The ratio of the two arms of the No. 2 chromosome found in the writer's cultures is 1.0:1.4 but McClintock has found certain strains of maize where the ratio is approximately 1.0:1.2.


---

**A SECONDARY TRISOME IN MAIZE**

BY MARCUS M. RHOADES

DEPARTMENT OF PLANT BREEDING, CORNELL UNIVERSITY

Communicated November 7, 1933

Three types of trisomes have been identified in Datura by the cytogenetic investigations of Blakeslee, Belling and others. The primary trisomes are those in which a member of the monoploid set is represented in triplicate rather than in duplicate as is the case for the remainder of the set. Primary trisomes have been isolated in Datura, Zea, Lycopersicum, Matthiola, Oenothera and other plants and in Drosophila melanogaster. The three homologous chromosomes in a primary trisome give characteristic configurations at pachytene, diakinesis and metaphase I. A closed ring of three at diakinesis should never be found in a primary trisome since the two ends in an open V or chain of three are not homologous.

A secondary trisome differs from a primary trisome in that the extra chromosome is not a replicate of one of the members of the monoploid set but has in some way become modified so that its two ends are homologous. The conclusion that the two ends are homologous was reached from a study of the configurations at diakinesis and metaphase I (Belling and Blakeslee) where a ring of three or a bivalent plus a closed univalent was commonly found. No adequate studies of the prophase synapsis have ever been made in secondary trisomes so Belling's conjecture that the extra chromosome is a double half chromosome has lacked convincing support. Secondary trisomes have been found previously only in Datura although Philp and Huskins may have a modified secondary in Matthiola.

A tertiary trisome is one in which the supernumerary chromosome is composed in part of one member of the monoploid set and in part of a different member of the monoploid set. Tertiaries have been found in...
Datura, Zea and possibly other forms. Tertiary trisomes give a range of configurations at diakinesis which is in accord with the theory that only homologous ends of chromosomes are attached. For a complete discussion of the types of configurations at diakinesis and metaphase I in primary, secondary and tertiary trisomes see Belling.3

This paper is concerned with the first secondary trisome which has been found in maize. Among the progeny from a selfed plant trisomic for chromosome 6 there occurred a variant which was strikingly different from its sibs. It resembled as a seedling some of the dwarf types of maize since it had an extremely stocky appearance with broad leaves which had blunt points. Somatic counts of root tips showed 21 chromosomes but the plant possessed only two satellited chromosomes so it probably was not trisomic for chromosome 6. Plants which are trisomic for chromosome 6 cannot be distiguished from disomic sibs. As the plants matured the differences between the variant and its sibs increased. At maturity the variant was of reduced stature, had thick leaves which were leathery in texture, and broad with extremely blunt points. The leaves were so stiff that they had no tendency to assume a pendant position near their tips. The tassel was not noticeably different from normal ones in appearance, although the presence of smut made this uncertain. This variant proved, when studied cytologically, to be a secondary trisome of chromosome 5.

Plants trisomic for chromosome 5 differ markedly from their disomic sibs in several ways. Their leaves are broader and have blunter tips than do the leaves of disomes. They tend to remain stiff and do not droop. The tassel of a trisome is more compact and sturdier in appearance. The stature of trisomes is less, giving them a stocky growth habit. They are several days later in flowering than their disomic sibs. Trisomic individuals as seedlings can usually be distinguished from disomes by the
broadness of the leaves and the bluntness of the tips, together with a somewhat reduced stature. The general difference in appearance and growth habit is so pronounced that an accurate classification of a segregating culture of mature plants into trisomic and disomic types can be made.

It is of interest to note that certain of the characteristics which distinguish the No. 5 primary trisomes were exaggerated in the secondary. This exaggeration of certain characters in the secondary is essentially

![Figure 3](image)

A camera lucida sketch at pachytene representing the synaptic relationships of two normal chromosomes 5 and the modified or secondary chromosome. The prominent knob in the long arm is in a heterozygous condition. This is one of the two types of pachytene association which were observed.

in agreement with the extensive work of Blakeslee on secondary trisomes in Datura. Knowing the characteristics of the primary and of one of the secondaries it should be possible to predict in advance the characteristics of the other secondary. Blakeslee accomplished this unique feat for one of the secondaries in Datura.

Chromosome 5 in Zea has an insertion region which is nearly median so that the two arms are nearly equal in length. The relative lengths of
the two arms from measurements at pachytene is 1.0:1.1. The longer arm carries in many strains of maize a large prominent knob. The morphology of chromosome 5 is shown diagrammatically in figure 1. One of the two chromosomes 5 present in the secondary trisome had the prominent knob in the long arm while the other did not. The morphology of the extra chromosome present in the secondary trisome is shown diagrammatically in figure 2. As the figure shows, the short arm of chromosome 5 is in duplicate and the insertion region is median.

Cytological studies of the secondary trisome were made at pachytene, diakinesis and metaphase I. The pachytene figures were the more illuminating since they made possible an exact determination of the morphology of the modified chromosome. At pachytene only two types of synaptic configurations were found, although other types may not have been detected. The first type is that represented in figures 3 and 3a. The insertion region of the modified chromosome occupies a terminal position with its two homologous arms synapsed for some distance. At a variable distance from the terminal insertion region the two arms of the modified chromosome cease their synaptic relationship with each other and pair, individually, with the short arms of the two normal chromosomes 5 to give a cross-shaped figure which resembles those found in heterozygous translocations in Zea. Twelve clear figures of this type of pachytene association were found but the position of the center of the cross varied considerably. In one figure the distance from the center of the cross to the terminal insertion of the modified chromosome was one-third of the length of the entire arm while in another figure the center of the cross was approximately three-fourths the length of the arm from the terminal insertion. The rest of the figures showed the center of the cross occurring between these two observed extremes. Burnham⁴ and McClintock⁶ have observed that in translocation figures the position of the center of the cross varies and interpreted it as the pairing of non-homologous parts. It is important to point out that in this secondary trisome
the varied positions of the center of the cross is not caused by non-homologous association as the two arms of the modified chromosome are homologous throughout their lengths with the short arms of the two chromosomes 5.

The other observed type of pachytene association was that in which the two normal chromosomes 5 had synapsed completely leaving the modified chromosome unpaired. In these figures, and they were seen more frequently than the first type since they were easier to find, the unpaired modified chromosome always had a terminal insertion with its two arms pairing evenly with one another to the distal end of the chromosome. Figure 4 represents the unpaired modified chromosome and the two synapsed normal chromosomes at pachytene. All of the cytological observations support the belief that the two arms of the modified chromosome were of equal length. Measurements of the first type of synaptic configuration at pachytene show that the distance from the terminal insertion region of the modified chromosome to the ends of its two arms is equal to the distance from the insertion regions of the normal chromosomes 5 to the end of their short arms. Likewise the measurements of the second class of configurations agree with the conclusion that the modified chromosome is composed of two entire short arms of chromosome 5 and has a median insertion region.
The types of configurations found at diakinesis are shown in table 1. The two commonest types were a ring of three, and a bivalent plus a closed univalent or circlet. Types 2 and 3 in table 1 undoubtedly arose from the pachytene configuration having a bivalent composed of the two normal chromosomes 5 with the modified chromosome unpaired. The remaining types in table 1 probably arose from the first type of pachytene association with the failure to form, or the breakage of, chiasmata giving the range of figures found at diakinesis.

**TABLE 1**

**DIFFERENT TYPES OF CONFIGURATIONS FOUND IN THE SECONDARY TRISOME AT DIAKINESIS. THE FREQUENCY WITH WHICH EACH OF THE DIFFERENT TYPES OCCURRED IS INDICATED BY THE NUMBER BELOW IT IN THE TABLE.**

<table>
<thead>
<tr>
<th>TYPE 1</th>
<th>TYPE 2</th>
<th>TYPE 3</th>
<th>TYPE 4</th>
<th>TYPE 5</th>
<th>TYPE 6</th>
<th>TYPE 7</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>27</td>
<td>20</td>
<td>5</td>
<td>7</td>
<td>1</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>

We will assume that a ring of three at diakinesis arises from a pachytene association of the first type in which at least three chiasmata are present. One of the chiasmata occurs in the long arms of the two chromosomes 5 and when it is terminalized will result in the ends of the two long arms being associated at diakinesis. A second chiasma occurs in that region between the center of the cross and the distal end of one normal chromosome 5 and one arm of the modified chromosome. The third chiasma occurs beyond the center of the cross between the short arm of the other normal chromosome 5 and the other arm of the modified chromosome. When these two chiasmata terminalize they will presumably result in the two arms of the modified chromosome being associated with the two short arms of the two normal chromosomes 5. The three chiasmata should then give a ring of three at diakinesis, and the observed frequency of rings was high. The pachytene figures clearly showed that the distance from the insertion regions to the center of the cross is, on the average, at least half the length of the short arm. There is no reason to suppose that the formation of chiasmata in the two regions from the center of the cross to the insertion of the modified chromosome or to the insertions of the two normal chromosomes is completely inhibited. The occurrence of chiasmata in the regions between the center of the cross and the distal ends of the short arms would, from analogy of genetic interference, tend to reduce the frequency with which chiasmata would be formed coinci-
dentally in the regions between the center of the cross and the insertions. The pairing at pachytene is of equal intimacy throughout the figure and the considerable distance from the insertions to the center of the cross would surely seem to permit the formation of chiasmata unless these regions in some way are restricted to few chiasmata. It is true that the genetic and cytological maps for the two autosomes in Drosophila melanogaster indicate that the amount of crossing-over per unit of physical length is low near the spindle fibre. We have some reason for believing that such a condition may hold for chromosome 2 in Zea but the evidence is not wholly convincing.** The genetic map of the long arm of chromosome 5 is at least 80 units long and the but-slightly shorter arm should have approximately the same length of genetic map so a large proportion of the figures should have two or more chiasmata in the short arm. The occurrence of a chiasma in either the region between the insertions of the two chromosomes 5 and the center of the cross or in the region between the center of the cross and the insertion of the modified chromosome coincidentally with the three chiasmata in the other three regions of the figure should give a figure eight (type 7 of table 1) at diakinesis. The most striking feature of the diakinesis configurations was the failure to find any figure eights. The number of observed figures in table 1 is small but many more cells were examined during the summer in an endeavor to find such a type of configuration. None was found, although it may be harder to detect and, therefore, overlooked. Unfortunately some of the temporary smears spoiled before counts could be made for the different types of figures present. The data in table 1 are, however, in the writer's opinion, a random sample and a fair representation of the types of figures found at diakinesis. The failure to find figure eights at diakinesis can be interpreted in two ways. Either no chiasmata are formed between the insertion regions and the center of the cross coincidentally with chiasmata in the other regions or else they are broken or cancelled at diplotene. It seems more probable that the rare, at best, occurrence of figure eights can be explained by the breaking or cancellation of chiasmata at diplotene. This conclusion would support Sax's theory of crossing-over and would be opposed to that of Darlington.

The only genetic factor in the fifth linkage group in maize whose location is with certainty known to be in the short arm of chromosome 5 is bm1 (McClintock8) and the position of this gene is close to the insertion region. But certain of the characteristics which distinguish the primary trisome of chromosome 5 must be assigned to genetic factors which are situated in the short arm of the chromosome.

* Paper No. 202 from the Department of Plant Breeding, Cornell University, Ithaca, New York.

** See preceding paper by the writer in this Journal.
THE COLOR CHANGES OF ELASMOBRANCH FISHES

BY G. H. PARKER

WOODS HOLE OCEANOGRAPHIC INSTITUTION

Communicated October 28, 1933

Very little work has been done on the color changes of elasmobranch fishes. In 1921 Schaefer reported in an appendix to an extended article on the color changes in flatfishes that the skates Raja clavata and Raja batis showed on being tested no such changes. A little over a decade later Lundstrom and Bard (1932) described striking color changes in the dogfish Mustelus canis and showed that in this fish the secretions from the pituitary gland were accountable for the dark phase of this fish. The light phase of Mustelus was studied in 1933 by Parker and Porter who in a paper now in press (1934) have demonstrated that this coloration is induced by the direct action of nerves. In the course of the work on dogfishes opportunity was found to test the possibility of color changes in the common skate Raja erinacea which was available in the laboratory at that time.

Two individuals, indistinguishably dark brown, were placed one in a white-walled sea-water tank illuminated from above and the other in a similar black-walled tank. After eighteen hours the skate in the white tank was light brown and that in the black tank was dark brown. The fishes were then transferred each to the other tank. After the light skate had been in the dark tank nine hours it became decidedly dark, but the dark skate after an equal interval in the light tank remained dark. Twelve hours later, however, this fish had become very light and of a hue that could be described as pinkish white. At this stage in the tests unfortunately the mate of this light fish died.

The light fish, now extremely pale in tint, was transferred to the black tank. In two hours it had darkened considerably and in twelve hours it was again dark brown. In consequence of the need of the tanks for other experimental work, tests on this skate had to be discontinued. Enough, however, had been observed on these two fishes to justify the conclusion that Raja erinacea, like Mustelus canis, is subject to reasonably striking color changes. From this standpoint it would seem desirable