METAPHASE I ORIENTATION OF CHAIN-FORMING INTERCHANGE QUADRIVALENTS: A THEORETICAL CONSIDERATION

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ABSTRACT

The orientation behavior of chain forming interchange quadrivalents at metaphase I was studied in three interchange heterozygotes of pearl millet [*Pennisetum americanum* (L.) Leeke] which involve chromosomes *1*, *3*, *6* and *7* in various combinations. Of these, two combinations predominantly produced rings and the third was a chain-forming type. The chain quadrivalents derived from the two ring-forming interchanges, as well as the chain quadrivalent generated by the third interchange, all showed one adjacent orientation at metaphase I (adjacent-1 or -2, depending upon the formation or failure of chiasmata and their positions in the different segments of the pachytene cross). Homologous centromere co-orientation leading to adjacent-1 and alternate-1 occurs following chiasma failure in the noncentric arms of the pachytene cross, and nonhomologous centromere co-orientation leading to adjacent-2 and alternate-2 occurs following chiasma failure in the centric arms of the pachytene cross. Thus, it has been proposed that, unlike in ring quadrivalents, a specific chain quadrivalent will have only homologous or nonhomologous centromere co-orientations at metaphase I.

DEPENDING on the position of break points and the location of chiasmata, reciprocal interchanges involving two chromosomes form associations of four, namely, the interchange quadrivalents, in heterozygotes. From the extensive sudies carried out on cytogenetic features of corn reciprocal interchanges it has been established unequivocally that ring quadrivalents exhibited adjacent-1 (homologous centromeres co-orient and pass to opposite poles leading to nondisjunction of translocated pieces), adjacent-2 (homologous centromeres pass to the same pole and nonhomologous centromeres co-orient leading to disjunction of translocated pieces) and alternate orientation at metaphase I (BURNHAM 1956). With 50% alternate disjunction (under random conditions of quadrivalent orientation) the heterozygote will be approximately 50% fertile because adjacent segregations lead to unbalanced (and hence lethal) gametes. From these it is logical to deduce that the centromeres of an interchange quadrivalent segregate in twos, *i.e.*, at anaphase I each pole receives two. Co-orientation in ring quadrivalents has been subjected to a considerable analysis

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in plants such as corn, rye and cotton. Based on a study of segregation of the nucleolar organizers in the spore quartets and the extent of pollen abortion, BURNHAM (1950) showed that in chain-forming interchange heterozygotes of corn adjacent-2 segregations did not occur.

During the course of a cytogenetic study of genotypic regulation of centromere co-orientation and fertility of two-chromosome and multiple-chromosome interchanges in pearl millet, we have observed differential metaphase I orientation behavior of chain quadrivalents. This behavior was analyzed in detail in order to examine the relationship between adjacent and alternate co-orientation types at metaphase I.

THE INTERCHANGES

Pearl millet has a somatic chromosome number of $2n = 14$. The haploid genome includes five, nearly metacentric, long and medium long chromosomes (nos. *1* to *5*), a nearly submetacentric medium-length chromosome (no. *6*) and a nearly submetacentric short (no. 7) chromosome that has the nucleolus organizer region situated in the short arm. During meiosis, the first six pairs form open ring bivalents with one terminal chiasma recognizable in each arm at diakinesis, whereas the seventh pair forms a rod bivalent with a single terminal chiasma in the long arm. Thus, the chiasma count per pollen mother cell (PMC) in a normal genotype is 13.

We isolated three spontaneously arisen interchanges. Interchanage *T(3-6)* occurred in the line IP 457, an inbred maintained by selfing for more than 15 generations. The inbred Vg 268 was obtained from the Millet Breeding Station at Vizianagaram (Andhra Pradesh) and also maintained by selfing. It was found when crossed with other inbreds to be a homozygote for an interchange involving chromosomes *1* and *3*, namely, *T(1-3)* (KODURU 1978). These two interchanges were intercrossed in order to study the behavior of the ensuing double heterozygotes that involved chromosomes *1*, *3* and *6*. In the selfed progeny of an F_1 plant from this cross, one of 60 plants (F_2 generation) was found to be heterozygous for a third interchange which involved the nucleolus organizer. The other 59 F_2 plants were either homozygous for the interchange or had the standard complement or were heterozygous (single or double) for the interchanged chromosomes. The interchange multiples in none of these plants, however, were associated with the nucleolus.

The relationship of the chromosomes involved in the new interchange with those of *T(1-3)* and *T(3-6)* was evaluated in appropriate crosses. These studies, reported elsewhere, showed that the new interchange involved chromosomes *1* (short arm) and 7 (long arm) (KODURU *et al.* 1984). The cytological behavior of *T(1-3)* and *T(3-6)* has been described by us (KODURU 1978, 1979; KODURU and KRISHNA RAO 1984). All interchanges were routinely maintained in the homozygous state by selfing. Morphologically, the different chromosomes involved in the three interchanges could be identified by differences in their size (chromosome *1*: approximately 52 μm long; chromosome *3*: approximately 40 μm long; chromosome *6*: approximately 26 μm long; chromosome 7: approximately 22 μm long). Furthermore, in the case of *T(1-3)* and *T(3-6)* the length

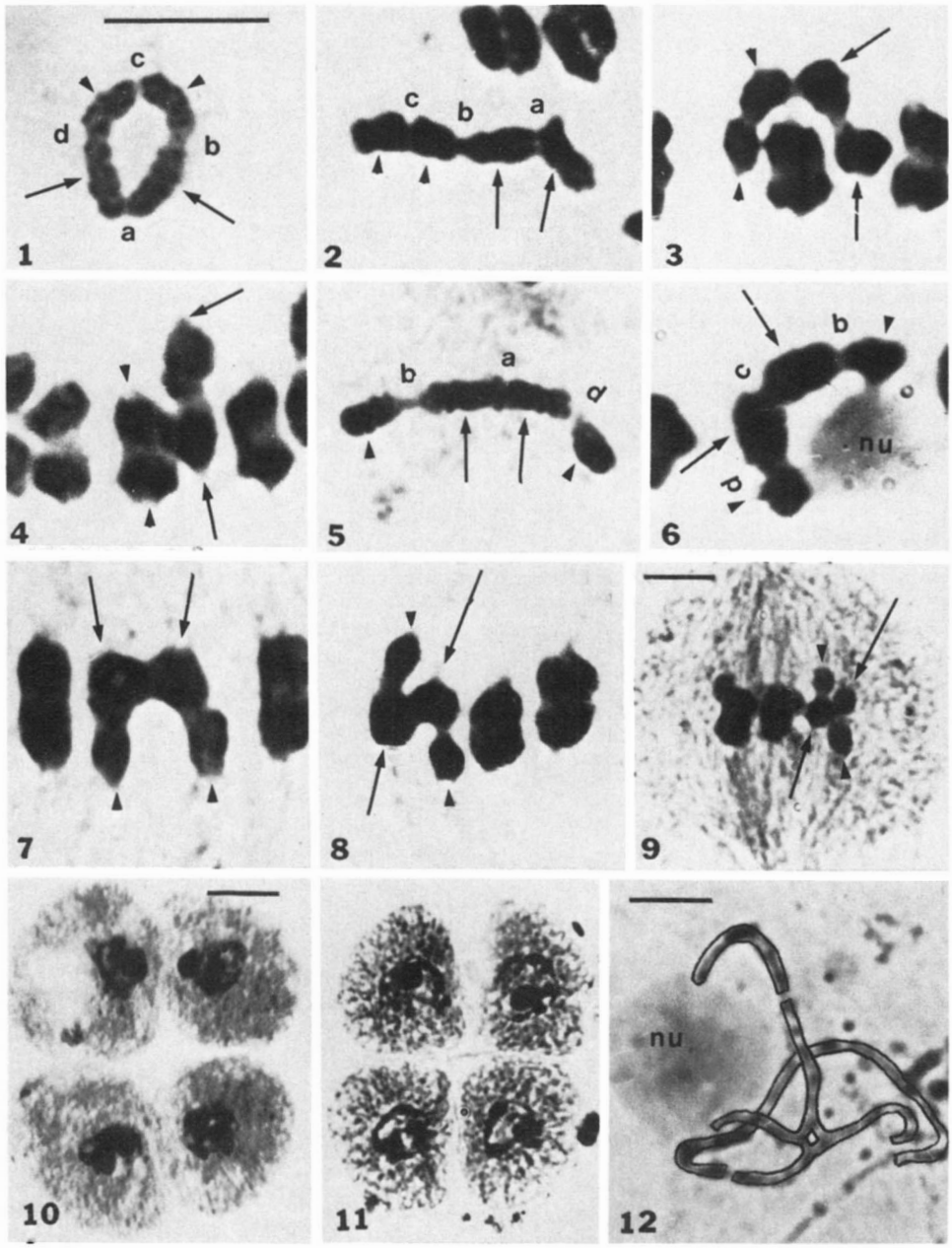
of the exchanged segments was almost equal (approximately 15 and 12 μm long, respectively); thus, the interchanges did preserve the original length differences between the nonhomologues. Although precise estimations were not made, the length of the exchanged segments of *T(1-7)* also appeared to be equal as the two nucleolar chromosomes in the quadrivalent did not differ much in size at diakinesis (Figure 6). From the three pachytene configurations of this interchange that we were able to analyze, it was tentatively concluded that the break point in chromosome 7 was in the long arm at a distance two-thirds of its length from the centromere and in chromosome *1* it was in the middle of the short arm (Figure 12). The interchanges *T(1-3)* and *T(3-6)* essentially formed rings (Figure 1), whereas *T(1-7)* essentially formed a chain (Figure 6, Table 1).

One common feature of these three interchanges was the confinement of chiasmata predominantly to the distal segments. Chiasma failure to an extent of about 5% was noticed in the case of *T(1-3)* and *T(3-6)*, which resulted in chain configurations (KODURU 1979). Depending on the location of chromosomes carrying the homologous centromeres (as determined by size of the chromosomes) these chains were grouped in two classes: (I) those in which adjacent end pairs of chromosomes carried homologous centromeres (Figure 2) and (II) those in which adjacent end pairs carried nonhomologous centromeres (Figure 5) (see LEWIS and JOHN 1963). In contrast to these two interchanges, *T(1-7)* formed one type, namely, type II in which adjacent end pairs carried nonhomologous centromeres (about 75% of PMCs). The remaining 25% of PMCs from *T(1-7)* had either ring types (about 10%), due to chiasma formation in the short arm or in the interstitial segment of the nucleolar bivalent, or other branched types (about 12%) or a trivalent and univalent (about 3%). The straight chain types were analyzed for their orientation at metaphase I.

ORIENTATION AT METAPHASE I

For convenience, the orientation of chain quadrivalents from *T(1-3)* and *T(3-6)* is considered in one group. Both of them formed the two chain types (I and II) due to chiasma failure in different segments of the pachytene cross (see KODURU 1979) in about 5% of PMCs. At metaphase I, 3378 PMCs were analyzed to accrue sufficient chain quadrivalents for subsequent classification into different orientation types (Table 2). The behavior of rings has been reported previously (KODURU 1979).

A total of 116 PMCs with type I chain configurations were analyzed for both interchanges. As shown in Table 2, they showed only two orientation types in which homologous centromeres co-oriented, either adjacent-1 (Figure 3) or alternate-1 (Figure 4) with about equal frequency. Likewise, for type II chains all of the 91 PMCs analyzed showed only nonhomologous co-orientations, namely, adjacent-2 and alternate-2. A more detailed analysis of chain orientation at metaphase I was possible with the *T(1-7)* interchange which formed type II chains (Figure 6). All of the 500 chains that were analyzed showed nonhomologous co-orientations (Figures 7 and 8).



FIGURES 1–5.—Chromosome pairing, chiasma formation and orientation behavior of chain interchange quadrivalents from *T(3-6)*. (1) Diakinesis: note the open ring is composed of two big and small chromosomes. Bar indicates 10 μm. (2) Type I chain at diakinesis with the adjacent homologous centromeres. (3) Adjacent-1 orientation with the co-orientation between adjacent homologous end pairs in type I chain at metaphase I. (4) Alternate-1 orientation with the co-orientation between adjacent homologous end pairs in type I chain at metaphase I. (5) Type II chain at diakinesis with the adjacent nonhomologous centromeres [for metaphase I orientation types refer to those of *T(1-7)*]. Figures 1–5 are all at the same magnification. The homologous

TABLE 1

Frequency of chain types at diakinesis in the three interchange heterozygotes of pearl millet

Genotype	PMCs scored	Chain types		% of PMCs with chains
		I[a]	II[b]	
T (3–6)	500	20	14	6.80
T (1–3)	500	16	12	5.60
T (1–7)	500	0	398	79.60

[a] Chain with adjacent end pairs carrying homologous centromeres.
[b] Chain with adjacent end pairs carrying nonhomologous centromeres.

TABLE 2

Metaphase I orientation types and frequencies of chain types in the three interchanges of pearl millet

Genotype	Chain type	PMCs[a] scored	Metaphase I orientation types				% Alternate	χ^2 (Adjacent/alternate)
			Adjacent-1	Alternate-1	Adjacent-2	Alternate-2		
T (3–6)	I	59	27	32	0	0	54.24	0.42
	II	42	0	0	24	18	42.86	0.86
T (1–3)	I	57	30	27	0	0	47.37	0.16
	II	49	0	0	22	27	55.10	0.51
T (1–7)	II	500	0	0	257	243	48.60	0.38

[a] From anthers with all PMCs at metaphase I; number of cells with chains alone is given.

Nucleolar composition of microspore quartets of *T(1-7)* was studied in 1756 quartets from four plants. Of these, 56% were of nondiffuse type, *i.e.*, all four spores had conspicuous nucleoli (Figure 10). In 44%, two microspores had conspicuously large nucleoli and the other two had either one small nucleolus or two small nucleoli (equivalent to two diffuse type, Figure 11); these would be expected to be derived from adjacent-2 segregation of chain quadrivalents. The frequency of adjacent-2 and alternate orientation of chain quadrivalents

centromeres are marked with similar arrows. The letters on quadrivalents indicate the position of chiasmata with reference to Figure 13.

FIGURES 6–12.—From the interchange *T(1-7)*. (6) Diakinesis showing type II chain with the adjacent nonhomologous centromeres. Note, the chain is associated with the nucleolus (nu). Bar indicates 10 μm. (7) Adjacent-2 orientation with the co-orientation between adjacent nonhomologous end pairs in type II chain at metaphase I. (8) Alternate-2 orientation with the co-orientation between adjacent nonhomologous end pairs in type II chain at metaphase I. (9) Metaphase I in an unflattened PMC of *T(1-7)* showing two-dimensional space arrangement of the components of chain quadrivalent to produce alternate orientation with co-orientation between adjacent nonhomologous centromeres. (10) Nondiffuse type microspore quartet. Bar indicate. 10 μm. (11) Two diffuse type microspore quartet; note the nucleoli in the upper pair of spores are bigger than those in the lower pair. (12) Interchange cross at pachytene showing break points in chromosomes *1* and *7* (*nu*, nucleolus). Bar indicates 10 μm. Figures 6–8, 10 and 11 are at the same magnification.

at metaphase I were 51 and 49%, respectively. The observed frequencies of chain orientation types and microspore quartet types differed significantly (contingency χ^2 4.06, $P < 0.06$). This predicts adjacent-1 segregation also in some PMCs. An examination of orientation types of quadrivalent configurations other than straight chains showed adjacent-1 orientation in 85% of rings and in almost all "Y"-shaped chains. Also, the linearly oriented (positioned perpendicularly to the equatorial axis of the spindle) straight chains contributed to adjacent-1 segregations and, hence, to the nondiffuse microspore quartets. Thus, the spore quartet data confirm the observed metaphase I orientation types of chain quadrivalent of *T(1-7)*. These results strongly suggest that for chain-forming two-chromosome interchange complexes two of the four expected metaphase I co-orientation types will be eliminated.

From the spore quartet analysis of corn interchanges involving the nucleolar chromosomes, BURNHAM (1950) determined that in rings with crossing over in the interstitial segment adjacent-2 frequency was low or none, whereas in chains little or no adjacent-2 segregations occurred. MCCLINTOCK (1934) also observed infrequent adjacent-2 segregations for *T(6-9a)* with a chain frequency of more than 50%. RICKARDS (1964, 1977) reported adjacent-1 orientation only for a chain interchange quadrivalent of *Allium triquetrum*. In a *T(4-5)* translocation of cotton, ENDRIZZI (1974) observed co-orientation of homologous centromeres situated on the end pairs of chromosomes (*i.e.*, adjacent-1) in chain quadrivalents. From the information presented on the orientation of chain and ring quadrivalents in the German cockroach it was seen that a specific chain type had only two of the four orientation types realized for ring configurations (Figure 2, a–h, COCHRAN 1977).

THEORETICAL CONSIDERATIONS

Apart from the genotypic control of segregational behavior of interchange complexes (THOMPSON 1956; LAWRENCE 1958; REES 1961; SAKAI *et al.* 1972; DENNHÖFER 1975; ROBINSON 1976; COCHRAN 1977; KODURU 1979; DIEZ ROSS and COCHRAN 1984), some authors traced the role of chiasmata in the induction of nondisjunction resulting from the rigidity of the ring complex in responding to the pulling forces of the spindle during the process of orientation (DARLINGTON 1937; ÖSTERGREN 1951). Under such conditions, a given interchange with a defined chiasma formation and terminalization should have a similar disjunction pattern irrespective of the genetic background in which it is situated, an unrealistic condition. Thus, it is logical to suggest that chiasmata have a role in the orientation pattern of the interchange complexes; however, chiasma formation cannot be regarded as the only cytological factor responsible for the generation of nondisjunctional types. Now, it is held that the presence of nondisjunctional types could have resulted from the behavior of "adjacent centromeres" (not necessarily homologous) "in pairs." The presence of a single chiasma in a bivalent ensures its regular orientation and disjunction, whereas its absence results in variable behavior of the univalents during meiosis.

If the same logic is extended to the orientation behavior of interchange complexes, it seems probable that the orientation behavior of a pair of cen-

tromeres in a complex hinges upon the way in which the two centromeres are linked by a chiasma, unrelated to homologies. This permits the components of complex configurations, such as interchanges, to have different orientation types according to the permissible combinations of two linked centromeres. Then in a quadrivalent ring complex, the four centromeres that are linked by adjoining chiasmata can act as four pairs of which two are homologous and two are nonhomologous combinations. These two principal pairs, when behaving independently should produce four co-orientation types: adjacent-1, alternate-1, adjacent-2 and alternate-2, in equal proportions. By means of distinct cytomorphological features these four co-orientation types of ring interchange quadrivalents were identified and their relative frequencies were documented in cotton (ENDRIZZI 1974), German cockroach (COCHRAN 1976, 1977, 1983), rye (LACADENA and CANDELA 1977; NARANJO and LACADENA 1979), pearl millet (KODURU 1979) and Pisum (LAMM 1981).

BOUSSY (1982) considered the theoretical aspects of two types of alternate orientations of ring complexes. He argued that the ring complexes, although having alternate orientation, will have three-dimensional space arrangement of four centromeres at metaphase I. Then, it is possible to change alternate-1 to alternate-2 and vice versa by rotating the axis of the meiocyte's spindle; hence, the distinction of alternate-1 and alternate-2 in ring complexes is actually a misconception resulting from the two-dimensional interpretation of three-dimensional figures.

Before the validity of these arguments of BOUSSY are accepted, two points should be considered: (1) The three-dimensional space arrangement of the four chromosomes of an alternately oriented ring quadrivalent cannot be a realistic one. As such it does not include the forces of the spindle fibers that pull the centromeres of the equatorially positioned quadrivalent to the opposite poles under great tension in a living cell. Under these dynamic forces, as in co-oriented bivalents, the two pairs of co-oriented centromeres of an alternate ring quadrivalent will align vertically and the arms connecting these two pairs take diagonal positions. Thus, in a living meiocyte an equatorially positioned 2:2 oriented alternate ring quadrivalent will be more a two-dimensional figure than a three-dimensional one. (2) At least in two organisms it was shown that the frequencies of disjunction types can be manipulated genotypically (COCHRAN 1977; KODURU 1979; DIEZ, ROSS and COCHRAN 1984). Here again, BOUSSY'S arguments fail to account for a precise shift in the frequency of four disjunction types through varied genetic background in the German cockroach (COCHRAN 1977; DIEZ, ROSS and COCHRAN 1984) or the changes in the frequency of adjacent-2 and alternate-2 in genotypes with directed segregation in pearl millet (KODURU 1979). This fact, namely, that the four co-orientation types exist in definite proportions and can be manipulated genetically, is evidence for the existence in nature of two alternate types.

Apart from these, a more direct cytological inference can be obtained by studying the orientation of interchange chain quadrivalents. These need not have three-dimensional space arrangement of the centromeres at metaphase I (Figure 9). Since the cytological distinction of the two types of orientations

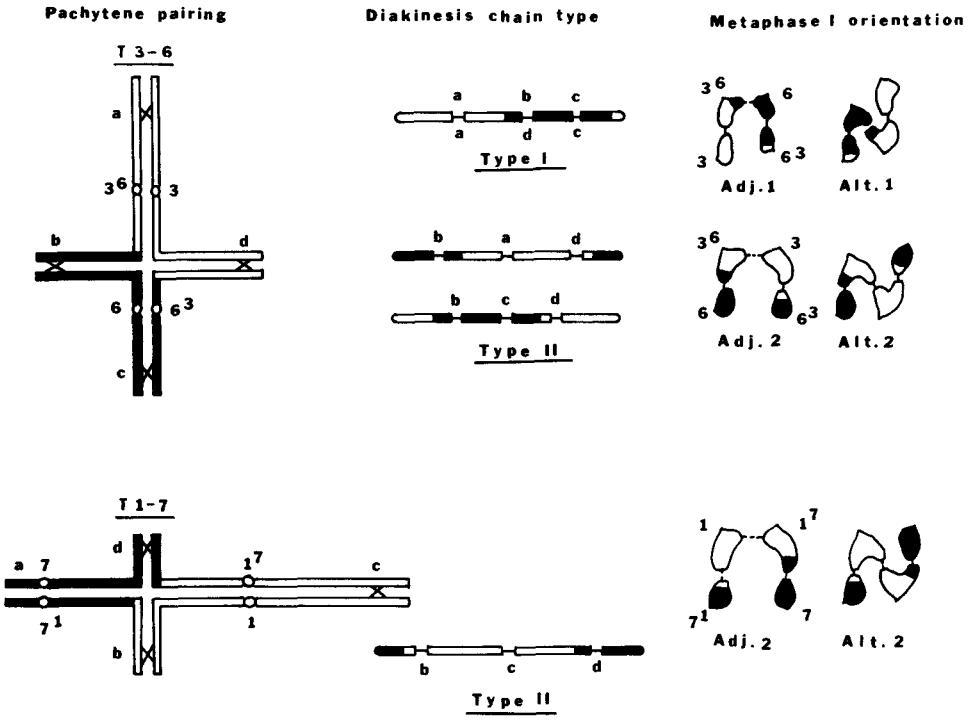


FIGURE 13.—Diagramatic pachytene configurations of the interchange *T(3-6)* and *T(1-7)*, the position of possible distal chiasmata, the derivation of different chain types from the pachytene pairing and their orientation behavior at metaphase I. In type I chain chiasma at b or d fails and in type II chain chiasma at c or a fails.

either in adjacent or in alternate configurations mainly rests on the co-orientation of homologous or nonhomologous centromeres, it is possible to classify the alternate configurations from chains into one of these two types provided that the chromosomes involved in the interchange could be precisely identified even at metaphase I.

The failure of chiasma formation in one of the four arms of a pachytene cross results in the formation of chain configurations. Such pachytene interchange cross configurations can have centromeres in two ways: (1) The axis of the arms carrying centromeres is perpendicular to the axis of the arms in which chiasma failure occurs [Figure 13, *T(3-6)*] and (2) the axis of the arms carrying centromeres is parallel to the axis of the arm in which chiasma failure occurs [Figure 13, *T(1-7)*]. The former configuration at diakinesis produces chains with adjacent chromosomes carrying homologous centromeres (type I, Figure 13), and the latter produces at diakinesis chains with adjacent chromosomes carrying nonhomologous centromeres [type II, Figure 13, *T(1–7)*]. For type I chains the four centromeres can be in three possible pairs of which two are homologous and one (the central) is nonhomologous, whereas for type II chains two of the three possible pairs are nonhomologous. As such, these chains, theoretically, should also show both homologous and nonhomologous

co-orientations in 2:1 and 1:2 proportions, respectively, for type I and type II chains.

Furthermore, when randomness for the four centromeres in the initiation of co-orientation of chain quadrivalents is considered, three classes of centromere orientation in relation to the poles can be visualized: (1) a 2:2 orientation in the two terminal pairs of chromosomes (adjacent-1 or adjacent-2 depending on the position of homologous centromeres) and an adjacent subclass with only the middle two chromosomes co-orienting (adjacent-1 or adjacent-2, again depending upon the location of homologous centromeres; see KODURU *et al.* 1984); (2) 3:1 orientation with co-orientation between the first and second and second and third centromeres or chromosomes only; (3) linear orientation of the four centromeres (or chromosomes) perpendicular to the equatorial axis of the spindle of the meiocyte. In view of the movement of the four centromeres of the interchange complex in twos to poles, only 2:2 types are considered stable either numerically or structurally, and the other two types are considered unstable and thus are argued to require undergoing reorientation before they pass through anaphase I (ROHLOFF 1970; RICKARDS 1977; KODURU 1984). Thus, the present arguments are limited to only 2:2 orientation types, whereas the reorientation phenomenon of 3:1 or other types is considered elsewhere (KODURU 1984).

The orientation pattern of such chains can be documented by direct cytological analysis if the identification of the position of the homologous centromeres on the spindle axis is possible by way of marked size differences between the chromosomes as was the case in the present study (Figures 1–9). When these predictions are compared with the observed data (Table 2) it is particularly interesting to note that each chain type had only one co-orientation, *i.e.*, either homologous (type I) or nonhomologous (type II). Nonhomologous co-orientations are eliminated for type II (Figure 13), in spite of the occurrence of one chiasma connecting the nonhomologous centromeres (central two) in the former case and homologous centromeres (again central two) in the latter. These findings suggest that in the chains there is 2:2 orientation with subclasses "homologous co-orientations" and "nonhomologous co-orientations" in equal numbers. In other words, there is consistent co-orientation between the adjacent pairs of centromeres at the end positions resulting in either adjacent or alternate configurations. Thus, it appears more reasonable that the failure of a connecting chiasma between the other nonhomologous centromeres at the end positions in the former case and homologous centromeres at the end positions in the latter case are the reasons for the elimination of one type of co-orientation.

The chain-forming corn interchanges were of two types: (1) those in which the break point in chromosome *6* was in the short arm (*T 5-6C, T 5-6 Inv5a, T 4-6 Li*) and (2) those in which the break was in the satellite (exclusively chain formers, *T 1-6b, T 3-6b, T 5-6*) or in the long arm (*T 1-6a, T 5-6a*) (see BURNHAM 1950). In type 1 translocations, chain formation was attributed to failure to remain associated in the short translocated arm of the pachytene cross, especially the one attached to the nucleolus (Figure 3, BURNHAM 1950). In type 2 translocations, chain formation was entirely due to the failure of

synapsis in the satellite arm of the pachytene cross or in the short translocated arm. In all of these translocations the frequency of adjacent-2 was reported to be nil or very low, if at all present. In type 1 crossing over in the interstitial segment will eliminate adjacent-2 segregations from ring quadrivalents. Considering the chains, in all of these translocations, chain formation was due to failure of chiasma formation in the translocated noncentric arm of the pachytene cross. This is contrary to the situation in *T(1-7)* of pearl millet, which also involves the nucleolar chromosome and in which chiasma failure was in the nontranslocated centric arm of the pachytene cross (Figure 13). Consequently, corn chains carry homologous centromeres on adjacent pairs of chromosomes at the end positions, *i.e.*, type I chains according to the present concept. When these end pairs carrying homologous centromeres co-orient, adjacent-1 segregations will occur and adjacent-2 will be eliminated. In *Vicia faba*, one chain former showed only 2% adjacent-1 orientation, whereas adjacent-2 was about 49%, and another chain former showed no adjacent-2 orientation (MICHAELIS and RIEGER 1959). SJODIN (1971) also noticed similar behavior with two translocations (*T 4-7i, T 1-3b*) of *V. faba*. From these data it appears that the general dogma that adjacent-2 segregations do not occur in chain-forming interchanges is applicable only to those cases in which the chain quadrivalents are of type I.

Another point to be considered is the frequency with which the homologous centromeres move to opposite poles. For type I chains 100% of meiocytes will receive the homologous centromeres at the opposite poles (as homologous co-orientations are the order for these chains), whereas only 50% of meiocytes show the segregation of homologous centromeres (contributed by only alternate orientations) in type II chains. Thus, the orientation and segregation behavior of chain-forming interchange complexes differ from the ring interchange complexes and is controlled by linking chiasmata relative to the centromere positions.

CONCLUSIONS

1. During co-orientation the centromeres of an interchange complex behave as adjacent pairs.
2. The orientation behavior of a pair of centromeres of an interchange complex is controlled by connecting chiasmata.
3. The homology of the centromeres is not a prerequisite for co-orientation.
4. Failure of chiasma formation in noncentric arm of the pachytene cross will lead to type I chains and homologous co-orientation; this is followed by adjacent-1 and alternate-1 disjunction.
5. Failure of chiasma formation in the centric arm of the pachytene cross will lead to type II chains and nonhomologous co-orientation; this is followed by adjacent-2 and alternate-2 disjunction.
6. Some amount of adjacent-2 segregation for type I chains and adjacent-2 segregation for type II chains may occur if the chain quadrivalent passes through anaphase I disjunction following linear orientation at the equator.

Thus, the co-orientation type to be eliminated is predetermined even at

pachytene by the way in which chiasma fails in relation to the pachytene axis carrying centromeres.

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LITERATURE CITED

BOUSSY, I. A., 1982 Alternate 2 disjunction does not exist. Genetics **100:** 505–509.

BURNHAM, C. R., 1950 Chromosome segregation in translocations involving chromosome *6* in maize. Genetics **35:** 446–481.

BURNHAM, C. R., 1956 Chromosomal interchanges in plants. Bot. Rev. **22:** 419–552.

COCHRAN, D. G., 1976 Disjunction types and their frequencies in two heterozygous reciprocal translocations of Blattella germanica (L.). Chromosoma (Berl.) **59:** 129–135.

COCHRAN, D. G., 1977 Patterns of disjunction frequencies in two heterozygous reciprocal translocations from the German cockroach. Chromosoma (Berl.) **62:** 191–198.

COCHRAN, D. G., 1983 Alternate-2 disjunction in the German cockroach. Genetics **104:** 215–217.

DARLINGTON, C. D., 1937 *Recent Advances in Cytology*, Ed. 2. J. & A. Churchill Ltd, London.

DENNHÖFER, L., 1975 Inherited preferential segregation in translocation heterozygotes of the mosquito, Culex pipiens. Theor. Appl. Genet. **45:** 250–253.

DIEZ, M., M. H. ROSS and D. G. COCHRAN, 1984 Genetically controlled differences in orientation in an interchange heterozygote of the German cockroach. J. Hered. **75:** 107–112.

ENDRIZZI, J. E., 1974 Alternate 1 and alternate 2 disjunction in heterozygous reciprocal translocations. Genetics **77:** 55–60.

KODURU, P. R. K., 1978 Cytogenetic studies on spontaneous mutant phenotypes of Pennisetum americanum (L.) Leeke. Ph.D. Thesis, Andhra University, Waltair, India.

KODURU, P. R. K., 1979 Metaphase I centromere co-orientation in interchange heterozygotes of pearl millet. Genet. Res. **34:** 69–76.

KODURU, P. R. K., 1984 Centromere orientation, reorientation and segregation in an interchange quadrivalent during anther development in pearl millet. Chromosoma (Berl.). In press.

KODURU, P. R. K. and M. KRISHNA RAO, 1984 Cytogenetics of a semi-dwarf phenotype in pearl millet, Pennisetum americanum (L.) Leeke. Can. J. Genet. Cytol. **26:** 272–278.

KODURU, P. R. K., M. KRISHNA RAO, K. V. LAKSHMI and J. SYBENGA, 1984 Anther development and the orientation of an interchange quadrivalent in pearl millet. Chromosoma (Berl.). In press.

LACADENA, J. R. and M. CANDELA, 1977 Centromere co-orientation at metaphase I in interchange heterozygotes of rye, Secale cereale L. Chromosoma (Berl.) **64:** 175–189.

LAMM, R., 1981 Giemsa C banding and silver staining for cytological studies in Pisum. Hereditas **94:** 45–52.

LAWRENCE, C. W., 1958 Genotypic control of chromosome behaviour in rye. IV. Selection for disjunction frequency. Heredity **12:** 127–131.

LEWIS, K. R. and B. JOHN, 1963 Spontaneous interchanges in Chorthippus brunneus. Chromosoma (Berl.) **14:** 618–637.

MCCLINTOCK, B., 1934 The relation of a particular chromosomal element to the development of nucleoli in Zea mays. Z. Zellforsch. Mikrosk. Anat. **21:** 294–328.

MICHAELIS, A. and R. RIEGER, 1959 Strukturheterozygotie bei Vicia faba. Zuchter **29:** 354–361.

NARANJO, T. and J. R. LACADENA, 1979 Analysis of centromere co-orientation in rye-wheat derivative by means of C-banding. Chromosoma (Berl.) **73:** 227–235.

ÖSTERGREN, G., 1951 The mechanism of co-orientation in bivalents and multivalents. The theory of orientation by pulling. Hereditas **37:** 85–156.

REES, H., 1961 The consequences of interchanges. Evolution **15:** 145–152.

RICKARDS, G. K., 1964 Some theoretical aspects of selective segregation in interchange complexes. Chromosoma (Berl.) **15:** 140–155.

RICKARDS, G. K., 1977 Prometaphase I and anaphase I in an interchange heterozygote of Allium triquetrum (Liliaceae). Chromosoma (Berl.) **64:** 1–23.

ROBINSON, A. S., 1976 Progress in the use of chromosomal translocations for the control of insect pests. Biol. Rev. **51:** 1–24.

ROHLOFF, H., 1970 Die Spermatocytenteilungen der Tipuliden. IV. Mitteilung. Analyse der Orientierung röntengenstrahleninduzierter Quadrivalente bei Pales ferruginea. Ph.D. Thesis, Eberhard-Karls Univsersität, Tübingen, West Germany.

SAKAI, R. K., R. H. BAKER, A. MILAN and S. SAID, 1972 Sterility enhancement in the mosquito, Culex tritaeniorhynchus. Can. J. Genet. Cytol. **14:** 215–220.

SJODIN, J., 1971 Induced translocations in Vicia faba L. Hereditas **68:** 1–34.

THOMPSON, J. B., 1956 Genotypic control of chromosome behaviour in rye. II. Disjunction at meiosis in interchange heterozygotes. Heredity **10:** 99–108.

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