A BIOMETRICAL STUDY OF CROSSING OVER. ON THE MECHANISM OF CROSSING OVER IN THE THIRD CHROMOSOME OF *DROSOPHILA MELANOGASTER*[1]

JOHN WHITTEMORE GOWEN
Maine State Agricultural Experiment Station, Orono, Maine

[Received November 23, 1918]

TABLE OF CONTENTS

INTRODUCTION

This paper is an attempt to analyze the current theories of crossing over by a study of its normal fluctuating variations in a particular chromosome. It is the direct outgrowth from, and indeed in some respects, a supplement to the studies of crossing over made during the past few years in this laboratory.. During this investigation, however, the problem has been approached from a different point of view and has made use of rather more adequate methods.

The problem and the point of view taken may be best defined by considering a few of the already known facts concerning crossing over in Drosophila. If one counts separately the offspring of a large number of back-crossed females heterozygous for a large number of factors, there

---

[1] A contribution from the Zoölogical Laboratory of COLUMBIA UNIVERSITY.

may be formed from the resulting data characteristic curves of variation of the number of breaks for each region of the chromosomes which were contained in the females under consideration. The precise form of these curves, as well as the location in them of the value calculated from the offspring of any particular female, is the result of two basic variables, environment and heredity;—environment, in that the conditions surrounding the germ cells of one female may be more favorable to crossing over in one region or mayhap in the whole chromosome than the conditions in another female; heredity, in that a gene may, when substituted for another gene in the same locus, influenced in a marked way the crossing over in a given region.

Little has been done toward a direct analysis of factors such as these in their bearing on the contending views of the mechanism behind the crossing-over phenomena. Yet clearly such an analysis offers one of the best means of extending our knowledge and furnishes critical evidence. The study of interindividual variation offers a way by which the problem of the mechanics of crossing over may be attacked.

Specifically, the direction of the attack on the general problem is that of the analysis of the variation curve in terms of its component individuals. A given individual in the frequency distribution may show a particularly high rate of crossing over for one section of the chromosome. Will it show the same high rate for other sections and, if so, will it also show this proportionately high rate for the double crossing over including these two regions? Does the substitution of other genes for those normally present affect the crossing over in an individual concerned in the formation of our variation curve? These examples will give a definite idea as to the general manner of approach to the problem of variation in crossing over followed in this paper.

MATERIAL AND METHODS

Most of the data contained in this paper were collected during the years 1915-'16 and 1916-'17 that the author has been a member of the Zoölogical Laboratory at Columbia, the rest was obtained at Cold Spring Harbor, Long Island, during the summer of 1916.

To make the conditions as nearly constant as possible with regard to temperature, all flies were bred and reared in an incubator controlled by a thermostat to maintain a temperature of 25° C. Even with this precaution, it is realized that this is not altogether satisfactory, for in summer the outside temperature often rises higher than 25° C. However this rise is slight, and it is thought that the conditions have been maintained so constant that temperature variations may be said to be negligible.

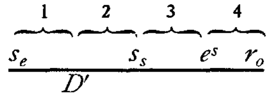
It is probable that food has no effect on crossing over. But as a change was made from fermented banana to an artificial food mixture of starch, sugar, peptone, yeast, and water, this factor will be discussed in connection with the data.

The factors used throughout were those which lie in the third chromosome. Enumerated in the order of their position, they are sepia (s_e), Dichaete (D'), curled (c_u), peach (p^p), spineless (s_s), hairless (H'), sooty (e^s), and rough (r_o). These factors are arranged in the chromosome as seen in diagram 1.

Several distinct sets of experiments were made, using different combinations of these factors. In all cases they were made as back-crosses of a heterozygous female to a male homozygous for the recessives carried by the female. The specific kind of cross that was used in each experiment will be given in connection with a discussion of the data.

For the data on the effect of selection on crossing over, all of the matings were made strictly brother and sister. For the rest of the data this practice has not always been followed, although it generally has been. In all cases the record for the output from each female, represents the offspring of that female mated to a single male. The time allotted for the hatching of the eggs which were laid is in every case ten days after the first fly hatches. Thus the count of a given female is obtained by counting all flies which hatch during the ten days following the emerging of the first offspring from the pupa case.

It hardly seems necessary to say that contamination was carefully watched as a source of error in the data. In every case all of the triple crossovers were tested to be sure that there were no mistakes. Any other cultures which gave extreme results were bred from to test the result. From this it is thought that the cultures included in these data are free from contamination and non-virginity errors.

In recording data, each region of the chromosome may be designated in one of two ways. Thus 

the first region would be either s_e D' or 1; the second region D' s_s or 2, etc. In this way the regions are designated from left to right numerically as 1, 2, 3, 4, etc. The double crossover may also be recorded as s_e D' and D' s_s where a break occurs in the two regions sepia Dichaete and Dichaete spineless simultaneously, or it may be recorded as 1, 2 (break in region 1 and break

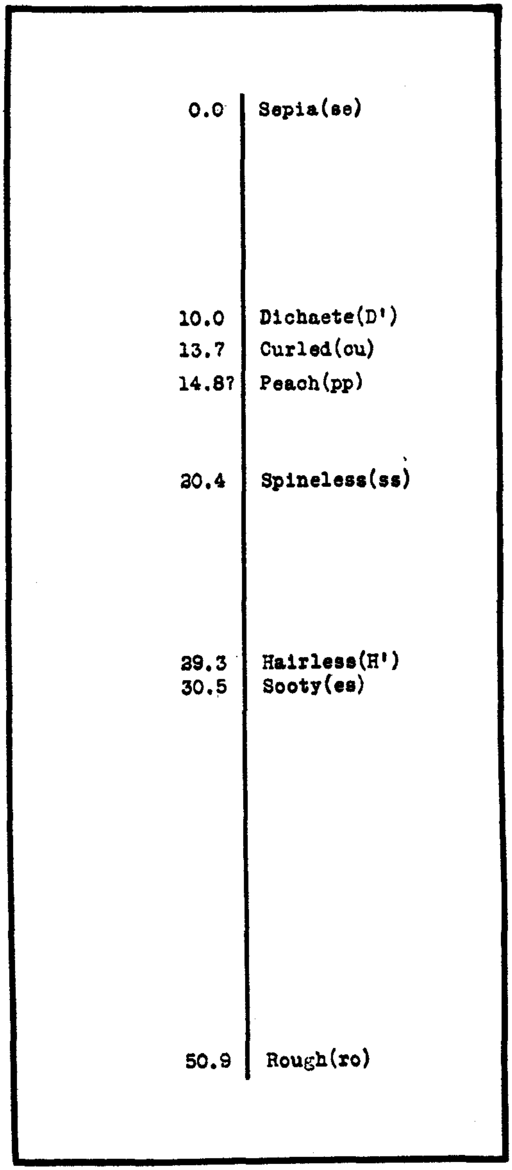


Diagram I

in region 2). The triple crossovers may likewise be recorded as 1, 2, 3, for one including the first three regions of the chromosome. Thus by an extension of this method all possible crossovers are recorded.

The biometrical methods used in the analysis of the statistical material are in general not different from those commonly in use. A few remarks may not be out of place, however, in regard to the computation of some of the constants in this paper. In the calculation of the standard deviation SHEPPARD'S correction for the second moment was not used as it is evident to anyone studying the distribution that there is no approach to high contact at one end of the distribution at least. In the back-cross test of heterozygous females, carrying the genes for sepia, curled, spineless, sooty, rough, in one chromosome, and for dichaete, and hairless in the other, by males homozygous for sepia, curled, spineless, sooty, and rough, all of the calculations were made from ungrouped frequency distributions. In the formation of the correlation tables all the data have been punched on cards and sorted, first into the frequency distribution for the first region, then the classes sorted into the frequencies for the second region to form the correlation surfaces. This sorting has all been done by the machine made by the Tabulating Machine Company. All of the calculation was done on one of the common calculating machines. It is hoped that there are no errors remaining in the computations, although it is impossible to be absolutely sure in a work as large as this that slight arithmetical slips have not gone by unnoticed.

THEORETICAL ASPECTS OF THE PROBLEM OF THE MECHANISM OF CROSSING OVER

Before proceeding to the direct analysis of the problem of crossing over, it may be well to consider what the different theories of crossing over should give as observed results in a theoretically perfect experiment. The theories to account for crossing over which are now extant may be reduced to two.[2] The first of these, brought forward by BATESON and PUNNETT, as the reduplication theory, attempts to account for crossing over as a differential rate of division in germ-cell formation. The second takes as its fundamental postulate a twisting of the chromosome threads in loose twists.

If we carry the analysis of what would be expected on the reduplication theory to include, besides the single separation, those double separations of coupled factors, we would expect only such correlation between single separations and the successive double separations as would be brought about by their being correlated to the same thing. In other words, we would expect this relationship to vanish when we used partial correlations to measure directly the single separations and double

---

[2] In view of the recent criticism by STURTEVANT and BRIDGES of the hypothesis to account for crossing over brought forward by GOLDSCHMIDT, it seems to me wise to await the reply before considering it further.

separations. This is just what we would not expect on the twisting hypothesis of crossing over. Let us consider the case of a fixed point of twist having a known variation around a mean ratio (a) from the fixed point for the second twist. Now, if we take successive ratios of crossing over along this chromosome, with a break at one fixed point, what is the likelihood of another simultaneous break in successive regions as we progress along the chromosome away from the fixed point? Surely, it will increase to the mode of our frequency curve of the ratio for twist, and diminish from that toward the further end. Thus one of the strongest pieces of evidence that can be given for the twisting hypothesis to account for crossing over will be given if we can show that there is such a rise and fall in single and double correlations.

There are, unfortunately, some difficulties in our data which should be pointed out. In the first place, it is impossible to limit our first break to a fixed point because there are not enough good factors close enough together to do this. It is necessary, therefore, to take a small segment of the chromosome from which to measure. The successive regions taken to divide the frequency distribution of twisting have to be uneven intervals and further the interval in one of our segments ($e^s\ r_o$) has to be quite long. These are physical difficulties which I see no way of overcoming. They are not difficulties which in any way vitiate the conclusions, however, for in every case the effect is such that it subtracts from the numerical value of the coefficients measuring the relationship. Thus conclusions drawn from these coefficients have a big margin of safety.

These difficulties should, however, be kept constantly in mind in weighing the value of the evidence. Specifically, in our data, region $e^8\ r_o$ is poorly suited to this study because it is so long that should twists occur between 25 and 30 units apart the second twist might fall in either of two regions (s_eD' or D'_8), depending on whether the first one is near e_8 or r_0. The mid-regions are also not well suited to this study as the regions on either side are not long enough to enable the mode of the curve to appear, if the modal frequency of twisting is about 25 units. The $s_e\ D'$ region considered in connection with the rest of the data is, however, well suited to the study, for here the first region is short and so located at the end of the chromosome that it has the whole length of the chromosome for the other twist to fall. Consequently, it is to that region which we will pay most attention in our subsequent analysis. Some other difficulties, such as genetic variations of crossing over, which if present materially influence our conclusions, will be the first to receive consideration.

FREQUENCY DISTRIBUTIONS OF THE VARIATION IN PERCENT OF SINGLE AND DOUBLE CROSSING OVER IN THE THIRD CHROMOSOME OF DROSOPHILA

The frequency of the percentage of crossing over for the various regions is shown in tables 1 and 2, both in absolute figures and in percentages.

TABLE 1

Percentage of single crossing over $\left(\frac{s_e \quad s_s \quad e^s \quad r_o}{D'}\right)$.

Percent crossing over	Region 1		Region 2		Region 3		Region 4	
	Frequency	Percent	Frequency	Percent	Frequency	Percent	Frequency	Percent
0-2	2	.83	2	.83	1	.41		
2-4	4	1.66	10	4.16	9	3.75		
4-6	18	7.50	30	12.51	18	7.50		
6-8	29	12.08	51	21.26	45	18.76	3	1.25
8-10	44	18.34	57	23.76	57	23.76	2	.83
10-12	55	22.93	31	12.92	44	18.34	5	2.09
12-14	38	15.84	27	11.25	29	12.08	13	5.41
14-16	30	12.51	16	6.66	19	7.91	15	6.25
16-18	13	5.41	9	3.74	11	4.59	38	15.84
18-20	3	1.25	5	2.09	4	1.66	34	14.17
20-22	3	1.25	1	.41	3	1.25	48	20.00
22-24	1	.41	1	.41			28	11.67
24-26							23	9.58
26-28							17	7.08
28-30							7	2.92
30-32							5	2.09
32-34								
34-36							1	.41
36-38							1	.41
Total	240	100.00	240	100.00	240	100.00	240	100.00

In engaging in any discussion of the distributions and the interrelations between them, it seemed advantageous to have the physical constants, mean, standard deviation, and coefficient of variation, before us. In the calculations of these constants SHEPPARD'S correction for the second moment was not used.

A number of interesting points are brought out by this table:

1. It will be seen that the crossing-over ratio for $D's_s$ obtained by summation of the values for $D'c_u$ and c_us_s that the sum is only 8.388 percent, as against 9.483 percent for the cross which does not contain

TABLE 2

Percentage of double crossing over $\left(\frac{s_o \qquad s_s \; e^s \; r_o}{D'}\right)$.

Percent double crossing over	Region 1, 2		Region 1, 3		Region 1, 4		Region 2, 3		Region 2, 4		Region 3, 4	
	Frequency	Percent	Frequency	Percent	Frequency	Percent	Frequency	Percent	Frequency	Percent	Frequency	Percent
0.0-0.5	96	40.00	92	38.31	35	14.59	152	63.34	67	27.91	154	64.17
0.5-1.0	45	18.76	26	10.84	14	5.84	42	17.50	31	12.92	39	16.25
1.0-1.5	27	11.25	38	15.84	40	16.66	26	10.83	41	17.09	31	12.93
1.5-2.0	30	12.51	30	12.51	38	15.84	11	4.59	32	13.33	5	2.09
2.0-2.5	16	6.66	19	7.92	33	13.75	5	2.09	24	10.01	6	2.50
2.5-3.0	16	6.66	18	7.51	20	8.33	1	.41	13	5.41	2	.83
3.0-3.5	3	1.25	5	2.09	20	8.33	1	.41	13	5.41	1	.41
3.5-4.0	3	1.25	5	2.09	14	5.84	2	.83	11	4.59	1	.41
4.0-4.5			1	.41	12	5.00			2	.83		
4.5-5.0	4	1.66	3	1.25	5	2.09			5	2.09		
5.0-5.5			2	.83	4	1.67						
5.5-6.0					1	.41					1	.41
6.0-6.5					2	.83						
6.5-7.0			1	.41					1	.41		
7.0-7.5												
7.5-8.0												
8.0-8.5												
8.5-9.0					2	.83						
Total	240	100.00	240	100.00	240	100.00	240	100.00	240	100.00	240	100.00

TABLE 3
Physical constants for the frequency distributions of the third chromosome.

Region	Mean	Standard deviation	Coefficient of variation
s_e D'§	10.900 ± .166	3.807 ± .117	34.923 ± 1.199
s_e s_s*	20.383 ± .276	6.332 ± .201	31.003 ± 1.074
s_e e^s*	30.458 ± .361	8.282 ± .263	27.189 ± .917
s_e r_o*	50.858 ± .420	9.654 ± .306	18.623 ± .624
D' c_u†	2.845 ± .297	2.680 ± .210	58.956 ± 5.885
D' s_s§	9.483 ± .170	3.907 ± .120	41.201 ± 1.468
D' e^s*	19.558 ± .258	5.916 ± .188	30.335 ± 1.034
D' r_o*	39.958 ± .330	7.568 ± .240	18.513 ± .624
c_u s_s†	5.543 ± .186	1.677 ± .131	40.823 ± 1.636
s_s H'†	9.862 ± .251	2.263 ± .177	23.558 ± .875
s_s e^s§	10.075 ± .165	3.785 ± .117	37.570 ± 1.310
s_s r_o*	30.475 ± .266	6.103 ± .192	19.427 ± .651
H' e^s†	1.173 ± .258	2.323 ± .182	62.980 ± 6.414
e^s r_o§	20.400 ± .216	4.957 ± .153	24.300 ± .791
s_eD' and $D'ss$§	1.065 ± .045	1.029 ± .032	96.651 ± 5.040
s_eD' and s_se^s§	1.273 ± .041	.950 ± .029	74.636 ± 3.341
s_eD' and e^sr_o§	2.170 ± .063	1.458 ± .045	67.178 ± 2.853
$D's_s$ and s_se^s§	.609 ± .027	.613 ± .019	100.766 ± 5.401
$D's_s$ and e^sr_o§	1.498 ± .053	1.210 ± .037	80.792 ± 3.777
s_se^s and e^sr_o§	.613 ± .029	.672 ± .021	109.750 ± 6.240

* Compound constants calculated from the separate components by summation.
† Calculated from ungrouped frequencies of table A (Appendix, p. 241).
§ Calculated from grouped frequencies of table D (Appendix, pp. 243-247).

the gene for c_u. Likewise, in the summation of the values s_sH' and $H'e_s$ there is quite a considerable difference from the result obtained in the cross without H' (11.035 to 10.075). It remains for a further section of this paper to discuss whether or not these differences are significant.

2. It will be noted that there is a very high coefficient of variability in practically every ratio, this variability being greatest when the mean crossing over ratio is small. Thus, it may be said that when dealing with factors which separate only rarely there is to be expected great fluctuation in the value of the ratio of crossovers to the total number of flies.

3. It is further to be noted that the variability in the number of double breaks is markedly higher than when the variability of the single break is considered. This high variability is no doubt due in part to the small absolute number of double crossovers which are expected. However, this does not in any measure account for the whole of it. From the table

we can safely say that double crossing over is an extremely variable character.

4. A comparative view of this variability will give us a better basis for judging of its real magnitude. A constant is so named because it has a low variability, and as this variability becomes greater , its action is measured by so-called laws. Now, it will be interesting to compare some of the morphological characters which more nearly approach physical characters and some more nearly physiological characters with the values for crossing over.

TABLE 4

Variation constants for various characters.

Subject	Character	Coefficient of variation	Authority
Poland-China swine	Size of litter	27.41	SURFACE (1909)
Man	Number of children	48.14	POWYS (1905)
English males	Heart weight	22.22	GREENWOOD and BROWN (1913)
Cattle	Rev. maximum daily milk yield	18.00	GAVIN (1913)
Domestic fowl	Shell weight of eggs	13.86	CURTIS (1914)
English	Length of skull	3.31	MACDONELL (1904)
Domestic fowl	Breadth of egg	3.29	PEARL (1914)
Drosophila	Single crossing over	18.51-58.96	This paper
Drosophila	Double crossing over	67.18-109.76	This paper

A glance at this table suffices to show how much crossing over in different females varies. Even the lowest values stand well up among the characters which are more purely physiological in character and the highest value is much above that which is ordinarily found even in the physiological characters. Such a high variability demands explanation, and it will be the function of a succeeding section of the paper, where the data has been collected for it, to attempt such explanation.

VARIATION IN CROSSING OVER BETWEEN TWO FIXED POINTS IN EXPERIMENTS CONTAINING OTHER INTERMEDIATE GENES

In undertaking a discussion of crossing over, a matter of prime importance is the question whether or not a change in the genes between two fixed points influences the amount of crossing over between these two fixed points.

It has already been shown by STURTEVANT (1917) and MULLER (1916) that there are disturbing factors in the second and third chromosomes which reduce the crossing over of the factors located in their respective chromosomes. In every case these disturbing factors have quite a considerable effect, as, for example, the cutting down of crossing over from about 50 percent to 1 percent. Now the question arises, do all factors influence crossing over? Is an effect on crossing over as much a function of a gene as the eye color or the body color that is given to an animal by its presence? A partial answer to this problem may be had by a comparison of the crossing-over value for two sets of data in which it is known that in the first set a given gene is present which is not present in the second set. To this end the following data were collected in which heterozygous females of the composition indicated for each distribution were crossed with males homozygous for the recessives carried by the female.

It will be seen on examination of these tables that they differ from each other in having a different set of factors run in combination with certain common factors. Thus, table 5 differs from table 6 in being formed from a cross which has a chromosome carrying dichaete sub-

TABLE 5

Genes, $\frac{se \quad ss \quad e^{s} \quad r_o}{D'}$.

Non-crossovers	Single crossovers				Double crossovers					
0	1	2	3	4	1, 2	1, 3	1, 4	2, 3	2, 4	3, 4
17,171	2,208	2,211	2,639	5,163	292	392	629	132	413	125

Triple crossovers				Quadruple crossovers	Total
1, 2, 3	1, 2, 4	1, 3, 4	2, 3, 4	1, 2, 3, 4	
11	39	17	13	1	31,456

TABLE 6

Genes, $\frac{se \quad ss \quad e^{s} \quad r_o}{H'}$.

Non-crossovers	Single crossovers				Double crossovers						Triple crossovers		Total
0	1	2	3	4	1,2	1,3	1,4	2,3	2,4	3,4	1,2,3	1,2,4	
1459	378	175	29	436	31	8	89	10	10	2	3	1	2631

TABLE 7

Genes, $\dfrac{D' \quad p^p \quad s_s \quad e^s \quad r_o}{\qquad}$.

Non-crossovers	Single crossovers				Double crossovers						Triple crossovers			Total
0	1	2	3	4	1,2	1,3	1,4	2,3	2,4	3,4	1,2,3	1,2,4	1,3,4	
1220	92	263	312	366	15	25	30	9	32	11	1	4	1	2381

TABLE 8

Genes, $\dfrac{s_c \qquad c_u \qquad s_s \qquad e^s \qquad r_o}{D' \qquad\qquad H'}$.

Non-crossovers	Single crossovers						Double crossovers													Triple crossovers									Total
0	1	2	3	4	5	6	1,2	1,3	1,4	1,5	1,6	2,3	2,4	2,5	2,6	3,4	3,5	3,6	4,6	1,2,3	1,2,5	1,2,6	1,3,4	1,3,6	1,4,6	2,3,6	3,4,6	3,5,6	
4664	534	112	319	689	77	1320	22	25	55	14	150	16	22	2	46	3	1	44	37	1	1	1	1	3	1	5	1	1	8167

stituted for one carrying hairless. Table 5 differs from table 8 in having a chromosome carrying dichaete substituted for one carrying both dichaete and hairless.

This, then, gives the data necessary to test out the previous question, Is an effect on crossing over as much a part of the function of a gene as the character produced by it? For if the gene is not an integral part of the mechanism, but is simply carried along by it, it would be expected that a gene's presence would have no effect on crossing over. But if allelomorphs are granules of varying physical characteristics in the chromosome and crossing over takes place by the breaking of finely spun-out twisted threads, it would be expected that one type of granule substituted for another type of granule would affect the position and number of breaks in a chromosome, much the same as the breaking of the strands of a wire cable in a given place is influenced by whether German silver or steel occupies that place. All that is necessary is to compare the constant elements of these distributions as they would have been, supposing that the gene in question had not been there. To compare the cross dichaete heterozygous with hairless heterozygous all that is necessary is to reduce the distribution of table 5 to what it would have been in a cross $\frac{s_e\ \ s_s\ \ k\ \ e^s\ \ r_o}{\quad}$ neglecting dichaete and hairless as in table 9. As it was impossible to follow the kidney factor (k) in the presence of rough, it was not counted.

TABLE 9

Formula of back-crossed female	Reduced formula	0	1	2	3	1, 2	1, 3	2, 3	1,2,3	Total
A. $\frac{s_e\ s_s\ e^s\ r_o}{D'}$	$\frac{s_e\ s_s\ e^s\ r_o}{\quad}$	17463	4419	2650	5202	524	1042	126	30	31456
B. $\frac{s_e\ s_s\ e^s\ r_o}{H'}$	$\frac{s_e\ s_s\ e^s\ r_o}{\quad}$	1469	381	197	443	39	89	12	1	2631

TABLE 10

Reduction of crossing over of table 9 to single crossover in each region.

Formula of back-crossed female	Reduced formula	0	1	2	3
A. $\frac{s_e\ s_s\ e^s\ r_o}{D'}$	$\frac{s_e\ s_s\ e^s\ r_o}{\quad}$	17463	6015	3330	4600
B. $\frac{s_e\ s_s\ e^s\ r_o}{H'}$	$\frac{s_e\ s_s\ e^s\ r_o}{\quad}$	1469	420	249	543

Without going into further detail,the eight possible arrangements of these five tables were made for the comparison of the effect of their different factors on the crossover ratios between the common factors. The measure used for this comparison was the well-known χ^2 test of PEARSON. Since none of these were theoretically fitted frequency curves, the comparison was made only between the non-crossovers and single crossovers (obtained by summation) of each distribution. In this way the danger of q being small in the case of double crossovers is avoided. In the following table are given the results of the comparisons of these distributions.

From this it is seen that even taking the greatest probability (that of the two curves D' heterozygous and H' heterozygous being the same), the odds against any of these curves coming from the same population are all more than three times the probable error (25 to 1). The disturbance

TABLE 11

Distributions compared	χ^2	P
$\frac{s_e \; s_s \; k \; e^s \; r_o}{D'}$ and $\frac{s_e \; s_s \; k \; e^s \; r_o}{H'}$	8.37	Less than .039859
$\frac{s_e \; s_s \; k \; e^s \; r_o}{D'}$ and $\frac{D' \; p^p \; s_s \; k \; e^s \; r_o}{}$	234.76	$1/10^{40}$
$\frac{s_e \; s_s \; k \; e^s \; r_o}{D'}$ and $\frac{s_e \; c_u \; s_s \; k \; e^s \; r_o}{D' \quad H'}$	82.81	$1/10^{14}$
$\frac{s_e \; c_u \; s_s \; k \; e^s \; r_o}{D' \quad H'}$ and $\frac{s_e \; s_s \; k \; e^s \; r_o}{H'}$	29.94	.000005
$\frac{s_e \; c_u \; s_s \; k \; e^s \; r_o}{D' \quad H'}$ and $\frac{D' \; p^p \; s_s \; k \; e^s \; r_o}{}$	307.05	$1/10^{64}$

does not necessarily confine itself to the region occupied by the gene, as a study of the distributions will show. It may be anywhere and its effect may be more or less pronounced. In general, however, the effect is not as great as that of the previously found modifiers for crossing over. From this it follows that each gene has been accompanied by a disturbance in the crossing-over mechanism. This disturbance, it seems to me, may be due to the difference in the strains and stresses set up in the chromosome by different types of particles.

The essential conclusions to be drawn from this section of the work is that only those experiments containing as nearly as possible the same genes can be used in any critical study of crossing over and that the amount of crossing over between two fixed genes is a variable quantity, depending on the genes which are present. This does not mean that the crossing-over ratio is not a good means of measuring the position of the factors in a chromosome, it merely means that the scale from experiment to experiment may vary. Thus we should carefully consider the factors present in every experiment.

DOES FOOD OR SEASON INFLUENCE CROSSING OVER?

To test this, it becomes necessary to divide our records (table D) at the places where a change of food occurred. The distributions resulting may then be compared by means of the previously described test, χ^2, for similarity. Table 12 gives the distributions and the χ^2 with the resulting probabilities that the various distributions can come from random sampling. Thus the χ^2 value of 9.78 obtained by the comparison of the distribution resulting from the use of fermented banana and of a starch-sugar mixture for food indicates that once in 22 such trials as good or worse a fit would be expected.

TABLE 12

	0	1	2	3	4	Total	Distributions compared	χ^2	P
Fermented banana I	4456	866	744	779	1691	8536	I & II	9.78	.045
Starch-sugar mixture II	4944	1009	922	959	1824	9658	II & III	5.78	.219
III	5797	1193	962	1132	2159	11244	I & III	6.91	.147

This gives a fair chance that all three curves are samples from the same population as would be expected *a priori*. The second and third distributions are the much better-fitting divisions. From this it may be concluded that the food used has little or no effect on crossing-over. Since the divisions may also represent divisions for different seasons, it follows from this that seasons have little or no effect on crossing over unless one takes the doubtful stand that the effect of food and season exactly counterbalance each other.

CROSSING OVER IN RELATION TO MODIFYING FACTORS

It is too obvious to require experimental demonstration that modifying factors for crossing over would influence in a marked way the data obtained for crossing over in a large number of females where such modifying factors were present.

In an earlier section of this paper it has been shown that such a crossing-over disturbance does occur when known and accompanying unknown genes are introduced between fixed points. Now, it is conceivable that there are unknown genes in any cross which may cause crossing-over disturbances and will be distributed unevenly in the female whose offspring are counted. This uneven distribution will make the results from such a cross heterogeneous. The test of whether or not the material to be used in the succeeding study of crossing over is homogeneous will be dealt with in this section.

If we select only the females giving the lowest total percent of crossing over in the chromosome in question, we should lower the percent of crossing over if modifying factors are present. Such a selection experiment has been performed, the selection continuing for six generations of strictly brother-and-sister matings. In some respects these data are unsatisfactory. The chief difficulty lies in the few individuals that it was possible to include in a given generation. In this way a large individual variation is possible which may in some cases obscure the results. However, taken as a whole, I think it will be found to answer the question, for the constants are rather uniformly the same in showing no effect of selection.

The material chosen for this selection experiment was the cross, male homozygous for sepia, spineless, kidney, sooty, rough, mated to a female heterozygous dichaete and sepia, spineless, kidney, sooty, rough. This cross is chosen as it is to be the cross used in the study of the mechanism of crossing over which is to follow. The reductions of the data to their means and correlations for each given generation are tabulated in table 13.

TABLE 13

Generation	1	2	3	4	5
Mean total of crossing over	37.97±.970	47.81±1.274	49.67±1.929	49.03±1.272	55.75±1.09

	1 and 2	2 and 3	3 and 4	4 and 5
Parent-and-offspring correlations	.1033±.1423	.1595±.1756	.3360±.1348	—.2107±.1177

A like experiment has been made for selection of females with high percent of crossing over; the results are seen in table 14.

TABLE 14

Generation	1	2	3	4	5	6
Mean	58.07±1.150	51.52±1.717	52.57±.587	49.85±2.769	51.16±.929	54.80±2.

	1 and 2	2 and 3	3 and 4	4 and 5	5 and 6
Parent-and-offspring correlations	—.0641±.1105	.0297±.3369	.1500±.2484	—.1348±.1912	—.0780±.2021

It is evident from this data that while the probable errors are large, the data are in accord in showing no effect of selection. This is even more striking when one considers the individual pedigrees where one generation may jump to the other extreme from its parent.

In this connection, it seems to me especially instructive to compare the correlations obtained by MACDOWELL (1917) during his selection experiment with those we have here. After selection had been continued for more than fifty generations, the parent and offspring correlations in one set of experiments for the bristle number were —0.1436 for the males and —0.1378 for the females, or correlation of about the same magnitude as those in the experiment given above. Thus we see that in actual magnitude the correlations are about the same size for our experiment as those for an experiment carried on for some fifty-four generations where it was shown that selection had no appreciable effect after the first six generations. It seems a justifiable conclusion to be drawn from the above, the origin of the stock from a single pair, and the subsequent long inbreeding, that the records are homogeneous and without heterozygous modifying factors for either reduction or increase in crossing over. The crossing-over mechanism is, then, working in a system of events controlled only by the mechanism used in crossing over for the particular set of factors.

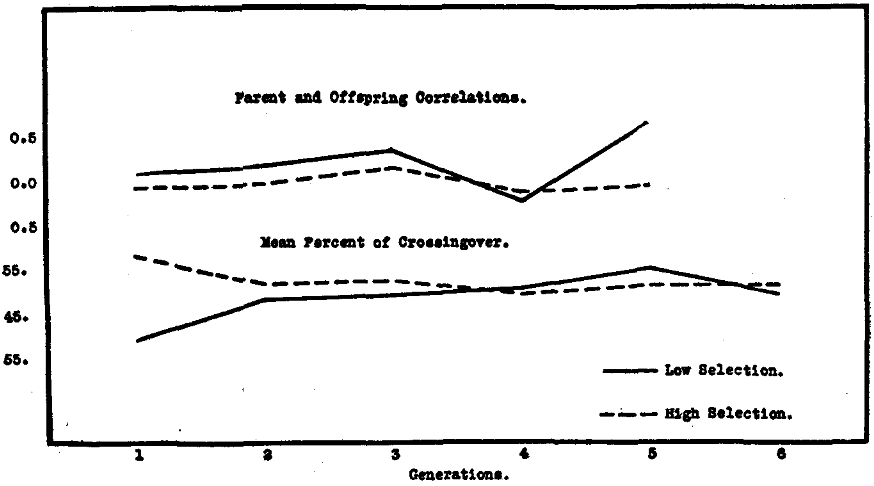


DIAGRAM 2

ON THE RELATION BETWEEN NUMBER OF OFFSPRING AND VIABILITY OF THE FACTOR COMBINATIONS USED

As an explanation of the difference of expected from obtained ratios in some crosses, the hypothesis of differential viability has been proposed. This is on the face of it a legitimate hypothesis for such results, as it is known that some combinations of factors are less viable than others. Now, in a bottle of a large number of flies, where crowding takes place, it is an easy step to consider that in the competition more of the less viable combinations of factors die. Since this cause might be a disturbing influence in the ratios obtained in these experiments, if one combination of factors were less viable than another, it becomes necessary to test for disturbances of linkage due to inviability. If it is considered that the number of flies produced by a bottle is a suitable measure of its condition, then if there is a disturbance of the linkage due to the viability in any given combination with variations in food or crowding, it would be expected that the ratios obtained for such bottles would be correlated. If we find no such correlation it is justified to conclude that no such difference in viability of factors remained unbalanced in our experiments. Table 15 shows the correlation for the given combinations of factors and the bottle output.

TABLE 15

Region	Correlation	Region	Correlation
1	.0670 ± .0433	1, 3	.1115 ± .0429
2	—.0622 ± .0433	1, 4	.0299 ± .0434
3	.1174 ± .0429	2, 3	—.0410 ± .0434
4	.0275 ± .0434	2, 4	—.0658 ± .0433
1, 2	.0119 ± .0434	3, 4	—.0436 ± .0434

Thus it will be seen that only in two cases does the correlation run as high as 0.1. Even this is only slightly above two times the probable error and therefore cannot be considered as significant. We may conclude with safety, then, that in no combination of factors which resulted from the crosses that were used did unbalanced differential viability exist.

The general conclusions which may be drawn from the first part of this paper are:

1. Crossing over between two fixed points is highly variable both relatively and absolutely.
2. A change in genes between two or more fixed points in the third chromosome may be accompanied by a slight disturbance of the crossing-over ratios between these fixed points.
3. The food used had no effect on crossing over.
4. It is highly probable that there were no unequally distributed modifying factors for crossing over at work in our data for the back-crossed females heterozygous for dichaete and sepia, spineless, kidney, sooty, rough, to be used for the critical study of crossing over in the succeeding section.
5. There is no effect of unbalanced differential viability resulting from any of our combinations of factors.

ON THE RELATION OF CROSSING OVER TO POSITION

In any study of the crossing-over mechanism an adequate analysis of the problem must include a knowledge of the relation between the total crossing over in one part of the chromosome and the total crossing over in the remaining regions. Toward the solution of this phase of the problem the data in table D (page 243) have been collected. The cross of a homozygous sepia spineless kidney sooty rough male mated to a heterozygous female sepia spineless kidney sooty rough on one side, dichaete on the other, is the same as that used in our selection experiment where the stock was shown to be free from factors modifying the crossing-over ratios. For want of space the formed correlation tables have been omitted. All correlation coefficients have been calculated by the usual formula,

$$r = \frac{s(xy)}{N\sigma_x\sigma_y}$$

The problem presents some difficulties as the above formula does not give the true correlation as uninfluenced by other associated variables. For obtaining these it is necessary to resort to the use of partial correlations. The fundamental correlations are shown in table 16 with their probable errors calculated by the help of the tables edited by PEARSON (1914).

TABLE 16

Coefficients of correlation for total crossing over in the different regions of the chromosome, together with those for number of offspring.

Section	Coefficient of correlation	Section	Coefficient of correlation
1 and 2	0.7136 ± .0213	2 and 4	0.5985 ± .0280
1 and 3	0.7888 ± .0164	2 and T*	0.6628 ± .0244
1 and 4	0.7426 ± .0195	3 and 4	0.7410 ± .0196
1 and T*	0.8108 ± .0149	3 and T	0.8335 ± .0133
2 and 3	0.6761 ± .0236	4 and T	0.8782 ± .0100

* T stands for the total offspring output per female.

In every case the correlations are high and many times their probable errors. This table furnished us the material for calculation of the correlations between the different regions when the effect of difference in number of offspring per mating, on the correlation between two given chromosome regions, is eliminated through the use of partial correlations.

TABLE 17
Partial correlations deduced from table 16.

Regions correlated	Partial correlations (Total constant)
1 and 2 .T	.4019 ± .0365
1 and 3 .T	.3492 ± .0382
1 and 4 .T	.1093 ± .0430
2 and 3 .T	.2988 ± .0396
2 and 4 .T	.0458 ± .0435
3 and 4 .T	.0341 ± .0435

The correlations range from 0.4019 to 0.0341, from nine times the probable error to insignificance. An interesting relationship is apparent in this range of correlation. Considering any given region correlated with the remaining regions, the algebraic value of the correlation coefficients is greatest for the first left-hand region and diminishes toward the right hand. This is clearly brought out in table 18, together with the differences and their probable errors calculated by the usual difference formulae.

TABLE 18
Correlation and differences for the single crossovers of successive chromosome segments.

Regions	Coefficient of correlation	Difference	Regions	Coefficient of correlation	Difference
1 and 2 .T	.4019		3 and 1 .T	.3492	
1 and 3 .T	.3492	.0527 ± .0528	3 and 2 .T	.2988	.0504 ± .0550
1 and 4 .T	.1093	.2399 ± .0575	3 and 4 .T	.0341	.2647 ± .0584
2 and 1 .T	.4019		4 and 1 .T	.1093	
2 and 3 .T	.2988	.1031 ± .0539	4 and 2 .T	.0458	.0635 ± .0611
2 and 4 .T	.0458	.2530 ± .5876	4 and 3 .T	.0341	.0117 ± .0615

The significance of these differences becomes apparent by a comparison with their probable errors. In each case the relation of the crossing over between the 1 and 3, 2 and 3, and 3 and 2, with the fourth 1 and 4, 2 and 4, and 3 and 4, is quite significant. The other values do not have such great significance, some of the greater difference in the case of the fourth region may be due to its greater length. The consistency of the relationship leads one to suspect that it is more than chance, even though the differences are not great in comparison with the probable errors.

The fact that all of the eight differences between adjoining sections arranged in order from left to right are positive when the likelihood *a priori* is equal, as to whether any given difference shall be an excess or defect, is greatly in favor of the view that this is not a chance relationship, but is one brought about by some inherent cause in the mechanism of crossing over. Taken at its face value, this graded scale of correlation means that the conditions in a given female favorable to a given grade of crossing over in the first region is in a less degree favorable to crossing over in the second region and to a still less degree to crossing over in the regions to the right of the second.

It is further brought out that the distribution of the single crossovers for the different segments of the chromosome is by no means a random sample. They are associated variates. This conclusion is important in a number of ways. The chief among these is that in treating any expectation for double crossovers as the product of the single crossovers, either as just the single observed crossovers or as the single crossovers obtained by summation, we are committing a grave error. The error lies in the fact that we do not take into consideration that they are in general correlated variates.

Because of the importance of this correlation and to further test its generality another experiment was performed, using a larger number of factors. The cross used for this was a male homozygous for sepia, curled, spineless, kidney, sooty, rough, mated to a female heterozygous for dichaete, hairless on one side, and sepia, spineless, kidney, sooty, rough, on the other. It is realized that this distribution is not comparable with the preceding one, yet should the mechanism of crossing over be the same, the manner of crossing over in the two cases should be alike, even though the absolute values were different.

The correlations for this cross are given below. It is realized only too keenly that they are based on rather small numbers; as measured by the standard of the probable error, however, they are significant. Not only that, but taken in consideration with the preceding data it is believed as greater numbers are gathered that the correlations will remain practically the same except for a little tendency to smooth. Table 19 gives the correlation for the successive regions calculated from the ungrouped frequencies by the use of the ordinary formula.

By examination of this table it is seen that it substantiates a former conclusion that the crossing-over values for various sections of the chromosome may be, and generally are, correlated variates. This corre-

TABLE 19

Coefficients of correlation for the successive regions of the third chromosome.

Section	Coefficient of correlation	Section	Coefficient of correlation
s_e D' and D' c_u*	0.5792 ± .0677	D' c_u and e_s r_o	0.0640 ± .1004
s_e D' and c_u s_s	0.3100 ± .0911	c_u s_s and s_s H'	0.1945 ± .0969
s_e D' and s_s H'	0.4440 ± .0809	c_u s_s and H' e^s	0.2752 ± .0932
s_e D' and H' e^s	—0.0070 ± .1003	c_u s_s and e_s r_o	0.2023 ± .0967
s_e D' and e_s r_o	0.1920 ± .0971	s_s H' and H' e^s	—0.2003 ± .0967
D' c_u and c_u s_s	0.2224 ± .0958	s_s H' and e^s r_o	0.1194 ± .0994
D' c_u and s_s H'	0.3970 ± .0849	H' e^s and e^s r_o	—0.2364 ± .0952
D' c_u and H' e^s	—0.1330 ± .0990		

* The total number of offspring for each section held constant by the method of partial correlations.

lation runs as high as 0.5792 and drops to —0.2364. The correlation for the $H'e^s$ distance is seen in most cases to be abnormal. This is probably due to the fact that the ratio for crossing over of this section is rather small in absolute magnitude and since there are only a few crossovers expected with the number of individuals small, the crossing-over values are subject to considerable variation. For this reason where more individuals are included in the data this discrepancy will straighten out and fall in line with the observations previously made. This conclusion is justified, it is thought, for when the data are plotted the curve of the successive regional correlations of the smaller series onto the curve of the successive regional correlations for the larger series of data, the curve of the larger series is seen to bisect the fluctuations of the smaller series as would be expected if they were samples of like populations governed by the same mechanical laws. Thus, barring the slight modifications of the double-crossover values caused by the kind of intermediate factors present, in general the relationship previously established is seen to hold.

Thus, there is a correlation between the crossovers in a given region and the crossovers in successive regions. In general, this relation between crossing over in the various regions is greatest between the region toward the left-hand end of the chromosome and the region under consideration. That is, high crossing over in region BC is more likely to be correlated with high crossing over in AB than in the region of CD.

ON THE RELATION BETWEEN CROSSING OVER IN ONE REGION AND CROSSING OVER INCLUDING TWO REGIONS AT A TIME

The question having most immediate bearing on the mechanism of crossing over is: What is the relation between crossing over in one region and crossing over including two regions at a time, for the successive segments of the chromosome? The importance of the question lies in the fact that if it can be shown that the value of the double crossovers falls in the ordinary cocked-hat frequency curve, it indicates that there is a definite modal length for maximum amounts of double crossing over. Such a modal length is accounted for by the twisting hypothesis of crossing-over as due to the chromosome threads lying across each other in loose twists during the stage at which crossing over takes place. If it can be shown that the double crossing-over ratios do rise and fall for each of the successive segments of the chromosome studied, it not only strengthens the twisting hypothesis, but puts the only other existing hypothesis of reduplication in the forced position of adopting another co-hypothesis to account for the fact, as has been shown in the previous discussion of the theory. To make a study of the crossing-over relationship secure and to be sure that our deductions are not based on a false groundwork, it is necessary to carefully consider how the experiment is performed. All factors that are to be compared should be put together in the same experiment and only data known to be alike in modifying factors used. Such data are at hand in the data on back-crossed females contained in our records for the back-crossed female sepia, spineless, kidney, sooty, rough, on one side, the dominant dichaete on the other, as has been shown by the previous parts of this paper. Before beginning the mathematical analysis of the data it may be well to consider some general aspects of the material as presented. There is one difficulty which must be taken into consideration when considering all measurements containing the region $e^s r_o$, that is, this region is about twice the value of the other regions under consideration. Unfortunately, it was impossible to get this region broken up into smaller parts, for as yet no good factor is known to occupy this region. This high ratio of crossing over means that if the length of the double crossing over is of a value such that the two extremes of the long $e^s r_o$ region fall so as to include two segments, the data will have a bimodal distribution and our observed correlation will have a distorted value. This possible distortion should be kept in mind when considering the data, and in general the main conclusions should rest on observations of the shorter distances.

The first difficulty confronted is the fact that the single crossovers in the various regions of the chromosome are correlated variates partly dominated in their position of breaking by some such cause as the plasma surrounding them. Thus it becomes necessary in a critical experiment to determine the mode of distribution of the breaks in a chromosome, to keep the single-crossover correlations constant throughout the length of the chromosome in females used in the experiment (constant with regard to its quality to influence double crossing over). Since the influence of this relation has been measured by the correlations of the different regions of the chromosome with one another, a mathematical universe may be formed to measure the double crossovers as they would have occurred in an experiment where the surroundings of the chromosomes are constant. In other words, in this way the obstacle of differential single crossing over as regards the various regions of the chromosome is removed. When this is done it is possible to measure the relation that exists in the double crossovers of the successive regions of the chromosome, knowing that it is only the effect of the chromosome mechanism that is studied.

To the end of establishing such a universe, it is necessary to obtain the relationship between the successive regions of the chromosome for double crossing over as they occur in a universe affected by the correlation of the single crossovers for the different regions. To this end the data given in table 20 were collected.

TABLE 20

Correlations between single and double crossovers and number of offspring per mating.

Doubles	Region 1 correlation	Region 2 correlation	Region 3 correlation	Region 4 correlation	Total offspring
1, 2	0.5578 ± .0300	0.6336 ± .0260	0.4421 ± .0350	0.3634 ± .0378	0.3857 ± .0371
1, 3	0.7724 ± .0176	0.6239 ± .0266	0.7073 ± .0218	0.5640 ± .0297	0.6180 ± .0269
1, 4	0.6483 ± .0253	0.4804 ± .0335	0.5730 ± .0292	0.6202 ± .0268	0.6224 ± .0267
2, 3	0.1795 ± .0421	0.3572 ± .0380	0.3285 ± .0388	0.1375 ± .0427	0.1734 ± .0422
2, 4	0.4810 ± .0335	0.6258 ± .0265	0.4472 ± .0348	0.4907 ± .0330	0.4249 ± .0357
3, 4	0.4220 ± .0358	0.4269 ± .0356	0.5336 ± .0311	0.4489 ± .0348	0.3830 ± .0372

Before tabulating the constants which will be necessary to the final study, the establishing of the linearity of regression for the tables from which the fundamental correlations of table 16 and table 20 have been deduced, is necessary. The constants to determine this are given in table 21.

TABLE 21

Criteria for linearity of regression.

Characters correlated	r	η	$\eta - r$	Σ_m	$\eta^2 - r^2$
T and 1	.8108 ± .0149	.8275 ± .0137	.0167	$.3287\sigma$	.0274 ± .0143
T and 2	.6628 ± .0244	.6733 ± .0238	.0109	$.2353\sigma$	.0140 ± .0102
T and 3	.8335 ± .0133	.8439 ± .0125	.0104	$.2611\sigma$	.0173 ± .0114
T and 4	.8782 ± .0100	.8847 ± .0094	.0066	$.2127\sigma$	.0115 ± .0093
T and 1, 2	.3857 ± .0371	.4085 ± .0363	.0228	$.2674\sigma$	.0181 ± .0115
T and 1, 3	.6180 ± .0269	.6563 ± .0248	.0383	$.4019\sigma$	.0488 ± .0187
T and 1, 4	.6224 ± .0267	.6394 ± .0258	.0172	$.2993\sigma$	.0227 ± .0123
T and 2, 3	.1734 ± .0422	.1971 ± .0418	.0237	$.1862\sigma$	.0088 ± .0081
T and 2, 4	.4249 ± .0357	.4436 ± .0350	.0187	$.2532\sigma$	.0162 ± .0109
T and 3, 4	.3830 ± .0372	.4008 ± .0365	.0178	$.2347\sigma$	.0140 ± .0102
1 and 2	.7136 ± .0213	.7307 ± .0203	.0172	$.2722\sigma$	.0247 ± .0135
1 and 3	.7888 ± .0164	.7993 ± .0157	.0105	$.2241\sigma$	.0167 ± .0112
1 and 4	.7426 ± .0195	.7472 ± .0192	.0046	$.1437\sigma$	.0069 ± .0072
1 and 1, 2	.5578 ± .0300	.5752 ± .0291	.0174	$.2438\sigma$	.0197 ± .0121
1 and 1, 3	.7724 ± .0176	.7788 ± .0171	.0064	$.1730\sigma$	.0099 ± .0086
1 and 1, 4	.6483 ± .0253	.6728 ± .0239	.0245	$.3123\sigma$	.0324 ± .0154
1 and 2, 3	.1795 ± .0421	.2227 ± .0414	.0431	$.2288\sigma$	.0174 ± .0113
1 and 2, 4	.4810 ± .0335	.4920 ± .0330	.0110	$.1797\sigma$	.0107 ± .0089
1 and 3, 4	.4220 ± .0358	.4796 ± .0335	.0576	$.3957\sigma$	.0519 ± .0190
2 and 3	.6761 ± .0236	.6847 ± .0231	.0086	$.1662\sigma$	.0117 ± .0094
2 and 4	.5985 ± .0280	.6238 ± .0266	.0253	$.2702\sigma$	.0309 ± .0150
2 and 1, 2	.6336 ± .0260	.6647 ± .0243	.0211	$.3086\sigma$	.0404 ± .0171
2 and 1, 3	.6293 ± .0266	.6580 ± .0247	.0341	$.3213\sigma$	.0437 ± .0177
2 and 1, 4	.4804 ± .0335	.5289 ± .0314	.0485	$.3399\sigma$	.0490 ± .0185
2 and 2, 3	.3572 ± .0380	.3724 ± .0375	.0152	$.1618\sigma$	.0111 ± .0091
2 and 2, 4	.6258 ± .0265	.6358 ± .0259	.0100	$.1725\sigma$	.0126 ± .0097
2 and 3, 4	.4269 ± .0356	.5018 ± .0326	.0749	$.4052\sigma$	.0690 ± .0217
3 and 4	.7410 ± .0196	.7483 ± .0192	.0073	$.1782\sigma$	.0109 ± .0089
3 and 1, 2	.4421 ± .0350	.4608 ± .0343	.0187	$.2220\sigma$	.0169 ± .0112
3 and 1, 3	.7073 ± .0218	.7161 ± .0212	.0089	$.1912\sigma$	.0125 ± .0097
3 and 1, 4	.5730 ± .0292	.6000 ± .0279	.0270	$.3040\sigma$	.0317 ± .0152
3 and 2, 3	.3285 ± .0388	.3618 ± .0378	.0333	$.2493\sigma$	.0230 ± .0124
3 and 2, 4	.4472 ± .0348	.4632 ± .0342	.0160	$.2063\sigma$	.0146 ± .0104
3 and 3, 4	.5336 ± .0311	.5584 ± .0291	.0247	$.2813\sigma$	.0271 ± .0139
4 and 1, 2	.3634 ± .0378	.3966 ± .0367	.0332	$.2229\sigma$	.0252 ± .0135
4 and 1, 3	.5640 ± .0297	.5857 ± .0286	.0217	$.2873\sigma$	.0249 ± .0135
4 and 1, 4	.6202 ± .0268	.6459 ± .0249	.0257	$.2533\sigma$	.0325 ± .0157
4 and 2, 3	.1374 ± .0427	.1846 ± .0420	.0471	$.1730\sigma$	.0152 ± .0106
4 and 2, 4	.4907 ± .0330	.5133 ± .0321	.0226	$.2114\sigma$	.0227 ± .0129
4 and 3, 4	.4489 ± .0348	.4837 ± .0333	.0348	$.2530\sigma$	.0325 ± .0153

It will be remembered that a regression to be linear must have the constants $\eta - r$, $\eta^2 - r^2$ and Σ_m equal to zero within the limits of random sampling. To obtain these, two new constants must be derived. The correlation ratio is obtained by the formula

$$\eta = \frac{\sigma_{my}}{\sigma_y}$$

where σ_{my} is the standard deviation of the weighted means of the y arrays about the mean of the population. Σ_m, the square root of the mean square deviation of the means of the arrays from the regression line, is derived by the formula

$$\Sigma_m = \sigma_y \sqrt{\eta^2 - r^2}$$

due to PEARSON (1905). The probable errors of $\eta^2 - r^2$ are calculated by the method of BLAKEMAN (1905).

The net result of the study of table 21 shows that all the tables on which our correlations are based have the regression lines linear. In no case is the value of the constant $\eta^2 - r$ greater than three times its probable error.

The point of linearity of regression established, we may now return to table 20. From these constants the singular partial correlation coefficients where the total offspring output per female is held constant, have been tabulated in table 22.

TABLE 22

Partial correlation coefficients for total single and total double crossing over in the third chromosome.

Doubles	Singles: Region 1 correlation Partial correlations	Region 2 correlation Partial correlations	Region 3 correlation, Partial correlation	Region 4 correlation, Partial correlation
1, 2 .T	0.4539 ± .0346	0.5471 ± .0305	0.2365 ± .0411	0.0560 ± .0434
1, 3 .T	0.5895 ± .0284	0.3640 ± .0378	0.4423 ± .0350	0.0564 ± .0434
1, 4 .T	0.3136 ± .0393	0.1158 ± .0430	0.1271 ± .0429	0.1966 ± .0419
2, 3 .T	0.0676 ± .0433	0.3286 ± .0388	0.3352 ± .0386	—0.0313 ± .0435
2, 4 .T	0.2576 ± .0406	0.5077 ± .0323	0.1860 ± .0420	0.2714 ± .0403
3, 4 .T	0.2062 ± .0417	0.2501 ± .0408	0.4200 ± .0359	0.2547 ± .0407

Study of this table reveals a general tendency on the part of crossing over in region 1, when correlated with doubles including region 1, to rise to a high point and then to decline from this point to the end of the chromosome. The same general tendency will be seen when region 4 is correlated with the successive doubles including 4. That is, the correlation rises to 2, 4, then declines toward 1, 4. In the middle of the chromosome both regions have their high correlations at the end of region 1. Thus it

TABLE 23

Singular partial correlation coefficients for table 22 (second order).

Double	Singles, region 1 correlation	Double	Singles, region 2 correlation	Double	Singles, region 3 correlation	Double	Singles, region 4 correlation
1, 2 .T2	0.3054 ± .0395	1, 2 .T1	0.4469 ± .0348	1, 2 .T1	0.0934 ± .0432	1, 2 .T1	0.0072 ± .0435
1, 2 .T3	0.4078 ± .0362	1, 2 .T3	0.5137 ± .0320	1, 2 .T2	0.0914 ± .0432	1, 2 .T2	0.0370 ± .0435
1, 2 .T4	0.4152 ± .0347	1, 2 .T4	0.5459 ± .0306	1, 2 .T4	0.2351 ± .0411	1, 2 .T3	0.0494 ± .0434
1, 3 .T2	0.5190 ± .0318	1, 3 .T1	0.1719 ± .0423	1, 3 .T1	0.3124 ± .0393	1, 3 .T1	—0.0099 ± .0435
1, 3 .T3	0.5170 ± .0319	1, 3 .T3	0.2709 ± .0403	1, 3 .T2	0.3752 ± .0374	1, 3 .T2	0.0427 ± .0435
1, 3 .T4	0.5872 ± .0285	1, 3 .T4	0.3624 ± .0378	1, 3 .T4	0.4413 ± .0351	1, 3 .T3	0.0461 ± .0434
1, 4 .T2	0.2936 ± .0398	1, 4 .T1	—0.0118 ± .0435	1, 4 .T1	0.0114 ± .0435	1, 4 .T1	0.1720 ± .0423
1, 4 .T3	0.2902 ± .0399	1, 4 .T3	0.0827 ± .0433	1, 4 .T2	0.0958 ± .0431	1, 4 .T2	0.1928 ± .0419
1, 4 .T4	0.2997 ± .0396	1, 4 .T4	0.1090 ± .0435	1, 4 .T4	0.1211 ± .0429	1, 4 .T3	0.1940 ± .0419
2, 3 .T2	—0.0745 ± .0433	2, 3 .T1	0.3299 ± .0388	2, 3 .T1	0.3365 ± .0386	2, 3 .T1	0.0241 ± .0435
2, 3 .T3	—0.0572 ± .0434	2, 3 .T3	0.2533 ± .0408	2, 3 .T2	0.2662 ± .0406	2, 3 .T2	0.0173 ± .0435
2, 3 .T4	0.0646 ± .0434	2, 3 .T4	0.3276 ± .0389	2, 3 .T4	0.3375 ± .0386	2, 3 .T3	0.0210 ± .0435
2, 4 .T2	0.0679 ± .0433	2, 4 .T1	0.4568 ± .0344	2, 4 .T1	0.1061 ± .0430	2, 4 .T1	0.2533 ± .0407
2, 4 .T3	0.2092 ± .0416	2, 4 .T3	0.4821 ± .0334	2, 4 .T2	0.0417 ± .0435	2, 4 .T2	0.2883 ± .0399
2, 4 .T4	0.2382 ± .0411	2, 4 .T4	0.5151 ± .0320	2, 4 .T4	0.1837 ± .0421	2, 4 .T3	0.2699 ± .0404
3, 4 .T2	0.1192 ± .0429	3, 4 .T1	0.1867 ± .0420	3, 4 .T1	0.3795 ± .0373	3, 4 .T1	0.2387 ± .0411
3, 4 .T3	0.0699 ± .0433	3, 4 .T3	0.1439 ± .0426	3, 4 .T2	0.3737 ± .0374	3, 4 .T2	0.2515 ± .0408
3, 4 .T4	0.1855 ± .0420	3, 4 .T4	0.2468 ± .0409	3, 4 .T4	0.4256 ± .0356	3, 4 .T3	0.2651 ± .0405

is seen that the relation of double crossovers to the regions surrounding them forms curves, the crest of the curves occurring between 20 and 30 units.

But there are discrepancies in the high point of this curve. It will be noticed that there is a significant correlation between region 1 and the double including regions 2 and 4. In the same way, 2 is correlated with 1, 3 and 3 with 1, 4 significantly as measured by its probable error. These correlations would not be expected, and the question arises as to what they are due.

We have seen that the single crossovers in the various regions are correlated variates in which the correlation is most pronounced between adjacent regions. If, then, crossing over in region 1 has a sufficiently high correlation with crossing over in region 2, it would be expected that double crossing over including region 2 would also be correlated with region 1. To test this hypothesis for this case and the similar cases as given above, it is necessary to form the previously described universe, in which the correlation between the two continuous variables 1 and 2, 4 for a constant value of a third variable 1 and 2 is determined, where all values of the offspring are held constant. The measure of such a correlation has been termed the singular partial correlation by PEARSON (1914).

The values for the successive singular partial correlation coefficients (second order) for the above data are given in the table below in which the terms held constant are separated from the correlated term by a dot.

For the complete analysis of the problem the third-order singular partial coefficients needed are given in table 24.

TABLE 24

Singular partial correlations for table 23 (third order).

Double	Singles region 1	Double	Singles region 2
2, 3 .2T3	—0.0845 ± .0432	1, 3 .1T3	0.1223 ± .0429
2, 4 .2T4	0.0421 ± .0435	1, 4 .1T4	—0.0123 ± .0435
3, 4 .3T4	0.0442 ± .0435	3, 4 .3T4	0.1834 ± .0421

Double	Singles region 3	Double	Singles region 4
1, 2 .1T2	0.0124 ± .0435	1, 2 .1T2	0.0070 ± .0435
1, 4 .1T4	0.0124 ± .0435	1, 3 .1T3	0.0119 ± .0435
2, 4 .2T4	0.0371 ± .0435	1, 4 .1T4	0.0169 ± .0435

A study of these tables shows that where before a significant correlation was observed between singles in one region and doubles not including this region as one of the breaking segments when coefficients of the first order were used, now a significant correlation is present only when the double also includes the single as one of the breaking segments. Thus the previous hypothesis to account for these discrepancies was correct. Two double crossovers correlated with a given region may have a significant correlation with that region due to their both being correlated with a third region.

The last difficulty in the study of the data at hand for the purpose of determining how double crossovers are related to the various regions of the chromosome is removed. The correlations of table 23 show that double crossing over, including region 1, is not distributed at random, but is more apt to have a second simultaneous break in region 3 than in any other, the difference in this case running as high as seventeen times the probable error.

Each of the end regions exhibit that rise in the relationship in the middle of the chromosome which, as has been previously pointed out in the first part of the paper, would be expected on the basis of the twisting hypothesis where there was a definite ratio of twist. These waves rise rather sharply to the mid-point and drop off rapidly in the other direction. The relations of region 1 to double crossing over including the other successive regions is that best suited to bring out this rise, for, as has been previously pointed out, the region 1 is so short that twists of the same length cannot extend into either of two regions. This, then, forms the best test of the hypothesis of twisting to account for crossing over versus any other hypothesis which calls for the distribution of crossovers at random. Region 1 correlated with the successive doubles rises sharply to 3 and falls rapidly to 4. Region 4 rises to 2 and falls to 1. The rise and fall in 4 is less rapid, due to its being so long a segment that it enables a twist falling within its bounds to fall in either of two regions, depending on whether or not its first break is near one end or the other, still even in this the mode is marked. The mid-regions also exhibit a rise toward the ends as would be expected, although as the number of factors is too few, no mode appears. This high point and this drop may then represent a twisting taking place about every 20 to 30 units in the third chromosome.

If these correlations are considered from the point of view of the reduplication theory to account for the interchange, what is it necessary to consider? Not only does the rise and fall of the correlation have to be taken into account but also account has to be taken of the whole correlation, for no correlation can be expected on the reduplication theory as previously shown. Correlations have then to consider nothing, even when ranging from twenty-four times the probable error to those four times the probable error. The odds against this being accidental are enormous. It may then be said that the twisting hypothesis for crossing over accounts for the facts remarkably well, while the reduplication theory accounts for them not at all. Consequently, the experimental facts here deduced in carefully controlled and analyzed experiments indicate crossing over to take place between loosely twisted, finely spun-out chromosome threads with between 25 and 30 units as the modal distance between successive crossovers. Because of the uneven intervals and the inaccuracy of the moments calculated from them due to the few classes on which they would have to be based, it is not the purpose of this paper to treat the frequencies other than by the use of correlation coefficients. It is, however, of interest to try the moment calculation for the position of mode for the best suited of these classes for analysis. The approximate ratio between the two twists when calculated for the s_eD' region by the formula: position of the mode $=$ mean $-$ $\frac{1}{2}\,\frac{1\mu_3(r-2)15}{2\mu_2(4+2)}$, is shown to be at 26.24 units, considering each class as distributed around the mid-ordinates (an hypothesis obviously untrue, but giving the best approximation to the true value which it is possible to obtain since the true mean of each class is not known). The use of the above formula for the mean is justified, as the curve is shown to be type IV by $\beta_1=+.057$ and $\beta_2=+68.313$.

DISCUSSION

The geometrical interpretation put upon the rise and fall of the double-crossover frequencies may seem rather speculative in character. It is, however, I venture to think, supported by a good deal of strong evidence. Since the idea that the chromosomes are the bearers of the determiners of hereditary characters was put forward by WEISMANN and ROUX and applied to Mendelian inheritance by SUTTON, there has been an ever increasing amount of evidence collected that it is to the chromosome we must look for the mechanism of heredity. As a basis for this conclusion the studies of STEVENS and WILSON have shown the parallel between sex and the behavior of a chromosome pair. This was followed by the work of MORGAN, showing that this parallel included the so-called sex-linked factors as well as sex. As direct evidence, we may draw first on that of BOVERI on multipolar mitosis, of BALTZER on reciprocal crosses of seaurchins and that of HERBST (1909) and GODLEWSKI (1911) on parthenogenesis and fertilization. Further evidence comes from the work of LUTZ (1912), GEERTS (1911) and GATES (1907, *et seq.*) in the study of Oenothera mutants. With all, perhaps the most brilliant piece of evidence is that of BRIDGES (1916) where proof is given that the sex chromosomes bear the sex-linked factors; for here by cytology and genetics he can follow the course of the sex-chromosomes and of the factors carried thereby. These names do not exhaust the list of those who have added materially to the proof that the chromosomes are the bearers of the hereditary characters, yet it seems to me that these constitute as complete a chain of crucial experimental evidence as would be required by the most rigorous logic, consequently the conclusion will not be crowded by presenting more. Should it be granted, however, that this does constitute proof, it requires that all hypotheses to account for the interchange of linked or coupled factors shall rest on the chromosome; it requires that the reduplication hypothesis shall segregate its genetic ratios through the agency of the chromosomes.

If other evidence is taken purely from the experimental side of genetics and consideration be given to STURTEVANT'S (1914) criticism, the reduplication hypothesis in what TROW (1912) and BAILEY (1913) have shown to be the general mathematical relations of its gametes, it is found that it is doubtful if reduplication is able to explain even the ratios that are obtained. Thus in the case of TROW'S special hypothesis STURTEVANT shows that in every case the calculated is greater than the observed ratios. The difference is significant in every case and in the same direction. Further, STURTEVANT shows that if the general hypothesis is used the number of cell divisions required are at hopeless variance when considered with the possible divisions. It may then be said that deduction from the theory leads to a poor agreement between this theory and fact.

The students of genetics who use the linkage hypothesis to explain their ratios have some evidence to show that the linkage hypothesis is also applicable to the same forms on which the reduplication hypothesis is based. BRIDGES (1914) has shown that in the experiments of PUNNETT (1913) on sweet peas and GREGORY (1911) on Primula the linkage hypothesis is at least applicable. Unfortunately, BRIDGES used as his measure of linkage the coefficient of association of YULE, which is in itself of rather doubtful value as a measure of relationship, as has been shown by HERON (1911), and HERON and PEARSON (1913). Fortunately, however, the conclusions of BRIDGES have been justified, since we now have some very excellent data presented by ALTENBURG (1916) in evidence that the linkage hypothesis can be applied to Primula. Data on some 3600 plants show clearly that it is exceedingly difficult to see how a reduplicating series can be made to fit.

ALTENBURG separates his cases in which the male plants were heterozygous and the cases in which his female plants were heterozygous. There seemed to be quite a difference in the amount of crossing over between them, so I thought it might pay to test each of the classes for the likelihood of this coming from random sampling. The table 25 shows the result of this test.

TABLE 25

	♂ Heterozygous	♀ Heterozygous	Percent ♂	Percent ♀	Difference	Diff. ÷ P.E.$_{\text{Diff.}}$
Non-crossovers	1829	266	55.558929	67.807132	12.298 ± 1.716	7.2
First single	1053	107	31.986633	27.295914	4.691 ± 1.437	3.2
Second single	325	11	9.872418	2.806122	7.066 ± 0.956	7.4
Double	85*	8*				

* Not calculated, as the value of q would be very small.

Thus it is seen that the difference is well above three times the probable error. The range of probability that these differences came from random sampling are 31 to 1 for the 3.2 times the probable error to 1,675,321 to 1 for the 7.2 times the probable error. This difference certainly looks significant. Since all of these plants were raised under the same conditions and cared for alike, it would seem that crossing over in the female is less than that in the male due to some differential effect of the sex. Such a graded effect, taken in connection with the other known facts for crossing over, indicates that when a sufficient number of animals and plants are known, a graded series of crossing-over values may be found, extending from Drosophila with crossing over only in the female, through sweet pea and Primula with crossing over in both sexes, to silk-worms and probably chickens, with crossing over only in the male. Such a series would then duplicate the series found for the Y chromosomes, although it would not parallel it.

To return to our general theme, in discussing this paper of ALTENBURG (1916), PUNNETT (1917) suggests that the reduplication hypothesis calls for a marked difference for the reduplicating series for the BC regions in the back crosses, $\frac{BAC}{bac} \times \frac{bac}{bac}$ and $\frac{BC}{bc} \times \frac{bc}{bc}$.[4]

---

[4] "On the chromosome hypothesis there is only one set of positions which allows of

At first sight the difference in crossing over shown when different genes are interpolated between two fixed genes would seem to agree with this expectation for the reduplication hypothesis as above stated. In non-conformity with the requirements of this hypothesis as stated by PUNNETT, the total crossing over may be significantly increased by the presence of A heterozygous and be diminished in a like case where another A is heterozygous as compared with the crossing over of the $\frac{BC}{bc} \times \frac{bc}{bc}$ condition. Further, the change of a factor outside the region BC may affect the crossing over of that region more than a similar change of a factor within the region itself. Let us now take the data in the tables and arrange two cases to conform with the needs of the reduplication hypothesis. There are several possible cases of this kind which could be made. The choice of the particular case seems immaterial, consequently let us confine attention to the back-crossed females heterozygous for sepia, spineless on one side, dichaete on the other, and females heterozygous for the genes sepia and spineless. For this table the data from appendix tables A, D, and C are available. The data collected and so reduced are given in tables 26 and 27.

two of the coupling values between three factors A, B and C to be equal, viz., when two loci are equidistant from the third, thus:

$$B \qquad\qquad\qquad A \qquad\qquad\qquad C$$

The coupling or linkage values between A and B, and between A and C, are here of the same value, but when this is so it follows of necessity that the value for B and C must be considerably lower than either of the other two. If a three-factor case were found of such a nature that two of the values were equal and the third definitely higher, such a case might serve as a criterion between the two hypotheses." Further, he says, "Such a case is probably to be found among Primulas in connection with the three pairs of characters, magenta (M) and red (r), short style (S) and long style (s), green stigma (G) and red stigma (g)." GREGORY and ALTENBURG have both published on these, but, as PUNNETT, says, "The figures" (ALTENBURG'S) "as they stand offer of course no criterion between the rival hypotheses, for the critical experiment is yet to be made. This consists in the cross between $SsGg$ plants (ex $SG \times sg$) and the double recessive $ssgg$, where all individuals used are homozygous for either M or m. On the chromosome hypothesis the linkage values should remain the same as those given above (where M is present in heterozygous forms); on the reduplication hypothesis we should expect to find the linkage higher, probably of the form $2SG$: $1Sg$: $1sG$: $2sg$." This statement has several obscure points more especially as to how this comparison of the two distributions is to be made. If, as the text would indicate, the comparison is to be between the reduplication series as applied to each set of data, instead of comparing the actual distribution of the data, the reasoning is in error for, as STURTEVANT has shown that the series obtained on TROW'S hypothesis, always is significantly too high. In our comparison we shall, therefore, consider only the actual figures.

TABLE 26

	D'	$s_e\ s_s$	$s_eD'\ s_s$	s_s	$D's_s$	s_e	$s_eD's_s$	N
Table A	3532	3257	381	368	244	307	27	26
Table D	12758	12357	1666	1583	1260	1507	145	196

For table C when dichaete is not present:

TABLE 27

	Non-crossovers		Single crossovers	
	s_es_s	N	s_e	s_s
Table C	968	1153	277	233

Considering only the series s_es_s which, according to PUNNETT's statement of the reduplication hypothesis, the series of A and D should differ from that of C we have:

TABLE 28

	$s_e\ s_s$	s_e	s_s	N
Table A	3284	688	612	3558
Best fitting series 5:1:1:5	*3395*	*679*	*679*	*3395*
Table D	12502	3173	2843	12954
Best fitting series 4:1:1:4	*12589*	*3147*	*3147*	*12589*
Table C	968	277	233	1153
Best fitting series 4:1:1:4	*1052*	*263*	*263*	*1052*

None of these expected series agrees with the actual series as well as could be wished. Thus table A could be best fitted by a series of about 4.6 to 1. Table C would have a better agreement between actual and expected, fitted with a series of 4.4 to 1. This is a fundamental drawback to the theory of reduplication, for the search for simple series often obscures real differences. Thus the Primula series treated by PUNNETT (1917) leads to a theoretical distribution on TROW's hypothesis of secondary reduplication which could have the actual distribution observed in the *SG* series selected from it in samples of 3684 individuals each in not more than 1 in 2500 such samples. Yet the uncritical nature of the hypothesis led PUNNETT to conclude that the result is in fair accord with expectation. Thus in our experiment there are significant differences in the distributions taken as a whole, but these differences follow no rule.

Comparing the reduplicating series above, it is seen that they lead to practically the same thing; that is, 4 : 1 : 1 : 4, instead of coming to markedly different series as the reduplication hypothesis calls for. The conclusion seems forced upon us by this test of the hypothesis that the facts of the several factor crosses do not agree with this hypothesis, but that the twisting hypothesis, based as it is on the known chromosome behavior, does fit the facts.

The conclusion that the reduplication hypothesis does not explain the several factor cases is further borne out by the fundamental experiments of PLOUGH (1917). In this investigation the temperature effect on crossing-over rate enabled him to show that crossing over does not occur in the early oögonial divisions, and there is good reason to believe that the percentage of crossing over is affected by temperature only in the growth period of the egg. Thus the long series of differential cell divisions necessary for the formation of the reduplicating series is shown to be absent in actual point of fact.

Adopting the explanation that it is the chromosomes that must be looked to for the mechanism of crossing over, the inquiry may be made as to how crossing over is brought about. STURTEVANT (1913) has shown that it is possible to map the position of the factors in the chromosome by crossing-over ratios. This principle has been extended and has been shown to be applicable to all the Drosophila chromosomes. The practical value of the hypothesis may thus be said to be proved, and through the work of MORGAN, STURTEVANT, BRIDGES and MULLER (1915) all of the chromosomes are mapped. As was pointed out in a preceding section of this paper, the ratios may vary, yet in no case does this variation affect the relative position of the factors.

It becomes important, then, to inquire how this exchange takes place. The function of this paper is a specific inquiry into what the ratios of the double crossovers to the different single crossover regions would show as to this interchange. Following the ideas of JANSSENS (1909) as elaborated by MORGAN (1916), MULLER, BRIDGES, and PLOUGH (1917), of a twisting of the chromosomes, although considering that this twisting takes place at an earlier stage and between the finer threads of the chromosomes, it has been possible to show that the results are what would be expected on the twisting hypothesis to account for crossing over. Turning more to the general aspects of the case, it is seen that this gives a strong foundation for a single mechanical explanation for the exchange of factors where there is only one scheme to account for the whole. It is not known why a fusion should take place where it does or why the genes should line up along the chromosomes as accurately as they do. These are problems of the future, but they do not in any way influence the fact that the hypothesis of loose twisting explains the observed ratios for the third chromosome in so many of its intricacies, as to carry the conviction that it is much more than just a chance relationship.

In conclusion, I wish to express my thanks to Prof. E. B. WILSON and Dr. C. B. DAVENPORT for opportunities accorded me for research; to Prof. T. H. MORGAN, Dr. A. H. STURTEVANT, and Dr. C. B. BRIDGES for their ever-ready assistance and suggestion, and to Dr. RAYMOND PEARL for his constant interest in my work.

SUMMARY

This paper is a contribution toward the analysis of the normal fluctuating variations in crossing over as seen in the third chromosome of *Drosophila melanogaster*. The third chromosomes of each female, as shown by her offspring, cross over a certain number of times. The variability is studied by comparing the results from different females. The association between the crossovers is studied by comparing the results within each given female.

1. The means, standard deviations, and the coefficients of variation are given for the distributions of each region in this chromosome under discussion. The features of chief interest are the great variability of both single crossing over and double crossing over. The coefficient of variability ranges between 18 and 59 for the single crossovers and 67 and 110 for the double crossovers. The actual amount of this coefficient is apparently dependent to some degree on the actual mean size of the crossing-over ratio.

2. A table is presented to show the relative variability of crossing over in comparison with that of other physiological and morphological characters. The table shows that crossing over is one of the most highly variable phenomena known, indicating that the mechanism behind crossing over is not as precise as that found in most physiological studies.

3. As a necessary preface to the analysis of the internal mechanism of variations of crossing over it has been pointed out that it is essential to know how much the ratios are influenced by external agencies. Toward this end it has been shown (page 214) that to some degree the absolute value of the crossing-over ratio varies according to the genes present in the chromosome. Further, it is shown that no significant

effect on crossing over was produced by the food or temperature used or by the variations of season or bottle output.

4. Since it had been shown that the crossing-over values are influenced by the known genes present, it became essential to know whether or not there were any modifying genes present influencing the ratios. A selection experiment was performed to test this. The parent and offspring correlations for this experiment ranged from + 0.336 ± .135 to — .0211 ± .118 for the selection for low crossing over; for high crossing over from + 0.150 ± .248 to — 0.134 ± .191. The conclusion is to be drawn that there were no differences in modifying factors for crossing over in the experiment.

5. In the resolution of the single crossing-over ratios into their component elements it was shown that there is a significant correlation between the crossing over in different regions. In general this difference progresses from the left-hand end of the chromosome to the right. Thus the correlation between region 1 and 2 is + 0.4019 ± .0365, between 1 and 3 is + 0.3492 ± .0382, and between 1 and 4 is + 0.1039 ± .0430. The explanation of this difference is obscure.

6. A relationship between single and double crossing over is shown to exist, such that a crossover in one region is more likely to be accompanied by another simultaneous crossing over in a region 25 to 35 units away than it is to be accompanied by a simultaneous crossing over in any other region. Thus when region 1 is correlated with its double crossover including regions 2, 3, and 4, respectively, the correlations are + 0.3054 ± .0395, + 0.5170 ± .0319, and + 0.2997 ± .0396. This rise and fall, together with a definite mode, is held to mean that there is a modal interval between two successive crossovers. Thus the two finely spun-out chromosomes, when they come together prior to crossing over, apparently twist about each other loosely and generally have the points of contact where breaking may take place about 25 to 30 units apart.

APPENDIX

TABLE B

$$\text{Cross: } ♀\ \frac{D'\ \ p^{p}\ \ s_{s}\ \ e^{s}\ \ r_{o}}{N} \times ♂\ \frac{p^{p}\ \ s_{s}\ \ e^{s}\ \ r_{o}}{p^{p}\ \ s_{s}\ \ e^{s}\ \ r_{o}}$$

References	0		1		2		3		4		1, 2		1, 3		1, 4		2, 3		2, 4		3, 4		1,2,3		1,2,4		1,3,4		Total
627	46	59	3	3	16	12	17	14	19	9	1	1	.	2	2	2	1	1	2	3	.	1	.	.	.	.	.	.	214
629	45	41	9	9	8	12	13	15	17	6	1	1	.	.	3	1	.	.	2	2	.	.	.	.	1	.	.	.	186
632	29	34	2	8	17	9	15	3	11	7	.	.	1	.	2	1	2	1	2	1	.	3	.	.	.	1	.	.	149
634	47	57	2	2	14	15	15	18	19	20	.	3	1	2	1	1	.	1	.	2	.	.	.	.	.	.	.	.	220
658	42	45	1	1	4	3	4	11	11	9	.	.	1	2	1	.	.	.	1	2	.	.	.	.	.	.	.	.	138
665	78	90	6	9	24	21	24	27	21	26	.	2	3	4	3	.	.	.	4	5	1	2	1	.	.	2	.	.	353
665b	51	64	2	5	13	15	16	11	17	16	1	.	1	1	.	.	1	.	1	.	1	.	.	.	.	.	.	.	216
665c	42	52	.	5	2	10	7	8	24	11	.	.	1	2	3	.	.	.	1	.	.	.	.	.	.	.	.	.	168
700c	22	27	1	1	4	3	4	3	9	5	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	80
706	25	18	2	.	2	1	4	7	6	8	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	74
708a	23	31	5	2	9	6	11	10	9	7	1	2	1	1	.	.	.	2	.	1	.	2	.	.	.	.	.	.	123
708b	15	25	2	1	4	3	5	5	5	6	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	71
708c	27	39	2	1	5	8	7	7	10	10	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	117
710	15	22	.	.	2	.	4	4	14	4	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	66
718b	23	34	1	2	8	8	6	9	8	5	.	1	.	.	1	4	.	.	.	.	.	.	.	.	.	.	1	.	111
728a	25	27	4	1	2	3	3	5	12	5	.	1	.	2	2	2	.	.	.	1	.	.	.	.	.	.	.	.	95
Total	1220		92		263		312		366		15		25		30		9		32		11		1		4		1		2381

TABLE C

$$\text{Cross: } ♀\ \frac{s_{e}\ \ s_{s}\ \ e^{s}\ \ r_{o}}{H'} \times ♂\ \frac{s_{e}\ \ s_{s}\ \ e^{s}\ \ r_{o}}{s_{e}\ \ s_{s}\ \ e^{s}\ \ r_{o}}$$

References	0		1		2		3		4		1, 2		1, 3		1, 4		2, 3		2, 4		3, 4		1,2,3		1,2,4		Total
1052	42	20	8	15	3	6	.	1	7	6	2	2	.	.	2	1	.	.	.	.	.	.	.	.	.	.	115
1157	56	55	6	13	5	10	.	.	9	16	.	.	1	.	1	5	1	2	.	.	2	.	1	.	.	.	183
1161	55	45	7	7	.	3	.	.	20	21	.	1	.	.	1	6	.	.	1	1	.	.	.	.	.	.	168
1162	57	51	20	12	10	6	1	.	18	18	1	3	.	.	1	1	.	.	.	.	.	.	.	.	.	.	199
1163	54	40	9	9	2	6	.	.	6	7	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	136
1189	60	58	18	14	10	5	.	3	19	18	1	.	.	.	4	7	.	.	.	.	.	.	.	.	.	.	217
1192	38	28	14	8	4	2	1	.	12	13	1	.	.	.	5	5	4	.	.	.	.	.	2	.	.	.	137
1193	58	66	21	18	7	14	.	2	25	17	1	2	.	.	3	8	.	1	1	.	.	.	.	.	.	.	244
1194	39	31	13	13	2	4	1	1	8	12	.	.	.	.	2	5	.	.	.	1	.	.	.	.	.	.	132
1195	66	40	12	10	4	15	.	.	23	24	3	1	3	1	5	1	.	.	2	1	.	.	.	.	1	.	212
1197	87	58	21	11	9	9	1	1	24	18	.	.	.	.	2	3	1	.	2	.	.	.	.	.	.	.	247
1229	17	20	7	2	2	1	1	.	2	2	2	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	58
1242	18	16	5	2	.	1	.	.	2	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	48
1249	39	27	13	9	4	4	.	1	10	15	.	1	.	.	3	1	.	.	.	.	.	.	.	.	.	.	127
1250	38	29	8	9	.	5	.	1	7	2	3	2	.	.	2	.	.	.	1	.	.	.	.	.	.	.	107
1251	27	21	12	8	5	2	2	1	7	6	.	.	.	.	3	1	.	.	.	.	.	.	.	.	.	.	95
1270	12	12	1	.	1	3	.	1	8	5	1	.	.	.	3	.	.	1	.	.	.	.	.	.	.	.	48
1273	15	15	7	6	2	2	.	1	4	6	.	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.	61
1280	15	13	1	3	2	3	.	.	9	7	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	56
1275	10	11	2	4	1	1	.	2	6	1	1	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	41
Total	1459		378		175		22		443		31		8		89		10		10		2		3		1		2631

TABLE A

Cross: ♀ $\dfrac{s_e \quad c_u \quad s_s \quad e^s \quad r_o}{D' \qquad H'}$ × ♂ $\dfrac{s_e \quad c_u \quad s_s \quad e^s \quad r_o}{s_e \quad c_u \quad s_s \quad e^s \quad r_o}$

References	0	1	2	3	4	5	6	1, 2	1, 3	1, 4	1, 5	1, 6	2, 3	2, 4	2, 5	2, 6	3, 4	3, 5	3, 6	4, 6	1,2,3	1,2,5	1,2,6	1,3,4	1,3,6	1,4,6	2,3,6	3,4,6	3,5,6	Total
1348	112 78	12 9	5 3	9 2	11 11	1 2	28 30	1 .	. .	1 .	. .	4 .	. .	. .	. .	2 .	. .	. .	1 1	1 .	. .	. .	. .	. .	. .	. .	. .	. .	. .	324
1349	104 97	12 11	1 .	10 10	20 20	2 6	26 33	. .	. 1	. .	. .	2 2	. .	. .	. .	. .	. .	. .	1 1	1 .	. .	. .	. .	. .	. .	. .	. .	. .	. .	360
1350	111 113	11 12	3 2	4 5	18 14	1 .	33 40	. .	. .	2 .	1 .	2 3	. .	. .	. .	1 .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	379
1351	107 86	13 9	1 1	6 5	15 13	3 1	34 29	2 1	. .	4 2	1 1	. 1	1 .	. .	. .	. 1	. .	. .	1 .	1 2	. .	. .	. .	. .	. .	. .	. .	. .	. .	339
1352	116 113	12 8	4 1	3 2	11 13	4 .	20 29	. .	. .	. .	. .	4 2	. .	. 1	. .	1 1	. .	. .	1 1	1 1	. .	. .	. .	. .	. .	. 1	. .	. .	. .	350
1363	66 57	13 3	2 1	1 2	7 8	. .	17 17	1 .	1 .	. 1	. .	2 4	. .	. 1	. .	. .	1 .	. 1	1 1	. .	. .	. .	. .	. .	. .	. .	1 .	. .	. .	209
1364	38 49	4 4	. 1	4 3	7 4	4 .	7 9	. .	1 .	. .	. .	. 2	. .	. .	. .	. 1	. .	. .	. .	2 .	. .	. .	. .	. .	. .	. .	. .	. .	. .	140
1365	78 77	11 13	4 1	6 8	15 9	5 1	13 13	3 1	. .	3 1	. .	. 2	. .	1 1	1 .	4 3	. .	. .	. 1	. .	. .	. .	. .	. .	1 .	. .	. .	. .	. .	276
1366	63 76	9 13	2 .	6 9	14 11	4 2	20 27	1 .	. 1	. .	. 1	2 2	. .	1 .	. .	. .	. .	. .	1 .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	265
1368	79 69	4 6	. .	4 3	11 6	3 .	18 27	. .	. .	. 1	. .	4 4	. .	. .	. .	. 2	. .	. .	. .	2 .	. .	. .	. .	. .	. .	. .	. .	. .	. .	243
1369	74 60	10 12	6 1	2 2	9 9	. 1	25 22	1 .	. .	1 3	. .	4 6	1 1	1 2	. .	2 .	. .	. .	1 1	1 .	. .	. .	. .	. .	. .	. .	. .	. .	. .	259
1372	51 44	8 6	2 2	4 3	11 5	2 2	14 20	. .	. .	. 2	. .	3 2	. .	. 1	. .	1 .	. .	. .	. 2	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	185
1382	58 69	6 7	. 3	6 4	10 9	1 1	21 18	. .	. 2	. 1	. .	1 3	. .	. 2	. .	. 1	. .	. .	. 4	1 .	.	. .	. .	. .	. .	. .	. .	. .	. .	228
1383	50 52	6 6	2 2	6 2	12 12	. .	22 22	. 1	1 .	1 .	. .	3 1	. 2	. .	. .	1 1	. .	. .	. .	2 1	. .	. .	. .	. .	. .	. .	. 1	. .	. .	209
1385	27 26	6 2	1 .	5 6	6 7	1 .	13 7	2 1	2 .	. 2	. .	. 3	. .	. 2	. .	. 2	. .	. .	. 1	1 1	. .	. .	. .	. .	1 .	. .	. .	. .	. .	125
1386	72 76	3 3	. .	4 2	12 4	. 1	9 27	. 1	. .	1 1	. .	2 3	. 1	1 .	. .	. 1	. 1	. .	1 .	1 1	. .	. .	. .	. .	. .	. .	. .	. .	. .	228
1387	70 65	12 9	2 .	7 2	11 9	1 1	13 14	1 .	. .	2 .	1 .	5 3	. 1	. .	. .	1 .	. .	. .	. .	1 .	. .	. .	. .	. .	. .	. .	. .	. .	. .	231
1388	69 54	7 5	4 .	. 6	12 10	. 1	22 23	1 .	. 2	. .	. 1	4 2	. .	. .	. .	1 .	. .	. .	. 1	1 .	. .	. .	. .	1 .	. .	. .	. .	. .	. .	227
1389	59 61	8 11	1 2	7 5	10 13	. .	12 20	. .	1 .	3 .	. 2	2 .	1 .	. .	. .	. 2	. .	. .	4 .	3 .	. .	. .	. .	. .	. .	. .	. .	. .	. .	227
1390	77 93	12 8	1 2	3 4	12 13	. .	19 19	1 .	. .	3 1	. .	1 4	. .	. .	. .	. .	. .	. .	. 1	. 1	. .	. .	. .	. .	. .	. .	. .	. .	. .	275
1391	49 35	5 11	2 3	6 3	5 4	1 3	7 17	. .	. .	2 .	. .	5 1	. 3	. .	. .	. 3	. .	. .	. 1	. .	1 .	. .	. .	. .	. .	. .	. .	. .	. .	167
1392	75 67	6 8	2 3	4 5	8 14	2 1	24 18	. .	. .	. 1	. .	1 3	. .	1 .	. .	. 2	. .	. .	. .	1 .	. .	. .	. .	. .	. .	. .	. .	. .	. .	245
1393	72 64	2 6	1 2	2 7	8 7	. .	8 21	. .	1 1	. 1	. 1	3 1	. .	. .	. .	. 1	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	210
1395	36 23	. 2	. 1	3 .	2 1	. .	2 7	2 .	. .	. .	. .	. .	. 1	. .	. .	1 .	. .	. .	1 .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	82
1396	53 40	5 8	3 1	4 4	6 8	1 1	21 13	. .	. .	1 2	. .	2 2	. .	. .	. .	1 .	. .	. .	1 1	2 1	. .	. .	. .	. .	. .	. .	. .	. .	. .	181
1397	40 46	6 8	2 .	2 3	8 10	1 .	7 10	. .	. .	1 .	. 1	1 2	. .	1 1	. .	2 .	. 1	. .	. .	. 1	. .	. .	. .	. .	. .	. .	. .	. .	. .	154
1415	62 54	10 1	3 .	4 3	7 11	3 .	20 10	. .	. .	. .	. 1	2 1	. .	. 1	. .	. .	. .	. .	1 .	1 .	. .	. .	. .	. .	. .	. .	. .	. .	. .	193
1417	71 58	8 6	2 5	10 8	11 12	. .	22 17	. .	. .	1 1	. .	1 2	. .	. .	1 .	. 2	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. 1	261
1420	67 73	5 12	4 .	8 1	13 12	. 1	16 20	. .	1 .	. .	1 .	1 .	. 1	1 1	. .	. 1	. .	. .	2 .	. 1	. .	. .	. .	. .	1 .	. .	. .	. .	. .	243
1422	79 72	11 7	1 4	6 5	12 12	1 .	18 25	. .	. 2	2 1	. .	5 4	. .	. 2	. .	. 2	. .	. .	1 1	. .	. .	1 .	. .	. .	. .	. .	. 1	. .	. .	275
1426	60 49	11 9	1 .	6 3	8 12	. 1	17 32	. .	. 1	1 2	. .	3 .	. 1	. .	. .	. .	. .	. .	. 1	3 .	. .	. .	. .	. .	. .	. .	. 2	. .	. .	221
1427	53 60	8 3	2 .	7 4	8 6	1 2	14 37	. 1	. 2	. .	. 1	1 1	. .	. .	. .	. 1	. .	. .	. 2	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	215
1428	54 20	. 4	. .	4 4	3 4	1 .	6 3	. .	. .	. .	. .	. 1	. .	. .	. .	. .	. .	. .	. 2	. .	. .	. .	. .	. .	. .	. .	. .	1 .	. .	105
1429	27 29	7 4	2 .	6 2	5 9	1 .	10 4	. .	2 .	. .	. .	. 1	1 .	. .	. .	1 .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	113
1431	22 12	2 1	. 1	2 1	2 1	. 1	3 3	. .	. 1	. 1	. .	1 .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	1 .	. .	. .	. .	. .	. .	. .	55
1432	75 62	5 5	1 1	1 5	4 7	2 .	17 16	. .	. .	. .	. 1	3 5	. .	. .	. .	. .	. .	. .	. .	1 .	. .	. .	. .	. .	. .	. .	. .	. .	. .	211
1473	45 44	7 5	2 .	2 2	7 8	1 1	11 12	. .	1 .	. 2	. .	2 1	. 1	. .	. .	. .	. .	. .	. 3	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	157

TABLE D

Cross: ♀ $\frac{s_s \quad e^s \quad r_o}{D'}$ × ♂ $\frac{s_e \quad s_s \quad e^s \quad r_o}{s_e \quad s_s \quad e^s \quad r_o}$

References	0		1		2		3		4		1, 2		1, 3		1, 4		2, 3		2, 4		3, 4		1,2,3		1,2,4		1,3,4		2,3,4		1,2,3,4		Total
588	27	25	5	5	6	3	10	4	8	2	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	97
666	14	14	2	2	3	4	4	5	2	.	3	.	1	.	.	.	.	1	.	4	.	.	.	.	.	.	.	.	.	1	.	.	60
737	8	12	3	1	1	1	2	5	8	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	44
740	53	63	7	14	10	10	6	17	26	28	3	2	1	3	3	3	1	.	1	2	1	.	.	.	.	.	.	.	.	.	.	.	244
741	4	6	.	1	.	1	1	.	1	3	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	19
747	53	47	8	10	9	9	6	6	23	25	.	1	4	3	.	1	.	.	1	5	.	2	.	.	.	.	.	.	.	.	.	.	213
748	11	4	1	2	1	2	1	3	4	4	1	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	36
750	43	36	6	4	5	3	2	7	16	7	.	1	2	.	1	2	.	.	1	2	1	.	.	.	.	.	.	.	.	.	.	.	139
751	55	20	.	1	2	.	2	4	8	6	.	.	.	.	.	2	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	102
754	74	66	3	2	1	2	3	.	6	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	45
756	15	11	4	7	3	8	10	7	28	24	.	.	1	.	1	1	1	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	238
757	26	29	4	2	4	6	2	4	9	6	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	94
758	6	6	2	.	1	.	2	1	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20
759	63	63	6	6	1	6	7	6	25	29	.	2	.	4	2	3	1	.	1	2	1	.	.	.	.	.	.	.	.	.	.	.	228
760	44	49	5	3	2	7	4	5	17	9	.	1	1	2	.	3	.	.	1	.	1	.	.	.	.	2	.	.	.	.	.	.	156
761	41	41	5	7	.	2	2	6	22	20	.	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	149
762	60	57	6	7	2	4	9	5	20	18	1	.	.	.	2	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	193
763	52	53	0	5	3	4	10	7	14	12	1	1	1	.	3	4	1	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	171
764	40	35	5	3	4	1	8	5	6	12	1	.	1	.	3	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	125
766	38	40	4	4	.	6	3	3	12	10	1	2	.	3	2	2	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	132
767	27	35	4	5	5	5	3	2	16	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	109
770	14	19	2	2	1	3	1	2	6	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	52
772	9	10	1	1	1	.	2	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	26
774	28	18	2	3	1	2	1	4	10	9	.	.	.	1	.	3	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	83
775	52	20	4	7	1	2	1	3	2	10	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	105
776	38	31	2	3	7	9	5	4	5	12	2	1	2	1	.	1	.	.	1	1	1	.	.	.	1	.	.	.	.	.	.	.	127
777	22	24	11	2	1	3	7	2	14	8	.	.	.	.	1	1	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	99
778	25	20	2	4	7	9	4	4	8	18	.	3	2	1	3	2	.	.	2	2	.	.	.	.	.	.	.	.	.	.	.	.	116
779	40	48	1	1	6	6	8	7	15	18	.	.	.	.	1	4	2	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	160
780	31	31	2	2	3	4	4	5	4	4	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	91
781	27	28	.	2	9	1	4	6	14	13	1	.	.	.	.	.	4	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	112
782	36	29	5	1	4	8	1	3	14	13	1	.	3	.	2	1	1	.	3	2	.	.	.	.	.	.	.	.	.	.	.	.	127
783	64	62	2	8	7	5	13	14	15	26	.	1	.	4	.	4	.	1	.	1	.	1	.	.	.	.	.	1	.	1	.	.	240
784	58	64	6	6	7	2	6	4	10	11	.	.	.	1	1	1	.	1	2	2	.	.	.	.	1	.	.	.	.	1	.	.	184
785	29	32	.	5	2	2	1	.	8	10	.	.	.	.	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	93
786	44	36	3	3	7	9	4	2	7	9	1	.	.	.	1	.	.	.	2	.	1	.	.	.	.	1	.	.	.	.	.	.	130
788	40	46	6	5	5	9	8	7	9	11	2	2	1	2	4	3	.	2	4	2	.	.	.	.	.	.	.	.	.	.	.	.	168
789	52	39	5	4	4	6	8	7	11	14	2	1	.	3	3	3	.	1	2	2	1	.	.	.	1	1	.	.	.	.	.	.	170
790	107	85	12	5	6	7	5	9	20	22	1	.	1	1	1	4	.	.	.	1	1	1	.	.	.	.	1	.	.	.	.	.	290
791	52	51	8	6	5	5	1	5	14	14	1	.	1	.	1	6	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	164
793	28	29	5	1	3	4	5	6	9	21	.	.	.	.	1	1	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	115
795	39	49	4	9	8	13	15	6	13	14	1	.	2	2	5	1	.	1	.	2	.	1	.	.	1	.	.	1	.	.	.	.	187
797	26	28	3	3	8	5	6	6	6	11	1	1	.	2	2	.	.	1	.	1	1	.	.	.	1	.	.	1	.	.	.	.	113
799	16	10	1	3	2	1	1	1	2	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	39
800	43	59	3	2	2	7	3	9	9	15	.	.	1	1	1	2	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	159
901	34	43	3	5	6	1	4	4	14	12	.	.	1	.	.	4	.	.	2	1	1	.	.	.	.	.	.	.	.	.	.	.	135
902	47	57	3	6	2	3	8	7	20	15	3	.	1	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	175
903	13	10	2	1	3	1	1	.	4	4	.	.	.	1	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	42
904	23	31	3	2	3	2	2	4	12	4	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	87
905	65	55	7	4	5	7	8	5	22	21	1	.	2	3	4	.	.	.	.	2	.	.	.	1	.	.	.	.	.	.	.	.	212
906	45	34	13	5	9	5	16	4	14	11	.	.	1	.	1	1	.	1	.	.	.	3	1	.	.	.	.	.	.	.	.	.	164
907	52	50	12	9	8	13	7	8	15	17	2	.	1	2	3	2	.	.	2	1	.	1	.	.	.	1	.	.	.	1	.	.	207
908	57	50	6	7	5	7	3	4	7	15	.	.	.	2	5	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	170
909	37	48	14	7	5	4	9	11	18	15	.	2	6	2	3	5	1	.	5	1	1	1	.	.	.	.	.	.	.	.	.	.	195
910	45	44	7	4	6	6	5	5	9	11	1	.	2	.	1	2	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	151
911	35	34	3	2	3	6	3	5	11	7	1	1	.	2	3	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	119
912	27	31	4	5	2	2	1	3	3	6	.	.	1	1	2	.	.	.	.	3	.	.	.	.	.	.	.	.	1	.	.	.	92
913	19	19	5	4	2	6	1	3	10	10	1	1	.	1	1	1	.	.	1	1	.	.	.	.	1	.	1	.	.	.	.	.	88
914	13	19	2	2	3	.	1	2	12	8	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	63

TABLE D (continued)

References	0		1		2		3		4		1, 2		1, 3		1, 4		2, 3		2, 4		3, 4		1,2,3		1,2,4		1,3,4		2,3,4		1,2,3,4		Total
916	39	52	3	5	2	6	7	8	9	13	1	.	1	2	2	1	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	154
917	41	29	5	3	5	5	12	10	6	11	1	.	.	.	1	1	2	.	1	.	1	.	1	.	.	.	.	.	.	.	.	.	135
918	15	28	4	1	2	1	2	1	5	6	.	1	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	68
920	21	22	4	3	1	5	3	.	3	6	1	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	71
921	21	17	2	4	6	3	3	5	3	2	1	1	1	1	2	2	.	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	78
922	58	61	8	5	7	8	13	10	26	13	.	.	2	1	4	3	.	.	2	2	.	.	.	.	.	.	.	.	.	.	.	.	223
923	15	6	1	.	1	1	2	1	2	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	31
924	28	51	4	6	10	9	7	6	9	14	.	1	2	.	.	2	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	151
925	36	33	1	8	6	7	2	7	18	9	2	1	.	.	.	4	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	136
926	36	33	6	2	7	4	5	9	5	15	.	.	1	1	2	1	.	.	2	1	.	1	.	.	.	.	.	.	.	.	.	.	131
927	18	7	2	3	1	1	3	1	4	2	.	1	1	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	47
929	63	39	1	2	3	3	3	4	10	10	.	.	.	1	.	4	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	146
930	39	35	6	6	.	2	8	6	17	10	.	1	1	1	3	3	1	.	2	1	.	2	.	.	.	.	.	.	.	.	.	.	144
931	26	32	2	4	4	8	2	4	4	15	1	1	.	1	.	1	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	107
932	16	17	.	.	2	3	2	2	8	5	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	58
933	21	36	2	.	6	2	2	5	5	6	.	.	2	.	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	91
934	15	18	2	4	.	1	2	7	4	8	.	.	.	1	1	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	67
935	15	18	2	4	.	1	2	7	4	8	.	.	.	1	1	2	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	67
936	22	23	4	6	5	2	.	4	6	1	.	1	.	1	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	77
940	30	20	4	2	.	2	6	1	7	6	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	80
941	19	29	3	6	3	5	6	1	2	6	1	.	1	.	.	1	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	86
942	21	23	3	4	6	7	5	9	11	9	1	1	2	1	2	2	2	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	112
943	21	20	4	3	5	3	1	3	6	9	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	77
944	9	19	3	1	2	1	2	4	10	8	.	.	.	.	2	2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	65
946	8	6	3	2	.	6	.	2	7	3	1	.	.	2	.	.	.	1	.	1	.	.	.	.	.	.	.	1	.	.	.	.	43
948	21	18	1	5	2	6	3	1	8	4	.	1	.	1	3	2	2	.	2	2	.	1	.	.	.	.	.	.	.	.	.	.	83
949	46	15	.	.	2	2	2	2	5	3	2	.	.	1	1	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	83
950	13	17	3	4	.	1	4	1	7	1	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	53
951	17	24	2	6	4	2	2	2	8	11	.	.	2	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	81
952	20	26	2	2	3	2	7	3	10	8	.	1	.	.	1	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	87
953	23	20	2	4	4	2	3	6	4	5	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	74
954	31	11	.	2	1	.	4	.	13	4	.	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	69
957	26	25	1	.	4	1	5	2	9	5	.	.	.	.	2	1	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	83
958	20	19	3	1	.	4	5	6	5	7	1	.	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	74
959	26	22	2	3	1	3	4	2	11	2	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	77
960	22	23	1	7	1	1	5	3	6	12	1	1	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	85
961	25	8	2	2	2	3	4	2	.	2	1	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	53
962	32	29	4	.	.	1	3	2	10	3	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	85
963	15	24	2	1	1	5	4	1	5	7	1	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	68
964	19	14	3	1	.	2	1	4	10	8	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	64
965	26	15	1	1	.	2	4	4	7	7	.	.	1	.	.	1	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	71
966	23	21	4	4	4	.	3	2	7	6	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	75
968	16	28	5	3	2	2	2	3	5	6	.	1	1	.	.	1	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	77
970	16	23	2	3	1	4	4	2	6	6	1	.	.	.	.	.	.	.	1	1	.	.	.	.	.	1	.	.	.	.	.	.	71
971	20	24	2	2	2	2	3	2	11	11	.	1	1	.	.	.	.	.	.	3	1	.	.	.	.	.	.	.	.	.	.	.	85
973	23	30	3	3	1	2	3	1	6	6	1	.	2	1	1	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	86
974	16	19	2	2	3	5	2	2	4	4	1	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	62
975	35	36	4	1	5	8	5	9	8	9	.	1	.	.	.	1	1	1	.	1	.	.	.	.	.	1	.	.	.	.	.	.	126
976	41	37	3	1	3	6	6	6	11	12	.	1	.	.	1	1	.	2	1	2	.	.	.	.	.	.	.	.	.	.	.	.	134
982	41	22	4	2	2	4	4	3	7	4	.	.	1	.	2	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	98
983	23	22	3	5	7	4	3	5	13	5	.	1	.	.	1	3	1	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	99
984	22	30	5	3	4	3	4	11	7	6	.	.	.	.	1	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	99
985	29	24	5	5	3	3	6	3	11	5	.	1	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	97
986	24	28	6	2	7	5	5	3	13	10	.	1	.	.	1	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	107
987	27	16	6	4	1	5	1	2	7	3	.	1	1	2	2	1	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	82
989	16	14	1	1	6	.	2	5	3	5	.	.	1	.	1	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	58
991	20	18	4	1	1	2	2	.	3	7	.	.	.	.	1	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	62
994	15	13	2	.	2	2	4	4	1	4	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	49
995	21	27	.	3	2	5	1	1	9	9	.	.	1	.	.	1	.	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	83

TABLE D (continued)

References	0		1		2		3		4		1, 2		1, 3		1, 4		2, 3		2, 4		3, 4		1,2,3		1,2,4		1,3,4		2,3,4		1,2,3,4		Total
996	21	24	3	4	4	4	6	.	10	11	1	.	.	.	.	1	1	.	1	1	.	.	.	.	1	.	.	.	.	.	.	.	93
997	29	28	2	1	8	6	3	3	7	3	2	.	.	.	.	2	1	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	98
998	26	26	3	.	2	1	1	8	14	9	.	.	.	.	2	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	94
999	24	27	4	7	2	5	1	4	6	5	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	87
1002	17	11	2	5	2	1	1	4	6	6	.	.	.	.	2	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	59
1003	29	13	2	2	1	3	4	5	5	5	1	.	2	.	1	6	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	80
1005	26	20	2	3	4	2	3	4	8	6	.	.	.	.	1	.	.	.	.	3	.	1	.	.	.	.	.	.	.	.	.	.	83
1010	10	16	3	1	3	4	7	.	1	6	.	.	.	.	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	54
1011	13	17	3	4	2	1	3	2	8	3	.	.	.	2	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	61
1014	26	19	1	.	1	4	2	1	7	7	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	70
1023	14	22	4	3	2	4	3	.	5	5	2	.	.	.	2	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	67
1025	18	20	1	4	2	6	2	4	11	7	1	1	.	.	1	1	.	1	1	.	.	.	.	.	.	1	.	.	.	.	.	.	82
1026	53	51	5	4	7	5	8	5	12	13	.	1	1	.	2	2	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	172
1027	47	41	5	2	7	4	5	8	8	7	1	.	1	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	139
1028	28	51	9	5	6	9	7	9	18	10	4	2	1	1	2	2	.	1	.	1	.	1	.	.	.	.	.	.	.	.	.	.	167
1029	40	35	5	6	5	2	9	10	11	9	2	.	1	.	2	2	1	.	1	1	2	1	.	.	1	.	.	.	.	.	.	.	146
1031	33	32	9	7	13	12	8	11	17	11	1	1	3	3	2	.	.	.	4	2	1	1	.	.	1	.	.	.	.	.	.	.	173
1032	33	45	10	9	13	11	8	5	14	16	1	1	.	3	3	1	.	.	3	2	1	1	.	.	.	.	.	.	.	.	.	.	180
1033	56	60	4	4	3	2	9	11	22	17	.	.	1	1	6	3	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	201
1034	35	49	9	11	4	1	4	10	14	16	1	.	3	1	.	.	1	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	162
1035	33	23	2	2	2	5	6	7	10	6	2	.	.	1	1	3	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	104
1036	58	52	4	4	9	8	6	8	7	13	2	1	1	2	2	3	2	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	185
1038	43	37	5	6	2	2	8	12	12	13	.	.	.	4	.	.	.	.	2	.	.	1	.	.	.	.	.	1	.	1	.	.	148
1040	37	37	4	5	2	6	7	12	7	16	.	.	.	1	.	3	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	140
1041	46	41	9	4	4	2	8	10	9	14	.	2	.	.	.	1	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	152
1042	35	48	5	2	6	4	6	4	1	20	.	1	.	.	.	.	.	.	3	1	1	.	.	.	.	.	.	.	.	.	.	.	137
1043	18	15	1	1	2	2	1	3	4	4	1	1	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	55
1046	28	35	6	4	2	7	10	6	4	3	.	.	.	2	3	2	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	114
1060	13	14	4	2	5	3	.	2	4	4	.	1	.	1	1	1	.	3	2	1	1	.	.	.	1	.	.	.	.	.	.	.	63
1063	25	43	6	4	4	12	4	8	2	6	1	2	4	2	1	3	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	128
1066	42	23	4	3	1	4	4	1	12	8	.	.	.	1	1	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	107
1071	46	50	5	4	3	4	5	7	17	21	1	.	.	3	1	.	.	.	3	3	.	1	.	.	.	.	.	.	.	.	.	.	174
1072	42	49	7	7	5	6	9	9	15	13	.	.	1	.	3	1	.	.	1	3	.	.	.	.	.	.	.	.	.	.	.	.	171
1075	63	56	13	8	7	5	5	8	17	23	.	5	5	2	1	2	1	1	1	1	2	1	.	.	1	.	.	.	.	.	.	.	228
1084	50	21	1	4	3	3	1	1	8	6	.	1	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	102
1088	68	59	7	7	7	3	10	9	15	21	2	.	1	1	.	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	214
1090	54	36	2	4	5	1	1	4	17	9	2	.	.	.	.	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	140
1093	48	35	4	3	5	8	7	6	15	9	1	1	.	1	.	2	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	147
1094	38	43	10	5	6	11	5	9	9	8	1	.	2	2	3	1	.	1	1	2	.	1	.	.	.	.	1	.	.	.	.	.	159
1095	56	58	4	8	8	5	7	5	11	8	5	.	1	1	2	2	.	.	4	1	.	.	.	.	.	.	.	.	.	.	.	.	184
1097	40	23	5	4	.	4	5	7	8	14	.	1	1	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	114
1101	82	61	12	7	9	10	11	18	29	15	2	1	4	.	5	2	.	.	.	2	.	.	1	.	1	.	.	.	.	.	.	.	272
1102	46	58	5	8	3	3	13	7	13	9	.	.	1	2	2	1	1	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	175
1103	66	67	13	8	4	12	11	13	31	18	.	1	.	1	.	3	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	249
1108	48	47	3	1	1	3	1	9	7	19	1	1	.	.	2	.	.	.	1	.	4	.	.	.	.	.	.	.	.	.	.	.	148
1109	52	51	7	5	8	9	8	10	23	19	2	1	3	1	3	.	1	.	1	1	1	1	.	.	.	.	1	.	.	.	.	.	208
1112	43	31	5	2	6	4	7	4	6	5	.	.	2	.	1	1	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	119
1113	80	49	3	1	3	5	7	10	15	15	.	.	.	1	3	5	1	.	.1		.	.	.	.	.	.	.	.	.	.	.	.	198
1116	48	47	2	2	5	6	7	11	19	15	.	.	1	1	1	1	.	1	1	1	.	1	.	.	.	.	.	.	.	.	.	.	170
1118	46	46	7	6	9	7	9	9	27	28	1	.	3	2	3	2	1	.	1	2	.	1	.	.	.	.	.	.	.	.	.	.	210
1119	28	36	3	8	4	3	3	6	7	8	1	.	.	1	2	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	113
1120	51	25	8	5	9	10	5	10	12	8	1	3	1	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	151
1121	68	70	6	9	4	13	10	6	18	14	1	1	2	2	2	.	1	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	229
1131	86	95	4	17	7	11	13	15	32	34	2	.	1	.	2	1	.	.	2	4	2	.	.	.	.	.	.	.	.	.	.	.	328
1133	81	90	17	12	11	10	16	13	31	31	3	.	3	3	3	3	.	.	5	4	.	.	.	.	.	.	.	.	.	1	.	.	337
1139	57	63	9	7	2	1	8	14	18	9	.	.	.	.	2	.	.	.	.	2	.	.	.	.	1	.	.	.	.	.	.	.	193
1141	31	26	6	5	.	4	6	4	8	10	.	.	1	1	2	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	107
1142	21	46	8	6	3	6	5	8	11	14	.	3	1	1	1	1	1	2	2	1	.	.	.	.	.	.	1	.	.	1	.	.	143
1148	38	37	6	1	1	3	8	9	10	11	.	.	.	.	1	1	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	128

TABLE D (continued)

References	0		1		2		3		4		1, 2		1, 3		1, 4		2, 3		2, 4		3, 4		1,2,3		1,2,4		1,3,4		2,3,4		1,2,3,4		Total
1150	30	50	4	4	4	5	10	6	15	14	1	.	.	.	.	2	.	.	.	3	.	.	.	.	.	.	2	.	.	.	.	.	150
1151	28	30	2	1	3	4	7	6	9	4	.	1	1	.	1	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	99
1152	71	60	6	7	6	8	17	10	14	18	1	1	2	3	2	3	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	231
1153	63	86	11	10	7	10	12	15	22	15	1	1	.	2	2	2	1	.	3	1	.	.	.	.	.	.	.	.	.	.	.	.	264
1154	44	45	6	10	4	3	8	12	15	14	.	2	2	2	4	1	.	.	.	.	.	2	.	.	1	.	.	.	.	1	.	.	176
1156	58	52	8	8	8	5	9	7	15	22	.	.	.	1	1	1	.	.	1	1	1	.	.	.	.	.	.	1	.	.	.	.	199
1158	33	18	2	3	5	5	.	2	9	7	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	85
1160	45	52	14	5	1	2	5	10	15	14	.	.	2	.	1	3	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	170
1165	32	16	4	1	5	5	15	1	11	11	1	.	1	.	1	.	1	1	2	2	1	.	.	.	1	.	.	.	.	.	.	.	112
1169	26	19	3	2	3	5	6	8	5	5	1	1	.	1	3	1	1	.	1	.	1	2	1	.	.	.	.	.	.	.	.	.	95
1173	63	53	10	11	1	7	4	12	20	20	.	2	.	3	3	4	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	214
1174	80	73	10	8	3	11	16	14	25	35	4	.	3	5	4	4	.	1	1	4	.	.	.	.	2		1	.	.	1	.	.	305
1177	18	16	3	3	1	3	2	1	7	2	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	59
1179	40	41	5	4	4	8	7	4	15	8	.	.	.	.	1	3	2	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	144
1181	107	98	15	9	11	17	12	20	18	32	3	3	3	4	6	4	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	364
1182	95	106	12	15	15	16	16	19	25	26	1	.	5	4	2	4	.	.	1	1	.	1	.	.	1	.	.	.	.	.	.	.	365
1187	51	51	4	8	3	8	5	6	14	9	.	.	.	2	3	3	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	169
1188	39	24	2	2	8	4	2	4	12	9	1	.	1	1	1	5	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	117
1199	46	39	6	5	8	12	8	15	25	19	1	.	.	.	1	3	.	1	1	.	1	1	.	.	.	.	.	.	.	.	.	.	192
1200	40	31	4	4	5	5	10	9	9	8	1	.	1	1	2	1	.	1	2	1	.	.	.	.	2	.	.	.	.	1	.	.	138
1201	34	25	4	6	6	3	2	3	9	15	.	1	.	.	1	2	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	113
1204	27	14	1	.	3	1	3	1	2	2	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	55
1206	21	16	5	4	3	2	4	2	3	12	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	73
1219	9	14	4	1	4	8	1	3	4	6	1	1	2	1	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	61
1220	44	40	4	4	6	9	1	6	14	14	1	.	.	.	2	4	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	152
1221	12	13	.	2	.	1	.	2	4	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	37
1222	31	18	4	1	.	4	1	6	5	9	1	.	.	1	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	83
1225	21	13	2	2	1	3	1	2	4	7	.	.	.	2	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	59
1230	11	20	1	7	5	3	2	1	4	7	1	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	64
1231	46	33	6	4	6	2	.	3	13	10	.	.	2	.	1	2	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	129
1232	11	13	1	3	3	3	1	3	8	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	50
1233	27	40	4	4	4	4	3	6	14	11	1	1	1	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	127
1235	12	16	3	6	2	5	4	1	3	4	1	.	1	.	2	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	62
1236	25	19	2	7	.	3	1	3	11	4	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	77
1237	10	7	2	4	5	2	4	1	6	7	.	.	1	.	1	1	.	.	1	.	1	.	.	.	.	.	.	1	.	.	.	.	54
1238	12	14	2	1	.	2	.	1	3	4	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	41
1240	27	27	3	4	4	9	.	5	4	10	.	.	1	.	1	2	.	1	2	3	.	.	.	.	.	.	.	.	.	.	.	.	103
1241	26	27	4	.	3	2	2	6	6	13	.	.	1	1	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	94
1243	44	36	5	3	4	3	7	2	18	15	2	.	2	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	147
1244	12	10	2	3	1	2	2	5	5	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	48
1247	30	30	2	5	4	5	4	4	9	9	.	.	1	.	.	4	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	109
1253	38	30	4	5	6	4	4	7	8	11	4	2	1	1	1	2	.	.	.	3	.	1	.	.	.	.	.	.	.	.	.	.	132
1254	33	28	7	8	2	6	4	8	7	11	.	.	.	.	.	.	1	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	118
1256	33	29	8	3	7	5	3	4	6	11	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	111
1257	27	37	8	5	5	5	6	4	7	14	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	120
1258	39	26	6	4	2	2	4	3	13	15	1	.	1	2	4	1	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	125
1259	22	15	6	4	1	5	2	.	12	14	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	72
1260	26	34	3	6	3	1	9	5	9	10	.	.	1	2	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	112
1261	22	16	3	7	2	.	2	6	6	8	1	.	.	1	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	77
1262	30	38	2	2	2	8	6	7	3	13	1	1	3	.	1	.	.	.	2	1	1	.	.	.	.	.	.	.	.	.	.	.	121
1263	40	46	4	3	5	7	9	6	11	8	2	.	1	1	3	2	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	150
1264	14	12	2	2	1	4	2	5	14	2	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	59
1265	12	8	2	2	1	9	2	2	2	4	1	.	.	.	.	2	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	49
1266	17	11	.	.	3	4	4	2	2	2	1	.	2	.	.	1	1	.	1	3	.	.	.	.	.	.	.	.	.	.	.	.	54
1267	23	20	5	2	6	7	4	6	9	8	.	2	1	2	1	1	.	.	1	.	.	2	.	.	.	1	.	.	.	.	.	.	101
1268	22	27	5	1	4	4	1	3	10	8	.	1	1	1	4	2	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	96
1281	39	50	8	14	7	6	4	10	10	17	.	1	.	2	1	4	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	174
1282	63	42	11	10	7	11	8	14	16	9	1	.	.	3	.	.	.	1	3	.	.	1	.	.	.	1	.	.	.	.	.	.	207
1283	17	20	12	7	.	4	3	3	4	6	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	72

TABLE D (continued)

References	0	1	2	3	4	1, 2	1, 3	1, 4	2, 3	2, 4	3, 4	1,2,3	1,2,4	1,3,4	2,3,4	1,2,3,4	Total
1284	28 9	2 2	1 5	2 .	4 2	3 .	2 1	1 .	1 .	. 1	1 .	. 1	. .	. .	. .	. .	66
1287	29 25	7 3	4 4	8 5	4 10	. 2	2 2	1 2	. 4	. .	. 1	. .	. .	. .	. .	. .	113
1288	64 21	1 2	4 4	5 6	7 8	2 1	1 .	1 .	. 1	2 .	. .	. .	. .	. .	. .	. .	130
1289	30 29	5 6	5 8	7 8	6 13	2 .	2 .	1 .	. .	. 1	. .	. .	. .	. .	. .	. .	123
1290	42 38	9 9	10 7	8 11	15 14	4 2	1 2	3 2	1 1	2 3	2 .	. 1	2 .	. .	. .	. .	189
1291	45 48	6 10	15 13	2 7	7 6	1 2	3 3	2 1	1 2	1 1	2 .	. .	. .	. .	. .	. .	180
1292	33 23	8 4	7 6	6 3	12 3	2 4	3 .	1 2	. 1	5 3	2 1	. .	. .	. .	. .	. .	129
1293	41 35	7 5	9 8	9 4	11 8	3 1	1 1	1 .	. 2	. 2	. 1	. 1	. .	. .	. .	. .	150
1294	39 41	4 4	10 13	12 6	15 15	. 1	3 3	3 1	. .	2 2	2 3	1 .	1 .	. .	. .	. .	181
1296	40 43	11 4	1 9	4 6	15 16	3 1	3 1	4 .	. .	. 2	. 2	. .	1 .	. .	. .	. .	166
1297	28 19	3 4	4 4	7 3	9 11	. .	. 1	1 .	. .	2 1	. .	. .	. .	. .	. .	. .	97
1298	47 71	6 8	6 6	11 8	11 12	1 .	. 1	4 2	. .	2 3	. .	. .	. .	. .	. .	. .	199
1301	35 29	5 7	1 6	5 4	9 18	. 2	1 1	1 3	. 1	. 2	. .	. .	. .	. .	. .	1 .	131
1302	32 24	6 2	2 5	2 2	2 11	. .	1 .	. 1	. .	1 .	. .	. .	. .	. .	. .	. .	91
1304	37 30	6 2	4 .	5 6	8 9	2 .	. .	1 .	. .	. .	. .	. .	. 1	. .	. .	. .	111
1305	33 30	6 7	3 7	9 7	6 5	. 4	1 2	2 2	1 3	. 2	. 1	. .	. .	. .	. .	. .	131
1306	14 14	2 3	1 3	3 3	2 1	. 1	2 1	. 1	. .	1 1	. 1	. .	. .	. .	. .	. .	54
1307	44 41	7 7	6 9	10 9	12 14	1 1	4 1	2 1	1 .	2 1	. 1	. .	1 .	. .	. .	. .	175
1308	38 34	9 6	6 9	4 6	12 15	1 .	2 .	1 1	. 1	1 .	. .	. .	1 .	. .	. .	. .	147
Total	17,171	2208	2211	2639	5163	292	392	629	132	413	125	11	39	17	13	1	31,456

LITERATURE CITED

ALTENBURG, EDGAR, 1916 Linkage in *Primula sinensis*. Genetics **1**: 354-366.

BAILEY, P. G., 1913 Primary and secondary reduplication series. Jour. Genetics **3**: 221-227.

BALTZER, F., 1909 Über die Entwicklung der Echiniden-Bastarde mit besonderer Berücksichtigung der Chromatinverhältnisse. Zoöl. Anz. **35**: 5-15.

1910 Über die Beziehung zwischen dem Chromatin und der Entwicklung und Vererbungsrichtung bei Echinodermenbastarden. Arch. f. Zellforsch. **5**: 497-621.

BATESON, W., and PUNNETT, R. C., 1911 On genetic series involving reduplication of certain terms. Jour. Genetics **1**: 293-303.

1911 On the interrelation of genetic factors. Proc. Roy. Soc. Eng. B **84**: 3-8.

BATESON, W., SAUNDERS, MISS E. R., and PUNNETT, R. C., 1906 Reports to the Evolution Committee. Experimental studies in physiology of heredity **3**: 8-11.

BAUR, E., 1911 Ein Fall von Faktorenkoppelung bei *Antirrhinum majus*. Verh. Naturf. Ver. Brünn. **49**: 130-138.

BLAKEMAN, JOHN, 1905 On tests for linearity of regression in frequency distributions. Biometrika **4**: 332-350.

BOVERI, TH., 1907 Zellen-Studien VI. Die Entwicklung dispermer Seeigel-Eier. Ein Beitrag zur Befruchtungslehre und zur Theorie Des Kerns. pp. 292. Jena: Gustav Fischer.

BRIDGES, C. B., 1914 The chromosome hypothesis of linkage applied to cases in sweet peas and Primula. **48**: 524-534.

1913 Non-disjunction of the sex chromosome in Drosophila. Jour. Exp. Zoöl. **15**: 587-606.

1914 Direct proof through non-disjunction that the sex-linked genes of Drosophila are borne by the X chromosome. Science, N.S. **50**: 107-109.

1915 A linkage variation in Drosophila. Jour. Exp. Zoöl. **19**: 1-21.

1916 Non-disjunction as proof of the chromosome theory of heredity. Genetics **1**: 1-53, 107-164.

1917 An intrinsic difficulty for the variable-force hypothesis of crossing over. Amer. Nat. **51**: 370-373.

CURTIS, M. R., 1914 A biometrical study of egg production in the domestic fowl. IV. Factors influencing the size, shape and physical constitution of eggs. Arch. f. Entwicklungsmech. d. Organ. **39**: 217-327.

GAVIN, W., 1913 The interpretation of milk records. Jour. Roy. Agr. Soc. **73**: 1-22.

GATES, R. R., 1907 Pollen development in hybrids of *Oenothera lata* × *Oe. Lamarckiana* and its relation to mutation. Bot. Gaz. **43**: 81-115.

1908 A study of reduction in *Oe. rubrinervis*. Bot. Gaz. **46**: 1-34.

1909 The behavior of the chromosomes in *Oe. lata* × *Oe. gigas*. Bot. Gaz. **48**: 179-199.

1911 The mode of chromosome reduction. Bot. Gaz. **51**: 321-344.

GATES, R. R., and THOMAS, N., 1914 A cytological study of *Oenothera* mut. *lata* and *Oe.* mut. *semilata* in relation to mutation. Quar. Jour. Micr. Sci. **59**: 523-573.

GEERTS, J. M., 1911 Cytologische Untersuchungen einiger Bastarde von *Oenothera gigas*. Ber. d. deutsch. bot. Gesell. **29**: 160-166.

GODLEWSKI, E., 1911 Studien über die Entwicklungserregung. I. Kombination der heterogenen Befruchtung mit der künstlichen Parthenogenese. Arch. f. Entwicklungsmech. d. Organ. **33**: 196-233.

GOLDSCHMIDT, R., 1917 Crossing over ohne Chiasmatypie. Genetics **2**: 82-95.

GOODALE, H. D., 1909 Sex and its relation to the barring factors for poultry. Science, N. S. **29**: 1004-1005.

1910 Breeding experiments in poultry. Proc. Soc. Exp. Biol. Med. **7**: 178-179.

1917 Crossing over in the sex chromosome of the male fowl. Science, N. S. **146**: 213.

GREENWOOD, M., and BROWN, T. W., 1913 A second study of the weight variability and correlation of the human viscera. Biometrika **9**: 473-485.

GREGORY, R. P., 1911 On genetic coupling and repulsion in *Primula sinensis*. Proc. Roy. Soc. B. **84**: 12-15.

HERBST, C., 1909 Die cytologischen Grundlagen der Verschiebung der Vererbungsrichtung nach der mütterlichen Seite. Arch. f. Entwicklungsmech d. Organ. **27**: 266-308.

HERON, DAVID, 1911 The danger of certain formulae suggested as substitutes for the correlation coefficient. Biometrika **8**: 109-123.

JANSSENS, F. A., 1909 La théorie de la chiasmatypie. Nouvelle interpretation des cinèses de maturation. La Cellule **25**: 389-414.

LUTZ, A. M., 1912 Triploid mutants in Oenothera. Biol. Centralbl. **32**: 385-435.

1916 Oenothera mutants with diminutive chromosomes. Amer. Jour. Bot. **3**: 502-526.

McCLUNG, C. E., 1899 A peculiar nuclear element in the male reproductive cells of insects. Zoöl. Bull. **2**: 187-197.

MACDONELL, W. R., 1904 A study of the variation and correlation of the human skull, with special reference to English crania. Biometrika **3**: 191-245.

MACDOWELL, EDWIN C., 1917 The bearing of selection experiments with Drosophila upon the frequency of germinal changes. Proc. Nation. Acad. Sci. **3**: 291-297.

MORGAN, T. H., 1910 a Sex-linked inheritance in Drosophila. Science, N. S. **32**: 120-122.

1910 b The method of inheritance of two sex-linked characters in the same animal. Proc. Soc. Exp. Biol. Med. **8**: 17.

1911 a An attempt to analyze the constitution of the chromosomes on the basis of sex-linked inheritance in Drosophila. Jour. Exp. Zoöl. **11**: 365-413.

1911 b Random segregation vs. coupling in Mendelian inheritance. Science, N. S. **34**: 384.

1912 a The explanation of a new sex ratio in Drosophila. Science, N. S. **36**: 718-719.

1912 b Complete linkage in the second chromosome of the male. Science, N. S. **36**: 719-720.

1915 The rôle of the environment in the realization of a sex-linked Mendelian character in Drosophila. Amer. Nat. **59**: 385-429.

MORGAN, T. H., and BRIDGES, C. B., 1916 Sex-linked inheritance in Drosophila. Carnegie Institution of Washington Publ. 237, 87 pp.

MORGAN, T. H., STURTEVANT, A. H., MULLER, H. J., and BRIDGES, C. B., 1915 The mechanism of Mendelian heredity. Pp. 262. New York: Henry Holt & Co.

MULLER, H. J., 1916 The mechanism of crossing over. Amer. Nat. **50**: 193-221, 284-305, 350-366, 421-434.

PEARL, R., 1909 The frequency constants of a variable. Biometrika **6**: 437.

PEARL, R., and SURFACE, F. M., 1914 A biometrical study of egg production in the domestic fowl. III. U. S. Dept. Agric. Bur. Animal Industry, Bull. 110, pp. 178.

PEARSON, KARL, 1914 Tables for statisticians and biometricians. Cambridge. pp. 143. Chicago: Univ. of Chicago Press.

1896 Regression, heredity and panmixia. Phil. Trans. Soc. A **187**: 253-318.

1895 Mathematical contributions to the theory of evolution. II. Skew variation in homogeneous material. Phil. Trans. Roy. Soc. A **186**: 343-414.

1900 On the criterion that a given system of deviations from the probable in the case of a correlated system of variables is such that it can be reasonably supposed to have arisen from random sampling. Phil. Mag., ser. 5, **50**: 157-175.

1905 Mathematical contributions to the theory of evolution. XIV. On the general theory of skew correlation and non-linear regression. Drapers Company Research Memoirs. Biometric Series II, pp. 1-54, *5 fig.*

1911 On the probability that two independent distributions of frequency are really samples from the same population. Biometrika **8**: 250-253.

PEARSON, K., and HERON, DAVID, 1913 On theories of association. Biometrika **9**: 159-333.

PLOUGH, HAROLD H., 1917 The effect of temperature on crossing over in Drosophila. Jour. Exp. Zoöl. **24**: 147-211. *9 fig.*

POWYS, A. O., 1905 On fertility, duration of life and reproductive selection. Biometrika **4**: 233-285.

PUNNETT, R. C., 1913 Reduplication series in sweet peas. Jour. Genetics **3**: 77-105.

1917 Reduplication series in sweet peas. II. Jour. Genetics **6**: 185-195.

SURFACE, F. M., 1909 Fecundity of swine. Biometrika **6**: 433-436.

STEVENS, N. M., 1905 Studies in spermatogenesis with especial reference to 'Accessory chromosomes.' Carnegie Institution of Washington, Publ. 36. 74 pp.

1908 A study of the germ cells of certain Diptera, with reference to the heterochromosomes and the phenomena of synapsis. Jour. Exp. Zoöl. **5**: 359-374.

STURTEVANT, A. H., 1913 The linear arrangement of six sex-linked factors in Drosophila as shown by their mode of association. Jour. Exp. Zoöl. **14**: 43-61.

1915 The behavior of the chromosomes as studied through linkage. Zeitschr. f. ind. Abstamm. u. Vererb. **13**: 234-287.

1914 The reduplication hypothesis as applied to Drosophila. Amer. Nat. **48**: 535-549.

1917 a Genetic factors affecting the strength of linkage in Drosophila. Proc. Nation. Acad. Sci. **3**: 555-558.

1917 b Crossing over without chiasmatype? Genetics **2**: 301-305.

SUTTON, W. S., 1902 On the morphology of the chromosome group in *Brachystola magna*. Biol. Bull. **4**: 24-39.

TANAKA, Y., 1913 a Genetic coupling and repulsion in silkworms. Jour. Coll. Agric. Sapporo **5**: 115-118.

1914 Sexual dimorphism of genetic series in reduplication. Trans. Sapporo Nat. Hist. Soc. **5**: 61-64.

TROW, A. H., 1912 Forms of reduplication—primary and secondary. **2**: 313-315.

1916 A criticism of the hypothesis of linkage and crossing over. Jour. Genetics **5**: 281-297.

WELDON, W. F. R., 1902 Mendel's laws of alternative inheritance in peas. Biometrika **1**: 228-254.

WILSON, E. B., 1905 a The chromosomes in relation to the determination of sex in insects. Science, N. S. **22**: 500-502.

1905 b Studies on chromosomes. II. The paired microchromosomes, idiochromosomes and heterotropic chromosomes in Hemiptera. Jour. Exp. Zoöl. **2**: 507-545.

1909 Studies on chromosomes V. The chromosomes of Metapodius. A contribution to the hypothesis of the genetic continuity of chromosomes. Jour. Exp. Zoöl. **6**: 143-215.

1912 Some aspects of cytology in relation to the study of genetics. Amer. Nat. **46**: 57-67.

WILSON, E. B., 1914 Croonian lecture: The bearing of cytological research on heredity. Proc. Roy. Soc. B **88**: 333-352.