CROSSING OVER AND GENE REARRANGEMENT IN FLOWERING PLANTS[1]

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HYPOTHESES OF CROSSING OVER

Kinds of gene rearrangement

"Crossing over" exists apparently in all those flowering plants which have been sufficiently investigated with regard to it. (By itself, it does not rearrange different genes, but only exchanges alleles.) Genetically it consists in exchange of normally equal and homologous segments of a gene string (MORGAN 1911, STURTEVANT 1915, MULLER 1916). It has been proved, by the microscope, to consist in the exchange, at meiosis, of normally equal portions of homologous chromonemas (CREIGHTON and MCCLINTOCK 1931, STERN 1931). It may thus be termed "homologous exchange". Since the process is a normal one, the mechanism is apparently so perfect that no genes are lost in the exchange.

"Reversed crossing over" consists in the exchange of different arms of homologous chromosomes, apparently at the fusal (spindle) constriction. It has been proved to occur at the origin of the secondary mutants of Datura, usually in trisomics, and probably at meiosis.

"Reciprocal translocation" (heterologous interchange) is much rarer than crossing over. It consists in the mutual substitution of usually unequal segments of heterologous chromosomes. It has been proved to occur cytologically as well as genetically (see BELLING 1927, STURTEVANT and DOBZHANSKY 1930, DOBZHANSKY and STURTEVANT 1931, MCCLINTOCK 1930). It seems to originate at both mitosis and meiosis. It may be caused by X-rays. Apparently genes may sometimes be lost in the process.

"Translocation" shows a segment of one chromosome terminally attached, usually to a heterologous chromosome (see especially PAINTER and MULLER 1929).

"Inversion" consists in a portion of the gene string or chromonema being turned round, end for end; genes being apparently sometimes lost in the process (see especially STURTEVANT 1931, and MCCLINTOCK 1931).

"Deletion" removes a non-terminal portion of the gene string, the gap closing up (see especially PAINTER and MULLER 1929). The portion removed may form a ring (MCCLINTOCK 1932).

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"Insertion" causes a segment of one chromonema to be placed within another gene string. Genes may be lost in the process. It seems quite rare.

"Deficiency" is usually the loss of a (terminal) segment of the gene string (see McCLINTOCK 1931). It originates at meiosis or mitosis.

The hypotheses

A successful hypothesis is normally based on *verae causae* (ascertained facts), while unsuccessful hypotheses are often marked by containing one or more *fictae causae* (imagined statements). The first hypothesis as to crossing over seems to have been that of JANSSENS (1909), who predicted exchange of parts of homologous chromosomes, from his observations of chiasmas. In this hypothesis he introduced the *fictae causae* of two strands first breaking accurately at corresponding points, and then these same two strands joining in an alternate way. These processes took place conjecturally at an overlap (or at a half twist). This "break and join" seems to the writer improbable mechanically. There would be needed an accuracy of position, in the two strands, of less than half a micron, with nothing to mark the breakage points. Without such accuracy, the crossing over would be unequal; which it is not (with one exception). Also the conditions required for a break are the reverse of those for a join.

A second hypothesis, stated in full by BATESON in 1911, demanded selective division of cells (somatic and gonial), in accurate ratios, precisely separating the pairs of alleles, and properly multiplying them, so as to result in numbers corresponding to the mathematical expression of certain combinations. This would seem to require unknown forces to bring it about, and was also contrary to the known relevant facts. It has been proved to be wrong.

A third composite hypothesis for crossing over required openings-out at diplotene, alternately at the primary split and the secondary split; these alternations being the *cause* of chiasmas. (It is possible that such alternations may occur as a *consequence* of the opening out of chiasmas at diplotene, in plants like Datura.) It also adopted the "break and join" of JANSSENS, the weak point of his hypothesis (SAX 1932). This alternate-opening hypothesis is negatived for certain liliaceous plants (and for Dendrocoelum) by the observed facts: that chiasmas are present at pachytene; that it is recognizably the primary split which opens out at early diplotene (a stage which has rarely been well figured); while the secondary split at this stage is responsible only for a two-lobed state of the chromomeres (GELEI 1921, BELLING 1931a). The sequence of these splits is especially clear in Lilium and Fritillaria, where the primary split can be followed from early pachytene to mid diplotene. This third hypothesis

thus contains three imaginary causes: alternate openings-out as a cause, not a consequence, of chiasmas; accurate double breaks; and special double joinings. Chromonemas have not been observed to break and join again at the chiasmas, as required by this hypothesis.

A fourth hypothesis, that of the present writer, attempts to postulate *verae causae*. It was framed after a study of the chromomeres and chromioles; and this was not the case with the three other hypotheses, which ignored the chromomeres. It also accounts for gene rearrangements, which the other hypotheses ignore. The chief supports of this fourth hypothesis are the following. (a) The absence of longitudinal division in the chromonema at leptotene; as observed especially by the writer (1931a), WENRICH (1917), GELEI (1921), and BELAR (1929a). (b) The proof of the complete equivalence of the two chromioles resulting from the secondary split in each chromomere (MENDEL 1866, SUTTON 1903, GELEI 1921). (c) The fact that only homologous chromomeres, including alleles, are connected transversely (that is, synapse) at zygotene; as observed by GELEI (1921), by the writer (1928, 1931a), and also by MCCLINTOCK (1931) in cases of inversion. (d) The fact that non-homologous chromomeres are connected longitudinally to their nearest neighbors by one, and only one, fiber; as observed especially by GELEI (1921) and by the writer (1928, 1931a). (e) That the *two* chromioles formed from each original chromomere by the secondary split are seen to have acquired a new fiber connection longitudinally (in addition to the old fiber), which joins *one* of them to the nearest non-homologous chromiole each way (GELEI 1921, BELLING 1928, 1931a, 1931b). (f) That such new connections are formed when the chromonema is dividing longitudinally (BELLING 1931a, 1931b). (g) That crossing over (exchange), inversion, translocation, interchange, and deletion can take place when the chromonemas are dividing longitudinally (BELLING 1931b).

PRELIMINARY KARYOLOGIC EVIDENCE

Chromonemas are normally unsplit at leptotene and during the resting stage

The writer has made a special investigation of this point, by means of smear preparations in iron-aceto-carmine, and also by smear preparations fixed with chromic-acetic-formalin and stained with iron-brazilin. The plants mostly used were *Tradescantia virginiana*, *Rhoeo discolor*, *Allium triquetrum*, *Lilium regale*, *Scilla sibirica*, and *Aloe striata*. The work resulted in the conclusion that the so-called telophasic split (SHARP 1929, ROBERTSON 1931, and KAUFMANN 1925) did not exist here; and that the spongio-reticular structures in the nucleus, commonly figured in sections from mass fixations, were artifacts of slow fixation. BELAR (1929a, 1929b)

came to a similar conclusion. The writer found (like MARTENS 1927, 1929, and BELAR 1929a) that living resting (non-dividing) nuclei (in cells showing cyclosis), which would not normally divide again, when examined in an aqueous medium by the best water-immersion objectives, with accurate microscopy, were seen to contain unsplit, loosely coiled and zigzagged chromonemas. The plant material in which this was observed included: stamen-hairs of *Tradescantia virginiana*, of *Tradescantia fluminensis* (in which the nuclei sometimes appeared blank, but at other times showed the chromonemas), and of *Rhoeo discolor;* the hairs on the labellum of *Cypripedium pubescens*, and the stinging hairs of *Urtica gracilis*. When such non-dividing nuclei were fixed and stained, with optimum fixation, the same unsplit chromonemas were seen in them; but with slow fixation the familiar spongio-reticular structure (seen in sections of material fixed in mass) regularly appeared.

Preparations made by sectioning from material fixed in bulk suffer from too slow fixation. In the telophases, chromatin is being lost, and it is not strange that the interior of the vanishing chromosome should sometimes be more or less unstained, and that by poor fixation a moniliform aspect should be caused. It seems to the writer premature to infer from such changes that there is a longitudinal split in the telophase. For no signs of such a split are seen in good smear preparations of telophases, as observed by BELAR (1929b) and by the writer.

In the leptotene of Lilium, Galtonia, Allium, Scilla, Hyacinthus, Tulipa, and Agapanthus, in smear preparations stained with iron-brazilin and showing the chromomeres, it was ascertained by the writer that there was no trace of a longitudinal or other split, in either the chromomeres or their connecting fibers. It was also seen clearly that the secondary split came subsequently, in mid pachytene; early pachytene having only the primary split (figure 1). In Allium, slow destaining (in hyrax) of the early pachytene (1931a) proved that each chromomere had only one stained submicroscopic core, which was, in the writer's opinion, a gene with a thin covering of chromatin. There being only one such core in a chromomere, in the early pachytene, proved, apparently conclusively, that the secondary split had not yet appeared.

Hence, the evidence from the best fixed preparations, namely smear preparations showing chromomeres, is against any general telophasic split; and the supposed split can be sometimes explained as an artifact of slow fixation, resulting from fixation in mass.

Crossing over probably occurs during pachytene

In Lilium the average longitudinal distance between the centers of adjacent chromomeres at late pachytene (figure 2) was under half a micron. It

was seen to be less than this in several other liliaceous plants (but not in Fritillaria). Hence a relative movement of the homologous chromonemas by half a micron would bring about unequal crossing over, if any crossing over should occur. But unequal crossing over seems rare, being only known in the bar locus. Thus, apparently, crossing over must take place at pachy-

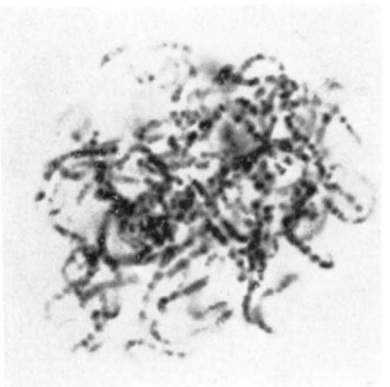

FIGURE 1.—Early pachytene of *Lilium regale*. Smear preparation, fixed in Navashin's mixture, stained with brazilin, and mounted in immersion oil. Pressed nearly flat. Photographed with Zeiss apochromatic 90 of 1.4 aperture, with homal. Enlargement near 1300. The chromomeres have *nearly* all synapsed. The secondary split has not yet appeared.

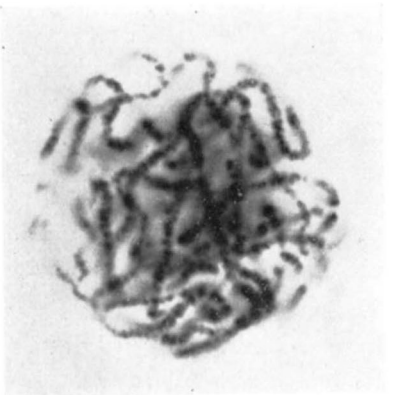

FIGURE 2.—Late pachytene of *Lilium regale*. Preparation as in figure 1, but not pressed. Focus somewhat below upper surface. All chromomeres have previously synapsed, and all are bilobed by the secondary split.

tene, when the homologous chromonemas are *fixed* together in the right positions by the connections between homologous chromomeres across the primary split. Any opening-out of the primary and secondary splits, or any sliding of the chiasmas, would apparently prevent that exact correspondence of the homologous chromomeres in the two homologous chromonemas, necessary to obviate unequal crossing over.

The two chromioles formed by the secondary split are equivalent

When a chromomere with its contained gene divides into two, genetic work has shown that there is no difference between the two products. One is apparently a replica of the other, as far as the evidence goes. Hence neither of them can truly be called the "old" chromomere or chromiole, or the "new" chromomere or chromiole. The same applies to chromonemas, which are strings of chromomeres. Two adjacent chromomeres at a certain minute distance apart, which is usually less than half a micron from center to center, can mutually form a connecting fiber. Such a fiber appears at zygotene between approaching homologous chromomeres, at first (sometimes) in the form of minute projections from the two adjacent chromomeres. Only one such fiber unites a pair of homologous chromomeres or a pair of chromioles. When the chromomeres divide at the secondary split, at mid pachytene, then a new fiber passes between two of the homologous chromioles transversely to the primary split. The new and the old fiber may thus form two transverse fibers at each locus. When the secondary split appears, a new *longitudinal* fiber is also formed. This passes between two adjacent non-homologous chromioles. The old fiber connects the other two adjacent chromioles. In all cases these fibers pass *the shortest way*, between chromioles that are nearly or quite touching; and do not pass diagonally, because this would be about four-tenths longer. (Thus there would not be normally half twists formed between sister chromonemas.)

Opening-out at earliest diplotene is (sometimes) at the primary split, and at first at many points

At earliest diplotene (schizotene) in *Allium triquetrum*, the homologous chromonemas of the nine bivalents begin to separate at about two hundred points (1931a), a number which is in excess of the total chiasmas, which may amount to near twenty at late diaphase. A large number of points of opening-out has also been seen at early diplotene (schizotene) in Lilium. At this stage, some of the pachytene chromonemas will not yet have opened-out completely, and all details of the process of opening-out can be traced (figure 3). In no case has the secondary split been seen to open-out in Lilium. (The chiasmas become visible at pachytene, before any opening-out.) The primary split is broad and clear, while the secondary split is hard to see (and has been so from its origin at mid pachytene), only consisting in the two-lobed condition of the chromomeres. In no case in liliaceous plants did four separate "opened-out" threads appear, as it would seem (as already stated) might occur at the points between the alternate openings-out presumed to exist in certain grasshoppers. McCLINTOCK (1931) proved that, in deficiencies in maize, only the primary split

showed at late pachytene at the point where the deficiency was. The same was the case with inversions. If the secondary split also opens out at diplotene, it is in bivalents which, at diaphase and metaphase, show normally no chiasmas but only terminal junctions (Datura).

In the supposed "break and join" of two or more chromonemas, the "break" apparently does not occur

In crossing over, translocation, interchange, inversion, and deletion, it has been supposed that the chromonemas first broke and then joined up in a different way. Since the breaks must correspond, in crossing over (as already stated), with an accuracy of less than half a micron, they are unlikely. Since breaks are presumably due to a tension, such tension will

FIGURE 3.—Stage (*L. pardalinum*) between pachytene and diplotene (early diplotene or "schizotene"). Prepared as in figure 1, but photographed with objective of 1.3 aperture. Slightly flattened. Focus just below surface. Thick (double) and thin (single) threads. In Lilium the opening-out seems to be only at the primary split.

render immediately subsequent joins improbable. Hence it is likely that the only disconnections that occur in chromonemas are between half of the newly formed chromioles, before they form a longitudinal connection with their nearest neighbors. In other words, chromonemas may join up from an unjoined state, but do not normally break after having joined.

ORIGIN OF CHIASMAS

Division of chromomeres, and formation of new fibers

For some time after the chromomeres have divided, at mid pachytene, only half the final number of longitudinal connecting fibers are clearly visible in each of the two synapsed chromonemas (as the writer has seen especially in Lilium). They are the old fibers. When the new fibers appear between the remaining half of the divided chromomeres (chromioles),

they are at first thin and inconspicuous. But they become indistinguishable from the old fibers at late diplotene (figure 4). Thus when the chromomeres of the two synapsed threads divide each into two chromioles, as they do in mid pachytene, there are only sufficient longitudinal threads for half of them. Each old chromomere forms two new chromioles, and there are no old chromomeres, old chromioles, old chromonemas, or old chromosomes left; only old connecting fibers are visible. Now, these old fibers cannot pass obliquely (as already stated) without an increase in length of about 40 percent. They do not seem to increase in length, but remain directly longitudinal between two of the chromioles (*which* two chromioles is apparently determined by chance). When, after a short time and during late pachytene, the *new* longitudinal fibers start their growth, they are forced

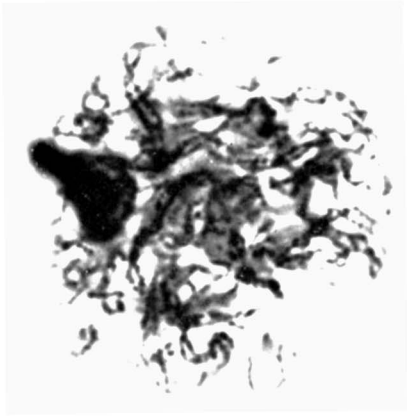

FIGURE 4.—Stage (*L. pardalinum*) when the opening-out is just complete (late diplotene, or "diplotene"). Preparation as in figure 1. Viewed below the upper surface. The bivalents form nodes and internodes. A node is not necessarily a chiasma, though many are.

to pass directly longitudinally because of the direct longitudinal position of the old fibers. Hence, there are, normally, no oblique connecting fibers between sister strands (in meiosis or mitosis); and no crossing over, twisting or overlapping of the sister strands.

Overlaps of the two homologous chromonemas

Overlaps of the two synapsing homologues seem likely to take place often enough to form the usual numbers of chiasmas. They will only form the diagonal X's if the chromomeres are sufficiently apart; for the formation of an X reduces the longitudinal distance between the centers of the chromomeres by about 30 percent. Thus if the centers of the chromomeres are 0.5 micron apart, and the connecting fibers are 0.2 micron long; then an overlap would form an X, with the chromomeres 0.05 micron apart. But if the chromomeres at 0.5 micron distance were connected by fibers only

0.1 micron long, then they could not form the diagonals of an X because these old connecting fibers would not be long enough. In this case the half twist or overlap would perhaps remain more or less external, without causing an X.

The X of the overlap may arise at zygotene with either of two directions of turn. When the chromomeres divide into two, the two diagonals of the X, like the normal direct longitudinal connections between the other chromomeres of the synapsed chromonemas, cannot become oblique, because this would require a growth of about 40 percent over the previous length. Hence they each remain in a plane with one of the two pairs of non-sister chromonemas (halves of synapsed partners). Which of the two planes any diagonal of the X is in, is apparently settled by chance. Thus the two diagonals may remain: (1) in both directions of overlap, together

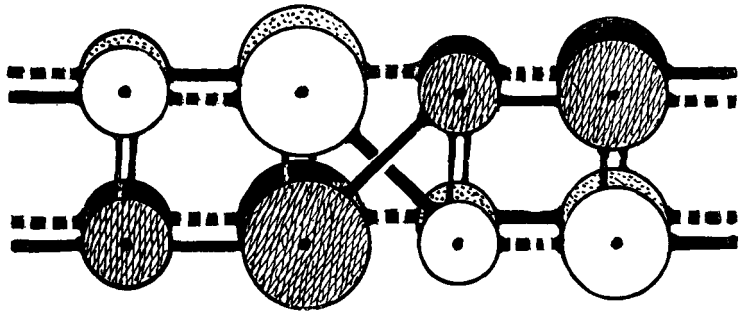

FIGURE 5.—Diagram of a direct chiasma, as seen at pachytene in Lilium. The solid lines are the old connecting fibers, the broken lines the new ones.

above; (2) in both directions of overlap, together below; (3) with one direction of overlap, *a* above and *b* below; or (4) with the other direction of overlap, *b* above and *a* below. These four kinds of X will occur equally frequently by chance, only if overlaps in different directions are equal in number. The first two kinds may be classed together as forming *direct* chiasmas (and direct crossovers), and the second two kinds as forming *oblique* chiasmas (and oblique crossovers). The writer has identified both kinds of chiasmas at pachytene in Lilium, in about equal numbers.

DIRECT AND OBLIQUE CHIASMAS

Direct chiasmas

Direct chiasmas may occur by chance in half of the overlaps which form chiasmas (this is shown by the study of ANDERSON'S genetic results with attached X's, which give equal numbers of direct and oblique chiasmas). When the two diagonals of an X are in the same plane at pachytene (as the writer has observed them sometimes in Lilium), then the two pairs of chromioles in the other plane are fairly close together longitudinally

(figure 5), and the new fibers are formed between these chromioles. (We may call the two sister chromonemas of one homologue, a and a'; and those of the partner b and b'.) This will give two direct crossover strands, $a+b$ and $b+a$ (or the converse), as well as two non-crossover strands, forming the diagonals of the X, namely a' and b' (or the converse). If we adopt the convention that the chromonemas a and b are above, and a' and b' below, we have: with the X above, direct crossovers $a'+b'$ and $b'+a'$, and non-crossovers a and b; and with the X below, direct crossovers $a+b$ and $b+a$, and non-crossovers a' and b'.

Oblique chiasmas

Here one diagonal of the X is above and one below, as the writer has sometimes observed in Lilium (figure 6), thus forcing the new longitudinal

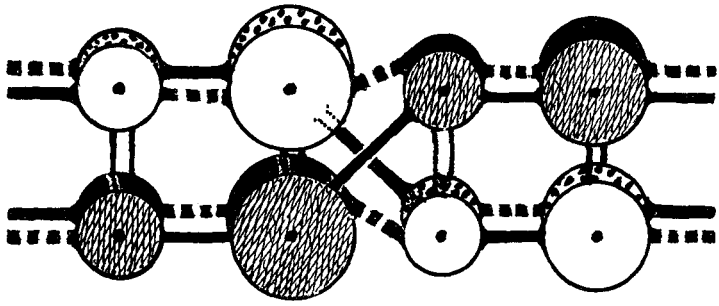

FIGURE 6.—Diagram of an oblique chiasma, as seen at pachytene of Lilium.

fibers to pass obliquely on each side between the unattached chromioles. (The old fibers of course cannot pass obliquely, because to do so they would have to increase 40 percent in length.) Here also the diagonals do not cross over, and the oblique chromonemas do. There are then two cases (given by the two directions of overlap), in which the top diagonal slants either from upper left to lower right, or from lower left to upper right. Diagonals a and b' give oblique crossovers $a'+b$ and $b+a'$, with non-crossovers a and b'. With the diagonals b and a', we have the oblique crossovers $a+b'$ and $b'+a$, with the non-crossovers b and a'.

Adjacent chiasmas

With two adjacent chiasmas we may have eight cases (and also eight converse cases, made by changing a to a', b to b', a' to a, and b' to b).

CHIASMAS	CROSSOVERS	
(1) Direct (A)+supplemental direct (A).	$\frac{a+b}{b+a}+\frac{a+b}{b+a}$	2 similar supplemental chiasmas.
(2) Direct (A)+complemental direct (B).	$\frac{a+b}{b+a}+\frac{a'+b'}{b'+a'}$	2 similar complemental chiasmas.

(3) Oblique (C)+supplemental oblique (C).	$\frac{a+b'}{b'+a}+\frac{a+b'}{b'+a}$	2 similar supplemental chiasmas.
(4) Oblique (C)+complemental oblique (D).	$\frac{a+b'}{b'+a}+\frac{a'+b}{b+a'}$	2 similar complemental chiasmas.
(5) Direct (A)+oblique (C).	$\frac{a+b}{b+a}+\frac{a+b'}{b'+a}$	2 unlike chiasmas.
(6) Direct (A)+oblique (D).	$\frac{a+b}{b+a}+\frac{a'+b}{b+a'}$	2 unlike chiasmas.
(7) Direct (B)+oblique (C).	$\frac{a'+b'}{b'+a'}+\frac{a+b'}{b'+a}$	2 unlike chiasmas.
(8) Direct (B)+oblique (D).	$\frac{a'+b'}{b'+a'}+\frac{a'+b}{b+a'}$	2 unlike chiasmas.

The supplemental similar chiasmas produce each two double crossovers and two non-crossovers. The complemental similar chiasmas give four single crossovers each. The four unlike pairs of chiasmas give each one double crossover, two single crossovers, and one non-crossover chromatid.

The four similar pairs of chiasmas have been called compensating, because the jugate chromatids, after crossing over, regularly separate or come together alternately, so that the two (conjunct) threads on one side of an internode adjacent to the left of the first chiasma are continuous with the two threads on one side of an internode adjacent to the right of the second chiasma. So too, the four unlike pairs are sometimes called non-compensating, because the jugate chromatids do not alternate in arrangement, and so two threads on the left of the first chiasma which are on the same side (conjunct) after diplotene will not appear to be conjunct on the right of the second chiasma.

Sometimes the double crossovers in cases of pairs of similar supplemental chiasmas (A+A, and C+C) are called "reciprocal". The double crossovers from the four pairs of unlike chiasmas (A+C, A+D, B+C, and B+D) have been called "diagonal"; but only one chiasma and crossover in each seems diagonal, and C+C is perhaps the truly diagonal chiasma pair.

Chiasmas and crossovers

Direct and oblique single chiasmas can be shown to be about equally numerous. With regard to pairs of chiasmas, when an overlap in one direction takes place, the next overlap, it seems probable, would occur in the opposite direction; for if it was in the same direction it would cause a twist, which seems unlikely, especially when the ends of the chromonemas synapse first. Hence usually there should be alternation of overlaps, and if every overlap forms a chiasma, there would be an alternation of direction of the overlaps of the diagonals of the X's in sequent chiasmas. This would not affect chance crossing over in direct chiasmas; but with a pair of se-

quent oblique chiasmas the results for crossing over would apparently differ from chance ones. For two sequent oblique chiasmas would most often be complemental rather than supplemental. This would lessen the number of double crossovers expected by chance, for complemental pairs of chiasmas have no double crossovers. If, however, we temporarily disregard this possible source of error, we have by chance 8 pairs of chiasmas occurring with equal frequencies. Having regard to the direction of overlap, we get 32 different pairs of chiasmas; but for the following we may consider only 8 main classes. These give 32 chromatids, and it can be reckoned (table 1) that there are normally, by chance, 8 non-crossovers, 16 single crossovers, and 8 double crossovers, among these.

TABLE 1

CHIASMAS	CHROMOSOMES		
	NON-CROSSOVERS	SINGLE CROSSOVERS	DOUBLE CROSSOVERS
Direct+supplemental direct	2	..	2
Direct+complemental direct	..	4	..
Oblique+supplemental oblique	2	..	2
Oblique+complemental oblique	..	4	..
2 (Direct+oblique)	2	4	2
2 (Oblique+direct)	2	4	2
Totals	8	16	8
Proportion	1	2	1

Thus the proportion for two sequent chiasmas, by chance, is 1 non-crossover, to 2 single crossovers, to 1 double crossover. With a third adjacent chiasma, the proportion would be (1:2:1) (1:1); or 1 non-crossover, to 3 single crossovers, to 3 double crossovers, to 1 triple crossover. For four sequent chiasmas, the chance proportion would be (1:2:1) (1:2:1); or 1 non-crossover, to 4 single crossovers, to 6 double crossovers, to 4 triple crossovers, to 1 quadruple crossover; and so on. (The percentage figures of the crossover chart of a chromosome are made to include the double crossovers, though these do not normally affect the recombinations.) So we have the results given in table 2, for bivalents with terminal fusal chromomeres, or single arms of J or V chromosomes. The distal recombinations are the sums of the odd-crossover chromosomes.

However, it does not seem commonly to happen that the same number of chiasmas occurs in all homologous bivalents. Thus the total chart crossovers may be somewhere between the numbers given in table 2. For the X chromosome of Drosophila, the numbers of crossovers in 100 chromosomes have long been published (see MORGAN 1926).

Chromosomes	Percentages	
Non-crossovers	43.5	Total chart crossing over = 70.5
Single crossovers	43	Distal recombinations = 43.5
Double crossovers	13	
Triple crossover	0.5	

Comparing this with the writer's chiasma theory, we note that the distal recombinations are 6.5 below 50 percent. Also the non-crossovers are in excess of the single crossovers, while the opposite happens on the chiasma theory (table 2). Taking the figures as given, we may deduce the following:

	Percentages
No-chiasma bivalents	13
One-chiasma bivalents	37
Two-chiasma bivalents	46
Three-chiasma bivalents	4

TABLE 2

Chart figures and recombinations in bivalents with terminal fusal attachment.

NUMBERS OF CHIASMAS	PERCENTAGES OF CROSSOVERS					CHART CROSSOVERS	DISTAL RECOMBINATIONS
	0	1	2	3	4		
(0)	(100)	..	..	..	..	(0)	(0)
1	50	50	..	..	..	50	50
2	25	50	25	..	..	100	50
3	12.5	37.5	37.5	12.5	..	150	50
4	6.25	25	37.5	25	6.25	200	50
And so on.							

However, since there is a proximal third or more of the X chromosome without sufficient mutants to detect double crossing over, it is possible that double crossing over is slightly more abundant than found. Perhaps some few distal crossovers are also undetected. No-chiasma bivalents do not seem to occur in attached X's, where their presence could be ascertained (see table 4). Hence, to agree with the writer's chiasma theory (neglecting the rare triple crossovers), the percentage of single crossovers should be increased by 7, and that of double crossovers by 2.

ATTACHED AND RING X CHROMOSOMES

Attached X's and crossing over

In the female Drosophila, three of the chromatids of the X bivalent usually pass into the polar bodies. So we cannot normally get both of the crossover chromatids from any crossover. But in the attached X's we regularly get two (non-sisters) of the four chromatids, and these serve to

show the distinction between direct and oblique crossing over. Direct crossovers, in attached X's, are between the two chromosomes of the V; and oblique crossovers are between two V's (but not between sister chromatids). If the attached X's are originally heterozygous for several loci, then single direct chiasmas do not change this heterozygosis: but single oblique chiasmas (that is 1/2 of the single chiasmas) make all heterozygous loci distal to them homozygous in the resulting attached X's. That is, if all chasmas are single, 50 percent of the attached X's (if heterozygous originally) are homozygous distal to the chiasmas. But, with all chiasmas single, 50 percent of the resulting chromosomes show one crossover, and 50 percent are non-crossovers. Hence the percentage of single-crossover chromosomes from single chiasmas is equal to the percentage of distally homozygous attached X's from single chiasmas. The percentage of *recessive* distally homozygous attached X's is half this (or half the percentage of single crossovers from single chiasmas).

Of the eight kinds of double chiasmas (table 1), two, both proximal direct plus distal oblique, give distal homozygosis of originally heterozygous attached X's. Of the 16 resulting attached X's, two are homozygous for recessives; that is, 12.5 percent. These 16 attached X's have 32 chromosomes, of which 8 (on the average) are non-crossovers, 16 are single crossovers, and 8 are double crossovers. This would yield a crossover chart total of 100 percent crossing over. It gives 25 percent double crossovers. Thus the percentage (due to double chiasmas) of attached X's distally homozygous for recessives is half the double crossovers (or a quarter of the total chart single crossovers due to double chiasmas).

Now the crossovers in the X of *Drosophila melanogaster* may be taken as (excluding the rare triple crossing over, and also the possibility of no-chiasma bivalents) nearly equal to,

Non-crossovers, 35 percent	Total chart crossing over = 80.
Single crossovers, 50 percent	
Double crossovers, 15 percent	Distal recombinations = 50.

These would arise from:

Single chiasmas, 40 percent
Double chiasmas, 60 percent

The distal recessive homozygosis for 100 resulting attached X's would be half the crossovers from single chiasmas, $20/2 = 10$ percent, plus half the double crossovers, 15/2 or 7.5; totaling 17.5 percent. The proximal parts of the attached X's, with about 10 percent of chart crossovers, should give about 10/2, or 5 percent of recessive homozygosis; since there are few or no proximal double crossovers to be reckoned with here.

Since the total chart crossovers are made up of the total single crossovers (s) plus twice the double (d) crossovers (that is, $s+2d=C$), the recessive distal homozygosis is $\frac{s-2d}{2}+\frac{d}{2}=\frac{s-d}{2}=\frac{50-15}{2}=17.5$; or $=\frac{C-3d}{2}=\frac{80-45}{2}=17.5$. STURTEVANT'S value for the *sc* locus is 17.1. The higher value of 19 for the locus *y* is probably due to differential viability (STURTEVANT 1931).

The values for *f* and *g* in table 3 (calculated from single chiasmas only) are over the values found. (It seems possible that there were a few double chiasmas proximal to these.) The data do not permit of the calculation of the values from *m* to *ec*.

TABLE 3

MUTANT LOCI	PROXIMAL CROSSOVERS FOUND	PERCENTAGES OF DISTALLY HOMOZYGOUS RECESSIVE ATTACHED X'S FOUND	PERCENTAGES CALCULATED FROM PROXIMAL CROSSOVERS AND CHIASMAS	
f	13.5	5.1	6.8	Mainly single crossovers
g	26	10.3	13.0	
m	33.9	13.5		
v	37	14.8		Single and double crossovers
t	42.4	16.1		
ct	50	16.4		
cv	56.3	15.9		
ec	64.5	16.5		More double crossovers
sc	70	17.1	17.5	
y	70	(19)	17.5	

For ANDERSON'S important experiments (1925), the attached X's may be divided into 3 regions: (A) from the fusal (spindle) chromomere to the locus of *f*, chart distance = 13.5; (B) from *f* to *ct*, chart distance = 36.5; and (C) from *ct* to *sc* (presumably near the distal end), chart distance = 20. In A the double crossovers are apparently unknown; in B they are ascertained; and in C they have not been measured in this experiment. However, we have assumed, for the X chromosome, that the total double crossovers are 15 percent. Those with both or the second crossovers in B are 5 percent. Thus 10 percent have their second crossovers in C. (Hence we can remove the second of the double crossovers from the chart distance in B and C, and consider only the proximal crossovers.)

Of the 13.5 single crossovers in A, 6.75 are probably oblique and produce homozygosis; and 6.75 would be direct. Taking the total double crossovers in B and C as 15, we may subtract the second (distal one) of these in

sections B and C; B having 5 known, and C therefore having the remaining 10.

TABLE 4

SECTION	CROSSOVERS IN ATTACHED X'S	ATTACHED CHROMOSOMES AND CHIASMAS
A	13.5	Direct, complementary non-crossovers, 6.75 Oblique, identical non-crossovers, 6.75
B	36.5−5=31.5	Direct, 15.75 { complementary crossovers, 7.88 complementary non-crossovers, 7.88 Oblique, 15.75 { crossovers and non-crossovers non-crossovers and crossovers } 15.75
C	20−10=10	{ Direct, Oblique, } complementary non-crossovers, 10

Thus we have the totals of attached X's:

(1) Complementary non-crossovers = 6.75 + 7.88 + 10 = 24.63
(2) Identical non-crossovers = 6.75
(3) Crossover and non-crossover = 15.75
(4) Complementary crossovers = 7.88

From this we get table 5. The fit would be somewhat closer if one or

TABLE 5

	CALCULATED FROM CHART DISTANCES	ANDERSON'S RESULTS FROM ATTACHED X'S
(1) Complementary non-crossovers	44.8	43.9
(2) Identical non-crossovers	12.3	10.8
(3) Crossover and non-crossovers	28.6	29.7
(4) Complementary crossovers	14.3	15.6

more of the double crossovers was found to be included in the 13.5 chart distance from *f* to the proximal end; for the chief difference is in the 5.4 percent of oblique crossovers found proximal to *f*, giving 10.8 (oblique + direct) crossovers; whereas the crossover chart has 13.5 crossovers here.

Ring X's and crossing over

L. V. MORGAN (1932, and *in litt.*) showed that when a ring X synapses with another ring X (or with a rod X) double-crossover X chromosomes survive, but no single crossovers appear in the progeny. Two chromonemas crossing over once would form one large ring (or one long rod) with two fusal chromomeres. This does not survive in the progeny. Double crossovers would form two rings (or a ring and a rod) and survive. But two

sister chromonemas crossing over would also form one inviable large ring (or long rod). If sister-strand crossing over occurred, the numbers of non-crossover chromosomes would be diminished with regard to the numbers of double-crossover chromosomes. This is not the case. Therefore sister-strand crossing over does not occur (normally) between two ring X's (or between the ring and the rod X). Hence it was not postulated above to solve the problem of attached X's, nor would it fit these. Therefore it probably does not occur in normal X's.

EXPLANATION OF GENE REARRANGEMENT

Reversed crossing over

This appears to originate usually at meiosis, and in a normal trisomic plant (Datura); but less commonly in a diploid (1927). On the writer's theory, if the fusal chromomeres synapsed, but the rest of the two chromonemas was in reverse order, crossing over could take place only close to the fusal chromomeres. Such reversed crossing over would give two chromosomes; one with two left arms, and the other with two right arms. The third homologous chromosome, in the trisomic plant, might help this process by synapsing first with one or both ends of one of the chromonemas concerned. Reversed crossing over in Datura appears to have occurred only next the fusal chromomere.

Reciprocal translocation

If any two heterologous chromonemas overlapped close enough when their chromomeres were first dividing, there might be (by the writer's theory) cross-connections found between two of the four, as in an ordinary chiasma (but not between sisters). Such cross-connections would produce reciprocal translocations, in which the interchanged parts were neither equal nor homologous. A bend at the point of overlap might result in a gene or more being omitted at the point of interchange.

It has been suggested that heterologous interchange results from interlocking of bivalents at meiosis. This seems possible; but it is also possible that some cases styled "interlocking" at meiosis may be due to interchange. If interchange occurs at *mitosis*, it cannot apparently be due to interlocking.

Terminal translocation

The writer has seen, in meiosis, the ends of the chromonemas resting laterally on other chromonemas. If cross-connections like those at a chiasma occurred during longitudinal divisions, chromonemas would result with terminal attachment of a heterologous segment. This might also occur at mitosis.

Inversion and deletion

If a dividing mitotic chromonema (or a bivalent at early pachytene) overlapped itself closely in a loop, when its chromomeres divided there might be formed cross-connections between two threads, as in a chiasma. This would result in an inversion (or a deletion). The deleted piece may form a ring (McCLINTOCK 1933). It is readily seen how a gene might be lost in the inversion, by the connecting fiber passing it by.

Insertion

This is perhaps a double interchange, where a loop of one chromonema overlaps another chromonema at two near places. The piece lost may be small. Insertion should be quite rare, since it requires two rare interchanges to cause it.

Terminal deficiency

This seems common. There are several possible ways in which it may arise. Every terminal translocation, for instance, is accompanied by a terminal deficiency in another chromonema.

OBJECTIONS TO THE THEORY

The following objections have lately been made to the present writer's modified Janssens' theory of crossing over; which accounts also for translocation, deficiency, interchange, inversion, deletion, and insertion.

First Objection. That direct chiasmas formed at overlaps, according to the writer's theory, can at most result in 50 percent of chromatids showing crossing over; whereas some chromosomes of Drosophila actually show a greater percentage than this. *Reply.* If the two pairs of sister chromatids at crossing over are a and a', and b and b', respectively; and a is opposite to b, and a' is opposite to b'; then, at the overlaps, direct chiasmas may be formed in which a crosses over with b, and also by chance, in equal numbers direct chiasmas in which a' crosses over with b'. So the four chromatids from a bivalent which has more than one direct chiasma, may sometimes all be crossovers; and it is possible that, in some cases of long chromosomes, the limit of 100 percent of crossover chromosomes may be reached. (Oblique chiasmas are left out of consideration here; but would, of course, add to the numbers of crossover chromosomes.)

Second Objection. That, on the writer's theory, the pairs of sister chromatids formed by the secondary split at meiosis should show half as many apparent twists as there are genes in the chromosome; and the same should happen between the two halves of a split chromosome in any mitotic division. *Reply.* It is a fact of observation that the longitudinal connection fibers between chromioles pass the shortest way (GELEI 1921, BELLING 1931a). The shortest way between any two homologous chromioles of a split chromonema and their two neighbors on either side is not obliquely

but longitudinally. Hence the old fiber will be longitudinal, and so force the new one to be so. Thus, also, there will be (normally) no twists between sister strands, though there may be rarely twists of the whole chromosome or bivalent. The difficulty with the objector, and this holds also for the first objection, is that there is no *old* chromiole when a chromomere has divided. The *old* chromomere has gone, and there are two new chromioles formed, which are equivalent. So also the old chromonema when divided changes into two new chromonemas. (There are, however, old connecting fibers, and subsequently new ones also, between adjacent chromioles.)

Third Objection. That there is always or usually a telophasic split in somatic divisions, and also that the leptotene of meiosis is always or usually split. *Reply.* A telophasic split has been predicated mainly by observers who have used sections of plant (or animal) material, fixed *en masse.* This method, in the writer's opinion, does not show fine nuclear details truly, but gives the alveolar artifacts of slow fixation. This is proved by comparison with similar material made into smear preparations by the best methods (see BELAR 1929a, 1929b). The writer has spent some months with smear preparations of mitosis (both diploid and haploid), especially of Tradescantia and Rhoeo, and has convinced himself that there is no telophasic split visible in his material. He is also satisfied that there is no longitudinal split to be seen, with good microscopy, in the leptotene threads of the liliaceous plants he has examined.

Fourth Objection. That bivalents with unequal homologues are inconsistent with the writer's theory of crossing over. *Reply.* It was the behavior of such bivalents which first led the writer to discredit the alternate-opening-out hypothesis of the origin of chiasmas. The effects of opening-out in these bivalents are visible at early diaphase. They do not show, in the cases examined, opening-out of the sister chromatids at the unequal free ends. They should show this is about half the cases, on the alternate-opening-out hypothesis, when sliding of the X's of chiasmas had not taken place. In WENRICH's excellent figures of Phrynotettix (1916), all the bivalents with unequal homologues show at early diaphase that the unequal extremities have not opened out at the secondary split. The writer has observed this same fact in a bivalent of Aloë with unequal homologues.

At the first anaphase, with a terminal (or sub-terminal) fusal point as in Phrynotettix, if there is no crossing over, or if there are two similar supplemental chiasmas, then the two long chromatids separate from the two short chromatids and pass to opposite poles (as in some of WENRICH'S figures). But if there is one chiasma, a long and a short chromatid pass together to each pole (as in other figures of WENRICH). The explanation of this is that there has been crossing over. The alternate-opening-out hypothesis of chiasma origin apparently cannot apply here, as already shown.

Fifth Objection. That the reduction in the number of nodes observed in some plants, from early diplotene to metaphase, is due to the breaking and rejoining of chiasmas; not to the disappearance of some loose twists, or overlaps, or of temporary lateral fusions. *Reply.* Since the nodes (apparently mostly temporary chromatin cross-connections) at early diplotene in *Allium triquetrum* seem somewhat over 200 in number (1931a), while the chiasmas at diaphase may be about 20, a loss of about 180 nodes results. It does not seem probable that these many lost nodes were chiasmas. For nodes are stated not to be lost in Stenobothrus from late diplotene to late diaphase (DARLINGTON and DARK 1932). Nor should it be assumed without proof that a node is a chiasma. That chiasmas break and join is improbable, for the writer knows no case of chromosomes joining after proved fracture. On the writer's hypothesis there is normally no fracture in crossing over, translocation, interchange, inversion, deletion, deficiency, or insertion.

Sixth Objection. If non-disjunction of the X chromosomes in Drosophila is attributed to the X's having so many chiasmas that they fail to disjoin; then, in the high non-disjunction line, why do the X's show less crossing over instead of more? *Reply.* The first part of this objection is a conjecture. Since the high non-disjunction is admittedly due to translocation or inversion, it seems probable that the apparent non-disjunction is sometimes non-conjunction, as the writer has noted in triploids and tetraploids (and also in Uvularia). If there are cases of whole or partial non-conjunction or asynapsis (compare MCCLINTOCK 1931), then the percentage of crossing over would be decreased.

Seventh Objection. The opening-out of the X of a chiasma towards the ends of the bivalent must separate the two chromosomes at this end, instead of giving a terminal junction. *Reply.* Since the terminal chromomeres visibly hold the leptotene-zygotene chromonemas together at the distal ends in a number of organisms, it is not improbable that the same distal chromomeres may hold the four jugate chromatids together when brought into contact at the ends. In this case the opening-out of the X of a chiasma at diplotene when it reaches the end of a bivalent will bring the terminal chromomeres of the chromatids into close proximity, and connection by new cross threads may result.

Eighth Objection. That the percentage of homozygosis of recessive alleles that were heterozygous in the parent, towards the distal (left) end of the attached X's of Drosophila, was found by ANDERSON, and also by others, to be slightly more than that calculated for random assortment of the recessive alleles. This was said to be inexplicable on the writer's hypothesis. *Reply.* The writer's hypothesis gives different grades of homozygosity of recessive alleles, according to the amount crossing over from proxi-

mal single chiasmas, equalling half of these crossovers, since only oblique (not direct) chiasmas cause homozygosis of heterozygous alleles in attached X's. There must be added to this half the double crossovers. For the X chromosome, terminal recessive homozygosity is about 17.5 percent on the writer's theory.

Ninth Objection. In the translocation of a terminal piece of one arm of the third chromosome to the fourth chromosome of Drosophila, crossing over was less in the proximal part of the attached portion of the third chromosome, in flies homosomic for the translocation, than in the normal flies. This was said to be inexplicable on the writer's theory. *Reply.* If synapsis begins with the small fourth chromosome in the combined piece (as it should, since the fusal point of the third chromosome is left behind), then there will be interference between this point and the first chiasma, and few crossovers will occur near this end; as perhaps happens also near the proximal end of the X, and near the fusal points of the second and third chromosomes (see also DOBZHANSKY 1931).

Tenth Objection. In haploid Zea, a split was found in the threads of the meiotic prophases. It was objected that this was contrary to the hypothesis of the writer, which is based on observations of an unsplit leptotene. *Reply.* The leptotene stage is more difficult to demonstrate than the pachytene, especially in aceto-carmine smears. The pachytene stage of the diploid Zea has been figured and photographed by MCCLINTOCK; but good figures and photographs of the leptotene are yet to be sought. The writer would suggest that further work might perhaps show a stage in the haploid Zea comparable with the leptotene of the diploid, as the split stage found in the haploid is perhaps comparable with the late pachytene of the diploid Zea.

Eleventh Objection. That a tertiary split has been demonstrated in the pachytene of one plant, and also that there were two split spiroid chromonemas in the first anaphase chromosomes. That this is contrary to the writer's hypothesis, in which the pachytene has only two splits, and the first anaphase chromosomes show two unsplit chromonemas. *Reply.* When the late pachytene is well enough fixed to show the chromomeres distinctly, only two splits are visible in Lilium and Fritillaria. Preparations which are to demonstrate a hitherto invisible tertiary split should perhaps show the chromomeres as distinctly as those obtained by the writer.

The spiroid threads found in the metaphase and anaphase chromosomes by appropriate destaining may perhaps appear with lighter centers when their chromatin is disappearing, as is the case from anaphase to telophase. Most workers however have found that the first-anaphase spiroid threads are only two in number. That this is the case in Rhoeo and Tradescantia, the writer also can testify, from iron-brazilin and iron-haematoxylin smears, fixed with Navashin's or with Flemming's mixture.

Twelfth Objection. That the genetic proof (PATTERSON 1933) of the chromosomes in the sperms of Drosophila being probably sometimes split, furthers the hypothesis of a telophasic split, and so is against the writer's hypothesis. *Reply.* The dense accumulation of chromatin in the sperms of most animals and some plants usually hides the state of the chromonemas. But when the sperm nucleus spreads out in the fertilized ovum, in plants and animals, it is usually found to be in the later prophase, and at a stage when the chromosomes are normally split. Hence the splitting of chromonemas may possibly take place in the spermatozoön. In a certain nematode, according to MULSOW, the chromosomes in the sperm are at the metaphase stage, and doubtless already split. PATTERSON's results also show that the chromonemas in the sperm are sometimes (in six-sevenths of the cases) *not* split, which is contrary to the "telophase-split" hypothesis of some writers.

Thirteenth Objection. That the chromomeres found in the pachytene of diploid Zea (by the acetic-alcohol and aceto-carmine method) do not correspond in the two synapsed threads. *Reply.* These "chromomeres" are often compound chromomeres run together during fixation, and then may be composed in different ways in the two threads. The same thing happens in Lilium, Fritillaria and Aloë, if the fixation is not rapid enough.

Fourteenth Objection. That no crossing over between sister chromatids was found either between two ring X's or between a normal and a ring X, in Drosophila. *Reply.* Sister-strand crossing over was, because of this fact, excluded from the writer's theory, which now uses equal numbers of direct and oblique chiasmas only, as calculated from ANDERSON's results with attached X's, and confirmed by observation of the pachytene of Lilium.

Fifteenth Objection. That the writer's theory does not fully explain ANDERSON's results with attached X's and equational exceptions. *Reply.* In the first form of the writer's hypothesis these could be only approximately explained by diagonal and sister-strand assortment at the spindle-fiber end. The present form of the theory enables ANDERSON's numerical results to be calculated with fair accuracy (see above).

Sixteenth Objection. That the late pachytene of Zea shows more nodes to a chromosome than the chiasmas seen at diaphase. *Reply.* A chiasma presumably arises only at an overlap, which is a kind of half-twist with no rotation in each chromonema. If the chromomeres are too close together, an overlap or half-twist may not result in a chiasma. Also at earliest diplotene, besides chiasmas, there are many (often hundreds of) chromatin connections across the primary split. A few of these may remain and hold the threads together for a time.

Seventeenth Objection. Since the action of X-rays of definite frequency in causing point mutation is taken as indicating that the bare genes are too

small to be visible with the microscope, therefore the genes cannot be directly counted. *Reply.* The writer's observations in destaining ultimate chromomeres in hyrax have shown that each contained one minute stainable central body (like a centriole). The cells were examined with the monobromide of napthalin objective, at a working aperture of 1.5. The central particles were probably over 0.07 micron across. They were doubtless covered with chromatin. The bare gene is then smaller than this. Hence, also, with regard to mutation, since the gene substance in one chromomere is not divisible by crossing over, this must be regarded as a whole; that is, as one gene. Whether the whole, or only part, of a gene is acted on by the X-rays does not seem generally ascertained. But in the formation of multiple alleles the action must apparently be partial. In this case the size of the whole gene does not seem deducible from the (direct or indirect) action of X-rays on a part of it.

Eighteenth Objection. It has been estimated that *Drosophila melanogaster* has over six times as many genes as the writer found in Lilium, and as seem to be about the number of ultimate chromomeres indicated in the grasshopper Phrynotettix (WENRICH 1916). *Reply.* This estimation seems to the writer to mingle point mutations with gene rearragements (deficiencies, inversions, interchanges) as causing dominant or recessive lethals. It also does not allow for the sperm chromonemas having sometimes split especially in the autosomes. Hence the resulting figure is too high (see PATTERSON 1933, MCCLINTOCK 1931).

SUMMARY

1. The writer's modification of JANSSENS' hypothesis explains crossing over, and also explains gene rearrangements, such as reversed crossing over, reciprocal translocation, inversion, deletion, and deficiency.

2. The chromonemas were proved to be unsplit at leptotene in certain plants.

3. Living (and also fixed) chromonemas of resting "final" nuclei showed no split, in the plants examined.

4. The secondary split was first seen at mid pachytene.

5. Both direct and oblique chiasmas were seen at pachytene in Lilium.

6. After the chromomeres have split, the old longitudinal fibers are either alone visible; or are seen to be thicker than the new ones.

7. In Lilium the opening-out at diplotene seems to be only at the primary split. (However, in plants such as Datura, with no chiasmas at diaphase, it is probable that the diplotene opening-out alternates at the chiasmas.)

8. Since chiasmas arise at pachytene in certain liliaceous plants, they cannot arise from alternate opening-out at diplotene.

9. Chiasmas seem to be due to overlaps, not twists. Overlaps may be sometimes mistaken for twists, under the microscope.

10. There are 8 main kinds of double chiasmas, equally numerous by chance.

11. Double chiasmas give, by chance, one non-crossover chromosome, two single-crossover chromosomes, and one double-crossover chromosome.

12. If crossovers arise from chiasmas, then the distal recombinations from the end to the fusal chromomere should be 50 percent.

13. If crossovers arise from chiasmas, then the chart crossovers divided by 50 should give the average number of chiasmas.

14. The ascertained numbers of crossover X chromosomes of *Drosophila melanogaster* appear to lack about 7 percent of single crossovers, and about 2 percent of double crossovers, if they arose from chiasmas (neglecting triple crossovers).

15. Flies with heterozygous attached X's in Drosophila (ANDERSON 1925), should (on the writer's theory) give distal recessive homozygotes in a percentage equal to half the chart length minus one and a half times the percentage of double crossovers. This would be 17.5.

16. On the writer's theory, the percentages of complementary and identical non-crossovers, of crossovers plus non-crossovers, and of complementary crossovers, in attached X's, have been calculated from the chromosome chart, and agree with ANDERSON's experimental results.

17. L. V. MORGAN's work with ring X's in Drosophila, like ANDERSON's results with attached X's, shows the absence of sister-strand crossing over. Therefore chiasmas formed by a half twist between the two homologues are absent, or rare (1931b).

18. It is possible to explain reversed crossing over, heterologous interchange, terminal translocation, inversion, deletion, and deficiency, by the overlapping of two chromonemas when their chromomeres are dividing. The result is equivalent to the formation of a chiasma between synapsed homologues; but is less regular, so that genes may be lost at the junctions.

19. Some objections to the writer's theory are briefly answered.

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