Studies on a case of high non-disjunction in *Drosophila melanogaster*[1]

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(With 2 Textfigures)

Table of contents

Introduction

Among a group of primary exceptional females of Drosophila melanogaster obtained after X-ray treatment was one which gave a high percentage of secondary exceptions. A preliminary mention of this high non-disjunction line has been made in two articles published in the papers of the Michigan Academy of Science, Arts and Letters

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(ANDERSON 1925, 1926). The origin of this line was as follows:
Echinus cut[6] garnet[2] *(ec ct g)* females were mated to scute crossveinless
vermilion forked *(sc cv v f)* males. Virgin Fl females were subjected
to X-ray treatment (ANDERSON 1924, 1925) and then mated to yellow
scute crossveinless Bar *(y sc cv B)* or yellow forked Bar *(y f B)* males.
The exceptional daughters (not-bar) were bred to determine their
X-constitution and incidentally their percentage of secondary non-dis-
junction. Most of them gave the normal low percentage of exceptions
averaging about three percent, which is somewhat lower than the 4·3
percent recorded by BRIDGES (1916). One vermilion equational except-
ional gave a much higher percentage and this line was continued over
the summer by breeding from exceptional daughters. The original primary
exception (No. 80) was of the constitution $\dfrac{sc \quad cv \; v \quad f\text{·}}{ec \quad v \; g}$ When the
analysis was begun in the fall of 1924 the constitution of the line was
$\dfrac{cv \; v \quad f,}{sc \; ec \quad v \; g}$ a reciprocal crossover having taken place between scute
and echinus. The line has since been continued in this form.

Crossing-over controls

The parents of the original cross from which the high non-disjunction
line arose were from the same stocks that were used by BRIDGES and
OLBRYCHT (1926) in their studies on crossing-over. Further data on
this cross have been published by the writer (1925 b). A map of the X
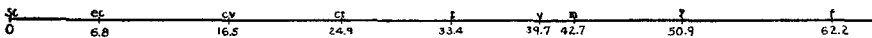
Figure 1.   Map of the X chromosome

chromosome is given in figure 1 showing graphically the position of
each of the genes used in this analysis. This map was compiled from
the data referred to above. Tan *(t)* and miniature *(m)* are interpolated
as they were used in the latter part of the analysis. The crossover
values given on this map will be referred to as control values.

The frequency of non-disjunction and of crossing-over in the high non-disjunction line

Table 1 presents the data accumulated on secondary non-disjunction
and crossing-over from $\dfrac{cv \; v \quad f}{sc \; ec \quad v \; g}$ mothers within the high non-dis-
junction line. All cultures with less than 100 offspring are omitted.

Table 1

Progeny of $\dfrac{cv\ v\ f}{sc\ ec\ v\ g}$ females from the high non-disjunction line

Culture number	Exceptions female	Exceptions male	Regular females	Regular males 0	1	2	3	4	1,3	1,4	2,3	2,4	3,4	1,2,4
a	40	35	74	40	3	9	10	4						
b	20	19	41	20	2	3	3	3						
c	24	22	69	47	3	4	3	1						
d	29	33	83	54	5	4	8	4						
e	27	14	59	40	2	5	4	—	—	—	—	—	—	1
f	51	28	62	45	5	7	2	3						
1	14	21	48	33	2	4	5	3	—	1				
2	28	23	64	30	1	3	3	3						
3	37	18	67	37	3	6	7	4						
4	23	14	62	27	2	3	6	3	—	1				
5	34	22	72	35	5	4	5	2	—	1				
6	26	16	48	31	1	4	11	—	—	—	—	1		
7	15	28	73	37	8	7	1	1						
8	23	19	61	45	—	5	8	3						
9	10	14	54	23	2	6	4							
10	22	22	58	45	2	3	4	5						
11	19	17	51	35	2	6	5	1	—	—	—	1		
13	26	24	57	31	2	2	3	3						
14	24	16	40	24	2	2	1	2						
15	13	17	46	30	2	2	5	2						
17	20	22	47	31	2	3	7	3						
18	23	17	34	25	3	1	2	2						
21	30	33	50	39	3	6	8							
22	13	16	38	33	—	3	3	1						
23	12	22	50	26	3	1	4	2	—	1				
29	32	28	59	48	1	3	6	1						
30	29	22	66	53	2	2	3	1						
31	18	19	48	42	6	3	6	1						
32	9	9	43	28	3	1	4	4						
33	23	11	48	29	2	2	3	2						
58	27	17	62	41	5	1	7	1	—	1				
101	10	16	42	30	4	3	6	6						
102	17	16	48	35	1	2	3	1						
103	28	25	51	32	3	3	4	1						
145	16	18	71	43	6	6	8	5						
148	13	15	57	38	6	3	7							
149	31	23	69	40	3	2	6	1	1					
150	21	22	36	34	3	8	1	2						

26*

Table 1 Continued

Culture number	Exceptions		Re-gular females	Regular males										
	female	male		0	1	2	3	4	1, 3	1, 4	2, 3	2, 4	3, 4	1, 2, 4
159	16	15	64	50	6	3	8	1						
160	29	24	43	29	1	8								
176	23	15	47	23	4	5	2							
177	33	22	64	34	4	1	3	1						
302	50	36	111	81	5	1	9	5	1	—	—	—	1	
327	49	36	105	70	8	7	12	3	—	1				
333	30	23	82	50	2	6	6	—	—	—	—	—	1	
349	52	28	89	61	9	7	13	3						
361	24	26	72	86	8	11	9	4	—	1	—	1		
362	36	25	127	94	3	7	11	5	—	—	—	—	1	
363	41	29	97	78	5	11	12	10						
364	31	22	79	71	5	10	7	5						
365	11	14	36	31	—	2	4	3						
366	26	20	65	48	2	—	8	6	—	—	—	—	1	
372	10	12	48	30	2	—	6	2						
373	23	15	69	50	1	5	9	8						
374	18	14	92	43	6	6	11	2	—	—	—	1		
413	28	25	90	54	6	6	6	1	—	1				
414	69	47	124	81	15	9	16	1						
415	40	33	69	61	1	2	6	3						
420	49	28	124	79	8	11	7	7						
429	73	49	117	69	6	6	7	4						
430	26	22	45	30	1	1	3	1	—	1				
486	24	15	60	36	7	3	5							
488	21	17	67	53	6	7	10	2	—	1				
489	45	50	121	81	6	4	17	5						
502	65	47	176	93	6	15	9	7						
522	11	14	57	32	2	1								
523	27	25	86	53	6	8	7	5						
524	31	26	96	83	9	6	9	8						
556	8	6	64	48	3	2	9	2						
572	12	11	59	38	4	5	5	1						
573	8	11	68	45	8	8	9	1						
574	45	29	128	74	9	10	10	6	—	—	—	—	1	
585	32	43	124	105	5	7	11	5						
589	37	27	103	71	3	7	8	2	1					
590	39	42	93	77	3	5	7	14						
591	12	15	62	26	4	4	9	6						
592	36	37	115	48	4	9	6	5	—	—	—	1		
593	18	13	44	29	2	3	2	5	—	—	—	—	1	

Table 1 Continued

Culture number	Exceptions		Re-gular females	Regular males										
	female	male		0	1	2	3	4	1, 3	1, 4	2, 3	2, 4	3, 4	1, 2, 4
594	12	13	62	40	—	5	3	3	—	1				
595	21	20	74	35	3	3	4							
597	26	21	118	61	8	7	6	5	—	—	—	—	1	
598	25	10	100	50	6	2	8	1	—	1	—	1		
599	37	32	144	86	5	6	10	6						
600	20	27	127	82	4	7	4	5						
603	42	25	96	73	6	5	8	1						
607	14	10	46	33	2	7	3	4						
608	11	5	65	41	3	3	4	3	—	1	1	1		
609	17	18	75	58	4	7	13	8	—	—		1		
610	22	21	108	94	6	6	10	9	—	1				
617	6	3	41	29	10	3	8	2	—	1	—	—	1	
618	48	46	172	114	7	8	15	14						
619	44	29	152	108	3	11	15	8	—	1				
621	15	13	81	39	10	8	9	2	—	—		—	1	
622	20	19	37	29	—	1	1	2						
624	31	22	86	51	8	6	10	1	—	—		1		
627	25	16	75	51	6	3	8	5						
631	21	25	57	43	2	—	5	3						
632	22	18	85	45	4	2	4	4	—	—	—	—	1	
633	18	19	112	49	6	3	5	4	—	1				
634	48	25	125	76	6	3	3	4						
635	19	15	77	45	8	7	3	2						
637	21	13	90	66	4	2	5	11						
639	22	17	62	54	5	5	9	6	—	1				
640	24	13	99	47	5	5	5	3	—	1				
641	18	18	98	53	13	8	10	—	—	—	1			
642	14	8	48	23	4	3	1	2						
643	11	10	49	29	4	11	4	1						
645	14	14	98	44	5	7	6	7	—	—	—	—	1	
646	26	15	109	58	8	8	9	3	—	—	—	—	1	
647	30	20	108	68	6	7	7	8						
648	16	11	72	56	5	3	4	6						
650	18	15	87	54	2	5	4	5	—	—	—	2	1	
665	24	21	101	64	5	10	4	8						
666	12	17	70	49	4	3	1	5						
668	29	14	89	46	6	9	7	4	—	—	—	1		
670	15	8	56	38	4	5	6	2	—	—	—	2		
686	37	23	64	52	3	8	4	1						
714	23	20	83	47	4	11	5	1	—	1	—	—	1	

Table 1 Continued

Culture number	Exceptions		Re-gular females	Regular males										
	female	male		0	1	2	3	4	1, 3	1, 4	2, 3	2, 4	3. 4	1, 2, 3
724	86	85	220	150	16	25	14	1	—	1	—	1		
725	46	56	193	124	17	12	17	11						
729	47	50	160	106	11	6	11	3						
730	13	9	63	41	7	3	4	6						
731	43	45	151	115	3	10	9	6						
770	35	23	76	50	3	3	7	1	—	1				
828	51	33	117	78	12	8	8	—	—	—	—	1		
829	47	41	175	96	13	10	12	3						
830	51	47	134	101	14	13	11	—	—	—	—	—	1	
831	33	55	121	81	15	16	3	2						
832	48	37	128	83	6	7	7	1						
833	55	53	152	95	9	18	14	4						
834	34	30	97	61	8	2	10	3						
835	62	49	165	109	15	9	20	3						
836	26	23	71	48	3	—	7	4						
838	20	17	62	33	6	4	6	7						
839	32	31	85	74	4	1	2	5						
840	46	52	156	89	7	10	14	2	—	2	—	—	2	
841	45	34	116	78	15	10	5	5	—	1	—	—	2	
842	36	34	129	68	8	8	7	7						
843	59	44	109	76	8	7	12	1						
844	34	32	118	86	8	12	18	4						
845	39	44	123	62	4	6	5	1	—	—	—	1	2	
846	46	36	118	71	8	9	12	2						
847	26	19	76	44	4	2	8							
848	18	8	31	38	2	1	4	2	—	1				
849	15	28	83	37	4	5	5	2						
850	33	29	109	90	7	10	6	6						
851	32	33	123	95	9	12	19	7	—	—	—	1		
853	48	38	113	84	9	7	6	3						
854	34	38	142	74	14	11	9	5						
855	42	31	97	75	11	8	8	1						
856	30	37	115	68	4	8	9	5						
857	36	27	105	65	6	6	4	2						
858	24	50	125	82	10	13	8	3						
859	35	25	110	62	6	5	8	2						
860	46	39	93	98	13	13	12	6						
861	32	25	101	68	10	10	14	3	—	1				
886	3	13	66	58	6	7	8	3						
887	37	23	91	70	4	7	11	8						

Table 1 Continued

Culture number	Exceptions		Re-gular females	Regular males										
	female	male		0	1	2	3	4	1, 3	1, 4	2, 3	2, 4	3, 4	1, 2, 4
983	34	24	117	82	8	8	8	6						
984	20	12	71	52	7	6	7	4						
1033	9	12	44	44	3	2	7	6	—	—	—	1		
1051	12	24	87	54	5	8	6	4	—	1				
1052	44	32	177	100	13	10	19	5	—	—	—	—	1	
1055	37	26	108	71	6	16	12	6	—	—	—	2		
1057	47	33	180	116	8	15	12	4	1	1	—	—	2	
1058	25	19	101	67	4	9	10	9						
1079	20	22	81	51	5	9	5	1						
1080	14	18	50	33	1	1	3	3						
1081	19	11	86	56	11	12	17	2						
1082	40	33	153	102	16	13	12	7	—	1	—	1	1	
1083	17	19	124	72	19	10	14	4	2	—	—	—	1	1
1084	35	37	152	90	14	17	11	1	—	—	1			
1086	31	30	129	113	18	12	15	5	—	—	—	1	1	
1087	35	30	232	127	16	18	17	10	1					
1088	42	40	221	121	17	21	21	9						
1089	13	9	57	42	9	5	9							
Total	5072	4344	15 758	10 307	1028	1120	1323	625	7	30	3	23	28	1

Where several broods were raised from the same mother, these have been combined, since it has been shown that there is no difference between successive broods within this line (ANDERSON 1926). Table 1 and succeeding tables include all of the data cited in the above paper where successive broods were compared.

Out of a total of 39669 flies listed in table 1, 9416 or 23·7 percent were exceptional. Many of the female exceptions were equational. These are included with the non-equational exceptions for the present and will be discussed in a later section.

Among the exceptions there were 4344 males to 5072 females, where equality is expected in secondary non-disjunction. The deficit of males is probably due to lower viability. In most of the cultures the exceptional males were either *y sc cv B* or *y f B*, both of which are well below normal in viability.

The percentages of crossing-over calculated from the regular males from table 1 are presented in table 2. For comparison the percentages of crossing-over in the controls are included. Crossing-over appears to

be about normal from scute to crossveinless, but shows a great reduction in the regions to the right of crossveinless.

Table 2. Summary of data on crossing-over from table 1

Region	Frequency	Total crossovers	Percentage	Coincidence	Controls
Non Crossovers	10307				
1. sc—ec . . .	1028	1066	7·4	—	6·8
2. ec—cv . . .	1120	1147	7·9	—	9·7
3. cv—g . . .	1323	1361	9·4	—	34·4
4. g—f . . .	625	707	4·9	—	11·3
1, 3 . . .	7	—	—	·07	
1, 4 . . .	30	—	—	·58	
2, 3 . . .	3	—	—	·03	
2, 4 . . .	23	—	—	·43	
3, 4 . . .	28	—	—	·42	
1, 2, 4 . . .	1				
Total	14495		29·6		62·2

Replacement of autosomes

Before the present data on high non-disjunction was collected, the line had been carried through the summer by out-crossing exceptional females to stock males. This stock was the same one used as a source of males for the X-ray work (ANDERSON 1924) and for mating to primary and secondary exceptions therefrom. It was thus known to be free from genes having any great effect on the percentage of secondary exceptions shown by normal low lines. Repeated mating to this stock should rapidly replace the autosomes of the original high non-disjunction line by those of the y sc cv B stock. Presumably the autosomes were all normal.

Later more definite tests were made for the effect of replacement of autosomes II and III. Exceptional females of the high non-disjunction line were mated to black vestigial males for two successive generations. Exceptional daughters which were also black vestigial were then mated to y sc cv B males and gave the same percentages of exceptions and crossovers as the rest of the high non-disjunction line. This shows that replacement of the original second chromosomes by those of the black vestigial stock did not alter either the percent of exceptions or the amount of crossing-over. A similar test was made using the third chromosome character sepia in place of the second chromosome characters black and vestigial. The results were the same.

Normality of the *sc ec v g* chromosome

All tests have shown the *sc ec v g* chromosome of the high non-disjunction line to be entirely normal. Data will be presented on one test only. This test was made by mating exceptional females to stock *cv ct f* males. Wild-Type regular daughters were mated to *y sc cv B* males. Their progeny are given in table 3. Equal proportions of XX and XXY cultures are expected. Five cultures gave no exceptions at all and were presumably from XX mothers. Six cultures gave typical low percentages of exceptions. An exceptional female from culture 341 gave only two percent (culture 419). The crossover percentages likewise approach the standard map values of figure 1 and are very different from those characterizing the high non-disjunction line.

Females homozygous for the *sc ec v g* chromosome gave only normal low percentages of exceptions. The *sc ec v g* males from high non-disjunction cultures were fertile. Replacement of the *sc ec v g* chromosome in the high non-disjunction line did not alter the behavior of the line.

The above results showed that the *sc ec v g* chromosome was entirely normal. So only tests involving the *cv v f* chromosome were continued.

Sterility of males from the high non-junction line

Many tests have been made for fertility of *cv v f* males from the high non-disjunction line. Most of these were made by putting several *cv v f* males in a culture bottle with a number of virgin females. Sometimes a single male with contrasting characters was added from some other source to give a supply of larvae to keep the culture bottle in good condition. In no case have any offspring been obtained from the *cv v f* males.

Tests of the *cv v f* chromosome

Exceptional females from the high non-disjunction line were crossed with stock *sc ec ct g* males and their wild type regular daughters mated to *y sc cv B* or *y f B* males. Half of these daughters should be XX in constitution, the other half XXY. The resulting cultures fell into two sharply contrasting lots according to the percentage of exceptions shown. One lot (see table 5) gave low percentages ranging from 0 to 5 percent, with a mean of 2,1 percent. The other lot (see table 6)

Table 3. Progeny of $\dfrac{se\ ec}{cv\ ct}\ \dfrac{v\ g}{f}$ cultures from the high non-disjunction line

	Exceptions		Regular females	Regular males																									
	Female	Male		0	1	2	3	4	5	6	1,3	1,4	1,5	1,6	2,3	2,4	2,5	2,6	3,4	3,5	3,6	4,5	4,6	5,6	1,4,6	2,3,6	2,4,6	3,5,6
36	—	1	120	37	5	7	12	9	15	15	—	—	—	—	—	1	—	2	—	2	1	3	3	—	—	—	—	1
39	—	—	83	38	—	7	8	11	5	17	—	—	2	1	1	—	1	2	1	1	2	—	3	—	—	—	1	—
44	4	2	266	72	8	14	17	30	20	26	—	4	3	3	—	1	6	4	1	4	1	4	3	—	—	—	—	—
59	—	1	141	35	10	12	13	25	11	12	1	1	1	1	—	2	2	1	—	2	2	5	5	—	—	1	—	—
61	1	—	108	38	3	7	7	7	5	5	—	2	3	3	—	2	2	1	—	2	1	2	2	—	—	—	—	—
62	—	—	129	42	2	6	11	14	9	10	1	1	1	1	—	2	—	1	—	2	1	4	4	—	—	1	—	—
338	—	—	130	60	4	7	7	10	7	13	—	—	1	2	—	1	—	2	2	2	1	—	—	—	—	—	—	—
339	—	—	135	66	7	7	9	15	11	9	—	—	1	1	—	1	1	1	—	2	—	1	1	—	—	—	1	—
340	4	14	143	58	7	10	7	19	10	6	—	1	2	1	—	—	1	1	—	3	—	1	1	—	—	—	—	—
341	3	3	106	46	6	6	8	16	5	5	—	1	1	1	—	1	2	2	—	3	1	1	1	—	—	—	—	—
342	—	—	124	59	—	8	7	6	4	11	—	—	1	1	—	1	1	1	—	—	2	2	2	—	—	—	—	—
419	5	1	167	53	9	13	12	13	13	13	—	—	1	1	—	2	1	2	—	1	1	2	2	—	1	—	—	—
Total	17	22	1652	604	61	104	118	175	115	142	1	10	14	16	1	13	17	18	4	21	14	10	24	4	1	1	2	1

gave high values resembling those listed in table 1. The former were interpreted as the expected XX cultures, the latter the XXY.

According to the above interpretation the small percentage of exceptions of table 5 should be due to primary non-disjunction in XX mothers. This was substantiated by tests of exceptional males and by growing cultures from both exceptional and regular daughters. The exceptional males were sterile indicating that they were XO in constitution. Fifty exceptional daughters were tested all giving high percentages of exceptions (cultures 83 to 890 of table 7). Five regular daughters not carrying the vermilion gene gave a total of 1267 regular offspring but no exceptions. Nine regular daughters heterozygous for vermilion were tested giving the results shown in table 4. Seven of the cultures gave low percentages of exceptions; the other two gave none at all. From these cultures, six exceptional sons tested proved sterile. Eleven exceptional daughters tested all gave high percentages of exceptions.

The data presented above are sufficient to show that the regular $\dfrac{cv \quad v \quad f}{sc \; ec \quad ct \quad g}$ daughters which give low percentages of exception are XX and that the exceptions they do give are primary. This is an

Table 4. Progeny of heterozygons vermilion regular daughters of
$$\text{XX} \; \frac{cv \quad v \quad f}{sc \; cc \quad ct \quad g} \; \text{mothers}$$

	Total	Ex-ceptions	Per-centage	Exceptional sons tested	Tests of exceptional daughters			
					culture number	Total offspring	Ex-ceptions	Per-centage
699	176	2	1·1	{	717	270	95	35·2
					736	214	63	29·4
700	195	0						
701	55	1	1·8		718	118	34	28·8
702	177	1	·6	1 sterile				
705	179	6	3·3	3 sterile {	737	102	32	31·4
					738	168	44	26·2
706	200	5	2·5		721	22	6	27·3
707	191	0						
708	150	4	2·7	1 sterile	739	139	13	9·4
709	171	6	3·5	1 sterile {	722	150	23	15·3
					723	130	21	16·2
					740	462	96	20·8
					741	172	29	16·9
Total	1493	25	1·7			2167	456	21·0

Table 5.　Progeny of $XX \dfrac{cv \quad v \quad f}{sc \quad ec \quad ct \quad g}$ regular daughters of outcrosses to $sc \; ec \; ct \; g$ males

Culture number	Exceptions female	Exceptions male	Regular females	Regular males 0	1	2	3	4	5	6	1,4	1,5	1,6	2,5	2,6	3,5	3,6	4,5	4,6
40	—	1	35	24	2	2	3	1	—	1									
41	4	3	140	102	5	5	7	—	4	3									
371	—	1	70	51	2	3													
375	1	1	127	64	—	4	3	—	—	4									
381	5	2	67	63	5	4	4	—	—	2									
403	4	1	116	80	—	2	2	—	—	2									
418	1	2	117	73	4	9	3	2	3	4	—	—	1						
684	1	2	68	67	2	4	2	1	2	1	—	—	1						
690	1	2	82	76	4	5	4	3	1	4	—	—	1						
693	3	1	70	52	6	5	7	1	—	2									
727	6	2	116	97	11	4	5	2	—	6	—	—	—			1	—		1
728	5	3	224	149	9	9	5	1	—	8									
743	2	1	110	92	8	7	4												
759	2	4	233	179	6	4	11	—	—	5									
761	1	2	138	132	3	8	4	—	—	2									
763	3	3	185	134	13	4	5	6	1	7	—	—		2					
764	4	4	193	113	6	10	2	—	—	7	—	—	—	—			1		
765	7	—	224	176	6	8	9	4	3	5									
766	4	3	171	122	11	10	5	—	1	7									
774	6	3	88	83	6	5	4	—	—	6									
786	1	1	70	56	3	2	5	—	1	1									
790	1	2	63	57	2	2	—	1	—	2									
791	5	2	241	188	7	14	7	1	1	6									
811	10	3	287	186	11	13	13	6	—	10									
814	1	1	70	56	2	2	2	1	—	1									
820	10	6	200	160	6	8	6	3	—	7	—	1							
1061	10	4	275	194	11	13	5	4	1	5									
1062	3	3	50	48	2	3	1	1	—	1	—	—	1						
1069	1	1	74	69	4	4	5	2	2	2									
1072	5	2	151	117	5	7	4	4	—	3	—	—	2						
1075	2	—	96	58	4	6	2	1	—	6	—	—	1						
1076	2	—	69	64	6	5	3	2	—	2	—	1	1						
1102	3	2	69	59	7	3	2	1	—	4									
1103	2	7	93	51	2	3	—	2											
1104	1	6	131	94	5	5	5	1	—	4	1								
1106	6	6	266	200	14	8	9	—	1	3	—	—	1						
1109	9	—	64	45	5	3	2	2	—	5									

Table 5. Continued

Culture number	Exceptions female	Exceptions male	Regular females	Regular males															
				0	1	2	3	4	5	6	1,4	1,5	1,6	2,5	2,6	3,5	3,6	4,5	4,6
1110	—	2	108	90	8	11	5	2	—	9	—	—	1						
1112	2	3	84	80	5	3	—	—	—	6									
1113	1	5	175	115	9	9	4	1	1	7	—	—	1						
1117	5	2	127	103	15	6	7	1	—	4	—	—	—	—	1				
1118	9	15	182	157	15	10	9	7	3	5	—	—	—	—	2	—	1		
1121	6	8	212	114	9	10	5	2	1	3	—	—	—	—	—	—	1		
1122	4	7	200	139	18	8	5	1	2	10	—	—	1	1					
1123	3	4	171	123	8	10	9	1	2	5	—	—	1	—	—	—	—	1	
1124	3	4	102	74	5	3	7	1	1	2									
1127	7	4	211	143	8	12	9	6	3	4	—	—	—	—	—	—	—	—	1
1129	4	3	197	157	13	8	9	1	—	13	—	—	—	1	1	—	2		
1131	7	6	216	167	16	18	9	3	1	9	—	—	—	1	—	—	1		
1133	9	7	246	195	15	22	11	4	1	9	—	—	—	—	2				
1134	2	1	93	88	5	7	6	—	—	1									
1135	2	5	105	56	5	8	2	3	—	4	—	—	—	—	1				
1137	5	6	183	153	10	8	7	3	1	4									
1140	3	3	154	101	7	5	9	—	2	6	—	1							
1142	6	7	245	188	15	12	12	3	2	7	—	—	1						
1143	3	8	247	169	11	6	6	4	3	6									
1144	8	5	216	171	15	20	10	6	1	9	—	—	—	1	1	—	—	—	2
1145	7	5	210	154	9	9	9	3	2	3	—	—	—	—	—	1			
1148	2	2	96	70	4	3	4	—	—	1									
1149	8	2	83	80	4	7	5	2	—	5									
1152	6	6	189	124	6	9	5	2	—	1	—	—	1	1					
1156	4	11	210	166	9	4	4	2	2	3									
Total	242	218	9105	6808	449	441	328	111	49	274	1	3	17	5	10	1	6	1	3

extremely high precentage of primary exceptions and shows that the
$cv\ v\ f$ chromosome of the high non-disjunction line has an affect on
primary non-disjunction even greater than its effect on secondary non-
disjunction.

Non-disjunction and crossing-over in $\dfrac{cv\quad v\quad f}{sc\ ec\quad ct\quad g}$ females

The purpose of outcrossing to $sc\ ec\ ct\ g$ males was to get all of
the original seven genes heterozygous in individuals carrying the $cv\ v\ f$
chromosome from the high non-disjunction line. The progenies from
regular females mated to bar males are given in tables 5 and 6. Those

Table 6. Progeny of XXY $\dfrac{cv \quad v \quad f}{sc \; ec \quad ct \quad g}$ regular daughters of outcrosses to $sc\;ec\;ct\;g$ males

Culture number	Exceptions		Regular females	Regular males													
	female	male		0	1	2	3	4	5	6	1,3	1,6	2,5	2,6	3,5	3,6	4,6
35	20	13	38	31	2		5	2		1							
42	18	17	39	28	2	4	5										
335	13	9	26	37	3	6	2		1	4							
370	21	18	63	42	2	8	1	2		6				1			
376	60	21	91	112	7	15	7	3		10			1	1			
377	22	10	83	44	6	3	4	2	1								
378	54	55	141	95	5	17	7	5		3							
379	21	19	57	44	3	2	3		1	2							
380	10	19	73	56	3	10	4	3	1	1			1				
402	21	26	57	50	3	2	4	1		1							
404	17	17	46	39	1	1		1		1							
405	32	28	52	32	7	3	4			1				1			
406	22	19	62	38	3	7	1			1							
416	32	30	78	54	3	3	6	3		1							
417	12	13	92	57	5	4	5			4							
682	20	22	59	34	8	3	4	1		3							
685	16	30	57	39	3	2	2	1		2			1				
687	31	18	42	60	8	4	1			2			1	1			
689	16	16	65	48	1	6	2			2							
692	9	16	31	34	8		2	1		3							
694	22	11	50	29	2		2		1	2							
696	13	13	62	43	5	5	2			2							
726	29	27	163	61	10	6	5	4		3			1				
742	36	29	148	104	9	8	8	2		6				1			
758	33	32	86	89	10	9	4	3		2			1				
760	42	30	107	79	6	12	6	1		1							
762	52	61	178	134	20	10	6	6		6							
773	39	35	75	56	11	6	2	2		2							
775	19	6	63	36	1	3	3			2							
777	34	15	49	42	5	4	1	1		1							
779	26	19	105	73	3	3		1	1	10						1	
780	65	49	170	140	16	13	9	4	1	8							1
781	23	22	51	38	4	5	1		1								1
782	26	14	66	59	11	9	1	1					1				
783	46	28	110	88	9	5	2	2	3					1			
784	32	25	98	68	4	6	6	5		3							
785	16	11	47	27	1	8				2				1			
787	36	35	114	54	10	8	3	2		4				1			
788	44	30	143	98	11	8	5	5		8				1			
789	55	43	121	93	7	11	6	1	2	5				1			

Table 6.   Continued

Culture number	Exceptions female	Exceptions male	Regular females	Regular males 0	1	2	3	4	5	6	1,3	1,6	2,5	2,6	3,5	3,6	4,6
810	45	41	129	97	6	7	10	3		2		1					
812	39	54	140	107	16	14	8	3	1	3							
813	44	45	118	93	11	9	5			2							
816	15	11	47	18	6	3	2	3									
818	33	32	112	82	3	10	2	2		8		1		1			
819	41	33	104	64	6	12	7	3		6				1			
1064	36	24	141	94	11	15	11	6		4			1				
1065	40	39	173	122	21	14	5	6	1	1						1	
1066	58	30	145	93	10	12	6	6	1	1							
1068	34	30	89	65	7	12	6			3							
1070	14	17	58	43	3	1	4	2		2		1					
1073	35	30	147	101	18	7	10	1	2	2							
1077	53	67	239	128	30	21	14	10		6							
1078	41	29	190	100	15	25	11	5	1	5	1	1			1		
1101	46	27	176	89	14	14	6	2		5				1			
1105	39	32	153	111	12	19	5	1		4				1		1	
1107	30	22	117	50	3	8	4	2		6		1					
1108	31	34	102	60	7	10	10	2	2	5							
1111	35	37	155	121	11	11	7	2	3	8		1					
1114	42	23	144	69	7	9	3	6	1	4							
1116	26	20	85	56	7	10	1			1							
1119	33	32	133	96	8	12	7	2		2				1			
1120	15	31	152	78	15	13	7	2		7							
1125	37	25	141	85	9	8	2	2	3	10		1					
1126	31	23	107	76	10	2	5	1	1	4				1			
1128	69	48	219	142	10	22	9	6	1	5						1	
1130	30	38	184	131	17	20	10	2	2	7						2	1
1132	25	18	62	54	2	11	4	2		5				1			
1136	52	61	191	142	18	19	15	2		9		2	1				
1138	12	17	88	51	4	3	3	1	1	4							
1139	53	34	99	71	6	10	11	4		2							
1141	34	23	105	68	6	8	4	3	1	5		1					
1146	41	31	226	143	24	16	11	3	1	12		1					1
1147	34	22	108	76	5	10	8	3	2	6		1	1				
1150	36	32	121	78	10	9	8	2	1	3							
1151	45	45	148	115	14	10	8	6	2	6		1					
1153	20	24	112	60	5	9	10	5		7							
1154	22	28	106	92	4	5	4	1		5		1					
1155	35	44	112	75	11	6	5			6							
1157	32	17	93	66	4	5	6	2		2		1				1	
Total	2588	2221	8529	5847	644	680	415	179	40	300	1	20	5	17	1	7	2

Table 7. Progeny of exceptional females of constitution $\dfrac{cv \quad v \quad f}{sc \ ec \quad ct \quad g}$

Culture number	Exception		Regular females	Regular males																	
	female	male		0	1	2	3	4	5	6	1,4	1,5	1,6	2,4	2,5	2,6	3,4	3,5	3,6	4,5	4,6
83	22	14	59	39	6	2	4	2													
505	16	14	51	31	3	3	3	3													
796	44	41	176	142	18	12	11	7	—	5	—	—	—	—	—	—	—	1	—	—	1
797	31	34	121	95	4	7	4	1	—	—	—	—	1								
798	27	26	70	67	4	7	4	1	1	4											
799	20	8	75	37	7	11	2	2	—	6											
826	60	70	175	110	19	16	14	4	—	4											
863	17	18	50	27	2	1	3	—	—	1											
865	50	31	101	74	11	6	7	2	1	7											
866	36	40	125	86	13	16	8	1	2	8	—	—	1								
867	32	33	117	57	7	4	11	1	2	5	—	—	1								
868	13	13	42	31	6	4	4	—	—	3											
870	30	27	108	68	4	5	3	—	—	1	—	—	1								
871	20	20	48	34	4	2	—	3	1												
873	8	11	35	35	2	5	3	—	—	1											
874	9	16	70	41	3	2	—	1													
884	35	24	165	93	6	10	11	—	—	3											
885	29	15	75	49	6	4	2	—	—	3											
888	46	22	87	46	5	7	3	1	2	2											
889	41	42	154	110	13	10	5	4	—	7											
890	12	12	66	42	6	1	1	—	2	5											
43	49	38	148	104	13	7	3	2	1	7	—	1	—	—	—	—	—	—	—	—	1
47	10	15	60	31	6	6	1	—	1	2	—	—	1	—	1						
48	30	28	125	72	14	8	8	5	1	10											
55	9	10	60	45	6	5	2	2	—	4	—	—	—	—	—	—	—	—	—	1	
56	12	11	55	22	5	2	1	3	—	5											
57	36	39	122	76	11	1	3	1	5	2	—	—	—	1	—	1					
75	17	12	81	37	10	8	5	—	1	5	—	1									
76	16	9	36	28	4	3	2	—	—	3											
78	26	22	68	61	3	8	2	2	2	2	—	—	—	—	—	—	—	—	—	—	1
79	12	22	71	49	4	2	2	—	1	3											
80	22	26	113	68	6	11	2	2	—	2											
304	34	36	130	91	6	8	10	1	2	10											
305	15	6	65	33	7	7	1	1	1	1											
307	24	33	155	79	9	13	7	3	—	5	—	1	1	—	—	3	1				
309	37	21	106	72	2	1	3	1	1	1											
311	38	33	101	76	7	3	1	5	3	8	—	—	1								

Table 7. Continued

Culture number	Exceptions female	male	Regular females	Regular males 0	1	2	3	4	5	6	1,4	1,5	1,6	2,4	2,5	2,6	3,4	3,5	3,6	4,5	4,6
312	15	16	51	41	11	4	3	1	—	1											
316	38	30	115	88	14	8	5	—	2	8											
320	48	42	143	96	8	10	5	4	2	6											
321	19	14	102	76	11	6	4	1	3	4	—	—	—	—	—	1					
323	12	10	43	30	1	5															
324	21	15	65	48	1	3	2														
325	18	29	83	45	3	4	3	1	—	2											
326	37	26	164	80	6	11	5	3	2	11											
334	24	13	71	56	2	6	3	5	2	4	—	—	—	—	—	—	—	—	—	—	1
367	22	18	66	42	4	2	5	1	—	4	—	1	1								
368	22	23	103	68	10	6	4	3	1	6	1										
369	24	24	52	39	1	1	6	1	-	6	—	—	—	—	1	—	—	1			
425	25	12	38	27	3	4	2	–	—	1											
454	21	19	38	26	3	2	—	1	—	1											
500	72	57	283	183	26	23	13	5	3	14	—	—	—	—	—	—	—	—	1		
503	23	17	75	52	10	5	4	—	1	2											
571	9	6	55	28	8	5	1	—	1	1	—	—	2	—	—	—	1				
580	39	34	169	127	4	13	10	2	1	14	—	—	—	—	—	1					
583	42	56	164	99	10	11	5	4	1	7											
657	9	14	51	30	2	3	4	2													
660	41	61	124	75	13	8	5	2	2	9	—	—	—	—	—	1	—	—	1		
676	11	6	60	29	1	2	1	1	1	4											
698	19	21	72	52	4	6	3	1	1	4	—	—	—	—	—	—	—	1	1		
713	25	29	81	53	3	6	4	4	2	7											
716	10	10	46	28	2	5	4	1													
862	42	23	82	66	6	10	2	3	—	3											
Total	1673	1517	5862	3842	429	397	259	107	55	254	1	4	10	1	2	7	2	2	5	1	3

in table 5 are XX, those in table 6 are XXY. Table 7 gives similar data for progenies of exceptional daughters of later generations. Cultures 83 to 890 (table 7 first part) were from primary exceptions from the cultures listed in table 5. Cultures 43 to 862 (table 7 last part) were from secondary exceptions. Table 8 gives data from similar exceptions mated to *sc ec cv ct v g f* males. In this table, all the regular offspring are classfied for crossing-over. As in table 1 all cultures with less than 100 offspring were discarded.

Table 8. Progeny of $\dfrac{cv\ \ v\ \ f}{sc\ \ ec\ \ ct\ \ g}$ females $\times$ *sc ec cv ct v g f* males

Culture number	Exceptions female	Exceptions male	Regular 0	1	2	3	4	5	6	1,3	1,4	1,5	1,6	2,3	2,4	2,5	2,6	3,4	3,5	3,6	4,6	5,6
435	28	23	146	21	8	5	10	5	9								1	1	1		1	
436	28	35	142	12	10	4	2	2	5								1					
446	14	13	71	12	5	5	5		2													
447	27	15	101	7	18	5	1	1	7													
470	15	16	101	11	10	7	3	3	6				1							1	1	
471	60	28	186	27	18	11	5	1	8				1			1	2					
472	16	4	57	3	5	7	4	4	4							1					1	
473	22	19	184	21	27	23	3	3	17				1				1					1
474	21	26	116	6	9	12	1		8								2					
475	42	23	161	10	11	10	4	1	10								2					
485	22	23	109	8	5	8		1	5													
561	29	35	155	15	27	12	3	4	13				1									
562	35	25	157	12	8	9	5	3	12										1			
563	54	44	294	25	33	19	3	6	21						1				1			1
564	73	26	320	53	27	22	9	5	17				1			1	2			1		
565	13	13	78	9	12	2	1	1	3													
566	19	13	75	5	13	9	1	1	7			1	1									
567	31	16	160	23	24	21	4	2	11	1		1	1				1					
568	30	19	153	23	19	12	9	2	8								2					
569	9	5	62	5	8	2	2		8		1											
732	29	30	170	16	24	9	1		9						2		2					
734	17	9	71	4	5	2	3	2	8								1					
735	36	37	198	15	12	12	9		8				1									
746	15	4	62	10	7	5	3		3								1					
747	63	50	264	27	31	18	6	4	17								1					
748	34	22	125	6	4	7	6	2	7								1			1		
749	20	17	132	17	13	5	4	2	10								1					
750	19	8	119	17	23	5	3	2	7							1	1					
752	12	9	64	5	7	9	1	1	9													
753	24	11	143	17	17	9	1	1	4		1						1			1		
754	26	16	107	8	21	4	5	2	7							1						
756	28	26	127	6	5	7	2	4	5					1								
757	56	32	231	30	19	12	3	2	11											1		
767	52	35	180	17	15	12	4	4	12				1									
769	52	23	158	11	14	9	2	2	8	1			1									
Total	1071	750	4979	514	514	330	128	73	306	2	2	2	11	1	1	5	23	1	3	5	3	2

The percentage of primary non-disjunction may be determined from the totals of table 5. There were 460 exceptions in a total of 18062 offspring or 2·5 percent. There is again a deficit of male exceptions due also to relatively low viability of the y sc cv B and y f B males which constitute the class of exceptional sons in this table. A striking feature is the apparent equality of male and female exceptions (or excess of females) as contrasted with the large excess of primary exceptional males in normal lines, where from 4 to 8 times as many males as females are obtained (BRIDGES 1916, SAFIR 1920, MAVOR 1924, ANDERSON 1924).

The percentages of secondary non-disjunction are summarized in table 9. The average for all data (tables 1, 6, 7 and 8) is 22·8 percent.

Table 9. Summary of the percentages of exceptional offspring
from XXY mothers

Source of data	Total Progeny	Exceptions	Percentage
Table 1	39669	9416	23·7
Table 6	21497	4809	22·4
Table 7	14433	3190	22·1
Table 8	8726	1821	20·9
Total	84325	19236	22·8

The data on crossing-over, summarized from tables 6,7 and 8 are presented in table 10. The percentages agree substantially with those of table 2. The greatest reduction of crossing-over occurs in the ct-v and v-g regions where the crossing-over is only one-sixth and one-tenth respectively of the normal amount.

The percentages of crossing-over in the XX females of table 5 are consistently lower than those summarized in table 10 from the regular offspring of XXY females of the same X constitution. These percentages are compared in table 11. The total crossing-over from scute to forked is 20,5 percent in the XX females as compared with 29,0 percent in the corresponding XXY females. Comparison of crossing-over in XX and XXY females in normal lines had shown no significant difference (MORGAN, BRIDGES and STURTEVANT 1925).

27*

Table 10.   Summary of data on crossing-over from tables 6, 7 and 8.

Region	Table 6	Table 7	Table 8	Total	Total crossovers	Per-centage	coin-cidence	con-trols
Non-crossovers .	5847	3842	4979	14668				
1. *sc—ec* . . .	644	429	514	1587	1641	8·0	—	6·8
2. *ec—cv* . . .	680	397	514	1591	1653	8·1	—	9·7
3. *cv—ct* . . .	415	259	330	1004	1031	5·0	—	8·4
4. *ct—v* . . .	179	107	128	414	431	2·1	—	14·8
5. *v—g* . . .	40	55	73	168	195	1·0	—	11·2
6. *g—f* . . .	300	254	306	860	975	4·8	—	11·3
1, 3 . . .	1	—	2	3	—	—	·04	
1, 4 . . .	—	1	2	3	—	—	·09	
1, 5 . . .	—	4	2	6	—	—	.38	
1, 6 . . .	20	10	11	41	—	—	·52	
2, 3 . . .	—	—	1	1	—	—	·01	
2, 4 . . .	—	1	1	2	—	—	·06	
2, 5 . . .	5	2	5	12	—	—	·76	
2, 6 . . .	17	7	23	47	—	—	·60	
3, 4 . . .	—	2	1	3	—	—	·14	
3, 5 . . .	1	2	3	6	—	—	·61	
3, 6 . . .	7	5	5	17	—	—	·35	
4, 5 . . .	—	1	—	1	—	—	·24	
4, 6 . . .	2	3	3	8	—	—	·39	
5, 6 . . .	—	—	2	2	—	—	·22	
Total	8158	5381	6905	20444	—	29·0	—	62·2

Table 11.   Comparison of crossing-over in XX and XXY females

of constitution $\dfrac{cv \quad v \quad f}{sc \quad ec \quad ct \quad g}$

Region	XY	XXY	Ratio XX to XXY
sc—ec	5·5	8·0	·69
ec—cv	5·4	8·1	·67
cv—ct	3·9	5·0	·78
ct—v	1·4	2·1	·67
v—g	·7	1·0	·70
g—f	3·6	4·8	·75
	20·5	29·0	·71

Localization

In order to determine what portion of the *cv v g* chromosome was responsible for the high non-disjunction and related effects, individuals were tested which contained only portions of that chromosome. These were selected from the regular offspring of $\dfrac{cv \quad v \quad f}{sc\ ec \quad ct \quad g}$ females by *sc ec cv ct v g f* males, listed in table 7. Only crossovers in the regions nearest to vermilion will be considered, and the genes *sc* and *ec* will be disregarded.

Crossing-over between cut and vermilion gives rise to *ct v f* and *cv g* combinations. Table 12 summarizes the progeny of *ct v f* females.

Table 12.   Progeny of *ct v f* regular females from table 8

Culture number	Total	Ex-ceptions	Per-cent-age	Re-gular males	cross-overs *cv—g*	Per-cent-age	Tests of *ct v f* sons	Tests of exceptional daughters		
								Total offspring	Percent exceptions	Percent crossovers *cv — g*
516	281	3	1·7	119	8	6·7	sterile			
531	158	2	2·7	76	1	1·3	sterile	202	25·3	8·2
532	299	77	25 8	97	8	8·2	sterile			
671	122	2	1·6	48	5	10·4				
677	189	6	3.2	93	1	1·1				
792	189	3	1·6	84	3	3·6	sterile			
804	230	4	1·7	98	5	5·1	sterile	119	28·5	5·6
821	66	3	4·5	34	2	5·9	sterile	85	18·8	3·6
Expectation control						34·4	—	—	4·0	34 4
Expectation high non-disjunction						8·1	—	—	22·8	8·1

These gave typical high non-disjunction progenies with high (XXY) or low (XX) percentages of exceptions, low crossing-over, and sterile *ct v f* males. In three cases exceptional daughters tested gave high percentages of exceptions and low crossing-over. Similar data for *cv g* females are presented in table 13. These progenies are normal, with low percentages of exceptions or none at all, normal crossing-over and fertile *cv g* males. Exceptional daughters from three of the cultures were tested, giving low percentages of exceptions. These tests show that te left end of the *cv v f* chromosomes is normal up to and including the locus of cut.

Table 13. Progeny of *cv g* regular females from table 8

Culture number	Total	Exceptions	Percentage	Regular males	Crossovers				Tests of *cv g* sons	Tests of exceptional daughters	
					ct—v	Percentage	*v—f*	Percentage		Total offspring	Percent exceptions
518	407	0	—	194	24	12·4	39	20·1			
536	260	0	—	125	20	16·0	36	28·8	fertile		
537	311	1	·3	139	16	11·5	35	25·2	fertile		
801	490	1	·2	232	24	10·3	53	22·8	fertile		
802	344	18	5·2	139	22	15·8	30	21·6	fertile		
824	383	25	6·5	165	27	16·4	37	22·4	fertile	499	7·6
825	228	19	8·3	74	13	17·6	17	23·0	fertile	159	2·5
878	156	0	—	83	15	18·1	19	22·9	fertile		
879	300	24	8·0	126	21	16·7	28	22·2	fertile	240	2·5
Expectation control						14·8	—	22·5	—	—	4·0
Expectation high non-disjunction						2·1	—	5·8	—	—	22·8

Crossing-over between vermilion and garnet gives rise to *cv v g* and *ct f* combinations. Tests of *cv v g* and *ct f* females are summarized in tables 14 and 15. The *cv v g* females gave typical high non-disjunction XX progenies while the *ct f* females gave normal progenies. These tests show that the region to the right of and including garnet is normal. No separation was found between *v* and the locus of the disturbing factor.

Tests for fertility of males from the high non-disjunction cultures listed in table 5, 6, 7 and 8 are in agreement with the data above.

Table 14. Progeny of *cv v g* regular females from table 8.

Culture number	Total	Exceptions	Percentage	Regular males	crossovers *ct—f*	Percentage	Tests of *cv vg* sons
678	112	3	2·7	45	1	2·2	
794	307	6	2·0	164	13	7·9	sterile
806	127	1	·8	55	5	9·1	sterile
876	128	1	·8	58	1	1·7	sterile
Expectation control						37·3	
Expectation high non-disjunction						7·9	

Table 15. Progeny of *ct f* regular females from table 8

Culture number	Total	Fx-ceptions	Per-cent-age	Re-gular males	crossovers				Tests of
					cv—v	Percent-age	*v—g*	Percent-age	*ct f* sons
680	158	6	3·8	57	11	19·	3	5·	
805	118	3	2·5	61	11	18·	6	10·	fertile
807	87	0	—	38	5	13·	5	13·	fertile
883	92	0	—	37	5	13·	2	5.	
Expectation control						23·2	—	11·2	
Expectation high non-disjunction						7·1	—	1·0	

No *ct v f* or *cv v g* males gave any offspring. Many were continued through successive culture bottles, some of which were kept in prime condition by adding a gravid female from some other stock. Offspring were obtained from most of the *cv g* and *ct f* males tested. The failures were cultures where the male died early without offspring and may or may not have been fertile.

The locus of the high non-disjunction modification is therefore restricted to the region between cut and garnet with sufficient distance between it and either of the two genes to allow occasional crossovers. The map distance between cut and garnet determined from the control data is 26·0 units. In addition to vermilion there are within this distance two usuable genes tan (33·4) and miniature (42·7) one of either side of vermilion. These two genes have been used to delimit more closely the affected region.

Localization with reference to tan and miniature

Exceptional females from the high non-disjunction line were mated to cut tan miniature garnet *(ct t m g)* males. Wildtype regular daughters were mated to cut tan vermilion miniature garnet *(ct t v m g)* males. Some of the exceptional daughters were again mated to *ct t v m g* males giving similar cultures. Thirty-one XXY cultures gave 7181 offspring of which 1626 or 22·6 percent were exceptional. Among these exceptions there were only 679 males to 947 females, a ratio of ·72 to 1·00. This ratio is lower than those given in the previous tables except table 8 where the exceptional males were the multiple recessive *sc ec cv ct v g f*. It probably represents only the relative viability of *ct t v m g* males versus wild-type females.

Forty-seven XX cultures gave 13214 offspring of which 262 or 2·0 percent were exceptional. There were only 66 males to 196 females or a ratio of ·34 to 1,0. This is much lower than the ratio above for secondary exceptions of the same X constitution. Throughout the work on high non-disjunction and on X-ray the primary exceptional males have appeared to be much feebler and less hardy than corresponding secondary exceptional males, though no attempt has been made to verify this impression. If true, it indicates that the absence of the Y chromosome in the males not only causes sterility but also reduces viability. Whether all of the observed deficit of males is to be accounted for thus is open to question but cannot be settled on the present data.

Data on crossing-over in the regions from cut to garnet are presented in table 16 which summarizes the regular progeny. The

Table 16. Summary of regular progeny of $\dfrac{cv \quad v \quad f}{ct \ t \ m \ g}$ females

Region	XX	XXY	Total Crossovers	Percentage	Controls
non-crossovers .	12708	5411			
ct—t . . .	105	72	178	·96	8 5
t—v . . .	31	10	41	·22	6·3
v—m . . .	4	1	5	·03	3·0
m—g . . .	104	60	165	·89	·8·2
ct—t, m—g .	—	1			
Total	12952	5555	18507	2·1	26 0

greatest reduction in crossing-over is found in the short regions neighboring vermilion. The *t-v* region shows only three and one-half percent of its normal amount of crossing-over, the *v-m* region only one percent.

The crossovers subjected to tests were those which occurred in the *t-v* and *v-f* regions. The former gave *ct t v f* and *m g* combinations. Six *ct t v f* males were tested for fertility. All proved sterile. Table 17 gives a summary of tests of four *ct t v f* females. All gave typical high non-disjunction XX progenies. Seven *m g* males were tested. Two died before the first examination of the cultures. Of the remaining five, four were fertile while one gave no offspring although transferred twice to new culture bottles. Table 18 gives the results of tests of four *m g* females. All gave apparently normal crossing-over, but the cultures were small. The percentage of exceptions could not be de-

Table 17. Progeny of *ct t v f* regular females from table 16

Culture number	Total	Ex-ceptions	Per-cent-age	Re-gular males	Cross-overs *m—g*	Per-cent-age	Tests of *ct t v f* sons	Tests of exceptional daughters		
								Total offspring	Percent exceptions	Percent crossovers *m—g*
1020	107	2	1·9	50	0	—	sterile	339	23·2	·8
1029	387	12	3·1	171	5	2·9	sterile	1340	22·8	1·1
1030	68	0	—	30	1	—	sterile			
1031	40	0	—	17	0	—	sterile			
Expectation control						8·2	—	—	4·0	8·2
Expectation high non-disjunction						·9	—	—	22·8	·9

Table 18. Progeny of *m—g* regular females from table 16

Culture number	Regular males	Crossovers			
		ct—t	Percentage	*t—v*	Percentage
1026	91	5	—	10	
1027	36	2	—	4	
1028	18	2	—	0	
1043	69	4	—	7	
Total	214	13	6·1	21	9·7

termined because of non-virginity. The *m g* sons of culture 1026 were
tested and proved fertile. Three regular daughters of culture 1026
were also tested (table 19) giving low percents of exceptions and normal
crossing-over.

Table 19. Progeny of regular daughters of culture number 1026

Culture number	Total	Exceptions	Percentage	Regular males	Crossovers		
					v—m	*m—g*	*g—f*
1038	308	4	1·3	135	0	15	18
1039	262	0	—	115	4	11	10
1040	510	2	·4	215	2	27	24
Total				465	6	53	52
Percent				—	1·3	11·4	11·2

One *ct t f* female was tested. The progeny consisted of 32 regular females and 20 regular males of which 2 were *m-g* cross-overs. The *ct t f* sons were fertile. Three of the regular daughters carrying the *ct t f* chromosome gave a total of 941 regular offspring and no exceptions. The males were classified for crossing-over giving the following percentages *cv-ct* 5·9, *ct-t* 5·0 and *t-v* 6·3. These data show the normality of the *ct t f* chromosome. One *v m g* male was put up in culture to test for fertility. No offspring were obtained but the male died so early that the results were not of significance. No other tests were obtained.

These tests show that the left end of the chromosome up to and including the locus of tan is normal. They also show that the right end is normal inclusive of the locus of miniature.

Inheritance of high non-disjunction

The localization tests have shown that all of the *cv v f* chromosome is normal except for a region of less than 9·3 units map distance between tan and miniature. Crossing-over has been demonstrated between tan and the affected region and also between this region and miniature, but crossing-over is so much reduced in this region that it is not possible to evaluate with any confidence the proportion of the region which is normal. The gene for vermilion is included in this region, no separation from vermilion having been demonstrated. No separation has occurred between the diverse characteristics of the high non-disjunction line, which include high primary non-disjunction, high secondary non-disjunction, high frequency of equational exceptions, low crossing-over, and sterility of males. These facts all point to the conclusion that all these characteristics behave as a single unit and are the result of a single gene or may be an inverted section or a deficiency. In the absence of any experimental method of distinguishing a gene mutation from a short inversion or deficiency covering no additional known loci, the simplest interpretation, that of a single gene mutation, is preferable because of its convenience. Throughout the remaining portion of this paper, it will be referred to as the gene for high non-disjunction.

The results of this study are in strong contrast to the results of BONNIER (1923, 1924) working on the line of high non-disjunction found by BRIDGES. In that line the high percentage of exceptions was recessive to the normal, males were fertile, and there was no correspondingly high primary non-disjunction shown.

Diverse effects of the high non-disjunction gene

In this section a summary will be made of the diverse differences which have been observed between high non-disjunction and normal cultures, differences which may be attributed to the gene responsible for high non-disjunction.

Sterility of males. All males which carry the high non-disjunction gene are sterile. There is however no apparent reduction in vigor or viability as shown by the regularity of the one to one ratio with normals.

Lethalness of homozygous female. No homozygous high non-disjunction females have occurred by equational non-disjunction. The expected number of these can be estimated from the observed number of exceptions equational for the corresponding region of the normal chromosome. From $\dfrac{ev}{sc\ ec}\ \dfrac{v}{ct}\ \dfrac{f}{g}$
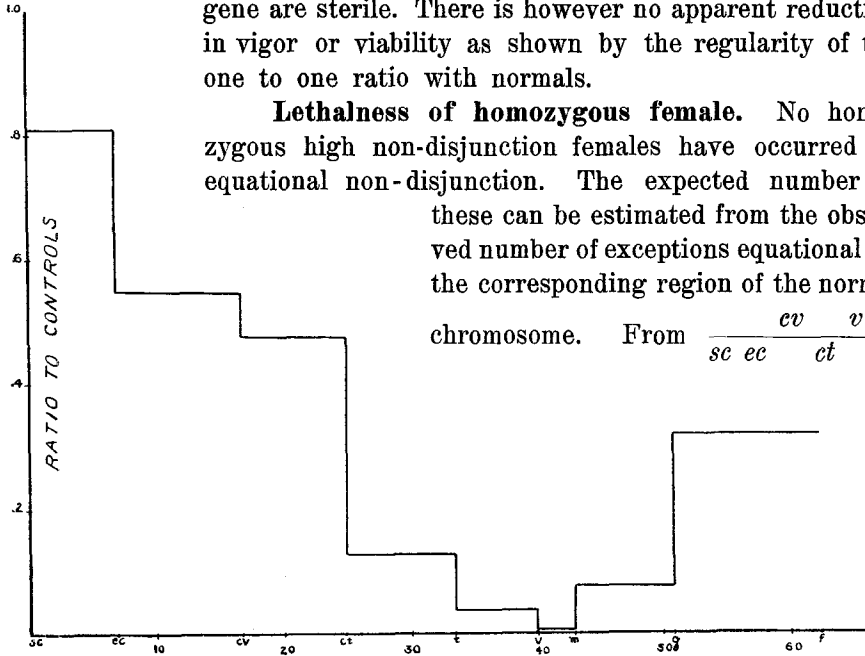
Figure 2.   Effect of the high non-disjunction gene on crossing-over

cultures, there were 22 exceptions equational for cut, and 18 for garnet (see table 22). The number expected for vermilion which is at or near the locus of high non-disjunction is about 20. The absence of equationals for vermilion is evidence of lethalness rather than sterility, which would only prevent a progeny test.

Reduction of crossing-over. The total amount of crossing-over between *sc* and *f* is only 20·5 percent in XX females heterozygous for the high non-disjunction gene as contrasted with 62·2 percent in the controls. The relative amounts of crossing-over are presented graphically in figure 2. The reduction is greatest in the regions adjacent to ver-

milion, rising gradually toward normal for regions further removed. The percentages of crossing-over in high non-disjunction cultures are those given in table 11. The values for the short distances involving *t* and *m* are obtained by dividing the *ct-v* and *v-g* percentages into parts proportional to the percentage of crossing-over in table 16.

High primary non-disjunction. Cultures from XX females carrying the high non-disjunction gene have given slightly over two percent of primary non-disjunction. Normal lines give much less than one-tenth of one percent of primary exceptions. Among the primary exceptions there is apparently an equal sex ratio (or excess of females) in contrast to normal lines where from 4 to 8 times as many males as females are obtained.

High secondary non-disjunction. The high non-disjunction of XXY females has given a mean of 22·8 percent of secondary exceptions in contrast to the usual 3 to 4 percent obtained in normal lines.

High percentage of equational exceptions. Among the secondary exceptions are many which are homozygous for a part of one of the parental chromosomes. In normal lines the secondary exceptions are rarely different in X constitution from their mother. In the high non-disjunction line the parental X constitution is altered in about ten percent of the exceptions by crossing-over.

Phenotypic constitution of exceptions

Many of the exceptional females obtained in the high non-disjunction line are equational. This is in sharp contrast to results obtained in normal lines where the exceptions are almost invariably of the same X constitution as their mother (BRIDGES 1916). Table 20 gives the distribution of phenotypes among the exceptional daughters of $\dfrac{cv\ v\qquad f}{sc\ ec\quad v\ g}$ females from the high non-disjunction line. Five percent of the exceptional daughters were equational for part of the chromosome thus adding to the evidence already adduced (BRIDGES 1916, L. V. MORGAN 1925, ANDERSON 1925, BRIDGES and ANDERSON 1925) for crossing-over in the four-strand stage. The frequency of homozygosis of the recessive genes *sc ec cv g* and *f* is given in table 21. No equational was obtained homozygous for *f*, indicating that the right end of the chromosome rarely, if ever, becomes homozygous. Proceeding toward the left end of the chromosome there was a regularly increasing frequency, reaching 3·7 percent

Table 20.   Exceptional daughters of $\dfrac{cv \quad v \quad f}{sc \quad ec \quad v \quad g}$ mothers

Phenotype	Number	Percentage
v	5455	94·85
$sc\ v$	70	1·22
$sc\ ec\ v$	138	2·40
$sc\ ec\ v\ g$	4	·07
$ec\ v\ g$	2	·03
$ec\ v$	1	·02
$v\ g$	18	·31
$cv\ v$	62	1·08
$sc\ cv\ v$	1	·02
Total	5751	100·00

Table 21.   Frequency of homozygosis of recessive genes in exceptional

daughters of $\dfrac{cv \quad v \quad f}{sc \quad ec \quad v \quad g}$ mothers

Gene	Number	Percentage
sc	213	3·7
ec	145	2·5
cv	63	1·1
g	24	·4
f	0	

for scute. The corresponding data for the exceptional daughters of $\dfrac{cv \quad v \quad f}{sc \quad ec \quad ct \quad g}$ females are presented in tables 22 and 23 (p. 330). Here the frequencies of homozygosis were not quite so high. About four and one-half percent were equational. Two were homozygous for forked. There was the same increasing frequency toward the left, reaching 3·1 percent for scute. However none was homozygous for vermilion. As there appears to be no reason why these should not be formed in the expected proportion, this may be taken as evidence that the high non-disjunction factor is lethal when homozygous in the female. The sterility of the males carrying this factor prevented a direct test such as would otherwise have been obtained by mating these males to exceptional females from the high non-disjunction line.

Table 22. Exceptional daughters of $\dfrac{cv \quad v \; f}{sc \quad ec \quad ct \quad g}$ mothers

Phenotype	number	percentage
+	5524	95·47
sc	78	1·35
sc ec	91	1·57
sc ec ct	7	0·12
sc ec ct g	4	0·07
ec ct g	1	0·02
ec	1	0·02
ct	3	0·05
ct g	7	0·12
g	6	0·10
cv	62	1·07
f	2	0·03
Total	5786	99·99

Table 23. Frequency of homozygosis of recessive genes in exceptional daughters of $\dfrac{cv \quad v \; f}{sc \quad ec \quad ct \quad g}$ mothers

Gene	number	percentage
sc	180	3·1
ec	104	1·8
cv	62	1·1
ct	22	0·4
v	0	
g	18	0·3
f	2	0·03

Genotypic constitution of exceptions

The genotypic constitutions of a number of exceptional females were determined from progeny tests. The results of these determinations are presented in tables 24 and 25. The percentage frequencies given are calculated as proportional parts of the percentage distribution of phenotypes in tables 20 and 22 respectively. For convenience in analysis there is included a schematic representation of the genotypic constitutions using 'a' to represent any gene from the *cv v f* parental chromosome and 'b' to represent any gene from the *sc ec v g* or *sc ec ct g* chromosome.

Table 24. Genotypic constitution of exceptional daughters of $\dfrac{cv \quad v \quad f}{sc \quad ec \quad v \; g}$ mothers

Phenotype	number tested	Genotype	Schematic representation	Cross-over	Frequency	Proportional percentage
v	229	$\dfrac{cv \; v \; f}{sc \; ec \; v \; g}$	$\dfrac{a \; a \; a \; a \; a}{b \; b \; b \; b \; b}$	0—0	219	90·71
		$\dfrac{sc \; ec \; cv v \; f}{v \; g}$	$\dfrac{b \; b \; a \; a \; a}{a \; a \; b \; b \; b}$	2—2	5	2·07
		$\dfrac{sc \; ec \; v \; f}{cv \; v \; g}$	$\dfrac{b \; b \; b \; a \; a}{a \; a \; a \; b \; b}$	3—3	2	0·83
		$\dfrac{cv \; v \; f}{ec \; v \; g}$	$\dfrac{a \; a \; a \; a \; a}{a \; b \; b \; b \; b}$	0—1	1	0·41
		$\dfrac{cv \; v \; f}{\sim \; v \; g}$	$\dfrac{a \; a \; a \; a \; a}{a \; a \; b \; b \; b}$	0—2	2	0·83
sc v	10	$\dfrac{sc \; cv \; v \; f}{sc \; ec \; v \; g}$	$\dfrac{b \; a \; a \; a \; a}{b \; b \; b \; b \; b}$	1—0	10	1·22
sc ec v	29	$\dfrac{se \; ec \; cv v \; f}{sc \; ec \; v \; g}$	$\dfrac{b \; b \; a \; a \; a}{b \; b \; b \; b \; b}$	2—0	18	1·49
		$\dfrac{sc \; ec \; v \; f}{sc \; ec \; v \; g}$	$\dfrac{b \; b \; b \; a \; a}{b \; b \; b \; b \; b}$	3—0	11	0·91
ev v	11	$\dfrac{cv \; v \; f}{cv \; v \; g}$	$\dfrac{a \; a \; a \; a \; a}{a \; a \; a \; b \; b}$	0—3	10	0.98
		$\dfrac{cv \; v \; f}{sc \; ec \; cv v \; g}$	$\dfrac{a \; a \; a \; a \; a}{b \; b \; a \; b \; b}$	0—2,3	1	0·10
v g	10	$\dfrac{cv \; v \; g}{sc \; ec \; v \; g}$	$\dfrac{a \; a \; a \; b \; b}{b \; b \; b \; b \; b}$	3—0	5	0·16
		$\dfrac{v \; g}{sc \; ec \; v \; g}$	$\dfrac{a \; a \; b \; b \; b}{b \; b \; b \; b \; b}$	2—0	1	0·03
		$\dfrac{cv \; v \; g f}{sc \; ec \; v \; g}$	$\dfrac{a \; a \; a \; b \; a}{b \; b \; b \; b \; b}$	3,4—0	1	0·03
		$\dfrac{cv \; v \; g}{sc \; ec \; v \; g f}$	$\dfrac{a \; a \; a \; b \; b}{b \; b \; b \; b \; a}$	3—4	2	0·06
		$\dfrac{v \; g}{sc \; ec \; v \; g f}$	$\dfrac{a \; a \; b \; b \; b}{b \; b \; b \; b \; a}$	2—4	1	0·03
sc ec v g		$\dfrac{sc \; ec \; v \; g}{sc \; ec \; v \; g}$	$\dfrac{b \; b \; b \; b \; b}{b \; b \; b \; b \; b}$	0—0	1	0·07

Table 25. Genotypic constitution of exceptional daughters of $\dfrac{cv \quad v \quad f}{sc \ ec \quad ct \quad g}$ mothers

Phenotype	number tested	Genotype	Schematic representation	Crossovers	Frequency	Proportional percentage
+	1005	cv v f / sc ec ct g	a a a a a a / b b b b b b	0—0	939	89·19
		sc cv v f / ee ct g	b a a a a a / a b b b b b	1—1	16	1·52
		sc ec cv v f / ct g	b b a a a a / a a b b b b	2—2	10	·95
		sc ec v f / cv ct g	b b b a a a / a a a b b b	3—3	4	·38
		sc ec ct v f / cv g	b b b b a a a / a a a a b b b	4—4	4	·38
		sc ec ct g f / cv v	b b b b b a / a a a a a b	6—6	1	·09
		ct v f / sc ec cv g	a a b b a a a / b b a a b b b	2,4—2,4	1	·09
		cv v f / ec ct g	a a a a a a / a b b b b b	0—1	14	1·33
		cv v f / ct g	a a a a a a / a a b b b b	0—2	16	1·52
sc	25	sc cv v f / sc ec ct g	b a a a a a / b b b b b b	1—0	24	1·30
		sc ec cv v f / sc ct g	b b a a a a / b a b b b b	2—1,2	1	·05
sc ec	61	sc ec cv v f / sc ec ct g	b b a a a a / b b b b b b	2—0	39	1·00
		sc ec v f / sc ec ct g	b b b a a a / b b b b b b	3—0	22	·57
sc ec ct	4	sc ec ct v f / sc ec ct g	b b b b a a a / b b b b b b	4—0	4	·12
ec ct g	1	ec ct g / sc ec ct g	a b b b b b b / b b b b b b	1—0	1	·02
ct g	4	ct g / sc ec ct g	a a b b b b b / b b b b b b	2—0	1	·03
		cv ct g / sc ec ct g	a a a b b b / b b b b b b	3—0	3	·09

Table 25. Continued

Pheno-type	number tested	Genotype	Schematic representation	Cross-overs	Fre-quency	Pro-portional per-centage
ct	2	$\dfrac{ct \quad f}{sc\ ec \quad ct \quad g}$	$\dfrac{a\,a\,b\,b\,b\,a\,a}{b\,b\,b\,b\,b\,b}$	2,5—0	1	·03
		$\dfrac{sc\ ec \quad ct \quad f}{ct \quad g}$	$\dfrac{b\,b\,b\,b\,b\,a\,a}{a\,a\,b\,b\,b\,b\,b}$	5—2	1	·03
g	4	$\dfrac{sc\ ec \quad ct \quad g\ f}{cv \quad g}$	$\dfrac{b\,b\,b\,b\,b\,b\,a}{a\,a\,a\,a\,b\,b\,a}$	6—4	1	·03
		$\dfrac{cv \quad g\ f}{sc\ ec \quad ct \quad g}$	$\dfrac{a\,a\,a\,a\,b\,b\,a}{b\,b\,b\,b\,b\,b}$	4,6—0	1	·03
		$\dfrac{cv \quad v\ g}{ec \quad ct \quad g}$	$\dfrac{a\,a\,a\,a\,a\,b\,b}{a\,b\,b\,b\,b\,b\,b}$	5—1	2	·05
cv	36	$\dfrac{cv \quad v \quad f}{cv\ ct \quad g}$	$\dfrac{a\,a\,a\,a\,a\,a\,a}{a\,a\,a\,b\,b\,b\,b}$	0—3	22	·65
		$\dfrac{cv \quad v \quad f}{cv \quad g}$	$\dfrac{a\,a\,a\,a\,a\,a\,a}{a\,a\,a\,a\,b\,b\,b}$	0—4	11	·33
		$\dfrac{cv \quad v \quad f}{sc\ ec\ cv\ ct \quad g}$	$\dfrac{a\,a\,a\,a\,a\,a\,a}{b\,b\,a\,b\,b\,b\,b}$	0—2,3	1	·03
		$\dfrac{sc \quad cv \quad v \quad f}{cv\ ct \quad g}$	$\dfrac{b\,a\,a\,a\,a\,a\,a}{a\,a\,a\,b\,b\,b\,b}$	1—3	1	·03
		$\dfrac{sc \quad cv \quad v \quad f}{cv \quad g}$	$\dfrac{b\,a\,a\,a\,a\,a\,a}{a\,a\,a\,a\,b\,b\,b}$	1—4	1	·03
f	2	$\dfrac{cv \quad v \quad f}{sc\ ec \quad ct \quad f}$	$\dfrac{a\,a\,a\,a\,a\,a\,a}{b\,b\,b\,b\,b\,a\,a}$	0—5	1	·02
		$\dfrac{cv \quad v \quad f}{sc\ ec \quad ct \quad g\,f}$	$\dfrac{a\,a\,a\,a\,a\,a\,a}{b\,b\,b\,b\,b\,b\,a}$	0—6	1	·02

The numbers involved in table 24 are comparatively few. The data from both tables will be used in the following section where the data can readily be combined. But in the sections dealing with crossing-over, only the data from table 25 will be used.

Equationals

The percentage of homozygosis of genes which were heterozygous in the parent may also be summarized from the genotypic frequencies of tables 24 and 25. Since these distributions are so largely controlled by the phenotypic frequencies of tables 20 and 22 respectively, the

percentages must parallel very closely those of tables 21 and 23. But they have the advantage that the homozygosis of normal allelomorphs can be tabulated as well as the recessive mutant genes. Such a tabulation has been made and is given in tables 26 and 27.

Table 26. Frequency of homozygosis of genes. Data from table 24

Locus	sc ec v g Chromosome	cv v f Chromosome
sc	3·7	2·2
ec	2·5	1·8
cv	1·0	1·1
g	·4	0
f	·3	0

Table 27. Frequency of homozygosis of genes. Data from table 25

Locus	sc ec ct g Chromosome	cv v f Chromosome
sc	3·0	3·9
ec	1·7	2·6
ev	·8	1·1
ct	·3	·4
v	·3	0
g	·2	·02
f	·2	·04

The *sc ec v g* and *sc es ct g* chromosomes are entirely normal and give a fairly regular distribution of frequencies. By combining the data from both tables we get the following

locus	percentage of homozygosis
sc	3·4
ec	2·1
cv	·9
g	·3
f	·2

The seriation is regular and indicates that the extreme right end, beyond *f* must seldom if ever become homozygous. The percentages increase regularly toward the left, rising to three percent at *sc*. The apparent absence of homozygosis at the right or spindle fiber end shows that the non-disjunction regularly takes place at the reductional division.

Crossing-over shown by exceptions

In normal non-disjunction lines the secondary exceptional daughters almost invariably have the same X constitution as their mother. Very little if any crossing-over has taken place in the X chromosomes which go into the exceptional (XX) eggs. This was shown by the direct test made by BRIDGES (1916) and by the very rare occurrence of equational exceptions in those lines.

The frequent occurrence of equational exceptions in the high non-disjunction line is due to the frequent occurrence of crossing-over in the X chromosomes which go into the exceptional XX eggs. The amount of crossing-over which occurs in these chromosomes can be determined from the data presented in table 25. This crossing-over is summarized in table 28. For comparison the percentages of crossing-over shown by the regular offspring are also given.

Table 28
The percentage of crossing over shown by exceptional daughters

Region	Exceptions	Regulars	Ratio
sc-ec	2·9	8·0	·36
ec-cv	2·4	8·1	·30
cv-ct	1·1	5·0	·22
ct-v	·7	2·1	·33
v-g	·1	1·0	·10
g-f	·1	4·3	·02
Total	7·3	29·0	·25

The percentages of crossing-over obtained are rather irregular but are all distinctly lower than the corresponding percentages for the regular offspring. They are especially low at the extreme right end. The total crossing-over from sc to f is only 7·3 percent as compared with 29·0 percent for the regular offspring.

Association of chromosomes

The decreasing percentage of exceptions homozygous for genes toward the right end of the chromosome map indicates that non-disjunction occurs at the reduction division and that it is always regular at the spindle fiber attachment. Equationals are obtained through the occurrence of crossing-over which disturbs the original arrangement of

28*

strands and tends to make the association of strands more and more random as we approach the left end. The rightmost crossovers are of special interest since in these we deal with the first disturbance of the original arrangement of strand. Table 29 gives a summary of rightmost crossovers.

Table 29. Association of crossovers. Rightmost crossovers only

Type of Association	Formula	1	2	3	4	5	6	Total
Equational	$\dfrac{a\ b}{a\ a}$	2·63	2·52	1·28	·48	·06	·06	7·03
Reciprocal	$\dfrac{a\ b}{b\ a}$	1·52	1·09	·38	·47	—	·09	3·55

In these crossovers the strands on the right are the original strands. If crossing-over takes place between identical strands no change will be apparent. If any one strand crosses over equally freely with each of the two strands from the opposite chromosome, it will result in a ratio of two $\dfrac{a\ b}{a\ a}$ combinations to one which is $\dfrac{a\ b.}{b\ a}$ The observed frequencies are 7·03 to 3·55 with a very slight error due to elimination of homozygous vermilion combinations.

This is a very close approximation and indicates that crossing-over is at random with reference to the strands which remain associated in the XX eggs.

Proceeding toward the left, the arrangement of strands becomes more and more disarranged through crossing-over, until a condition should be reached where the assortment of strands at the spindle fiber end should have no influence. Here random assortment should give a ratio of four $\dfrac{a\ b}{a\ a}$ and $\dfrac{b\ a}{a\ a}$ combinations to one $\dfrac{a\ b}{b\ a}$ combination when all crossovers are considered. This condition however should not be reached until the percentage of homozygosis becomes random (16·7 percent). The observed data (table 30) give a ratio of only 2·13 to 1. The ratios for the two leftmost regions average only 2·1 to 1. These low values are in accord with the phenotypic data of tables 20 to 23 in showing that the influence of the association of strands at the spindle fiber end is very strong even to the extreme left end of the chromosome.

Table 30. Association of crossovers. All crossovers

Type of Association	Formula	1	2	3	4	5	6	Total
Equational	$\dfrac{a\ b}{a\ a}$	2·73	2·52	1·28	·48	·06	·06	7·57
	$\dfrac{b\ a}{a\ a}$	·08	·12	·09	·06	·07	·02	
Reciprocal	$\dfrac{a\ b}{b\ a}$	1·52	1·09	·38	·47	—	·09	3·55

Crossing-over in XX and XXY females

In the preceding sections crossing-over has been computed from the regular offspring alone. When thus computed, crossing-over in high non-disjunction XX females is shown to be consistently lower than in XXY females of corresponding constitution. The ratios obtained when comparing the crossing-over in the XX and XXY cultures have been presented in table 11. In XX females there was 20·5 percent of crossing-over between sc and f; in the XXY females there was 29·0 percent. The ratio is thus ·71 to 1·00.

A similar comparison may be made between XX and XXY cultures from $\dfrac{cv\qquad v\qquad f}{ct\ \ t\quad m\ g}$ females (table 16). Here the XX cultures gave 1·88 percent of crossing-over between cut and garnet. The XXY cultures gave 2·61 percent. The relative amount is ·72, almost the same as in the preceding data.

As shown in table 28 the percentage of crossing-over calculated from the secondary exceptions is much lower than that calculated from regular offspring. For the entire distance from sc to f it is only 7·3 percent as compared with 29·0 percent for the regular offspring. If the calculation is based on both regular and exceptional offspring, the total crossing-over from sc to f is 20·9 percent[1]), very close to the

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[1]) In the calculation above it is necessary to double the frequency of the exceptions to correct for the elimination of one-half of the exceptional eggs.

$$7·3 \times 228 \ \ldots \ldots \ldots \ \ 3·33$$
$$29·0 \times ·772 \ \ldots \ldots \ \ \ 22·39$$

total crossovers . . . . . 25·72
total frequency . . . . . 122·8
percent of crossing-over . . 20·9

20·5 percent obtained in the regular offspring of XX females. The total percentage for XX females would not be appreciably altered by including the primary exceptions. Table 31 gives a comparison of crossing-over in XXY and XX females for each region.

Table 31.   Crossing over in xxy and xx females

Region	xxy regulars	xxy exceptions	xxy combined	xx
sc-ec	8·0	2·9	6·1	5.5
ec-cv	8·1	2·4	6·0	5·4
cv-ct	5·0	1·1	3·6	3·9
ct-v	2·1	·7	1·6	1·4
v-g	1·0	·1	·6	·7
g-f	4·8	·1	3·0	3·6
Total	29·0	7·3	20·9	20·5

The close correspondence of the total amounts of crossing-over in XXY and XX females suggests the interesting hypothesis that crossing over is identical in both cases and is independent of the presence or absence of the Y chromosome; but that the chromosomes which go into exceptional eggs are selected preponderantly from the non-crossover classes. This virtually means that of the two processes, crossing-over is the first to take place or at least to be determined and secondary non-disjunction is a subsequent process. On this hypothesis the presence of the Y chromosome could have no influence on the synapsis of the two X chromosomes nor on the interchange of material between them (i. e. crossing-over). The role of the Y chromosome would come later in causing many of the more loosely paired X chromosomes to be distributed to the same pole.

The mechanism of crossing-over and non-disjunction

Abundant evidence has been presented by BRIDGES (1916), L. V. MORGAN (1925), ANDERSON (1925 a), BRIDGES and ANDERSON (1925), STURTEVANT (unpublished) and in the present paper to show that crossing-over in the X chromosomes occurs regularly at the four strand stage, and that generally only two of the four strand cross over at any one level.

The attached-X cases (L. V. MORGAN 1922, 1925, ANDERSON 1925 a and unpublished data of STURTEVANT) and the attachment of the X and

Y chromosomes (STERN 1926, 1927) show that the spindle fiber is attached at the right or $f\,B$ end of the chromosomes. They also show that attachment at this end does not prevent or greatly alter the normal amount of crossing-over. In the attached-X cases where assortment is determined by the permanent attachment of the chromosomes at the spindle fiber end, genes near the point of attachment seldom become homozygous. This is taken to show that the separation of chromosomes is controlled at the spindle fiber end and perhaps by the spindle fibers themselves. Proceeding to the left, away from the spindle fiber end, there is an increasing percentage of homozygosis, approaching randomness near the middle of the chromosome.

If crossing-over between the different strands is at random, the ratio of $\dfrac{a\ b}{a\ a}$ to $\dfrac{a\ b}{b\ a}$ combinations should be two to one [1]) and the percentage of homozygosis of any gene near the point of attachment should equal one-half of the percentage of crossing-over between it and the spindle fiber attachment. Both expectations are realized in the observed data. As the distance from the point of attachment is increased, the percentage of homozygosis drops below one-half of the percent of crossing-over due to multiple crossing-over.

A study of crossing-over in triploids (BRIDGES and ANDERSON, 1925) has shown almost the same seriation in percentages of homozygosis, indicating that the distribution of chromosomes may be as regular at the spindle fiber end as in the attached-X cases. But the complexity of the data due to the presence of six strands rather than four makes it difficult to compare with the attached-X data.

The data on exceptions presented in this paper are more readily compared with the attached-X data. Here again the percentages of

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[1]) This relation can best be illustrated by an example. If there is 20 percent of crossing-over between a and the spindle fiber attachment, then there should be 20 crossovers among 100 chromosomes (50 attached pairs). These should be distributed as follows;

$5\ \dfrac{a\ b}{b\ a}$

$5\ \dfrac{a\ b}{a\ a}$ (homozygous for a)

$5\ \dfrac{b\ b}{b\ a}$ (homozygous for normal allelomorph of a)

Thus 5 out of 50 individuals will be homozygous for the recessive allelomorph a. This is equivalent to 10 percent of homozygosis.

homozygosis form a decreasing series converging upon the calculated right end of the chromosome map as the zero point. This indicates that the behavior at the spindle fiber end is just as regular as if the chromosomes were permanently attached i. e. one strand is always distributed with its complement.

The data on rightmost crossovers (table 29) show $7 \cdot 03 \; \dfrac{a \; b}{a \; a}$ to $3 \cdot 55 \; \dfrac{a \; b}{b \; a}$ combinations. This is a close approximation to the random expectation of two to one, therein agreeing with the attached-X data.

In the attached-X cases the split presumably goes continuously through the point of attachment thereby determining which of the two sister strands b and b' will be associated with a given a strand, as shown in the accompanying diagram.
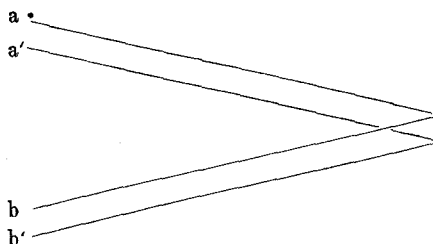
The association should always be a with b and a' with b'. In the case of free chromosomes it is uncertain if any such association is predetermined. With predetermined association, the random assortment of rightmost crossovers $\left(2 \; \dfrac{a \; b}{a \; a} \text{ to } 1 \; \dfrac{a \; b}{b \; a} \right)$ would indicate that strand a crossed over equally freely with strands b and b', a condition which has been shown to hold true in the attached-X cases. But if the chromosomes appear as two separate pairs in the homotypic division, then we should expect a to be distributed equally freely with b and b', since their orientation would not be predetermined. In this case the observed results should always show a random assortment of rightmost cross-overs. While the observed random proportions among the high non-disjunction exceptions are in accord with either condition, they at least suggest a mechanism of distribution of strands very similar to that in the attached-X cases.

In the attached-X cases, all of the X chromosomes were distributed to the exceptional daughters; and their genetic composition as determined from progeny tests appeared to be a random sample of the X constitution of the regular offspring of the controls. In the high non-disjunction line the exceptions differ in X constitution from the regular offspring of the same culture in that they show only 30 percent as many crossovers. The percent of crossovers among the regular offspring is higher than that of corresponding XX cultures. The percent of crossovers among the combined regular and exceptional offspring of XXY cultures is approximately equal to that of the XX cultures. It seems probable that the presence of a Y chromosome does not modify crossing-over but that after crossing-over has taken place, it may cause both X chromosomes (each consisting of two strands) to be distributed to the same pole. Such "exceptional" distributions occur much less frequently where crossing-over has taken place than where there has been no crossing-over as shown by the low percentage of crossovers among the exceptions. The X chromosomes which are crossovers near the spindle fiber end, very rarely go into exceptional eggs.

If the percentage of crossing-over be taken as an index of the closeness of synapsis, then we may say that those X chromosomes which synapse most intimately, especially in the region near the spindle fiber, are distributed most regularly to opposite poles at the reduction division. The presence of a Y chromosome acts as a disturbing element in the distribution chiefly of those X chromosomes which synapse or pair most loosely with each other. Whatever decreases the intimacy of synapsis especially at nor near the right end of the X chromosome should give rise to a decrease in the percentage of crossing-over and likewise a corresponding increase in the amount of secondary non-disjunction. This interpretation brings into simple relationship most of the apparently diverse effects of the high non-disjunction gene.

Constitution of primary exceptions

The XX regular daughters of constitution $\dfrac{cv \quad v \quad f}{sc \;\; ec \quad ct \quad g}$ from the crosses of high non-disjunction exceptions with *sc ec ct g* males (table 5) gave 244 primary exceptional daughters. These fell into the following phenotypes:

wild type 221

sc 4

sc ec 6

sc ec ct 4

sc ec ct g 1

ct g 3

g 3

cv 2
_____

244

Twenty three of these are equational. This is equivalent to 9·4 percent which is somewhat greater than among the secondary exceptions. The percents of homozygosis of the recessive genes in the *sc ec ct g* chromosomes are

sc . . . . 6·1

ec . . . . 4·5

ct . . . . 3·3

g . . . . 2·9

There is present the same decreasing frequency toward the right end. All of these percentages are much higher than among the secondary exceptions but none of them approach the 16·7 percent which would be expected on random assortment. All of the numbers are so low that not much importance can be attached to the observed ratios. Crossveinless became homozygous only twice, vermilion and forked not at all.

The genotypic constitutions of 158 of these exceptions were determined. These are given in table 32. The total crossing-over shown is 12 percent as compared with 7·3 percent for the secondary exceptions. Among the rightmost crossovers there were $16 \frac{a\ b}{a\ a}$ to $9 \frac{a\ b}{b\ a}$ combinations, very near the random proportion of two to one. Although the numbers involved are few, the distribution of genotypes appears to be very similar to the distributions obtained in the secondary exceptions. except for the increased frequencies due to a greater amount of crossing-over.

Table 32. Genotypic constitution of primary exceptions

from $\dfrac{cv \quad v \quad f}{sc \ ec \quad ct \quad g}$ mothers

Phenotype	number tested	Genotype	Schematic representation	Crossovers	Frequency
+	146	$\dfrac{cv \quad v \quad f}{sc \ ec \quad ct \quad g}$	$\dfrac{a\ a\ a\ a\ a\ a\ a}{b\ b\ b\ b\ b\ b\ b}$	0 - 0	131
		$\dfrac{sc \quad cv \quad v \quad f}{ec \quad ct \quad g}$	$\dfrac{b\ a\ a\ a\ a\ a\ a}{a\ b\ b\ b\ b\ b\ b}$	1—1	2
		$\dfrac{sc \ ec \ cv \quad v \quad f}{ct \quad g}$	$\dfrac{b\ b\ a\ a\ a\ a\ a}{a\ a\ b\ b\ b\ b\ b}$	2 - 2	2
		$\dfrac{sc \ ec_{\,} \quad v \quad f}{cv \ ct \quad g}$	$\dfrac{b\ b\ b\ a\ a\ a\ a}{a\ a\ a\ b\ b\ b\ b}$	3—3	2
		$\dfrac{sc \ ec \quad ct \ v \quad f}{cv \quad g}$	$\dfrac{b\ b\ b\ b\ a\ a\ a}{a\ a\ a\ a\ b\ b\ b}$	4—4	3
		$\dfrac{cv \quad v \quad f}{ec \quad ct \quad g}$	$\dfrac{a\ a\ a\ a\ a\ a\ a}{a\ b\ b\ b\ b\ b\ b}$	0—1	3
		$\dfrac{cv \quad v \quad f}{ct \quad g}$	$\dfrac{a\ a\ a\ a\ a\ a\ a}{a\ a\ b\ b\ b\ b\ b}$	0—2	3
sc ec	5	$\dfrac{sc \ ec \ cv \quad v \quad f}{sc \ ec \quad ct \quad g}$	$\dfrac{b\ b\ a\ a\ a\ a\ a}{b\ b\ b\ b\ b\ b\ b}$	2—0	3
		$\dfrac{sc \ ec \quad v \quad f}{sc \ ec \quad ct \quad g}$	$\dfrac{b\ b\ b\ a\ a\ a\ a}{b\ b\ b\ b\ b\ b\ b}$	3—0	2
sc ec ct	2	$\dfrac{sc \ ec \quad ct \ v \quad f}{sc \ ec \quad ct \quad g}$	$\dfrac{b\ b\ b\ b\ a\ a\ a}{b\ b\ b\ b\ b\ b\ b}$	4—0	2
ct g	2	$\dfrac{ct \quad g}{sc \ ec \quad ct \quad g}$	$\dfrac{a\ a\ b\ b\ b\ b\ b}{b\ b\ b\ b\ b\ b\ b}$	2—0	1
		$\dfrac{ct \quad g \ f}{sc \ ec \quad ct \quad g}$	$\dfrac{a\ a\ b\ b\ b\ b\ a}{b\ b\ b\ b\ b\ b\ b}$	2,6—0	1
cv	1	$\dfrac{cv \quad v \quad f}{cv \ ct \quad g}$	$\dfrac{a\ a\ a\ a\ a\ a\ a}{a\ a\ a\ b\ b\ b\ b}$	0—3	1
g	2	$\dfrac{cv \quad g}{sc \ ec \quad ct \quad g}$	$\dfrac{a\ a\ a\ a\ b\ b\ b}{b\ b\ b\ b\ b\ b\ b}$	4—0	1
		$\dfrac{sc \ ec \quad ct \quad g \ f}{cv \quad g}$	$\dfrac{b\ b\ b\ b\ b\ b\ a}{a\ a\ a\ a\ b\ b\ b}$	6—4	1

Summary

Studies are reported on a high non-disjunction line, the progeny of an equational exceptional daughter from an X-rayed mother.

The X constitution of females in this line was $\dfrac{cv \quad v \quad f}{sc \quad ec \quad ct \quad g}$.

The high non-disjunction and related effects were due to a gene in the $cv\ v\ f$ chromosome at or near the locus of vermilion. No crossing-over was obtained between this gene and vermilion. All of the left end of the chromosome up to and including the locus of tan was shown to be normal. The right end of the chromosome including the locus of miniature was also normal.

The high non-disjunction gene has the following diverse effects:
1. Males carrying this gene are sterile.
2. It is lethal when homozygous in females.
3. Heterozygous XX females give about 2 percent of primary non-disjunction, with nearly an equality of males and females.
4. Heterozygous XXY females give about 23 percent of secondary non-disjunction.
5. Among the secondary exceptional daughters about 5 percent are equational due to crossing-over in chromosomes which go into XX eggs.

Studies on crossing-over in both regular and exceptional offspring gave the following results:
1. Crossing-over in XX females is about two-thirds as great as shown by the regular progeny of XXY females.
2. Among the progeny of XXY females, the exceptional daughters show only twenty five percent as many crossovers as do the regular offspring.
3. When the regular and exceptional progeny of XXY cultures are combined, the computed crossing-over is approximately equal to that of the corresponding XX cultures.

Among the exceptional daughters of XXY cultures, the left end of the X chromosome was frequently equational, the right end only rarely so. The distribution of chromosomes was about the same as in the cases of attached X chromosomes except for the reduced percentage of crossing-over.

The mechanism of crossing-over and non-disjunction is discussed. The data presented are further evidence that the distribution of the X chromosomes is determined at the right or spindle fiber end, that

crossing-over occurs at the four strand stage but only two strands cross over at any one level, and that crossing-over occurs freely between any two strands.

The hypothesis is suggested that crossing-over is independent of the presence of a Y chromosome, and prior to the processes which determine the distribution of the X and Y chromosomes; and that the type of distribution where the two X chromosomes go to the same pole occurs most freely in those cases where little or no crossing-over has taken place near the spindle fiber end.

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