

# PREFERENTIAL SEGREGATION IN TRIPLO-IV FEMALES OF *DROSOPHILA MELANOGASTER*

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## INTRODUCTION

THE occurrence of non-random segregation in triplo-IV females of *Drosophila melanogaster* was reported in a preliminary note (STURTEVANT 1934) of which this is the full account. As there shown, and elaborated below, all the tested fourth chromosomes may be arranged in a series, of such a nature that each chromosome will (in a triplo-IV female) pass to the haplo-IV pole at meiosis more often than will any chromosome that lies above it in the seriation. Expressed in another way, if two chromosomes (A and B) are tested against any third chromosome (C), then C will "prefer" that one of the other two that lies higher in the series.

These relations are first described in the case where one of the IV chromosomes concerned carries genes from the X chromosome. The data on other triplo-IV females are then presented. An algebraic analysis that leads to quantitative predictions is then developed.

It should be remembered throughout that the relations discussed are between whole chromosomes, not individual loci—a circumstance made experimentally feasible by the fact that crossing over in this chromosome is negligible in frequency. The chromosomes concerned are designated by the names of the mutant genes they carry, but these genes are to be regarded only as convenient markers, making it possible to follow the behavior of the chromosomes concerned.

## DUPLICATION EXPERIMENTS

Males from the stock of *scute-10* (= *achaete-2*) were X-rayed and mated to yellow *scute-D1* females. There resulted numerous wild type daughters, and two that showed some of the characteristics of *scute*. These proved to have two separate modifications of the *scute* locus added to the *achaete* of the rayed males; they are designated *scute-10-1* and *scute-10-2*. The latter (*scute-10-2*) was found to be associated with a reciprocal translocation between the X and IV chromosomes. The break in X lies between the loci of *silver* and *broad* (to the right of the so-called "viability gene" of PATTERSON); that in IV lies between the known loci and the spindle attachment. Dr. J. SCHULTZ has examined the salivary glands of this

translocation, and informs me that it is more complex than this, there being a second break in IV beyond the loci of the known genes (the piece of X being intercalated between the two ends of IV). The two new chromosomes (X with left end replaced by IV, left end of X on spindle-attachment of IV) may be obtained separately; the present study is based on flies carrying the shorter of the two as a duplication: that is, diploids plus left end of X on an extra IV spindle attachment. The "normal" X's of such hyperploids carried yellow in the experimental cultures, so that wild type body-color served as an index of the presence of the duplicating fragment.

When such flies (females) were made heterozygous for the "normal" IV chromosomes it was found (STURTEVANT 1934) that the duplication did not segregate at random with respect to these IVs. The two IVs themselves pass to opposite poles in 95 percent or more of the eggs (see below); but the duplication regularly shows a *preference* for one of them. To use the same example as previously cited, in the case of females of the constitution  $\frac{y}{y}$  dupl  $\frac{ey^D}{gvl}$  crossed with  $y$  (not  $ey^D$ ) ♂, there resulted 673 +<sup>u</sup>  $ey^D$ , 372 +<sup>v</sup> +<sup>ev</sup>, 354  $y ey^D$ , 806  $y$  +<sup>ev</sup>; that is, the duplication passed

TABLE I

Percentage of cases in which the scute-10-2 duplication went to the same pole as the IV chromosome entered in each column heading, when that chromosome was tested against the ones indicated in the first column. The values entered as probable errors are the probable deviations from 50.0 percent—i.e.,  $67.45\sqrt{1/n}$ . The significance of the various symbols, where these are not standard designations for mutant genes, are indicated in the text and in the heading of table 2.

OPPOSED CHROMOSOME	PREFERRED CHROMOSOME								
	+ <sup>ci</sup> $ey^R$	<i>sv</i>	<i>ci</i> $ey^R$	$ey^D$	<i>ci</i>	X <i>ci</i>	<i>stn</i> <sup>a</sup>	<i>bt</i>	$ci^D$
+ <sup>ci</sup> $ey^R$	50.0		48.5 ± 1.8		48.5 ± 1.4			41.4 ± 1.8	
<i>sv</i>		50.0	47.2 ± 1.3	47.8 ± 1.6	52.2 ± 2.5				43.9 ± 2.4
<i>ci</i> $ey^R$	51.5 ± 1.8	52.8 ± 1.3	50.0	49.1 ± 1.8	51.1 ± 1.0	47.4 ± 1.2	43.2 ± 0.7	40.4 ± 2.0	
$ey^D$		52.2 ± 1.6	50.9 ± 1.8	50.0			45.0 ± 1.2	39.2 ± 1.6	39.5 ± 1.5
<i>ci</i>	51.5 ± 1.4	47.8 ± 2.5	48.9 ± 1.0		50.0		46.9 ± 1.0		
X <i>ci</i>			52.6 ± 1.2			50.0	48.2 ± 1.3		
+ <sup>u</sup> , <i>y sc w</i> <sup>a</sup>			58.7 ± 1.4	49.2 ± 1.9			47.5 ± 1.1		34.7 ± 1.9
<i>sv</i> <sup>na</sup>			56.8 ± 0.7	55.0 ± 1.2	53.1 ± 1.0	51.8 ± 1.3	50.0		43.0 ± 1.4
+ <sup>u</sup> , San G.			51.9 ± 1.3	61.1 ± 1.8			52.7 ± 2.2		46.3 ± 2.1
+ <sup>u</sup> , Bham			60.6 ± 1.6	52.6 ± 1.5			57.6 ± 1.7		51.3 ± 1.3
<i>bt</i>	58.6 ± 1.8		59.6 ± 2.0	60.8 ± 1.6				50.0	44.0 ± 1.2
$ci^D$		56.1 ± 2.4		60.5 ± 1.5			57.0 ± 1.4	56.0 ± 1.2	50.0
+ <sup>u</sup> , Tonto			63.0 ± 1.7	59.0 ± 1.7	53.9 ± 2.0				
<i>bt</i> <sup>D</sup>			58.7 ± 1.3	61.7 ± 2.1			56.6 ± 1.7		50.4 ± 1.8
+ <sup>u</sup> , Réd. M.			68.0 ± 3.1	60.4 ± 1.6			50.6 ± 1.9		51.5 ± 2.6
+ <sup>u</sup> , Arr. S.			61.6 ± 2.9	59.0 ± 2.0			63.1 ± 1.4		50.3 ± 1.9
+ <sup>u</sup> , Fla.			62.1 ± 1.9	58.4 ± 1.8					
<i>ey</i>		62.4 ± 2.7	59.2 ± 1.2				56.7 ± 1.3	43.7 ± 2.5	60.4 ± 2.7
+ <sup>u</sup> , Seattle			61.4 ± 1.8	62.9 ± 1.7			54.9 ± 1.3		
+ <sup>u</sup> , Sch. X			64.3 ± 1.3	61.9 ± 1.8					
<i>gvl ey</i> <sup>R</sup>			63.8 ± 1.6	65.2 ± 1.4		62.5 ± 1.4	56.0 ± 1.7	55.0 ± 1.4	56.5 ± 1.7
<i>ar</i>	69.1 ± 1.5		70.0 ± 1.3	62.6 ± 2.2			58.0 ± 1.9		59.2 ± 1.8
<i>gvl</i>		65.2 ± 1.7	67.8 ± 0.9	67.0 ± 0.7	60.7 ± 2.6		57.8 ± 1.2	57.0 ± 1.3	55.3 ± 1.4
$ey^A$		66.4 ± 1.9	66.4 ± 2.2	64.0 ± 2.9			61.3 ± 3.5	57.2 ± 1.7	
<i>M</i> <sup>A</sup>							69.4 ± 1.5	60.6 ± 2.7	
$ey^2$			64.5 ± 1.6	65.8 ± 2.4	65.8 ± 1.7		64.9 ± 1.5	65.8 ± 1.8	62.2 ± 2.5

TABLE 1 (Continued)

OPPOSED CHROMOSOME	PREFERRED CHROMOSOME								
	<i>bt<sup>D</sup></i>	<i>ey</i>	+, Sch. X	<i>gvl ey<sup>R</sup></i>	<i>ar</i>	<i>gvl</i>	<i>ey<sup>A</sup></i>	<i>M<sup>A</sup></i>	<i>ey<sup>2</sup></i>
<i>+ci ey<sup>R</sup></i>				30.9 ± 1.5					
<i>sv</i>		37.6 ± 2.7				34.8 ± 1.7	33.6 ± 1.9		
<i>ci ey<sup>R</sup></i>	41.3 ± 1.3	40.8 ± 1.2	35.7 ± 1.3	36.2 ± 1.6	30.0 ± 1.3	32.2 ± 0.9	33.6 ± 2.2		35.5 ± 1.6
<i>ey<sup>D</sup></i>	38.3 ± 2.1		38.1 ± 1.8	34.8 ± 1.4	37.4 ± 2.2	33.0 ± 0.7	36.0 ± 2.9		34.2 ± 2.4
<i>ci</i>						39.3 ± 2.6			34.2 ± 1.7
X <i>ci</i>				37.5 ± 1.4					
+, <i>y sc w<sup>A</sup></i>				43.6 ± 1.8		45.0 ± 1.2			
<i>sv<sup>na</sup></i>	43.4 ± 1.7	43.3 ± 1.3		44.0 ± 1.7	42.0 ± 1.9	42.2 ± 1.2	38.7 ± 3.5	30.6 ± 1.5	35.1 ± 1.5
+, San G.		45.0 ± 1.1		42.3 ± 1.4		42.7 ± 1.5			31.4 ± 2.7
+, Bham		44.0 ± 2.5		43.7 ± 1.4		42.7 ± 1.3			39.8 ± 2.1
<i>bt</i>		56.3 ± 2.5		45.0 ± 1.4		43.0 ± 1.3	42.8 ± 1.7	39.4 ± 2.7	34.2 ± 1.8
<i>ci<sup>D</sup></i>	49.6 ± 1.8	39.6 ± 2.7		43.5 ± 1.7	40.8 ± 1.8	44.7 ± 1.4			37.8 ± 2.5
+, Toronto		49.4 ± 2.1		47.2 ± 1.7		42.7 ± 1.5			
<i>bt<sup>D</sup></i>	50.0	52.1 ± 1.7		43.2 ± 1.5		39.0 ± 2.1			
+, Red. M.		48.9 ± 2.3		47.8 ± 1.9		40.7 ± 1.4			
+, Arr. S.		50.1 ± 1.6		44.7 ± 1.7		47.6 ± 2.2			35.1 ± 1.9
+, Fla.				42.9 ± 1.3		50.2 ± 1.3			
<i>ey</i>	47.9 ± 1.7	50.0	47.5 ± 1.5	44.9 ± 1.1		44.7 ± 1.1			
+, Seattle				51.1 ± 2.1		50.6 ± 2.1			
+, Sch. X		52.5 ± 1.5	50.0	53.1 ± 1.4		41.4 ± 4.4	50.0 ± 3.7		
<i>gvl ey<sup>R</sup></i>	56.8 ± 1.5	55.1 ± 1.1	46.9 ± 1.4	50.0	46.9 ± 1.3	47.3 ± 0.9	41.7 ± 2.4		43.2 ± 2.3
<i>ar</i>				53.1 ± 1.3	50.0	49.5 ± 1.1	44.7 ± 1.8		46.5 ± 1.7
<i>gvl</i>	61.0 ± 2.1	55.3 ± 1.1	58.6 ± 4.4	52.7 ± 0.9	50.5 ± 1.1	50.0	50.8 ± 1.1		51.3 ± 1.1
<i>ey<sup>A</sup></i>			50.0 ± 3.7	58.3 ± 2.4	55.3 ± 1.8	49.2 ± 1.1	50.0	53.0 ± 3.8	
<i>M<sup>A</sup></i>							47.0 ± 3.8	50.0	47.8 ± 3.5
<i>ey<sup>2</sup></i>				56.8 ± 2.3	53.5 ± 1.7	48.7 ± 1.1		52.2 ± 3.5	50.0

to the same pole as the *ey<sup>D</sup>* chromosome in 67.0 percent of the cases. The result was the same whether the duplication was received from the same parent as *ey<sup>D</sup>* (918/1398 = 65.7 percent) or from the same parent as *gvl* (561/807 = 69.5 percent), though in the latter case there resulted more than 50 percent recombination. The result was also the same in attached-X females carrying a Y chromosome (1118/1674 = 65.8 percent) and in separate-X females with no Y (361/531 = 67.9 percent).

TABLE 2

Preference ratios for scute-10-2 duplication in tests concerning a series of wild type IV chromosomes. These came from a mutant stock (yellow<sup>6</sup> scute<sup>12</sup> apricot) and from the following wild stocks: San Gabriel Canyon, California; Birmingham, England; Tonto, Arizona; Redwood Meadow, California; Arroyo Seco, Pasadena, California; St. Augustine, Florida; Seattle, Washington.

OPPOSED CHROMOSOME	PREFERRED CHROMOSOME								
	+, <i>y sc w<sup>A</sup></i>	+, San G.	+, Bham.	+, Tonto	+, Red. M.	+, Arr. S.	+, Fla.	+, Seattle	
<i>ci ey<sup>R</sup></i>	41.3 ± 1.4	48.1 ± 1.3	39.4 ± 1.6	37.0 ± 1.7	32.0 ± 3.1	38.4 ± 2.9	37.9 ± 1.9	38.6 ± 1.8	
<i>ey<sup>D</sup></i>	50.8 ± 1.9	38.9 ± 1.8	47.4 ± 1.5	41.0 ± 1.7	39.6 ± 1.6	41.0 ± 2.0	41.6 ± 1.8	37.1 ± 1.7	
<i>ci</i>				46.1 ± 2.0					
<i>sv<sup>na</sup></i>	52.5 ± 1.1	47.3 ± 2.2	42.4 ± 1.7		49.4 ± 1.9	36.9 ± 1.4		45.1 ± 1.3	
<i>ci<sup>D</sup></i>	65.3 ± 1.9	53.7 ± 2.1	48.7 ± 1.3		48.5 ± 2.6	49.7 ± 1.9			
<i>ey</i>		55.0 ± 1.1	56.0 ± 2.5	50.6 ± 2.1	51.1 ± 2.3	49.9 ± 1.6			
<i>gvl ey<sup>R</sup></i>	56.4 ± 1.8	57.7 ± 1.4	56.3 ± 1.4	52.8 ± 1.7	52.2 ± 1.9	55.3 ± 1.7	57.1 ± 1.3	48.9 ± 2.1	
<i>gvl</i>	55.0 ± 1.2	57.3 ± 1.5	57.3 ± 1.3	57.3 ± 1.5	59.3 ± 1.4	52.4 ± 2.2	49.8 ± 1.3	49.4 ± 2.1	
<i>ey<sup>2</sup></i>		68.6 ± 2.7	60.2 ± 2.1			64.9 ± 1.9			

Tables 1 and 2 show the results of the tests of this kind that have been carried out. Examination of these tables will show that the 26 kinds of IV chromosomes that have been tested fall into a series, approximately in the order in which they are listed in the rows of table 1. The nature of this series is such that the duplication "prefers" any chromosome to those that lie below it in the series, and this preference is greater the further apart the two chromosomes concerned lie in the series. This is shown by the fact that the values entered in each column gradually increase from the top to the bottom of the column. There are irregularities in this increase, often great enough to be statistically significant; but the general trend is unmistakable. It is probable that the discrepancies, so far as they lie beyond those to be expected from errors of random sampling, are due to differential viability or (in a few cases) to uncertainties of classification for some of the IV chromosome characters concerned.<sup>1</sup>

The exact seriation shown in the tables is not to be taken as accurate in detail, though the general neighborhood in which each chromosome is placed is clearly correct. The method used in obtaining this sequence, together with a numerical scale for judging the relative degrees of difference concerned, will be described below.

It will be observed that there is no evident relation between the position of a chromosome in the seriation and the mutant genes it carries. The top and the bottom chromosomes are both characterized by carrying recessive eyeless mutants, as is also *ey*, that lies near the middle of the series. Seventh from the top is a wild type chromosome, seventh from the bottom is another; and between these lie several other wild-type chromosomes, at least some of which certainly differ from each other.

Several of the tested chromosomes are derived ones. The first,  $+^{ci}ey^R$ , (from Dr. C. B. BRIDGES), arose by reverse mutation from the third, *ci ey<sup>R</sup>*. It is probable that these two are really identical in their preference properties. The *gvl ey<sup>R</sup>* chromosome (also from Dr. BRIDGES) arose by crossing over between *ci ey<sup>R</sup>* and *gvl*; it is intermediate, definitely different from both, and much more like *gvl*, from which its spindle-attachment is derived. The "+, Sch. X" chromosome was obtained (by Dr. J. SCHULTZ) by crossing over between *ey<sup>D</sup>* and *ci*. Here the crossover is much lower in the seriation than either of the chromosomes from which it was derived. Its spindle-attachment comes from *ey<sup>D</sup>*, which BRIDGES (1935) has shown to be a compound chromosome, with a diploid laterally attached duplication. This duplication may be important in determining the properties of the *ey<sup>D</sup>* chromosome; it is not present in the "+, Sch. X" chromosome.

<sup>1</sup> The position of *ey<sup>D</sup>* is different from that reported earlier (STURTEVANT 1934). This is because one of the earlier experiments was carried out with another chromosome ("Scutenick"), not further studied here, that sometimes gives a slight eye defect. These data have been discarded.

The "X *ci*" chromosome arose as a crossover in one of my triplo-IV experiments. The *ci* (and the spindle-attachment) came from *ci ey<sup>R</sup>*, the +<sup>ev</sup> either from *ci<sup>D</sup>* or from *gvl*. In either case the crossover is intermediate but more like the chromosome from which its spindle-attachment came. Evidently there is no one locus responsible for the preference properties of a chromosome, but it is possible that the spindle-attachment end is most important.

The relation of the duplication to the IV chromosomes is evidently due to the fact that it contains IV chromosome materials. A similar (undescribed) duplication, found in the "shaven" stock, carries the loci from *y* to silver, inclusive, but presumably has an X spindle-attachment. Experiments with it, comparable to those in table 1, gave the following values (the numbers given represent percentage preference for the first-named chromosome, which is the higher one in the seriation): *sv - ci ey<sup>R</sup>*,  $54.0 \pm 3.2$ ; *sv - ey*,  $46.6 \pm 1.9$ ; *ci<sup>D</sup> - ey*,  $48.7 \pm 2.7$ ; *sv - ci<sup>D</sup>*,  $47.5 \pm 4.3$ . These values are clearly not significantly different from 50.0. Similar results were obtained with duplications 107 and 118 (DOBZHANSKY 1934), though here one of the IV chromosomes concerned was a wild type of unknown position in the series.

On the other hand, another duplication derived from an X-IV translocation (an undescribed mottled notch received from DEMEREC) gave clear indications of preference, although the fragment of X concerned is considerably longer than that of scute-10-2. The values obtained here were: *ci ey<sup>R</sup> - +y sc w<sup>a</sup>*,  $60.0 \pm 2.0$ ; *+y sc w<sup>a</sup> - gvl ey*,  $57.4 \pm 1.9$ ; *+y sc w<sup>a</sup> - gvl*,  $66.9 \pm 1.8$ . These are clearly significant deviations from randomness, in the same direction as the corresponding *sc<sup>10-2</sup>* values.

#### TRIPLO-IV FEMALES

When three IV chromosomes are present in a single female, there are three possible types of segregation that give two chromosomes to one pole and one to the other (AB/C, AC/B, BC/A). With the existing material it has not been possible to determine the relative frequencies of all three types of segregation simultaneously in experiments in which contrary classes gave a viability control (except by the use of progeny tests, which have not been carried out). In some of the data the three frequencies were determined (without the viability control), while in others the viability control was obtained but only one of the three frequencies was determined.

Two samples of the raw data are shown in tables 3 and 4. In table 3 appear the results of testing a series of different chromosomes against *ey<sup>D</sup>* and *ci<sup>D</sup>*.<sup>2</sup> Here the type of segregation determined is *ey<sup>D</sup>ci<sup>D</sup>/x* (x indicates

<sup>2</sup> Both *ey<sup>D</sup>* and *ci<sup>D</sup>* are fully dominant when present in single dose in triplo-IV flies. It has not been found possible to distinguish such specimens from the corresponding diplo-IVs.

any other chromosome listed in table 3); the viability control is similar to that in a linkage backcross. Contrary classes should be equal; inspection of the table shows that in every case the  $ey^D$  character reduced the viability materially. Other experiments indicate that this is not due to the fact that the gene occurs most often in triplo-IV flies, for this condition evidently does not interfere with the viability appreciably—in some cases at least it appears to improve it slightly. The table shows a general tendency for the percentage of tested segregation type to increase as one passes from the top to the bottom of the series of table 1. As in that table, there

TABLE 3

*Offspring of triplo-IV females of the constitution  $ey^D/ci^D/x$ , mated to diplo-IV males not carrying  $ey^D$  or  $ci^D$ .*

x	$ey^D ci^D$	+	$ey^D$	$ci^D$	TOTAL	PERCENT $ey^D ci^D/x$
<i>sv</i>	181	242	250	347	1020	41.5
<i>ci ey<sup>R</sup></i>	67	82	163	168	480	31.1
<i>ci</i>	41	57	97	128	323	30.3
<i>+</i> , <i>y sc w<sup>a</sup></i>	44	36	49	97	226	35.4
<i>sv<sup>na</sup></i>	95	110	170	195	570	36.0
<i>+</i> , SanG.	64	125	111	157	457	41.4
<i>+</i> , Bham	66	84	60	140	350	42.8
<i>bt</i>	127	187	188	270	772	40.7
<i>ey</i>	71	89	77	115	352	45.5
<i>+</i> , Seattle	187	204	232	263	886	44.1
<i>gvl ey<sup>R</sup></i>	129	158	131	179	597	48.1
<i>gvl</i>	144	252	148	238	782	50.6
<i>ey<sup>A</sup></i>	101	137	56	98	392	60.7
<i>ey<sup>2</sup></i>	110	180	77	144	511	56.8

TABLE 4

*Offspring of triplo-IV females of the type A/A/B, mated to BB males.*

A	B	NOT B	B	TOTAL	PERCENT B
<i>sv</i>	<i>gvl ey<sup>R</sup></i>	181	74	255	29.0
<i>sv</i>	<i>gvl</i>	577	144	721	20.0
<i>sv</i>	<i>ey<sup>A</sup></i>	174	42	216	19.4
<i>sv</i>	<i>ey<sup>2</sup></i>	202	49	251	19.5
<i>ci ey<sup>R</sup></i>	<i>sv<sup>na</sup></i>	633	163	796	20.5
<i>sv<sup>na</sup></i>	<i>ci ey<sup>R</sup></i>	1227	183	1410	13.0
<i>ci ey<sup>R</sup></i>	<i>gvl</i>	791	243	1034	23.5
<i>gvl</i>	<i>ci ey<sup>R</sup></i>	771	92	863	10.7
<i>gvl ey<sup>R</sup></i>	<i>ci ey<sup>R</sup></i>	185	26	211	12.3
<i>sv<sup>na</sup></i>	<i>gvl ey<sup>R</sup></i>	976	213	1189	17.9
<i>sv<sup>na</sup></i>	<i>gvl</i>	1494	415	1909	21.8
<i>sv<sup>na</sup></i>	<i>ey<sup>A</sup></i>	1160	389	1549	25.1
<i>ey<sup>A</sup></i>	<i>sv<sup>na</sup></i>	659	58	717	8.1
<i>sv<sup>na</sup></i>	<i>ey<sup>2</sup></i>	440	155	595	26.0

are exceptions; here the value for *sv* is most aberrant. The explanation of this aberrant value is unknown, though it occurred in several independent tests and appears to be real. The general rule suggested by these results and by those of table 1 is: chromosomes high in the series tend to pass to the diplo-IV pole, those low tend to pass to the haplo-IV pole.

Table 4 shows the results from experiments of the type AAB, where the frequency of B eggs is determined. The frequency of this type of segregation is twice this value; the other two types of segregation are equivalent

(AB/A), and their frequency may therefore be calculated ( $= \frac{1-2B}{2}$ ). Here

TABLE 5  
Frequencies of types of segregation from triplo-IV females.

FEMALE AND TYPE OF SEGREGATION	NUMBER OFFSPRING	PERCENT	FEMALE AND TYPE OF SEGREGATION	NUMBER OFFSPRING	PERCENT
<i>sv sv/gul ey<sup>R</sup></i>	255	58.0	<i>ey<sup>D</sup> ci<sup>D</sup>/bt</i>	772	40.7
<i>sv sv/gul</i>	721	40.0	<i>ey<sup>D</sup> ci<sup>D</sup>/ey</i>	352	45.5
<i>sv sv/ey<sup>A</sup></i>	216	38.9	<i>ey<sup>D</sup> ci<sup>D</sup>/+Seattle</i>	886	44.1
<i>sv sv/ey<sup>2</sup></i>	251	39.0	<i>ey<sup>D</sup> ci<sup>D</sup>/gul ey<sup>R</sup></i>	597	48.1
<i>sv ey<sup>2</sup>/ci ey<sup>R</sup></i>	770	21.6	<i>ey<sup>D</sup> ci<sup>D</sup>/gul</i>	782	50.6
<i>ey<sup>D</sup> ci<sup>D</sup>/sv</i>	1020	41.5	<i>ey<sup>D</sup> ci<sup>D</sup>/ey<sup>A</sup></i>	392	60.7
<i>sv gul/gul ey<sup>R</sup></i>	276	26.8	<i>ey<sup>D</sup> ci<sup>D</sup>/ey<sup>2</sup></i>	511	56.8
<i>sv ey<sup>2</sup>/gul ey<sup>R</sup></i>	493	23.5	<i>ci ci<sup>D</sup>/ey<sup>A</sup></i>	249	48.2
<i>sv gul/ey<sup>2</sup></i>	278	45.0	<i>sv<sup>na</sup> sv<sup>na</sup>/gul ey<sup>R</sup></i>	1189	35.8
<i>sv ey<sup>2</sup>/gul</i>	278	35.2	<i>sv<sup>na</sup> sv<sup>na</sup>/gul</i>	1909	43.5
<i>gul ey<sup>2</sup>/sv</i>	—	19.8	<i>sv<sup>na</sup> sv<sup>na</sup>/ey<sup>A</sup></i>	1594	50.2
<i>ci ey<sup>R</sup> ci ey<sup>R</sup>/sv<sup>na</sup></i>	796	41.0	<i>sv<sup>na</sup> sv<sup>na</sup>/ey<sup>2</sup></i>	595	52.1
<i>ci ey<sup>R</sup> ci ey<sup>R</sup>/gul</i>	1034	47.0	<i>gul ey<sup>R</sup> gul/sv<sup>na</sup></i>	573	25.4
<i>ey<sup>D</sup> sv<sup>na</sup>/ci ey<sup>R</sup></i>	341	28.2	<i>sv<sup>na</sup> gul/gul ey<sup>R</sup></i>	1022	29.5
<i>ey<sup>D</sup> ci<sup>D</sup>/ci ey<sup>R</sup></i>	480	31.1	<i>sv<sup>na</sup> gul ey<sup>R</sup>/gul</i>	—	45.1
<i>sv<sup>na</sup> sv<sup>na</sup>/ci ey<sup>R</sup></i>	1410	26.0	<i>gul ey<sup>R</sup> ey<sup>A</sup>/sv<sup>na</sup></i>	338	22.4
<i>ci ey<sup>R</sup> bt/sv<sup>na</sup></i>	320	35.6	<i>sv<sup>na</sup> ey<sup>A</sup>/gul ey<sup>R</sup></i>	361	30.4
<i>sv<sup>na</sup> ci<sup>D</sup>/ci ey<sup>R</sup></i>	820	23.9	<i>sv<sup>na</sup> gul ey<sup>R</sup>/ey<sup>A</sup></i>	—	47.2
<i>sv<sup>na</sup> bt<sup>D</sup>/ci ey<sup>R</sup></i>	280	22.6	<i>sv<sup>na</sup> gul/ey<sup>A</sup></i>	398	35.2
<i>ci ey<sup>R</sup> sv<sup>na</sup>/gul ey<sup>R</sup></i>	217	36.8	<i>sv<sup>na</sup> ey<sup>A</sup>/gul</i>	398	32.6
<i>sv<sup>na</sup> ey<sup>A</sup>/ci ey<sup>R</sup></i>	1074	17.4	<i>gul ey<sup>A</sup>/sv<sup>na</sup></i>	—	32.2
<i>ci ey<sup>R</sup> ci<sup>D</sup>/gul</i>	831	54.2	<i>ey<sup>A</sup> ey<sup>A</sup>/sv<sup>na</sup></i>	717	16.2
<i>ci<sup>D</sup> gul/ci ey<sup>R</sup></i>	831	19.1	<i>ci<sup>D</sup> ey/gul</i>	247	38.0
<i>ci ey<sup>R</sup> gul/ci<sup>D</sup></i>	—	26.7	<i>ci<sup>D</sup> gul/ey</i>	247	33.2
<i>bt<sup>D</sup> ey<sup>A</sup>/ci ey<sup>R</sup></i>	484	27.3	<i>ey gul/ci<sup>D</sup></i>	—	28.8
<i>gul ey<sup>R</sup> gul ey<sup>R</sup>/ci ey<sup>R</sup></i>	211	24.6	<i>ci<sup>D</sup> gul/ey<sup>A</sup></i>	260	43.2
<i>ci ey<sup>R</sup> gul/gul ey<sup>R</sup></i>	1852	36.1	<i>ci<sup>D</sup> ey<sup>A</sup>/gul</i>	260	31.4
<i>gul ey<sup>R</sup> gul/ci ey<sup>R</sup></i>	1110	25.6	<i>gul ey<sup>A</sup>/ci<sup>D</sup></i>	—	25.4
<i>ci ey<sup>R</sup> gul ey<sup>R</sup>/gul</i>	—	38.3	<i>ci<sup>D</sup> gul/ey<sup>2</sup></i>	763	37.4
<i>gul gul/ci ey<sup>R</sup></i>	863	21.4	<i>ci<sup>D</sup> ey<sup>2</sup>/gul</i>	763	42.2
<i>ey<sup>D</sup> ci<sup>D</sup>/ci</i>	323	30.3	<i>gul ey<sup>2</sup>/ci<sup>D</sup></i>	—	20.4
<i>ey<sup>D</sup> ci<sup>D</sup>/+y sc w<sup>2</sup></i>	226	35.4	<i>ey gul/gul ey<sup>R</sup></i>	222	30.6
<i>ey<sup>D</sup> ci<sup>D</sup>/sv<sup>na</sup></i>	570	36.0	<i>gul ey<sup>A</sup>/gul ey<sup>R</sup></i>	1174	25.2
<i>ey<sup>D</sup> ci<sup>D</sup>/+San G.</i>	457	41.4	<i>gul ey<sup>2</sup>/gul ey<sup>R</sup></i>	1653	27.8
<i>ey<sup>D</sup> ci<sup>D</sup>/+Bham</i>	350	42.8			

there is no viability control, though in every case it may be surmised that the "B" class is slightly decreased from the true value by this factor.

Table 5 summarizes all the data available from triplo-IV experiments (of whatever type) in which as many as 200 flies were recorded. The final column gives the frequencies of the segregation-types concerned (that is, the values of table 3, twice those of table 4). These values have not been corrected, in cases where the viability correction is absent from the experiment itself; but the probability is that such corrections, were it possible to estimate them quantitatively, would be small in most cases.

Many of the values recorded in table 5 are strikingly different from the 33.3 percent that would result from random segregation. Analysis shows that these deviations are in general in agreement with the principle stated in discussing table 3. If A, B, and C represent the three chromosomes concerned, in the order of their position in the seriation, then the three types of segregation occur in the relative frequencies  $AB/C > AC/B > BC/A$ . More exact quantitative analysis will be discussed below.

#### ALGEBRAIC ANALYSIS OF THE DATA

Given three IV chromosomes (A, B, and C), the simplest assumption seems to be that when A and B pass to opposite poles at meiosis, C goes

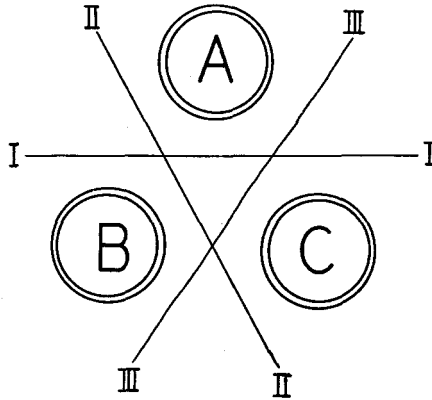


FIGURE 1. Three types of segregation of three IV chromosomes.

to the same pole as A in a fixed proportion of the eggs that is independent of the nature of C. It is clear, from even a cursory examination of the data, that the nature of C does influence the frequency with which A and B separate, so the absolute frequency of AC/B separation will be influenced by the nature of C; the assumption is that the nature of C does not influence the *relative* frequency of AC/B and A/BC.

The testing of this assumption may be approached by an analysis of the three types of segregation into certain possible components. In figure 1 these three possible types are labelled I, II and III.



The terminology used follows:

Let  $k = I + II$  (i.e., frequency of separation of A and B)

$l = I + III$  (i.e., frequency of separation of A and C)

$m = II + III$  (i.e., frequency of separation of B and C)

What will hereafter be referred to as the "preference ratios" may then be defined as follows:

$$r = \text{proportion of } k \text{ in which C goes with A } \left( \frac{II}{I+II} \right)$$

$$s = \text{proportion of } l \text{ in which B goes with A } \left( \frac{III}{I+III} \right)$$

$$t = \text{proportion of } m \text{ in which A goes with B } \left( \frac{III}{II+III} \right).$$

Then

$$I + II + III = 1$$

$$I = l(1 - s) = k(1 - r)$$

$$II = kr = m(1 - t)$$

$$III = ls = mt.$$

These equations may be shown to lead to the following results:

$$I = 1 - \left( \frac{r+s-2rs}{1-rs} \right) \quad (1)$$

$$II = \frac{r-rs}{1-rs} \quad (2)$$

$$III = \frac{s-rs}{1-rs} \quad (3)$$

$$t = \frac{s-rs}{r+s-2rs} \quad (4)$$

The first three numbered equations are of interest in dealing with triplo-IV cases; (4) has been used in the analysis of the  $sc^{10-2}$  duplication series. The original assumption was that the values of  $r$ ,  $s$ , and  $t$  were independent of the nature of the third element concerned—i.e., that  $r$  is a constant property of the pair A B, whether they be tested against C, D, or Z. Therefore equation (4) furnishes a method of calculating the preference between

B and C when that between A and B and between A and C is known. The duplication series may be taken as giving such preference values directly, since one type of segregation is rare and does not enter into the calculations. If C (figure 1) be taken as the duplication, the rare type of segregation is III, and the definition of  $r$  is that it is equal to  $II/I + II$ . However, in most

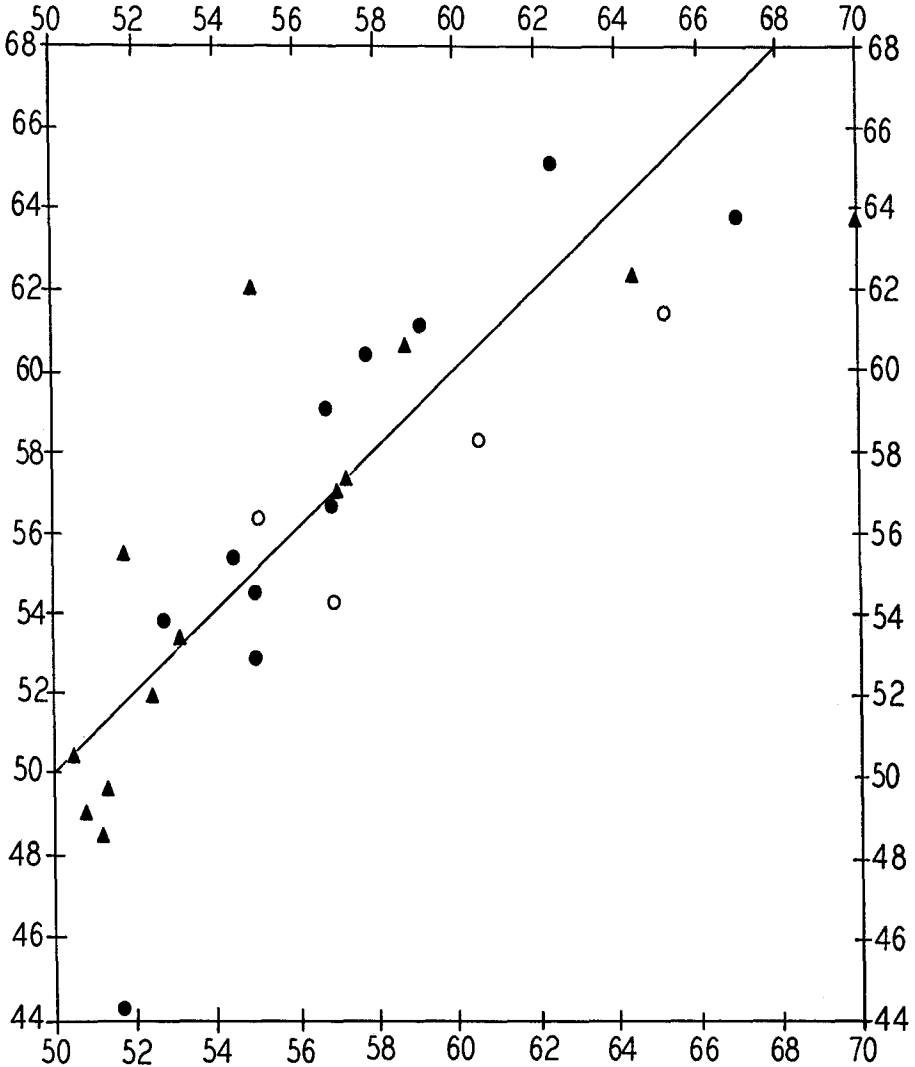


FIGURE 2. Comparison of observed (horizontal axis) and calculated (vertical axis) preference values for the scute-<sup>10-2</sup> duplication. Solid circles represent cases where the probable error of the observed value is 1.3 or less and the calculated value is an average of 9 or more determinations; solid triangles, cases where the probable error of the observed value is 1.3 or less, the calculated value the average of 5 to 7; open circles, cases where the probable error of the observed value is 1.4 or 1.5, the calculated value the average of 12 or more determinations.

cases the occasional occurrence of III will give rise to two classes, one of which will be indistinguishable from one of those resulting from I or II. Nevertheless, since III is infrequent, the data of tables 1 and 2 may be taken as giving direct determinations of preferences, and equation (4) may be applied to them. (See discussion below.)

Table 6 shows the calculated values of  $t$  for each of the 26 tested chromosomes in combination with the five most thoroughly tested chromo-

TABLE 6

*Average of calculated preference values (directly observed values also included), based on tables 1 and 2.*

OPPOSED CHROMOSOME	$ci\ ey^R$	$ey^D$	PREFERRED CHROMOSOME $sv^{na}$	$gv\ ey^R$	$gv$
+ $ci\ ey^R$	50.4	47.6	41.7	36.7	34.8
$sv$	48.1	49.6	44.9	36.0	36.4
$ci\ ey^R$	50.0	48.6	44.4	36.7	35.3
$ey^D$	51.4	50.0	45.5	38.1	36.0
$ci$	51.0	51.0	44.6	40.3	37.8
$Xci$	53.0	54.8	45.8	39.4	38.7
+ $y\ sc\ w^a$	55.7	54.3	47.9	40.2	39.2
$sv^{na}$	55.6	54.5	50.0	41.2	39.6
+San G.	55.1	56.3	51.1	42.2	40.4
+Bham	57.2	58.5	52.9	44.3	42.7
$bt$	58.8	56.7	54.7	46.3	43.3
$ci^D$	59.2	58.4	54.4	45.5	43.7
+Tonto	58.2	60.9	52.1	45.9	45.0
$bt^D$	60.2	59.5	54.0	45.4	44.5
+Red. M.	59.1	60.4	54.2	46.1	45.5
+Arr. S.	59.9	59.4	55.4	46.7	45.1
+Fla.	60.5	61.3	53.6	46.7	45.3
$ey$	60.8	60.2	56.9	47.0	44.6
+Seattle	62.9	63.3	56.5	49.7	48.2
+Sch.X	62.4	63.2	57.2	50.2	47.8
$gv\ ey^R$	63.3	61.9	58.8	50.0	47.2
$ar$	64.6	65.0	60.1	52.6	49.6
$gv$	64.7	64.0	60.4	52.8	50.0
$ey^A$	67.1	66.1	62.2	53.8	50.8
$M^A$	67.7	67.3	64.0	57.7	51.0
$ey^2$	68.0	68.4	64.8	55.5	55.1

somes. (See column headings.) From tables 1 and 2 were extracted all cases in which pairs of chromosomes entered in the cells of table 6 were each tested against a common third chromosome. From such combinations  $t$  was calculated (for example,  $sv/ey^D$  gave 52.2,  $ci\ ey^R/ey^D$  gave 50.9;  $sv/ci\ ey^R$  may be calculated from equation (4), substituting 52.2 for  $r$ , 50.9 for  $s$ ). The various possible calculated values for each cell of table 6 have been averaged; averages of this type have been used directly in figure 2, but in table 6 the observed values from tables 1 and 2 have been averaged in, each being given the same weight as a single calculated value.

The values in this table are clearly self-consistent, each of the columns giving a regularly increasing series of values as one reads from top to bottom. The discrepancies that exist are all small in amount. In effect this table represents a "smoothing" of the raw data of tables 1 and 2. The regularity of the gradation of values is in part inevitable, since the final seriation is based on these data; the essential point is that it is possible to get so nearly a perfect gradation for all five columns simultaneously.

When either r or s is close to 50, equation (4) is approximated by the equation

$$t = 50 + r - s. \tag{5}$$

That is, t differs from 50 by an amount equal to r - s. This relation is useful in checking calculations; and has also been made use of in applying arbitrary numerical values to the various chromosomes in table 7. This table in appearance, in method of construction, and in practical application, has a resemblance to the familiar "chromosome maps" that are based on crossover values. It is necessary to keep in mind, however, that no spatial relations are represented, and that the table concerns properties of whole chromosomes, not of loci.

TABLE 7.  
*Preference table (Description in the text).*

<b>+ci<sup>c</sup>ey<sup>R</sup></b>	20.6	<b>+Bham.</b>	11.2	<b>+Seattle</b>	6.3
<i>sv</i>	19.8+	<i>bt</i>	10.4	<b>+Sch. X</b>	6.2+
<b>ci ey<sup>R</sup></b>	19.8	<b>ci<sup>D</sup></b>	10.1	<b>gvl ey<sup>R</sup></b>	6.2
<b>ey<sup>D</sup></b>	18.6	<b>+Tonto</b>	9.9	<i>ar</i>	4.2+
<i>ci</i>	17.4	<i>bt<sup>D</sup></i>	9.6	<b>gvl</b>	4.2
<i>Xci</i>	16.2	<b>+Red. M.</b>	9.3	<i>ey<sup>A</sup></i>	2.5
<b>+y sc w<sup>a</sup></b>	14.9	<b>+Arr. S.</b>	9.0	<i>M<sup>A</sup></i>	1.0
<b>sv<sup>na</sup></b>	14.2	<b>+Fla.</b>	8.8	<b>ey<sup>2</sup></b>	0.0
<b>+San G.</b>	13.5	<b>ey</b>	8.4		

The table is based primarily on the relations of the eight most-studied chromosomes; these are represented in bold-faced type. The values of t for each successive pair of these were calculated from the values of table 6—i.e., "second order" calculations were made and averaged. The differences between these values and 50 were then taken as representing the differences between the chromosomes concerned. The interval concerned was first estimated by comparing the totals of the rows in table 6, and assuming the seriation to be such as to give a regularly ascending series of such totals. Each of the remaining 18 chromosomes was then fitted into the scheme by making "second order" calculations (from table 6) for its relations to the two of the chosen 8 better-studied chromosomes between which it lies. When the sum of the values so obtained was not equal to the

difference between the two chosen chromosomes (in no case did it differ markedly) the fitting was done by the method of proportional parts. These calculations resulted in a seriation of the chromosomes, with a set of relative differences. One of the terminal chromosomes (*ey*<sup>2</sup>) was arbitrarily taken as the zero point, and numerical values were assigned to each of the other 25 chromosomes, corresponding to the sum of the differences appearing in each interval between them and the arbitrary zero point.

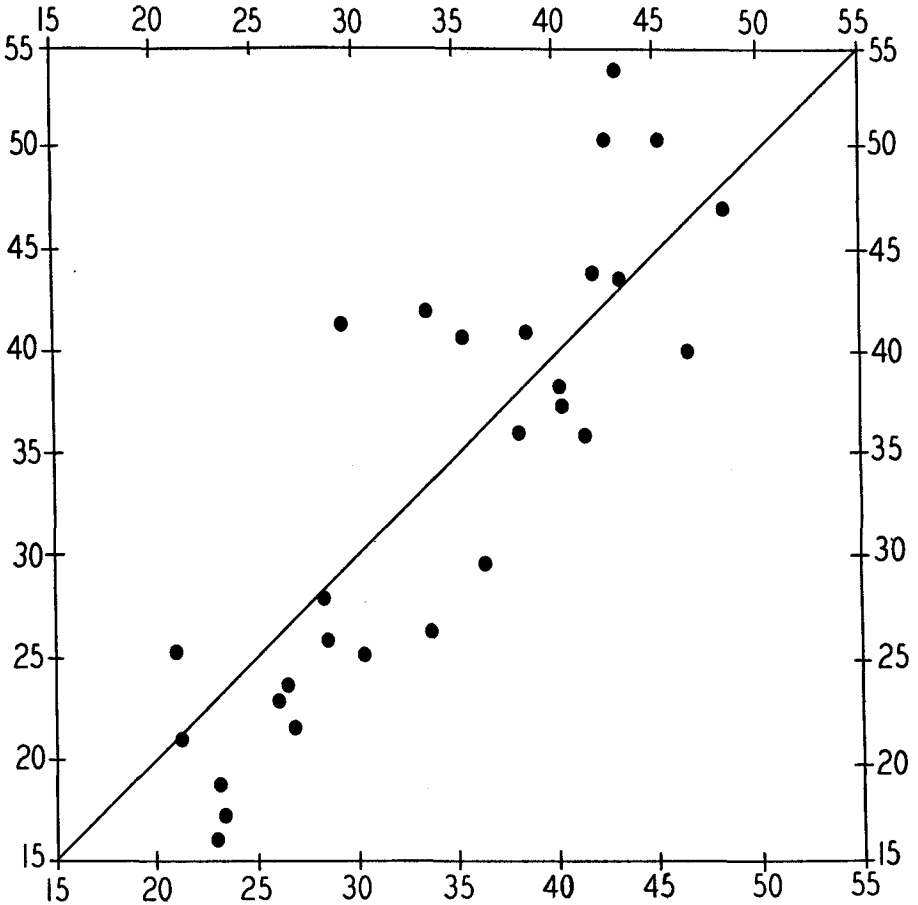


FIGURE 3. Comparison of observed (vertical axis) values for frequencies of segregation types in triplo-IV females with values calculated (horizontal axis) from the scute-10<sup>-2</sup> duplication experiments. Includes all cases where the observed value is based on 700 or more flies.

Table 7 may be used to give a prediction of the behavior of any three IV chromosomes when tested together. The differences between the values given in the table for any two chromosomes, when added to 50, give the preference ratio for those two. Three such values may be read off (for the possible combinations by two) for any three chromosomes; these, substi-

tuted for  $r$ ,  $s$ , and  $t$  in equations (1), (2), and (3), give the required prediction. Furthermore, any IV chromosome not listed in table 7 may be entered in its proper place by means of very few (theoretically by any single one) combinations with known chromosomes; it will then be possible to predict its behavior with any listed chromosomes.

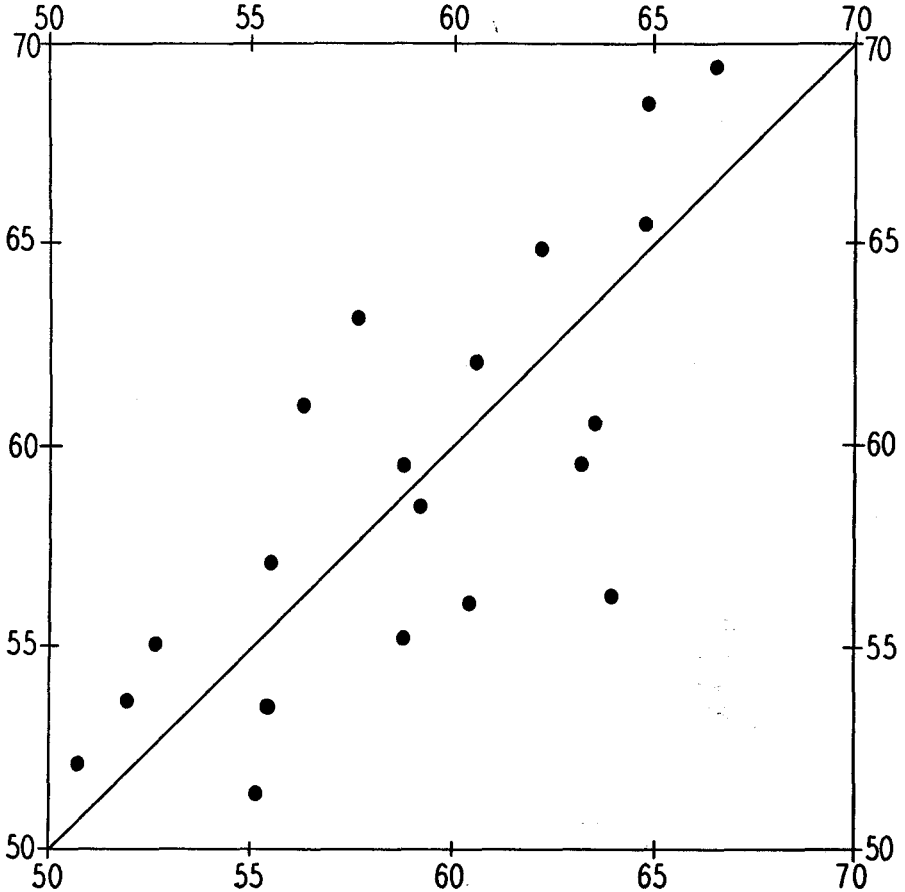


FIGURE 4. Preference ratios calculated from triplo-IV experiments (vertical axis) plotted against those calculated from scute- $10^{-2}$  duplication experiments (horizontal axis).

#### CORRELATION OF DUPLICATION AND TRIPLO-IV DATA

The equations developed in the preceding section were assumed to apply both to the duplication experiments and to those with triplo-IV females. It is possible to test this directly, by calculating from one series the results to be expected from the other. Figures 3 and 4 show the results of such a procedure.

Equations (1), (2), and (3) make it possible to calculate the types of segregation expected from triplo-IV females, given the preference ratios

of table 6. In some cases the necessary values are not included in table 6; such values were calculated by the same method as that used in deriving table 6. The observed frequencies are recorded in table 5. Figure 3 shows the relations here; all cases where the observed value is based on 700 or more flies are entered. The agreement is evidently satisfactory—calculations based wholly on scute-10-2 duplication data do in fact give good agreement with observations on triplo-IV.

There is, however, a suspicion of a systematic deviation in figure 3, such that observation gives a greater deviation from randomness than cal-

TABLE 8  
*Preference ratios calculated from triplo-IV data of table 5.*

CHROMOSOMES		NUMBER OF DETERMINATIONS	AVERAGE PREFERENCE RATIO
<i>sv</i>	<i>gvl ey<sup>R</sup></i>	1	56.1
<i>sv</i>	<i>gvl</i>	2	60.5
<i>sv</i>	<i>ey<sup>2</sup></i>	1	69.4
<i>ci ey<sup>R</sup></i>	<i>sv<sup>na</sup></i>	2	57.0
<i>ci ey<sup>R</sup></i>	<i>ci<sup>D</sup></i>	1	58.3
<i>ci ey<sup>R</sup></i>	<i>gvl ey<sup>R</sup></i>	2	59.5
<i>ci ey<sup>R</sup></i>	<i>gvl</i>	4	65.4
<i>sv<sup>na</sup></i>	<i>gvl ey<sup>R</sup></i>	3	55.1
<i>sv<sup>na</sup></i>	<i>gvl</i>	3	56.0
<i>sv<sup>na</sup></i>	<i>ey<sup>A</sup></i>	4	64.8
<i>sv<sup>na</sup></i>	<i>ey<sup>2</sup></i>	1	68.5
<i>ci<sup>D</sup></i>	<i>ey</i>	1	53.5
<i>ci<sup>D</sup></i>	<i>gvl</i>	4	61.0
<i>ci<sup>D</sup></i>	<i>ey<sup>A</sup></i>	1	63.0
<i>ci<sup>D</sup></i>	<i>ey<sup>2</sup></i>	1	62.1
<i>ey</i>	<i>gvl</i>	1	53.4
<i>gvl ey<sup>R</sup></i>	<i>gvl</i>	2	55.0
<i>gvl ey<sup>R</sup></i>	<i>ey<sup>A</sup></i>	2	59.4
<i>gvl</i>	<i>ey<sup>A</sup></i>	1	51.9
<i>gvl</i>	<i>ey<sup>2</sup></i>	2	51.2

ulation would lead one to expect. The problem was therefore approached in another way. From the definitions of r, s, and t it is possible to calculate them from triplo-IV data in cases where the frequencies of all three types of segregation are known. Table 5 includes a number of such cases. The preference values from these were calculated; where several determinations for the same two chromosomes were available these were averaged. The results are shown in table 8, and are plotted against the corresponding values of table 6 in figure 4. Here there is clearly no systematic deviation, so the indication of one in figure 3 is probably not significant. It may be noted that, if a table analogous to table 6 is constructed from the data of table 8, the same seriation of the nine chromosomes concerned will be

found to fit, with surprisingly few discrepancies and these of small magnitude. If the seriation is deduced solely from the data of table 8, it is found to agree with that shown in table 7, with the exceptions that *sv* might be placed below *ci ey<sup>R</sup>*, *ey* below *gvl ey<sup>R</sup>* (only one comparison possible), and *ey<sup>4</sup>* below *ey<sup>2</sup>*. In all these cases table 7 indicates only slight differences; the rearrangements suggested by the triplo-IV data would not seriously disturb them.

The calculations from the two series thus agree quantitatively as well as could be expected from the nature of the data.

#### INFLUENCE OF DUPLICATION ON SEGREGATION OF FOURTH CHROMOSOMES

It has been assumed, up to this point, that in diplo-IV females carrying the scute 10-2 duplication the frequency with which the two IVs go to one pole and the duplication goes to the other is negligible. It was clear, when the experiments of table 1 were carried out, that this type of segregation does occur; since these experiments regularly gave a few haplo-IV flies (more than the occasional ones found in any experiment), and such flies were always not-yellow (that is, carried the duplication). These flies were recorded, but have not seemed worth dealing with, since the viability of haplo-IV is extremely low and is also quite variable. In one of the experiments of table 1, however, it is possible to identify the other (triplo-IV) product of such segregation, namely in the combination *ey<sup>D</sup>/ci<sup>D</sup>/dupl*. From this combination there were recorded 146 *ey<sup>D</sup>*, 106 *ci<sup>D</sup>*, 94 *y ey<sup>D</sup>*, 160 *y ci<sup>D</sup>*, 11 *y ci<sup>D</sup>ey<sup>D</sup>*. The latter class results from the type of segregation under discussion; an equal number of (not-yellow) haplo-IV must have been produced but failed to survive. From these data one may deduce that the three types of segregation occurred with the following frequencies: *ey<sup>D</sup> dupl/ci<sup>D</sup>* = 57.9; *ci<sup>D</sup> dupl/ey<sup>D</sup>* = 37.8; *ey<sup>D</sup> ci<sup>D</sup>/dupl* = 4.2. It should be noted that the experiment suffers from the low viability of *ey<sup>D</sup>* referred to before.

Several experiments were carried out in an attempt to determine the frequency of this type of segregation in another way. Females of the type studied in table 1 were mated to males of the constitution *ey<sup>D</sup>/M<sup>4</sup>*. *M<sup>4</sup>* is completely suppressed in triplo-IV flies; accordingly any wild type flies must have arisen by the production of a diplo-IV egg by the mother. Since both *ey<sup>D</sup>* and *M<sup>4</sup>* have reduced viability, these experiments give maximum values, the haplo-IV eggs always giving less viable zygotes than the diplo-IV ones. The procedure adopted has been to double the number of + zygotes (since a corresponding number of haplo-IVs are lost), and add this number to that one of the two diplo-IV classes that was largest, in order to obtain a total number of zygotes. The data are given in table 9. The average value from this table is 4.55 percent non-disjunction, none



having been found in the few offspring studied from females with no duplication. It may be noted that the highest frequency of non-disjunction was obtained from the combination involving the highest members of the IV chromosome seriation, as might have been expected. Taking this and the  $ey^D/ci^D/dupl$  experiment together, we may conclude that 4 percent represents a fair estimate of the usual frequency of this type of segregation.

If 4 percent is taken as the frequency of AB/dupl segregation, it is possible to estimate the error introduced by its occurrence in the experiments of tables 1 and 2. If A and B each carry a recessive gene ( $a$ ,  $b$ ), the calculated preference will differ according as the male used in the test is

TABLE 9  
*Diplo-IV females  $\times$   $ey^D/M^4$  *males.**

CONSTITUTION OF MOTHER	$ey^D$	$M^4$	+	CALCULATED NON-DISJUNCTION
$sv/ey^4/dupl$	90	67	1	2.2
$+$ , $y\ sc\ w^a/sv^na/dupl$	129	99	6	8.5
$sv^na/sv^na/dupl$	204	231	7	5.7
$sv^na/bt/dupl$	102	100	3	5.6
$+$ , $SanG/ey^2/dupl$	90	67	1	2.2
$gvl/gvl/dupl$	188	160	3*	3.1
Average	—	—	—	4.55
$sv/ey^4$	191	149	0	0
$sv^na/sv^na$	85	80	0	0

\* These flies, being  $gvl/gvl/M^4$ , were expected to show the grooveless character, as do  $gvl/M^4$  flies. No trace of grooveless was found; the constitution of one of the three flies was verified by tests of its offspring. This result is presumably related to the fact that the grooveless character is often slight in haplo-IV  $gvl$ .

$y a$  or  $y b$ . If  $r$  represents the true preference ratio (for A over B), then in backcrosses to  $y a$  males the observed ratio will be  $r + 2/102$ ; in backcrosses to  $y b$  males it will be  $r/102$ . These expressions give the following values:

Male	$r = 50$	$r = 60$	$r = 65$	$r = 70$
$y a$	51.0	60.8	65.7	70.6
$y b$	49.0	58.8	63.7	68.6

Table 10 shows the results from all experiments in which females of a given constitution were mated to both kinds of males. The average difference between the two types of experiments, instead of being 2.0 as expected, is only 0.2; evidently this source of error in tables 1 and 2 is too slight to be further considered.

## POSITION OF THE DUPLICATION IN THE SERIATION

It is clear that the duplication may be placed in the same seriation as the other IV chromosomes. Since, as just shown, it almost always goes to the diplo-IV pole, it belongs at the top of the series, far above the other chromosomes dealt with. There is too much uncertainty about the values to enable one to place it numerically in relation to table 7.

TABLE 10  
Females *A/B/dupl* mated to males *y a* or *y b*.

<i>a</i>	<i>b</i>	BACKCROSS TO <i>a</i>		BACKCROSS TO <i>b</i>		<i>a</i> MINUS <i>b</i>
		N	CALC. PREFERENCE	N	CALC. PREFERENCE	
<i>ci ey<sup>R</sup></i>	<i>gvl</i>	625	67.2	583	68.5	-1.3
<i>ci ey<sup>R</sup></i>	<i>sv<sup>na</sup></i>	1979	56.0	361	55.1	+0.9
<i>gvl</i>	<i>ey<sup>2</sup></i>	821	48.2	203	50.8	-2.6
<i>gvl</i>	<i>ey<sup>A</sup></i>	378	50.2	587	48.6	+1.6
<i>ey</i>	<i>gvl</i>	200	58.0	802	54.6	+3.4
<i>Xci</i>	<i>sv<sup>na</sup></i>	505	52.3	216	48.1	+4.2
<i>sv<sup>na</sup></i>	<i>ey</i>	149	53.6	532	57.5	-3.9
<i>sv<sup>na</sup></i>	<i>ey<sup>2</sup></i>	201	64.1	306	65.4	-1.3
<i>sv<sup>na</sup></i>	<i>gvl</i>	174	58.6	678	57.5	+1.1
Average						+0.23

## IV CHROMOSOME TRANSLOCATIONS

Several reciprocal translocations between the IV and the II or III chromosomes have been tested for preference. They have not given consistent results, presumably because in all such cases there are types of gametes that are not recovered (or have greatly reduced viability). Until these complications can be eliminated it does not seem necessary to present what data were obtained.

## NO INFLUENCE OF AGE AND TEMPERATURE

Two separate experiments were carried out to test the effects of age of female and of temperature on the preference ratios. In the first case the tested females were *sv/ey<sup>D</sup>*, carrying the scute 10-2 duplication. Here controls (25°) and females treated for two days at 27°C immediately after emergence showed no clear differences from the usual value of 52 percent in daily transfer cultures run for 12 days. In the second series the females were *ci<sup>D</sup>/gvl*, with the duplication. The temperatures used were 19°, 25°, and 28°; the first and last were applied for three days that included the emergence from the pupae. Again there were no evident deviations from the usual value (55 percent) in daily transfer cultures made for 12 days. These temperatures and ages are evidently without effect on the preference ratios.

## PREFERENCE TESTS IN MALES

The results described in the preceding pages have been based entirely on tests of females. The results obtained from tests of males are shown in tables 11 and 12. Table 11, dealing with scute-10-2 duplication males, suggests that there is no preference in the male, none of the values being clearly different from randomness (50.0). However, it is to be noted that the four combinations that give over 66.0 in females all give above 50.0

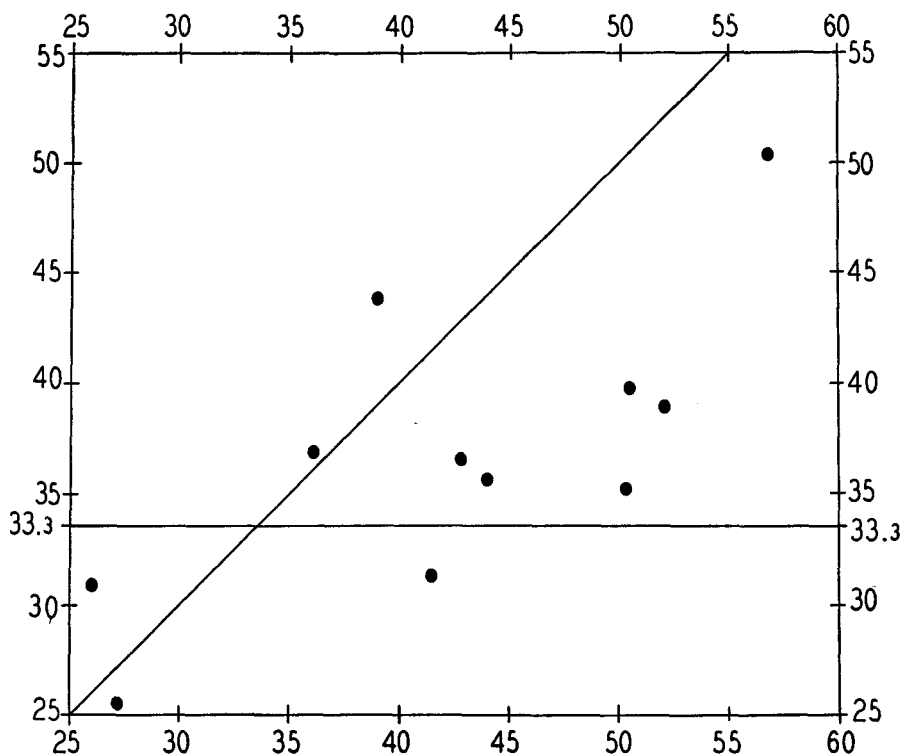


FIGURE 5. Frequencies of segregation types in triplo-IV males (vertical axis) plotted against the corresponding frequencies from triplo-IV females (horizontal axis).

in males, while the four that give 57.0 or less in females all give less than 50.0 in males.

Table 12, showing the results from triplo-IV males, indicates the existence of a preference in males that is less than that in females. The correlation between comparable values for the two sexes is obvious in figure 5. The numbers of combinations are too few to warrant presentation of the results of application of the preference formulae to males; the deviations from randomness are so slight that very large numbers would be required to furnish an adequate test of these formulae.

PREFERENCE OF THE DUPLICATION WITH RESPECT TO X AND Y

Tables 11 and 12 suggest that preference is more marked in triplo-IV males than in diplo-IV males carrying scute-10-2 duplication. One interpretation of this result might be that the unpaired X, having genes in common with the duplication, affects its behavior by reducing its de-

TABLE 11

*Preference values for the scute-10-2 duplication in males and in corresponding females.*

PREFERRED CHROMOSOME	OPPOSED CHROMOSOME	VALUE OBSERVED	
		MALE	FEMALE
<i>ci ey<sup>R</sup></i>	<i>ar</i>	52.7 ± 1.6	70.0 ± 1.3
<i>sv<sup>na</sup></i>	<i>bt<sup>D</sup></i>	49.5 ± 1.4	56.6 ± 1.7
<i>sv<sup>na</sup></i>	<i>ci<sup>D</sup></i>	49.2 ± 2.1	57.0 ± 1.4
<i>ci ey<sup>R</sup></i>	<i>gvl</i>	52.6 ± 0.8	67.8 ± 0.9
<i>ey<sup>D</sup></i>	<i>gvl</i>	52.0 ± 1.1	67.0 ± 0.7
<i>ci ey<sup>R</sup></i>	<i>sv<sup>na</sup></i>	49.7 ± 1.7	56.8 ± 0.7
<i>ey<sup>D</sup></i>	<i>sv<sup>na</sup></i>	46.3 ± 2.1	55.0 ± 1.2
<i>sv</i>	<i>ey<sup>A</sup></i>	50.8 ± 1.9	66.4 ± 1.9

TABLE 12

*Frequencies of segregation types in triplo-IV males and females compared.*

	MALES		FEMALES	
	OFFSPRING	PERCENT	OFFSPRING	PERCENT
<i>sv sv/ey<sup>2</sup></i>	488	43.8	251	39.0
<i>ey<sup>D</sup> ci<sup>D</sup>/sv</i>	346	31.3	1020	41.5
<i>bt<sup>D</sup> ey<sup>A</sup>/ci ey<sup>R</sup></i>	343	25.6	484	27.3
<i>sv<sup>na</sup> sv<sup>na</sup>/ey<sup>A</sup></i>	300	35.4	1594	50.2
<i>ey<sup>D</sup> ci<sup>D</sup>/sv<sup>na</sup></i>	597	36.8	570	36.0
<i>ey<sup>D</sup> ci<sup>D</sup>/+Bham.</i>	382	36.7	350	42.8
<i>ey<sup>D</sup> ci<sup>D</sup>/+Seattle</i>	639	35.7	886	44.1
<i>ey<sup>D</sup> ci<sup>D</sup>/ey<sup>2</sup></i>	253	50.5	511	56.8
<i>ey<sup>D</sup> ci<sup>D</sup>/gvl</i>	384	39.7	782	50.6
<i>sv<sup>na</sup> sv<sup>na</sup>/ci ey<sup>R</sup></i>	592	31.1	1410	26.0
<i>sv<sup>na</sup> sv<sup>na</sup>/ey<sup>2</sup></i>	704	38.9	595	52.1

pendence on IV. If this were correct one might expect a relation of the duplication to the X-Y segregation in such males. The available data on this relation follow.

Male y, carrying scute-10-2 dupl

	+ <sup>v</sup> ♀	y ♀	+ <sup>v</sup> ♂	y ♂	Total
♀ yy (X's separate)	854	1010	772	1031	3667
♀ $\bar{y}\bar{y}$ (X's attached)	252	350	314	368	1284

Analysis shows that in both series the duplication more often goes to the same pole as the Y ( $51.4 \pm 0.6$  percent and  $51.7 \pm 0.9$  for the two series,  $51.5 \pm 0.48$  for the two taken together). The deviation from randomness is very slight, and is doubtfully significant; since it is in the same direction in both series I am inclined to suppose that it is real.

Nevertheless the suggestion that such a relation is responsible for the difference between triplo-IV and duplication males cannot be taken as verified; for there is a more marked relation of the duplication to the sex-chromosomes in attached-X females, where its preference ratios for IV are unaffected. The data on this relation are as follows:  $\bar{y}\bar{y}$  dupl ♀ crossed with  $y\sigma$  gave  $+ \bar{y}$  1914,  $y \bar{y}$  1793,  $+ \sigma$  1872,  $y \sigma$  2162; preference of duplication for  $\bar{X}\bar{X}$  (as opposed to Y) =  $4076/7741 = 52.6 \pm 0.38$  percent. That the result is not due to viability complications is shown by two facts. First, similar experiments using females with separate X's gave the same four classes as above in the frequencies 1099; 1178; 939; 1076. Here there can be no question of preference, since the mothers carried the duplication, whereas the fathers were responsible for the sex of the offspring. The percentage corresponding to the preference ratio above must then be 50.0 except for deviations due to viability. It is  $50.6 \pm 0.52$ . Second, other duplications, that have X spindle-attachments, similar in gene-content to the scute-10-2 duplication, give similar preferences for  $\bar{X}\bar{X}$  as opposed to Y. My own observations on duplication 118 give  $307/555 = 55.4 \pm 1.4$ ; the data published by DOBZHANSKY (1934, p. 149) show similar relations for duplications 101, 106, 107, 118 and 136. The interpretation of these relations awaits further experiments.

#### DISCUSSION

The algebraic analysis of the data from triplo-IV females given above has been tested and shown to be adequate. However, the IV chromosomes concerned are cytologically visible bodies, and a satisfactory description of their behavior must have a geometrical basis.

In the earlier account (STURTEVANT 1934) it was indicated that 66.7 was the limiting preference ratio, and that an interpretation might be approached from this observation as a starting point. The more extensive data here presented do not bear out the suggestion of such a limiting value; tables 1 and 6 suggest rather that the value is slightly exceeded and that there is no approach to a limit. If the duplication itself be considered as a IV chromosome, then the preference ratio for it as compared to any other IV chromosome is nearer 90 than 66.7.

One natural assumption is that two of the IV chromosomes pair and pass to opposite poles, leaving the third to go to either pole at random. The preference seriation would then be an indication of the strength of

pairing affinity. This hypothesis alone is inadequate; for if, in *ABC*, pairing is always between *A* and *B*, there will result two types of segregation in equal numbers, and this value of 50 percent is the maximum that can be obtained. Since 50 percent is clearly exceeded in most of the duplication experiments and in several of those with triplo-IV, this hypothesis alone is inadequate.

Perhaps the most attractive of the remaining possible hypotheses is that all three chromosomes conjugate, as in figure 1, and preference is due to non-random orientation of the resulting hexad on the first meiotic spindle. One may suppose that the orientation is always such that one chromosome is directed toward one pole of the spindle, two toward the other. On this basis, a chromosome near the bottom of the preference seriation is one that is more likely to be directed toward a pole; it may be looked upon as being in some sense the equivalent of more than a single one of any type of chromosome lying above it in the seriation. It is probable that a workable model of this type could be imagined in terms of electrical charges.

The scute-10-2 duplication probably has nothing in common with the other IV chromosomes except its inert material and its spindle-attachment. The data on crossover IV chromosomes (of which more are needed) suggest also that these regions of normal IVs may be especially important in determining preference properties. Since the segregation relations of X and Y are also related to inert material and spindle-attachments, it seems likely that they are essential in the relations described in this paper. The spindle-attachment alone cannot be solely responsible, since the crossovers show that more than one locus must be involved. Since BRIDGES (1935) has shown that there is inert material at both ends of the IV chromosome, this demonstration does not weaken the argument for its importance.

#### SUMMARY

1. Segregation in triplo-IV females of *Drosophila melanogaster* usually gives two chromosomes to one pole, one to the other.
2. The three resulting types of segregation do not usually occur with equal frequencies.
3. The IV chromosomes studied may be arranged in a definite seriation, such that any chromosome will, in a triplo-IV female, pass to the haplo-IV pole more often than will any chromosome that lies above it in the seriation (when the two are tested in like experiments or in the same experiment).
4. If two chromosomes, *A* and *B*, are tested against any third chromosome, *C*, then in those cases in which *A* and *B* separate, *C* will go with *A*

in a proportion of the cases,  $r$ , that is independent of the nature of  $C$ —that is,  $r$  is a constant property of the pair  $AB$ .

5. If the preference ratio for  $A$  as opposed to  $B$  is called  $r$ , that for  $A$  as opposed to  $C$  is called  $s$ , and that for  $B$  as opposed to  $C$  is called  $t$ , then

$$t = \frac{s - rs}{r + s - 2rs} .$$

6. From this and related equations it is possible to show that the data form a consistent whole, and to predict the results that will be given by any combination of three tested chromosomes.

7. The segregation in triplo-IV males is also non-random. It deviates from randomness in the same direction as that in corresponding females, but less markedly.

8. More than one locus is concerned with the preference properties of a IV chromosome.

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