CHIASMA TERMINALIZATION IN A STRUCTURAL HETEROZYGOTE IN *SECALE*

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TERMINALIZATION of chiasmata which originate in structural heterozygotes between centromeres and points of non-homology is said to be arrested at such points. The hypothesis that terminalization stops at points where chromosome homologies change (DARLINGTON 1929) is based on two assumptions: (1) That point-by-point attractions which cause homologous chromosome segments to conjugate in pairs continue to exert a force through late prophase and that after chromosomes are effectively doubled the attractions hold chromatid pairs together rather than chromosome pairs; and (2) that attractions of like chromatids cannot be overcome by terminalization which, should it proceed beyond a point where chromosome homologies change, would cause a change from association of identical chromatids to an association of unlike chromatids. However, contradictions to the hypothesis have been reported by MARQUARDT (1948) and by HAGBERG (1954). The contradiction reported by HAGBERG was based on observations of certain chiasmata in heteromorphic bivalents, but no assurance was given that the chiasmata originated in segments proximal to changes in homology. MARQUARDT, on the other hand, observed multiple terminal chiasmata in translocation configurations, which clearly required the interpretation that chiasmata originated at interstitial sites and moved through non-homologous segments to terminal positions.

While studying meiosis in pollen mother cells of *Secale cereale* L. $\times$ *S. montanum* Guss. hybrids, the writer observed a translocation association comparable with those described by MARQUARDT. The association occurred in *r* hybrid No. 168-1, a plant obtained by pollinating *S. cereale* with X-rayed pollen of *S. montanum*. A first metaphase cell showed a 5-chromosome chain, a 4-chromosome "frying-pan-shaped" association, two bivalents, and one univalent (PRICE 1955, Figure 8). The univalent and the 5-chromosome chain resulted from naturally occurring structural differences—reciprocal translocations—which distinguish the chromosomes of the two species (SCHIEMANN and NURNBERG-KRUGER 1952; PRICE 1955; RILEY 1955; NAKAJIMA 1956; STUTZ 1957). The "frying-pan" configuration resulted from heterozygosity for an induced interchange between chromosomes not involved in naturally occurring translocations. This 4-chromosome induced-translocation configuration has special significance relative to the hypothesis that chiasma terminalization stops where chromosome homologies change.

The significance of the "frying-pan" configuration lies in its 3-chromosome terminal chiasma (Figure 2). A 3-chromosome terminal chiasma at first metaphase presupposes early prophase chiasmata in both segments of a chromosome arm which is paired in one segment with a second chromosome and in another segment with a third chromosome. In a translocation heterozygote such an association shows that chiasmata originate in segments both distal and proximal to the point of interchange. As Figure 1 illustrates, a completely terminalized 3-chromosome connection in a translocation configuration must result from movement of a chiasma through a point where chromosome homologies change.

Having recently reviewed MARQUARDT's contribution, the writer was prompted

FIGURE 1.—Diagrams of 4-chromosome associations in a translocation heterozygote with points of interchange in median positions: A, Pachytene association with chiasmata located so that a "frying-pan" configuration would result at first metaphase; B, first metaphase with terminalization of proximal chiasma arrested at the point of interchange; C, first metaphase with terminalization completed despite changes of chromosome homology.

FIGURE 2.—A 4-chromosome "frying-pan" configuration at first metaphase showing a completely terminalized 3-chromosome chiasma. $\times 3200$.

FIGURE 3.—A 4-chromosome "figure-of-eight" at first metaphase. $\times 3200$.

FIGURE 4.—A 4-chromosome "Y-shaped" configuration at first metaphase. $\times 3200$.

FIGURES 5 and 6.—First metaphase cells with "Y-shaped" configurations. $\times 1600$.

FIGURES 7, 8, 9, and 10.—First metaphase cells with "frying-pan" configurations. $\times 1600$.

FIGURES 11, 12, and 13.—First metaphase cells with "figures-of-eight." $\times 1600$.

to return to permanent preparations of pollen mother-cell divisions in *r*-hybrid No. 168-1. The permanent slides were re-examined, particular attention being given to the behavior of the four chromosomes involved in the induced translocation association.

In Table 1, diagrams show first metaphase configurations that could be expected if chiasma formation were variable in the several segments of a translocation association such as the one illustrated in Figure 1-A. The diagrams show interstitial chiasmata only where terminalization might be arrested by homology changes. These diagrammed expectancies can be compared with configurations actually formed by the four chromosomes involved in the induced translocation association.

OBSERVATIONS

Configurations formed in the first meiotic metaphase by the four chromosomes under investigation and the frequencies in which they were observed are shown in Table 2. In all, 482 cells in which the chromosome associations could be interpreted were found; in 172 of these cells, however, the four chromosomes of the induced translocation association could not be distinguished from the six chromosomes involved in the naturally occurring translocation association.

TABLE 1

Diagrams of first metaphase configurations expected if chiasmata fail in certain segments of four-chromosome translocation associations

DISPOSITION OF CHIASMATA IN STRUCTURALLY HOMOZYGOUS ARMS AND IN DISTAL SEGMENTS OF HETEROZYGOUS ARMS	DISPOSITION OF CHIASMATA IN PROXIMAL SEGMENTS OF THE STRUCTURALLY HETEROZYGOUS ARMS				
	CHIASMATA LACKING IN PROXIMAL SEGMENTS	A CHIASMA IN ONLY ONE PROXIMAL SEGMENT		CHIASMATA IN BOTH PROXIMAL SEGMENTS	
		ARRESTED	TERMINAL	ARRESTED	TERMINAL
CHIASMATA IN BOTH HOMOZYGOUS ARMS AND IN BOTH DISTAL SEGMENTS					
CHIASMATA IN BOTH HOMOZYGOUS ARMS BUT LACKING IN ONE OR BOTH DISTAL SEGMENTS					
CHIASMATA IN BOTH DISTAL SEGMENTS BUT LACKING IN ONE OR BOTH HOMOZYGOUS ARMS					
CHIASMATA LACKING IN ONE OR BOTH HOMOZYGOUS ARMS AND LACKING IN ONE OR BOTH DISTAL SEGMENTS					

TABLE 2

*Frequencies with which the induced translocation association forms various configurations in first metaphase cells**

OR	UN- CERTAIN
18	17	5	5	2	4	136	1	122	172

* Here the distinction between complete and incomplete terminalization is made only for "frying-pan" and "Y-shaped" configurations.

Chromosome associations in 122 other cells showed that the four chromosomes of the induced-translocation association formed two bivalents, but it was uncertain whether one bivalent or both were open or whether one or both were closed. In 136 cells the four chromosomes definitely formed two closed bivalents, and in one cell they formed two open bivalents. The induced translocation association produced 4-chromosome configurations in 51 cells. These 4-chromosome associations were in the forms of rings, "frying-pans," "figures-of-eight," and "Y-shaped" configurations (Figures 2-13). No univalents or 3-chromosome associations could be attributed to the four chromosomes under investigation.

Many of the configurations theoretically possible were not observed. The absence of univalents, 3-chromosome configurations, and certain types of 4-chromosome configurations indicates that chiasmata rarely failed in the structurally homozygous arms. Variable chiasma failure did occur in the distal and proximal segments of the heterozygous arms, however.

The "figures-of-eight" (Figures 3, 11, 12, 13) resembled a figure "8" only roughly. The induced reciprocal translocation was probably asymmetrical, and very likely this asymmetry was responsible for the appearance of the "figures-of-eight." They were not the kind of configuration expected if chiasmata in proximal segments were arrested at points of non-homology; neither could these configurations be interpreted as having completely terminalized 4-chromosome chiasmata. Because of this difficulty, arrested chiasmata are not distinguished from terminal multiple chiasmata in listing "figures-of-eight" in Table 2.

Five "frying-pan" configurations were seen with completely terminalized 3-chromosome chiasmata, but none of them could be so clearly photographed as the configuration first described (Figure 2). The multiple connections in 17 other "frying-pan" configurations were incompletely terminalized or were obscure. Two of the seven "Y-shaped" configurations had completely terminalized 3-chromosome chiasmata.

When two of the four chromosomes of the induced translocation association form a closed bivalent, a chiasma must have originated in the homologous proximal segments of chromosome arms whose distal segments are non-homologous. Complete terminalization in both arms of such a bivalent requires movement of

a chiasma past a point where homologies change. Two cells which provided critical evidence of this sort were observed. The first cell contained a 6-chromosome translocation chain (the naturally occurring translocation association) and four closed bivalents. In three of the closed bivalents the chiasmata in both arms were completely terminalized. The second cell contained a 5-chromosome chain (part of the naturally occurring association), three closed bivalents, one open bivalent, and a univalent. Terminalization was complete in both arms of all three closed bivalents. Thus, in each of these cells, there was at least one closed and completely terminalized bivalent composed of chromosomes that differed in the distal segments of one arm.

DISCUSSION

After terminalization had been demonstrated in several species, an explanation was sought for chiasmata in other species that appeared to be localized or failed to terminalize completely. DARLINGTON (1929) recognized that genic and environmental influences might control terminalization in some cases but suggested that incomplete terminalization might also result from the arrest of chiasmata at points where homologies change. Later, DARLINGTON (1931) supported his suggestion with observations of interstitial chiasmata at first metaphase in *Oenothera* translocation heterozygotes. Terminalization in *Oenothera* is usually complete, but concurrence of structural hybridity and persistent interstitial chiasmata should not have been regarded as conclusive supporting evidence for his hypothesis. Nevertheless, this case was cited later (DARLINGTON 1937, p. 511) as an "established" example of the arrest of terminalization by change of homology. Of the other "established" cases cited, only SANSOME's (1932) observations in *Pisum* provided any real support for DARLINGTON's hypothesis. When a 6-chromosome translocation association formed "figures-of-eight" in SANSOME's material, the interstitial chiasmata seemed to occur in a constant position at first metaphase. This suggested to SANSOME that terminalization had been stopped at a point where homologies changed.

The other "established" cases cited by DARLINGTON are much less conclusive. CATCHESIDE (1935) illustrated an interstitial chiasma in a "frying-pan" translocation association in X-rayed *Oenothera* but made no point of interpreting this configuration. CATCHESIDE's earlier study (1932) of haploid *Oenothera* and ERLANSON's (1931) study in *Rosa* were also cited as "established" cases; however, both of the authors accepted DARLINGTON's hypothesis as their basic tenet and interpreted their observation in the light thereof. It is interesting that in both cases completely terminal multiple chiasmata were described and illustrated in configurations which, it appears, should have been recognized as translocation associations. However, these configurations were not recognized as contradicting DARLINGTON's hypothesis. Instead, the validity of the hypothesis remained unquestioned, and the configurations were interpreted as evidence for segmental duplication.

DARK (1936) in a study of *Paeonia* and DARLINGTON and GAIRDNER (1937)

in a study of *Campanula* made similar interpretations. Translocation configurations were described in both materials; and when incompletely terminalized chiasmata were observed in these configurations, they were ascribed to the interruption of terminalization at non-homologous points. Completely terminalized 4-chromosome chiasmata were found in both studies; but in spite of the translocation configurations in the same materials, the 4-chromosome terminal chiasmata were regarded as evidence for duplicated terminal segments. DARLINGTON and GAIRDNER asked themselves why the four duplicated chromosome ends did not regularly pair, and answered that the parts assumed to be in common must have been very small. Such an interpretation requires that three chiasmata involving four chromosomes originate in a very small chromosome segment, an unlikely event.

Possibly non-homology arrests terminalization in certain cases. SANSOME's observations in *Pisum* seem to provide an example. However, the general validity of the idea that changes in homology stop terminalization must be rejected. One reaches this conclusion not only because of the contradicting evidence presented first by MARQUARDT and again in the present article, but also because of the inconclusiveness of the evidence on which the hypothesis was formed.

SUMMARY

Heterozygosity for an induced reciprocal translocation in a *Secale cereale* L. $\times$ *S. montanum* Guss. hybrid resulted in first-metaphase configurations which show that the point of translocation is so located that chiasmata form both proximal and distal to it. Several of the configurations exhibit terminal multiple chiasmata. Such configurations refute the hypothesis that terminalization of chiasmata is arrested at points where homologies change. Literature supporting the hypothesis is reviewed and found to be wanting in conclusive evidence.

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