THE MEIOTIC BEHAVIOR OF TANDEM ACROCENTRIC COMPOUND X CHROMOSOMES IN *DROSOPHILA MELANOGASTER*¹

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EXCHANGE in compound X chromosomes [the compounds have been described by NOVITSKI (1954)], with two exceptions, is similar in frequency and distribution to that in normal free X chromosomes. The two exceptions, the reversed acrocentric [symbolized $C(1)RA$] and the reversed ring [$C(1)RR$], behave differently from free X chromosomes in that they exhibit few or no single-exchange tetrads and equal frequencies of double- and no-exchange tetrads (SANDLER 1954, 1957). Although $C(1)RA$ without an extra arm yields this bimodal exchange distribution, the same compound with the long arm of the Y chromosome appended as an extra arm from the centromere [$C(1)RA \cdot Y^L$, centromere position designated by the period], yields a monomodal distribution similar to that in free X chromosomes (SANDLER 1958). A subsequent $C(1)RR$ obtained by SANDLER (1965) differs in meiotic behavior from his previous $C(1)RR$ (1957) and that of NOVITSKI (1954), for unknown reasons, in that it too has a normal exchange distribution. Thus, it appears likely that some insight into the control of exchange and crossing-over may be obtained from the study of the meiotic behavior of compound chromosomes in general, and specifically from the effect of extra arms, which are not themselves involved in exchange, on the exchange distribution. A detailed review is presented by SANDLER and LINDSEY (1967).

Previous analyses of tandem acrocentric compound X chromosomes [$C(1)TA$'s = two euchromatically complete X chromosome arms attached in tandem so that the pairing configuration is a spiral, with a single subterminal centromere] were consistent with the idea that the exchange distribution is similar to that in free X chromosomes whether or not a Y^L is appended to the centromere of the $C(1)TA$ chromosome as an extra arm (NOVITSKI 1954; SANDLER and LINDSEY 1963). These analyses were not conclusive, however, since (1) NOVITSKI's $C(1)TA \cdot Y^L$, $In(1)EN$ was analyzed before the importance of a free Y homologue on exchange was realized, and an unknown fraction of his $C(1)TA$ -bearing females did not carry a free Y homologue, and (2) SANDLER and LINDSEY's $C(1)TA$ (without Y^L) did not carry heterozygous markers. Therefore, neither the importance of

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Y^L for the exchange behavior nor the meiotic behavior of $C(1)TA$'s in general is fully established. This report is designed to answer both of these questions; it presents the results obtained with well-marked $C(1)TA$'s with and without an extra heterochromatic arm.

There are, in addition, two problems of current interest to which the behavior of $C(1)TA$'s is of consequence. One is the possibility of loss from the oocyte nucleus of the newly generated single-X products of exchange in tandem compounds. NOVITSKI and SANDLER (1956) originally described such loss of single-X products both for their tandem metacentrics [$C(1)TM$] and for NOVITSKI's $C(1)TA \cdot Y^L$, $In(1)EN$ when the compound-bearing mother did not carry a free Y homologue. SANDLER (1965) has subsequently demonstrated meiotic loss of ring chromosomes from heterozygous ring/rod females homozygous for $c3G$ (a third chromosome mutant which prevents meiotic exchange). This he feels might indicate some natural meiotic instability of ring chromosomes that causes them to be lost or lethal in the absence of exchange and, further, may be equivalent to the loss of newly generated *rings* at the second meiotic division in tandem compound-bearing females. However, loss of the single-X rods produced by exchange within $C(1)TA$ would not be consistent with this notion. There is no observed loss of newly generated single-X rods from SANDLER and LINDSLEY's $C(1)TA/Y$ females, although the crucial test [i.e. of $C(1)TA/0$ females] was not possible since their $C(1)TA$ was bb^- and required a free bb^+ homologue for survival.

The second problem involves the degree of nonrandom disjunction of asymmetric dyads at anaphase II (NOVITSKI 1951, 1967). In general, the shorter chromatid is preferentially recovered in the functional egg nucleus, and the degree of nonrandom disjunction (with the coefficient symbolized by c) is about 67% for free X dyads differing by the length of the proximal X heterochromatin. However, LINDSLEY and SANDLER (1965) and SANDLER and LINDSLEY (1967) estimate $c = 1.0$ (approximately) for $C(1)TM$ and tandem ring [$C(1)TR$] dyads which differ by a single X chromosome. Thus, does the degree of nonrandomness, as well as the fact of nonrandom disjunction, represent a meiotic process, other than length, which is not the same in compound X chromosomes and free X chromosomes? $C(1)TA$'s generate two types of asymmetric dyads: those composed of single- and double-length rods and those composed of single- and triple-length rods. There is no *a priori* reason to suspect that the degree of nonrandomness will be the same for the two kinds of dyads; therefore, an analysis of the data requires considering two different coefficients of nonrandomness, which are referred to as c_1 and c_2 for 1X-2X and 1X-3X dyads, respectively. Both the NOVITSKI (in SANDLER and LINDSLEY 1963) and the SANDLER and LINDSLEY (1963) $C(1)TA$ analyses estimated $c_2 = 1.0$; neither analysis was able to estimate c_1 , which is the parameter more directly comparable with the c 's for $C(1)TM$ and $C(1)TR$.

The results below indicate (1) that the exchange distribution is normal, both with and without an extra arm; (2) that there is no evidence of loss of newly generated single-X rods from females with or without a free homologue (thus,

the loss of newly generated rings is consistent with the notion of a natural meiotic instability of ring chromosomes); and (3) that nonrandom disjunction of 1X-2X asymmetric dyads is not affected by the addition of a heterochromatic second arm and the degree of nonrandomness (estimated at 0.79) is more characteristic of free X chromosomes than of the other types of tandem compounds.

ORIGIN AND CYTOLOGY OF $C(1)TA \cdot Y^L$ AND $C(1)TA \cdot sc^{v1}$

All the markers and chromosomes used are described in LINDSLEY and GRELL (1968). Females of the constitution $X \cdot Y^S$, $Ins(1)sc^{sL}EN^R \cdot Y^S/X \cdot Y^L$, $\gamma cv v f car \cdot Y^L$ (no $U-8e$) were mated to attached XY, $\gamma B/0$ males. Several γ , non- B , females were recovered spontaneously. One of these was unstable meiotically, yielding four segregation classes: 70 γB patroclinous males, 17 γ , non- B [one γf] females, 32 γ , heterozygous B females, and 31 γ males, many of which also carried some of the cv , v , f , and car markers. The breakdown products proved to be single-X rod chromosomes in normal sequence with Y^L at the centromere end, which is the expected breakdown product generated by exchange in a tandem acrocentric compound X chromosome with the components in normal sequence and with Y^L appended to the centromere as an extra arm (designated $C(1)TA \cdot Y^L$). This structure has been confirmed cytologically (see Figure 1). The proposed heterochromatic and euchromatic exchanges that could have given rise to $C(1)TA \cdot Y^L$ are shown in Figure 2; the arrangement of markers present in the rod-bearing male breakdown class indicates that f and car are in coupling on the proximal arm, and cv and v are in coupling on the distal arm of the recovered female.

The detachment of Y^L from $C(1)TA \cdot Y^L$ was effected by a recombination between the proximal arm of $C(1)TA \cdot Y^L$ and a duplication consisting of the X-centric piece of $T(1;4)B^S$ marked with car and with γ^+ from $In(1LR)sc^{v1}$ [= $Dp(1;f)16A1;20,B^S car \cdot \gamma^+$]. This is shown diagrammatically in Figure 3. The resulting $C(1)TA \cdot sc^{v1}$ now carries γ^+ instead of Y^L , and tests on single-X breakdown products from this compound confirm that they are rods in normal sequence with γ^+ at the centromere end and do not carry the fertility factors of Y^L . X0 sc^{v1} rod-bearing males are highly variegated for yellow, which is to be expected if little or no Y^L material remains. The removal of Y^L from this compound has also been confirmed cytologically (see Figure 1).

EXPERIMENTAL RESULTS

The key to classification of progeny types in succeeding crosses is given in Table 1. The results of crosses with $C(1)TA \cdot Y^L$ and $C(1)TA \cdot sc^{v1}$ with and without a free Y homologue are given in Tables 2, 3, and 4. The numbers in parentheses refer to the year (and order) in which crosses were performed. Tables 2 and 3 present the results of crosses of $C(1)TA$ -bearing females to $Y^S X \cdot Y^L$, $In(1)EN, \gamma B$ males with or without FR2 (= $\gamma^+ Y^L$), and Table 4 lists crosses of $C(1)TA \cdot Y^L$ -bearing females to $X \cdot Y^L$, $sc cv v f B car/Y''$ males ($Y'' = Y^S \cdot Y^S$) and of $C(1)TA \cdot sc^{v1}$ -bearing females to $X \cdot Y^L$, $\gamma cv v f B car/Y''$ males. The coupling relations of maternal markers are given in the table headings. The arrangement

FIGURE 2.—The proposed origin of $C(1)TA \cdot Y^L$. (For simplicity, only two of the four strands are shown.) Wide lines represent heterochromatin; narrow lines, euchromatin.

FIGURE 1.—Mitotic cytology of tandem acrocentric compound chromosomes. A-C, $C(1)TA \cdot Y^L$. D-F, $C(1)TA \cdot sc^{v1}$. (Arrows point out centromere positions.)

FIGURE 3.—The origin of $C(1)TA.sc^{v1}$ by exchange between $C(1)TA.Y^L$ and $Dp(1;f)16 A1;20,B^scar.y^+$.

TABLE 1

Key to progeny class numbers and classification of progeny for Tables 2, 3, and 4

Classification	Cross*				
	A	B	C	D	E
Regular patroclinous males	I	II	I	I	II
Exceptional patroclinous males	..	I	..	..	I
Regular, nonhomozygous matroclinous females	III	III	IV	IV	IV
Exceptional nonhomozygous matroclinous females	..	IV	..	..	..
Regular, homozygous matroclinous females	V	V	V	V	V
Regular, rod X-bearing females	VI	VI	VI	VII	VII
Exceptional, rod X-bearing females	..	VII	..	..	..
Rod X-bearing males, single crossover	VIII	VIII	VIII	VIII	VIII
Rod X-bearing males, triple crossover	IX	IX	IX	IX	IX

* $A = TA.Y^L/0('64)$, $TA.Y^L/0('67)$, $TA.sc^{v1}/0('67b)$ and $TA.sc^{v1}/Y''('67b)$;
 $B = TA.Y^L/FR2('64)$ and $('65)$; $C = TA.Y^L/0('65)$; $D = TA.sc^{v1}/0('67a)$;
 $E = TA.sc^{v1}/FR2('67a)$.

TABLE 2

Results of crosses with C(1)TA·Y^L, y cv v/y f car·YL/0 and C(1)TA·Y^L, y cv v/y f car·Y^L/FR2 ♀ ♀ to XY, y B/0 ♂ ♂

Progeny class	Phenotype	TA·Y ^L /0('64)	TA·Y ^L /FR2('64)
I	γ B ♂ ♂	1141	27
II	B ♂ ♂	..	1269
III	γ ♀ ♀	415	274
IV	+ ♀ ♀	..	4
	{ γ cv ♀ ♀	1	1
	{ γ cv v ♀ ♀	5	7
	{ γ v ♀ ♀	7	15
V	{ γ f ♀ ♀	7	2
	{ γ f car ♀ ♀	4	7
	{ γ car ♀ ♀	1	1
VI	γ B ♀ ♀	617	792
VII	B ♀ ♀	..	9
	{ γ f car ♂ ♂	96	117
	{ γ cv f car ♂ ♂	156	182
VIII	{ γ cv v f car ♂ ♂	220	179
	{ γ cv v car ♂ ♂	36	46
	{ γ cv c ♂ ♂	39	34
	{ γ ♂ ♂	1	2
IX	{ γ f ♂ ♂	1	0
	{ γ car ♂ ♂	0	1
	{ γ v f car ♂ ♂	0	1

of the four heterozygous markers in any C(1)TA-bearing female can be determined unequivocally by any three classes of single crossover rod-bearing sons. Five classes of single crossover rod-bearing sons, representing five genetic intervals, are recovered for each coupling relation; the number of triple crossovers recovered is negligible and does not affect the determination of the maternal genotype (thus, also, $E_0 + E_1 + E_2 = 100\%$ which is noted below).

Exchange and recombination are normal in both C(1)TA·Y^L and C(1)TA·sc^{V1} in that they do not involve preferential crossover regions. The proportions of recombinants distributed among the various classes of single-crossover rod-bearing sons, which do not differ noticeably from C(1)TA·Y^L to C(1)TA·sc^{V1} with or without a free Y homologue, are (average) γ-cv = 12%, cv-v = 33%, v-f = 42%, f-car = 8%, and car-centromere = 5%, in reasonable agreement with proportions based on standard map values. Likewise, the frequencies of homozygosis through double exchange, given in Table 5, are approximately equal for C(1)TA·Y^L and C(1)TA·sc^{V1}, although there is an increase when the mother carries a free Y (= fragment effect, SANDLER 1954). The difference in homozygosis with and without a free Y is consistently greater with C(1)TA·sc^{V1} than with C(1)TA·Y^L, which may suggest that the fragment effect depends in part on the presence of Y chromosome material in the genome. However, C(1)TM of LINDSLEY and SANDLER (1965), which does not carry known Y material, shows no fragment effect.

TABLE 3

Results of crosses with C(1)TA·Y^L, y/y cv v f car·Y^L/0 ♀♀ to X,Y y B/FR2 ♂♂ and C(1)TA·Y^L, y/y cv v f car·Y^L/FR2, C(1)TA·sc^{V1}, y/y cv v f car·y⁺/0 and C(1)TA·sc^{V1}, y/y cv v f car·y⁺ FR2 ♀♀ to XY, y B/0 ♂♂

Progeny class	Phenotype	TA·Y ^L /0('65)	TA·Y ^L /FR2('65)	TA·sc ^{V1} /0('67a)	TA·sc ^{V1} /FR2('67a)
I	γ B ♂♂	2481	56	1458	31
II	B ♂♂	..	4857	..	5686
III	γ ♀♀	..	1266	..	..
IV	+ ♀♀	313	6	627	1652
V	cv ♀♀	1	6	1	7
	cv v ♀♀	6	22	6	27
	cv v f ♀♀	0	6	2	9
	cv v f car ♀♀	0	2 *	0	3
	v ♀♀	12	36	1	32
	v f ♀♀	2	9	3	8
	v f car ♀♀	1	15	3	9
	f ♀♀	0	10	0	9
	f car ♀♀	3	11	0	9
	car ♀♀	0	3	0	0
VI	γ B ♀♀	1552	2858	..	..
VII	B ♀♀	..	22	806	3688
VIII	cv v f car ♂♂	263	284	59	421
	v f car ♂♂	539	811	253	1123
	f car ♂♂	629	1330 *	364	1439
	car ♂♂	93	276	69	261
	+ ♂♂	73	211	42	212
	cv v ♂♂	1	2	0	1
IX	cv v car ♂♂	0	5	0	1
	cv f car ♂♂	1	0 *	0	1
	cv car ♂♂	0	1	0	1
	v ♂♂	2	3	0	2
	v car ♂♂	0	3	0	1

* = γ body color.

It is apparent from the relative frequencies of the various classes summarized in Table 6 that *C(1)TA·Y^L* and *C(1)TA·sc^{V1}* behave alike. Exceptional classes are low in each cross and are therefore added into regular classes. It will first be noted that nullo-XY and XY-bearing sperm are recovered in equal frequencies from XY/0 males (see also LINDSLEY and SANDLER 1965; SANDLER and LINDSLEY 1967). Thus, the number of newly generated single-X rods recovered as females or males is nearly the same with XY/0 or XY/FR2 fathers. (Small differences between the sexes do not depend on whether or not the father carries a free Y homologue and, hence, the larger number is used to estimate rods.) Therefore, the best estimate of the number of X-bearing ova produced is the number of Y-bearing (or zero) ova recovered, which is the number of patroclinous males. Secondly, there does not appear to be any loss of the newly generated single-X rods as described by NOVITSKI and SANDLER (1956) for NOVITSKI's (1954)

TABLE 4

Results of crosses with C(1)TA·Y^L, y/y cv v f car·Y^L/0 ♀♀ to X·Y^L, sc cv v f B car/Y'' ♂♂ and C(1)TA·sc^{V1}, y/y cv v f car·y⁺/0 ♀♀ and C(1)TA·sc^{V1}, y/y cv v f car·y⁺/Y'' ♀♀ to X·Y^L, y cv v f B car/Y'' ♂♂

Progeny class	Phenotype	TA·Y ^L /0('67)		TA·sc ^{V1} /0('67b)		TA·sc ^{V1} /Y''('67b)	
I	γ or sc, cv v f B car ♂♂	5028		1053		6652	
III	γ or + ♀♀	1076		387		2065	
V	cv ♀♀	5		2		9	
	cv v ♀♀	14		3		43	
	cv v f ♀♀	5		2		12	
	cv v f car ♀♀	6		2		7	
	v ♀♀	41		7		36	
	v f ♀♀	8		2		14	
	v f car ♀♀	6		3		10	
	f ♀♀	10		0		7	
	f car ♀♀	3		0		11	
	car ♀♀	0		0		1	
	Single-X's	B ♀♀	γ ♂♂	B ♀♀	+ ♂♂	B ♀♀	+ ♂♂
	cv v f car	418	443	93	77	653	613
	v f car	994	1017	276	257	1449	1513
	f car	1346	1318	327	336	1819	1846
VIII	car	265	284	63	55	318	288
	+	165	145	43	44	237	247
	cv	1	1	0	0	1	2
	cv v	0	3	0	0	1	3
IX	cv v f	0	0	0	0	1	0
	cv v car	0	1	1	0	3	2
	cv f car	4	2	0	0	2	2
	cv car	1	2	0	0	3	0
	v	5	5	0	0	1	2
	v car	3	4	0	1	1	4

* γ body color.

TABLE 5

Comparison of percent homozygosis among matroclinous females of markers cv, v, f and car for C(1)TA·Y^L and C(1)TA·sc^{V1} with and without a free homologue

Cross	Percent homozygosis			
	cv	v	f	car
TA·Y ^L /0('64)	1.4	2.8	2.5	1.1
TA·Y ^L /FR2('64)	2.6	7.2	2.9	2.7
TA·Y ^L /0('65)	2.1	6.3	1.8	1.2
TA·Y ^L /FR2('65)	2.6	6.5	3.7	2.2
TA·sc ^{V1} /0('67a)	1.5	3.3	1.3	0.5
TA·sc ^{V1} /FR2('67a)	2.6	5.0	2.7	1.4

TABLE 6

Summary of $C(1)TA \cdot Y^L$ and $C(1)TA \cdot sc^{V1}$ data by major segregation classes
(Values in parentheses are fractions of patroclinous males)

Cross	Compound-bearing females*		Rods		Sum of X-bearing ova	Patroclinous males
	"Heterozygous"	Homozygous†	Female	Male		
$TA \cdot Y^L/FR2('64)$	403(0.311)	32(0.025)	792	562(0.611)	1227	1296
$TA \cdot Y^L/FR2('65)$	1781(0.363)	168(0.034)	2858	2926(0.594)	4875	4913
$TA \cdot sc^{V1}/FR2('67a)$	1652(0.289)	115(0.020)	3688	3463(0.645)	5455	5717
$TA \cdot sc^{V1}/Y''('67b)$	2065(0.310)	150(0.023)	4489	4522(0.680)	6737	6652
$TA \cdot Y^L/0('64)$	598(0.524)	18(0.016)	617	549(0.541)	1233	1141
$TA \cdot Y^L/0('65)$	438(0.177)	41(0.017)	1552	1601(0.645)	2080	2481
$TA \cdot Y^L/0('67)$	1506(0.300)	137(0.027)	3202	3224(0.641)	4867	5028
$TA \cdot sc^{V1}/0('67a)$	627(0.430)	22(0.015)	806	787(0.553)	1455	1458
$TA \cdot sc^{V1}/0('67b)$	387(0.368)	21(0.020)	803	770(0.731)	1178	1053

* $C(1)TA \cdot Y^L$ females increased by 1.4 as noted in text.

† Only homozygotes for cv and v in '64 crosses.

$C(1)TA \cdot Y^L$, $In(1)EN$ in the absence of a free Y homologue. In the crosses described here the number of rods produced (fraction of patroclinous males) is nearly the same for $C(1)TA/0$ mothers as for $C(1)TA/FR2$ mothers, and for both maternal genotypes, the number of rods recovered is always more than 50% of the number of patroclinous males recovered (indicating nonrandom disjunction of asymmetric dyads at anaphase II). $C(1)TA/FR2$ females produce on the average slightly more rods and proportionally fewer nonhomozygous matroclinous daughters than do $C(1)TA/0$ females; these slight changes may probably be due to exchange differences. Moreover, the number of exceptional patroclinous males, which in $C(1)TM$ and $C(1)TR$ are derived in part from nullo-X, nullo-Y eggs produced by the loss of newly generated single-X rings, is almost insignificant for $C(1)TA$'s and therefore is probably of nondisjunctional origin. The difference in behavior, in this respect, between $C(1)TA \cdot Y^L$ and $C(1)TA \cdot sc^{V1}$ of this report and Novitski's $(1)TA \cdot Y^L$, $In(1)EN$ is not understood.

$C(1)TA \cdot Y^L/Y$ females homozygous for $c3G$, which prevents almost all meiotic exchange, crossed to $XY/0$ males produced matroclinous females and patroclinous males in the ratio of 420:562 instead of the expected 1:1 ratio. Similarly, in crosses with a $C(1)RA \cdot Y^L$ line recovered as a spontaneous stabilization of $C(1)TA \cdot Y^L$ (unpublished), females homozygous for $c3G$ yielded matroclinous females and patroclinous males in the ratio of 1039:1462, whereas sisters heterozygous for $c3G$ yielded 1437 (with 138 v homozygotes) females and 2849 males. Thus, in two chromosomes which are structurally dissimilar but identical in terms of gene content, there is a deficiency of the same degree in the recovery of the attached-X $\cdot Y^L$ chromosome. No such deficiency of $C(1)TA \cdot sc^{V1}$ matroclinous females is noted (see below); therefore it is assumed that attached-X $\cdot Y^L$ females are somewhat less viable than patroclinous males in the same cross and their number needs to be revised upwards. For both $c3G$ crosses, summed recovery of the compound X chromosome is 71% of expected which is used to arrive at the

values given in Table 6 for each of the $C(1)TA \cdot Y^L$ matroclinous female classes.

Finally, it can be seen in Table 6 that, with one exception, the sum of X-bearing ova is close or equal to the number of patroclinous males. (The one exception, the cross $C(1)TA \cdot Y^L/0$ females to XY/FR2 males ('65) yielded a deficiency in the number of matroclinous females recovered; whereas, the number of rods recovered is normal. This is probably due to the matroclinous daughters receiving two doses of Y^L , which would make them even more inviable than usual, but would not affect the number of sons or daughters receiving single-X rods.) The equality in the observed and expected numbers of X-bearing ova confirms the conclusion reached above that all segregation classes, with the exception of $C(1)TA \cdot Y^L$ matroclinous females, are produced and recovered in the same relative frequencies and, therefore, that there is no loss of any single-X rods newly generated by exchange. It follows that in asymmetric dyads of single- and triple-length rods, the single-length rod is always found in the functional egg nucleus (i.e. $c_2 = 1.0$), since recovery of a triple-length rod in the functional egg nucleus would give rise to a lethal zygote, decreasing the number of observed X-bearing ova relative to patroclinous males. NOVITSKI and SANDLER (1956) and SANDLER and LINDSLEY (1963) also found $c_2 = 1.0$, at least when the mother carries a free Y homologue.

ANALYSIS OF EXCHANGE

The products of no, single, and double exchange in a tandem acrocentric compound X, as previously described by NOVITSKI (1954) and SANDLER and LINDSLEY (1963), are shown in Figure 4. Four different classes of double-X chromosomes may be derived by exchange within a $C(1)TA$; these are (1) homozygous for markers on the proximal arm (in this case cv, v, f , and/or car), (2) homozygous for markers on the distal arm (in this case = + alleles), (3) transposed $C(1)TA$ = markers transposed from the proximal arm to the distal arm and *vice versa*, and (4) matroclinous $C(1)TA$ = all markers heterozygous in coupling on the proximal arm. Classes (2), (3), and (4) are identical phenotypically and are collectively considered as "heterozygous" $C(1)TA$ -bearing females. Four phenotypically distinct classes are obtained following the various types of exchanges shown in Figure 4; their expected recovery frequencies together with the expected frequency of patroclinous males are given in Table 7, where E_i is the frequency of tetrads of rank i ($\sum_i E_i = 1$), and c_1 and c_2 are the coefficients of nonrandomness. Collecting terms for the expected frequencies of ova carrying each of the possible derivatives of a $C(1)TA$, plus patroclinous males (assuming $E_o + E_i + E_2 = 100\%$) yields

$$2 \times \text{homozygous } TA = 1/16 E_2 (3 - 2c_1)$$

$$2 \times \text{total matroclinous } TA = 2 \times \text{homozygous } TA + 2 \times \text{"heterozygous" } TA = \\ E_o + 1/2(1 - c_1)E_i + 1/4(2 - c_1)E_2$$

$$2 \times \text{rods} = 1/2(c_1 + c_2)E_i + 1/4(1 + c_1 + c_2)E_2$$

$$2 \times \text{patroclinous males} = E_o + E_i + E_2$$

Solving for the E_i 's and c_2 , these equations become

$$E_o = \text{pat. } \delta \delta - E_i - E_2$$

FIGURE 4.—The meiotic products of tandem acrocentric compound X chromosomes with no, single, and double exchange. The exchanges from which each product may be derived are indicated.

TABLE 7

Consequences of exchange and regular disjunction in TA/FR2 females. Crossovers involved are shown in Figure 4

Tetrad types		Products of meiosis and the probability that each will be included in the functional egg nucleus			
Rank and frequency	Crossover involved	Second meiotic division	First meiotic division	Second meiotic division	
E_0	None	Heterozygous TA (1/4)	Heterozygous TA (1/4)	FR2(1/4)	FR2(1/4)
$1/2 E_1$	A	Heterozygous TA $1/2(1-c_1)$	Single X $1/2(c_1)$	FR2(1/4)	FR2(1/4)
$1/2 E_1$	B	Triple X $1/2(1-c_2)$	Single X $1/2(c_2)$	FR2(1/4)	FR2(1/4)
$1/8 E_2$	A + C	Heterozygous TA (1/4)	Heterozygous TA (1/4)	FR2(1/4)	FR2(1/4)
$1/8 E_2$	A + D	Triple X $1/2(1-c_2)$	Single X $1/2(c_2)$	FR2(1/4)	FR2(1/4)
$1/8 E_2$	A + E	Homozygous TA $1/2(1-c_1)$	Single X $1/2(c_1)$	FR2(1/4)	FR2(1/4)
$1/8 E_2$	A + F	Single X (1/4)	Single X (1/4)	FR2(1/4)	FR2(1/4)
$1/8 E_2$	B + C	Homozygous TA $1/2(1-c_1)$	Single X $1/2(c_1)$	FR2(1/4)	FR2(1/4)
$1/8 E_2$	B + D	Homozygous TA (1/4)	Homozygous TA (1/4)	FR2(1/4)	FR2(1/4)
$1/8 E_2$	B + E	Single X (1/4)	Single X (1/4)	FR2(1/4)	FR2(1/4)
$1/8 E_2$	B + F	Triple X $1/2(1-c_2)$	Single X $1/2(c_2)$	FR2(1/4)	FR2(1/4)

$$E_1 = \frac{2(\text{pat. } \delta \delta - \text{mat. } \varphi \varphi) - (1 + 1/2c_1)E_2}{1 + c_1}$$

$$E_2 = 16 \text{ homozygous } \varphi \varphi / (3 - 2c_1)$$

$$c_2 = 1 - \left[\frac{(\text{pat. } \delta \delta - \text{mat. } \varphi \varphi - \text{rods})(1 + c_1)}{(\text{pat. } \delta \delta - \text{mat. } \varphi \varphi - 1/4E_2)} \right]$$

The coefficient c_1 may be independently estimated by the simultaneous measurement of transposed and homozygous $C(1)TA$'s. Thus

$$2 \times \text{transposed } TA = 1/16E_2$$

$$2 \times \text{homozygous } TA = 1/16E_2(3 - 2c_1)$$

and

$$c_1 = 3/2 - \text{homozygous } TA / \text{twice transposed } TA$$

Samples of the "heterozygous" matroclinous females from crosses given in Tables 3 and 4 and from several preliminary crosses not listed were progeny-tested to determine the coupling relations of the heterozygous markers. In effect, this is the fifth observation necessary for solution of the system of five equations (viz. E_0 , E_1 , E_2 , c_1 and c_2). These data are listed in Table 8 together with the number of homozygotes originally observed. For any cross the observed "heterozygous" females ($= X$) plus the observed homozygous females ($= H$) constitute the total number of matroclinous females; the sampled "heterozygous" females ($= X^*$) is a subset of observed "heterozygous" females, and observed transposed females ($= T^*$) is the number observed among the sampled "heterozygous" females. Assuming a true relation between the ratios of observed transposed females/sampled "heterozygous" females and observed homozygous females/observed "heterozygous" females [i.e. $T^*/X^* = k(H/X)$ for some constant k], then the estimate of $c_1 = 3/2 - \frac{H/X}{2T^*/X^*} = 3/2 - 1/(2k)$. Comparison of columns

TABLE 8

Results of progeny testing a sample from observed "heterozygous" matroclinous daughters for transposed genotypes (= markers in repulsion to centromere)

Cross	Observation No.	Observed "heterozygous" ♀ ♀ X	Observed homozygous ♀ ♀ H	Sampled "heterozygous" ♀ ♀ X^*	Observed transposes T^*	T^*/X^*	H/X
$TA \cdot sc^{V1}$ ('67b)	1	387	21	234	12	0.05128	0.05426
$TA \cdot Y^L$	2	284	29	137	13	0.09489	0.10211
$TA \cdot sc^{V1}$ ('67a)	3	627	22	74	2	0.02703	0.03509
$TA \cdot sc^{V1}$	4	192	7	151	4	0.02649	0.03646
$TA \cdot sc^{V1}$	5	87	1	29	1	0.03448	0.01149
$TA \cdot sc^{V1}$	6	105	5	65	2	0.03077	0.04762
$TA \cdot Y^L$	7	140	20	57	5	0.08772	0.14286
$TA \cdot Y^L$ ('65)	8	313	29	107	8	0.07477	0.09265
$TA \cdot sc^{V1}$ ('67b)	9	2065	150	332	14	0.04217	0.07264
$TA \cdot sc^{V1}$ ('67a)	10	1652	115	153	5	0.03268	0.06961
$TA \cdot Y^L$ ('65)	11	1272	120	155	9	0.05806	0.09434

* See text for explanation.

T^*/X^* and H/X in Table 8 shows a definite correlation between the size of the ratios for each cross but that, with one exception of a cross with small numbers, the ratio T^*/X^* is less than the ratio H/X . Values for $C(1)TA \cdot Y^u$ and $C(1)TA \cdot sc^{v1}$ are alike and, hence, c_1 is assumed to be the same for these two compounds. NOVITSKI and SANDLER (1956) also have concluded that the addition of a heterochromatic second arm to both chromatids of an asymmetric X dyad does not alter its degree of nonrandomness. It will be noted from the above equations that $c_1 = 1$ when $T^*/X^* = H/X$ (i.e. when transposed and homozygous $C(1)TA$'s are produced in equal frequency) and that $c_1 = 0.50$ when $2(T^*/X^*) = H/X$ (i.e. when twice as many homozygous $C(1)TA$'s are produced as transposed $C(1)TA$'s). The observed relations in Table 8 are for the most part intermediate (T^*/X^* less than H/X but more than half H/X) and, therefore, the coefficient c_1 is intermediate between 0.50 and 1.0.

It is necessary to consider whether the presence of a free Y homologue changes the value of c_1 from the value without a free Y homologue. The first eight observations in Table 8 are from crosses of females without a free Y homologue, and the last three observations are from crosses of females with a free Y homologue, and in every case the ratio of T^*/X^* to H/X is greater for $C(1)TA/0$ females than for $C(1)TA/Y$ females, suggesting a higher value of c_1 for $C(1)TA/0$ females. However, these observations are not sufficient to demonstrate a significant difference between the least-squares estimates of the relations for $C(1)TA/0$ and $C(1)TA/Y$ females, and therefore, we tentatively assume the model $T^*/X^* = k(H/X)$ with $k = 0.70138$ (least-squares estimate) for all 11 observations. From this estimate $c_1 = 0.79$ for $C(1)TA$ females with or without a free Y homologue. For the least-squares estimate of k , the 95% confidence interval is approximately 0.58 to 0.83, from which the value of c_1 would be significantly different from 1.0, but not from 0.66, for $C(1)TA$ females with or without a free Y homologue. Thus, TA compound X chromosomes differ at least from $C(1)TM$ and $C(1)TR$ but may be similar to free X chromosomes in terms of nonrandomness.

It should be pointed out that 1X-2X asymmetric dyads are not completely comparable between the TM , TR , and TA compound X chromosomes. In the case of $C(1)TM$ and $C(1)TR$, asymmetric dyads consist of a single-X ring (= one arm) and its sister chromatid with two arms; whereas in the case of $C(1)TA$ and in free X chromosomes, asymmetric dyads consist either of short and long one-armed sister chromatids or of short and long two-armed sister chromatids. Thus, the greater degree of nonrandomness in the TM and TR compound X chromosomes may reflect extra "dragging" due to the second unequal arm (see NOVITSKI, 1967). It is not possible to determine from the observations in Table 8 whether the degree of nonrandomness is exactly the same in $C(1)TA$ and in free X chromosomes, or if the degree of nonrandomness increases somewhat with increasing asymmetry in relative length. That nonrandom disjunction from 1X-3X dyads approaches unity does suggest the latter. Either case, however, is consistent with a mechanical notion of nonrandomness, and does not require a specific genetic control of this aspect of chromosome behavior.

TABLE 9

Solutions in E_1 and c_2 (as fractions) for the equations in text with data summarized in Table 6, using $c_1 = 0.79$; map distance computed as $(1/2 E_1 + E_2)$

Cross	E_0	E_1	E_2	c_2	Map distance
$TA \cdot Y^L/FR2('64)$	0.20	0.52	0.28	0.84	0.54
$TA \cdot Y^L/FR2('65)$	0.24	0.37	0.39	0.97	0.58
$TA \cdot sc^{V1}/FR2('67a)$	0.18	0.59	0.23	0.87	0.53
$TA \cdot sc^{V1}/Y''('67b)$	0.20	0.55	0.25	1.04	0.53
$TA \cdot Y^L/0('64)$	0.45	0.37	0.18	1.35	0.37
$TA \cdot Y^L/0('65)$	0.06	0.75*	0.19	0.62	0.57*
$TA \cdot Y^L/0('67)$	0.18	0.51	0.31	0.90	0.57
$TA \cdot sc^{V1}/0('67a)$	0.34	0.49	0.17	0.99	0.42
$TA \cdot sc^{V1}/0('67b)$	0.27	0.51	0.22	1.38	0.48

* Values for E_1 and map distance probably too large, as noted in text.

With $c_1 = 0.79$, solutions for the equations in E_i (divided by the numbers of patroclinous males to arrive at frequencies) and c_2 above when applied to each cross of Table 6 are given in Table 9 along with map values. These estimates agree with the conclusions developed above that the rank and frequency distribution of exchange are similar to those of free X chromosomes and that $c_2 = 1$ for both compounds. [For $C(1)TA \cdot Y^L/0('65)$, the value of c_2 is low and that of E_1 high because of the decrease in matroclinous females, as noted above.] Moreover, the map values for $C(1)TA/FR2$ females are slightly higher than map values for $C(1)TA/0$ females, which is consistent with the observations of more products of exchange (rods and homozygous $C(1)TA$'s) among the progeny of $C(1)TA/FR2$ females.

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SUMMARY

Well-marked tandem acrocentric compound X chromosomes with and without an extra heterochromatic arm (Y^L) were synthesized, and their behavior in crosses was investigated. With one exception, the results for both $C(1)TA$'s agree with those of previously studied $C(1)TA$'s. The exception is that there is no loss of newly generated single-X rods from mothers without a free Y homologue, as observed by NOVITSKI and SANDLER (1956). Although this difference in behavior is not understood, it is concluded that loss of newly generated, single-X rings from tandem-metacentric and tandem-ring compound X chromosomes may reflect a natural meiotic instability of rings, as proposed by SANDLER (1965).—The exchange distribution in both tandem acrocentrics with and without an extra heterochromatic arm, unlike reversed acrocentric compound X chromosomes without an extra arm, is comparable with that of free X chromosomes.—The coefficient of nonrandom disjunction from 1X–2X asymmetric dyads (estimated

at 0.79) is more characteristic of nonrandomness in free X chromosomes than of the other tandem compounds where it approaches unity. It is suggested that the degree of nonrandomness for the other tandem compounds reflects the asymmetry of a second euchromatic arm as well as the asymmetry in distal length.

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