragment visible (Fig. 1); where the association to opposite chromatids is approximately equal, the fragment would be expected to be left in the central region of the spindle.

Additional predicted effects (of little consequence to the problems addressed here) are described in the earlier work (Maguire, 1982).

Again, the differing expectations of bridge and fragment associations thought to result from the three chiasma maintenance models depend upon persistence of chiasma maintenance function into anaphase I under these circumstances. It can be argued (with due reservations stemming from the obvious circularity) that since there seems to be no obvious, acceptable alternative explanation for such associations, their existence here, with relative frequencies within the predicted range, supports the notion of such persistence. Actually, poleward migration of the acentric fragment is conventionally attributed directly to persistence of a true chiasma into anaphase I (in contrast to the mechanism proposed here). The view has been that an additional chiasma in the region distal to the inversion directly associates the fragment to a poleward dyad in such cases. However, the multiple crossing over necessary for such a relationship is expected to be rare, especially when the distal region is short, as is the case with all of the chromosome 1 inversions studied, and with the assumption of no chromatid interference, would be expected only half the time to involve appropriately the chromatids predicted to be associated. In fact, evidence was reported early (McClintock, 1938) that the fragment produced by three-strand double crossovers, with one crossover within an inversion and one proximal to it, tended to progress at anaphase I to the pole opposite prediction of direct chiasmate association.

Mention should be made of the fact that there are no apparent heterochromatic regions, which might conceivably provide basis for associations or for neocentric activity, in any of the chromosome arms containing the inversions. It should also be noted that previous observations of cells at diakinesis (Maguire, 1982) suggests that there is little or no terminalization of chiasmata within the inversions.

3. MATERIALS AND METHODS

Paracentric inversion Inld utilized in this study has breakpoints in the long arm of chromosome 1 at 55% and 92% of the distance from the centromere, giving lengths of the proximal, distal and inverted segments of the long arm of chromosome 1 of 69·5%, 10·1% and 46·7% respectively, of the total length of chromosome 10 as a reference. This inversion is 1·4*X* as long as the longer chromosome 1 inversion of the previous study (Maguire, 1982) and has a very similar distal break-point position. Maize plants heterozygous for inversion Inld, and with the same genetic background (KYS) as the plants used in the previous

study, were grown in a growth chamber. Microsporocyte samples were collected at meiotic stages and fixed in ethanol:chloroform 3:1 mixture, which seems to provide superior fixation (particularly for the crucial anaphase II observations of this study) to that of the conventional ethanol:acetic 3:1 mixture. The samples were stored in a freezer until examination in acetocarmine squash preparations

Table 1. *Frequencies of cells in various categories at Anaphase I*

Categories	No.	%
No bridge or frag.	301/545	55·2
Bridge, but frag. poleward or not seen	62/545	11·4
Bridge and frag., frag. free	95/545	17·4
Bridge and frag., frag. assoc.	36/545	6·6
Frag. only (centre)	31/545	5·7
Double bridge, 2 frags., all assoc.	7/545	1·3
Double bridge, 2 frags. assoc. only with each other	2/545	0·4
Double bridge, 2 frags., all free	8/545	1·5
Double bridge, 2 frags., each frag. assoc. with a separate bridge	1/545	0·2
Double bridge, 2 frags., one bridge and frag. assoc., others free	2/545	0·4

Table 2. *Frequencies of cells in various categories at Telophase I*

Bridge remnant and frag. assoc.		Single free frag.		Two frags		All others	
No.	%	No.	%	No.	%	No.	%
17/463	3·7	130/463	28·1	12/463	2·6	304/463	65·7

Table 3. *Frequencies of cells in various categories at prophase II*

No frag. visible		Frag. in cytoplasm		Free frag. in nucleus	
No.	%	No.	%	No.	%
619/750	82·5	112/750	14·3	19/750	2·5

with high-resolution light microscopy (1·4 N.A). Slides at anaphase I, teolophase I, prophase II, metaphase II and anaphase II were systematically scanned. Records were kept for number of cells at each stage in the readily scorable, important categories (with predicted characteristics which differ for the three models). Findings are listed in Tables 1–5. Since bridges tend to disappear at telophase I, no effort was made to record number of cells with a bridge at this stage.

4. RESULTS

Numbers of cells observed in different categories at the various stages are listed in Tables 1–5. Estimated frequencies of poleward movement of fragments are presented in Table 6.

Results show higher frequency of total cells with any class of crossover event within the inversion than was found for the longer of the other two chromosome 1 inversions. Overall, the apparent increased frequency of crossover events of any kind within the inversion was somewhat less than proportional to its additional

Table 4. *Frequencies of cells in various categories at metaphase II*

No frag. visible		Visible frag.	
No.	%	No.	%
757/892	84·9	135/892	15·1

Table 5. *Frequencies of cells in various categories at anaphase II*

No bridge, on frag.		No bridge, frag. off spindle		No bridge, frag. on spindle		Bridge, no frag.		Bridge and frag., frag. off spindle		Bridge and frag., frag. on spindle	
No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
588/786	74·8	87/786	11·1	26/786	3·3	74/786	9·4	11/786	1·4	0/786	0·0

Table 6. *Estimated poleward movement of fragments at anaphase I*

(The number of cells in which a fragment from a single crossover within the inversion progressed poleward at anaphase I is taken to be equal to the number of cells with a bridge, but fragment poleward or not seen, and the total number of cells with a single crossover within the inversion was assumed to be represented by the sum of this number and the number of cells with a bridge and fragment, fragment free. The number of cells in which three-strand doubles occurred with one crossover within the inversion and one proximal to it was estimated to represent twice the frequency of cells with a bridge at anaphase II; the number of these in which the fragment progressed poleward at anaphase I was estimated at the difference between this number and the number of cells observed to have a fragment only at anaphase I.)

Fragments from single crossovers within the inversion calculated to have progressed poleward at anaphase I		Fragments from three-strand double crossovers, one within inversion, one proximal, calculated to have progressed poleward at anaphase I	
No.	%	No.	%
62/157	39·5	87/118	73·7

length (observed was about 94 % of expected if crossover frequency per unit length were the same in Inld as in the longer of the other chromosome 1 inversions). This is consistent with expectation of lower crossover frequencies for the more proximal additional region.

Particular attention is directed to data for easily scored, diagnostic features (for which the models generate differing expectations). These are: (1) the frequency

with which anaphase II cells which contain a bridge (from an anaphase I loop dyad) also contain a fragment, (2) the frequency of anaphase I cells in which there is a bridge, but the fragment has moved poleward, and (3) the frequency of anaphase I cells containing a single bridge and fragment in which the fragment is clearly (centrally) associated with the bridge.

5. DISCUSSION

Findings are not in accord with predictions of the chiasma maintenance model which invokes installation of binding specifically at crossover locations only. This is the case most impressively because these findings imply a strong tendency for poleward progression at anaphase I of a single fragment (in cells where no bridge is present) toward the pole opposite the pole to which the loop dyad had progressed. That result is, however, expected (Fig. 4) if the fragment tends to be associated with the normal chromatids, with which it has complete sister chromatid relationship (the prediction of the 'generalized sister chromatid cohesiveness model' and of the 'late functional doubling of the telomere model'). There was apparently a strong tendency for the fragment (in this crossover class) to be included in the second division cell which does not contain the second division bridge-forming loop dyad, as described below in detail.

In reasonable accordance with the predictions (Fig. 1) of the 'sister chromatid cohesiveness' and 'late functional doubling of telomeres' models (but not predicted by the 'binder only at crossover location' model), there was a marked tendency for the fragment, in those cells with a single bridge and a separate fragment, to move poleward (Fig. 5*a*). This motion is predicted if the association between the fragment and one chromatid is stronger than the association of the fragment with the other chromatid, a condition which might arise either from eccentric position of the crossover within the inversion (if sister chromatid cohesiveness prevails), or from earlier doubling of one telomere than the other (if there is late functional telomere doubling). It can be suggested that longer inversions, with enhanced opportunity for eccentric positioning of a single crossover within the inversion, might be expected to show a higher frequency of poleward progression of such a fragment, if a sister chromatid cohesiveness system prevails. The findings of the previous study conformed to this prediction, with a higher frequency of poleward progression in the case of the longer chromosome 1 inversion. The present study included an attempt to extend observations for chromosome 1 inversions of similar genome position but differing extent. However, in this study where the inversion was substantially longer, a very similar (but slightly lower) frequency of poleward progression of a fragment (from this crossover class) was estimated to have occurred, than in the case of the longer chromosome 1 inversion of the previous study (39·5% and 40·8% respectively). Evaluation of this result is hampered by the inherent difficulty of predicting the frequency distribution of the position of single crossovers within longer inversions, but it fails to provide support for the existence of a linear relationship between fragment length and frequency of poleward progression of fragments in cells of this crossover class.

Association of a fragment with a bridge at anaphase I approached expectation

in frequency if this association results from generalized sister chromatid cohesiveness following three-strand double crossovers within the inversion rather than from installation of binder at the site of a single crossover within the inversion (Figs. 3 and 1). Notably, such associations are not accounted for by the 'late functional doubling of the telomere model' (Figs. 1–4).

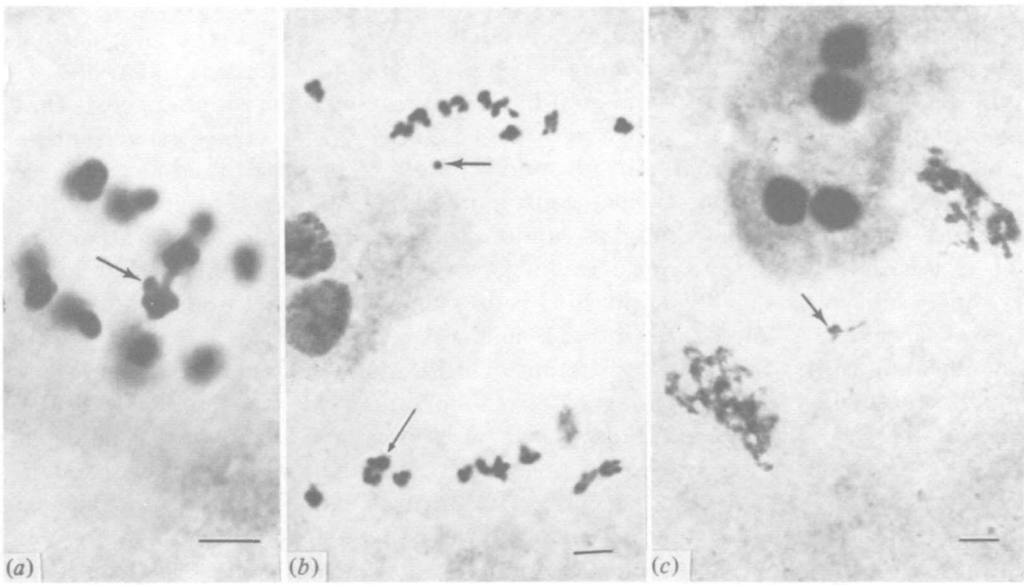

Fig. 5. Photomicrographs of Inld heterozygote microsporocytes. Magnification bars represent 5 μm (*a*) Early anaphase I with a single bridge and a fragment (arrow) associated with a normal, poleward chromatid of the bridge-containing configuration. (*b*) Anaphase I following 3-strand double crossing over with one crossover within the inversion and one proximal to it. A free fragment (large arrow) is in the vicinity of dyads progressing to one pole, and a loop dyad (small arrow) is in a corresponding position among the dyads progressing to the opposite pole. (A tapetal cell overlaps the central left portion of the cell.) (*c*) Telophase I showing a fragment associated with a bridge remnant (arrow). (Tapetal cells overlap the central upper portions of the cell.) Note that the examples illustrated here are short, transitory but interesting stages, seen relatively infrequently. Conclusions do not rely upon these (and similarly suggestive) demonstrations, but upon data from frequently occurring, easily scored stages from which appropriate deductions can be made.

Quantitative comparisons among the three chromosome 1 inversions (In5083 and In4305–25 of the previous study and Inld of this study) with respect to estimated poleward progression of fragments produced by three-strand double crossovers with one crossover within the inversion and one proximal to it are of special interest. Observations of fragment presence at telophase I (Table 2) suggest that more than half (estimate = 62 %) of the fragments which migrate toward a pole at anaphase I are not actually included in a nucleus and that physical association of a fragment with a poleward dyad must be disrupted before migration is complete in these cases. It is probably reasonable to expect that fragments included within a nucleus at telophase I have greater likelihood of appearing on

a second division spindle than in the cytoplasm. Also, fragments are apparently lost from the cytoplasm of a small proportion of cells (estimate = 2·3 %) between telophase I and prophase II, and an estimated 2·7 % of nuclei, expected to contain a fragment at prophase II, either do not, or contain it in unrecognizable configuration (Table 3). Overall, it is estimated that by anaphase II (Table 5) 6·6 % of total cells, expected on the basis of anaphase I information to contain a fragment, do not, indicating an effective loss or disappearance of fragments from 29·5 % of cells, initially destined to contain a fragment. This is the information, together with the data on distribution and position of a fragment at anaphase II in bridge containing, compared to non-bridge containing cells, which suggests that fragments produced by three-strand double crossovers with one crossover within the inversion and one proximal to it tend strongly to be distributed at anaphase I to the pole opposite from the loop containing dyad (Fig. 5*b*). If fragments of this derivation were even distributed at random to the cell with the loop dyad and to the cell without it, and loss of the fragment were randomly distributed among the various cell types, then 30 anaphase II cells which contained a bridge should also have contained a fragment. Only 11 such cells were found ($\chi^2 = 18{\cdot}6$, highly significant). Also, with random distribution of fragments of this derivation, some might reasonably have been expected to be found on the spindle of bridge containing cells at anaphase II, as a result of having been included in the nucleus with the loop containing dyad at telophase I. No such anaphase II cells were found. Thus, as indicated above, findings do not conform to expectations of the chiasma maintenance model of 'binder installation at crossover sites only', which predicts migration of fragments of this derivation toward the same pole as the loop dyad at anaphase I in most cells where chiasmate association persists into this anaphase stage, and deposition of the fragment in the central region of the spindle where such association does not persist. However, if the findings were to conform to the predictions of the sister chromatid cohesiveness model in simple linear fashion, frequencies of poleward migration of fragments of this derivation might be expected to vary in proportion to fragment length in the three differing chromosome 1 inversions which have now been studied. Such fragments are entirely sister chromatid to distal portions of the two chromatids of the normal (non-loop) dyad, partly to one chromatid and partly to the other, with precise extents apportioned between the two chromatids by the position of the crossover within the inversion (Fig. 4). Estimated lengths of the fragment for the three inversions, expressed as a percentage of the total length of the chromosome 10, vary from 37·9 for In5083 and 44·2 for In4305–25 (the two chromosome 1 inversions of the previous study), to 56·8 for Inld of the present study. When poleward migration frequencies for In5083 vs. Inld and for In4305–25 vs. Inld are compared, the results differ very significantly from this expectation ($\chi^2 = 13{\cdot}46$ and 70·94 respectively), although they do not differ significantly for the comparison In5083 vs. In4305–25 ($\chi^2 = 0{\cdot}75$). It can be suggested that beyond a threshold, increased extent of sister chromatid cohesiveness does not increase stability of association of the fragment to the normal poleward dyad, or that there are unknown relevant differences between the Inld and other materials, especially perhaps with respect to efficiency of installation of sister chromatid cohesiveness (Maguire, 1979). Further speculation at this time does not seem warranted.

In general, observations reported here confirm and extend earlier findings. Results are consistent with expectations of the 'generalized sister chromatid cohesiveness model' and depart drastically from expectations of the other two models. These results are considered to be strongly suggestive rather than conclusive, and it is hoped that further study of the mechanism of chiasma maintenance will be encouraged.

I am very grateful to Gregory G. Doyle for supplying the seeds used in this study. This work was supported by grant GM 19582 from the U.S. Public Health Service.

REFERENCES

DARLINGTON, C. D. (1932). *Recent Advances in Cytology*. Philadelphia: Blakiston.

EGEL, R. (1979). Telomeres and chiasma terminalization. *Hereditas* **91**, 138–140.

HOLM, P. B., RASMUSSEN, S. W., ZICKLER, D., LU, B. C. & SAGE, J. (1981). Chromosome pairing, recombination nodules and chiasma formation in the basidiomycete *Coprinus cinereus*. *Carsberg Res. Commun.* **46**, 305–346.

MAGUIRE, M. P. (1974). The need for a chiasma binder. *J. theoret. Biol.* **48**, 485–487.

MAGUIRE, M. P. (1978). Evidence for separate genetic control of crossing over and chiasma maintenance in maize. *Chromosoma* **65**, 173–183.

MAGUIRE, M. P. (1979). An indirect test for a role of the synaptonemal complex in the establishment of sister chromatid cohesiveness. *Chromosoma* **70**, 313–321.

MAGUIRE, M. P. (1982). The mechanism of chiasma maintenance. A study based upon behavior of acentric fragments produced by crossovers in heterozygous paracentric inversions. *Cytologia* **47**, 699–711.

MCCLINTOCK, B. (1938). The fusion of broken ends of sister half-chromatids following chromatid breakage at meiotic anaphases. *Research Bulletin of the University of Missouri Agricultural Experimental Station* **290**, 3–48.