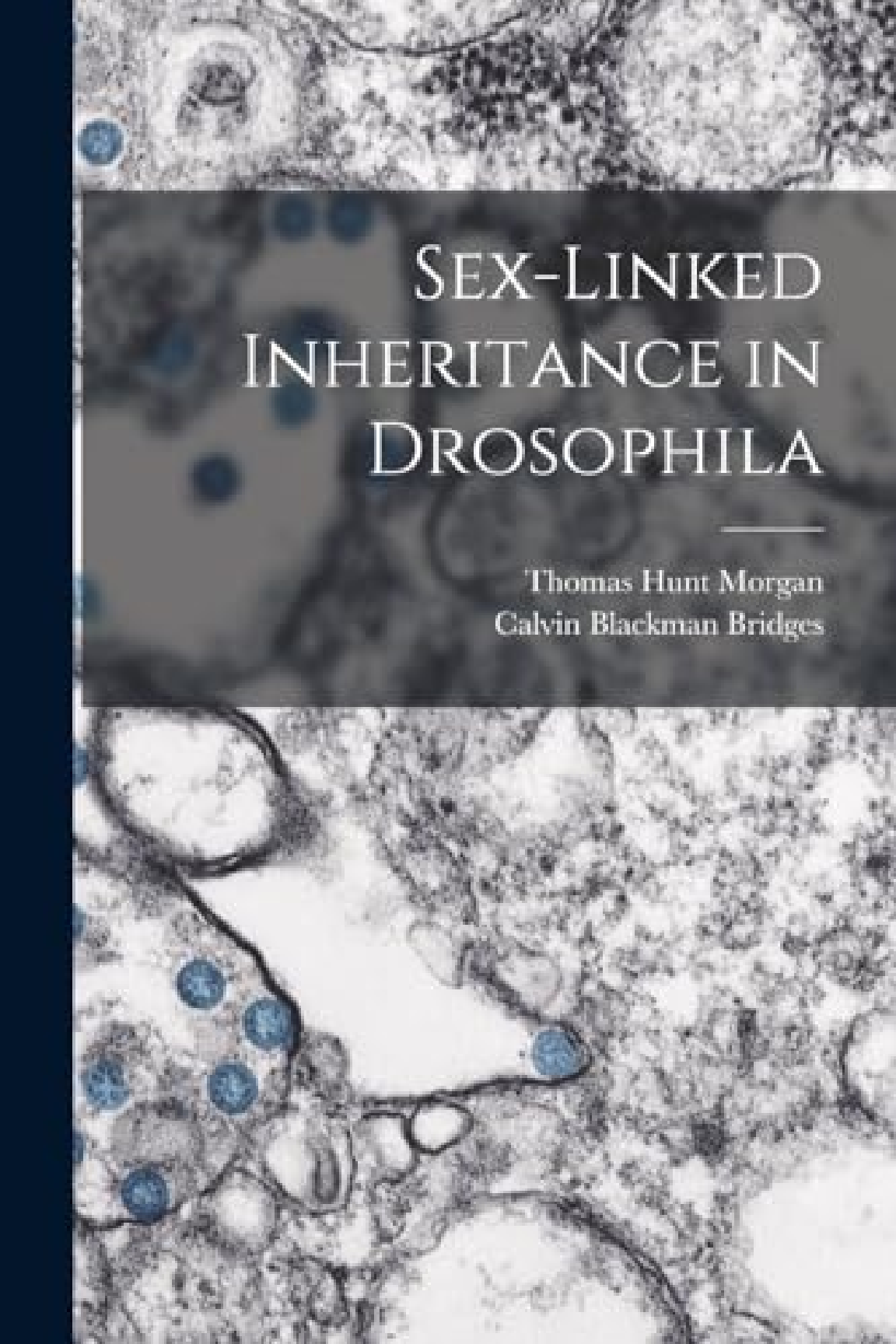


Sex-Linked Inheritance in Drosophila

Thomas Hunt Morgan
Calvin Blackman Bridges

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SEX-LINKED INHERITANCE IN DROSOPHILA ***

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SEX-LINKED INHERITANCE IN DROSOPHILA

BY

T. H. MORGAN AND C. B. BRIDGES



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PART I. INTRODUCTORY.

MENDEL'S LAW OF SEGREGATION.

Although the ratio of 3 to 1 in which contrasted characters reappear in the second or F_2 generation is sometimes referred to as Mendel's Law of Heredity, the really significant discovery of Mendel was not the 3 to 1 ratio, but the segregation of the characters (or rather, of the germinal representatives of the characters) which is the underlying cause of the appearance of the ratio. Mendel saw that the characters with which he worked must be represented in the germ-cells by specific producers (which we may call factors), and that in the fertilization of an individual showing one member of a pair of contrasting characters by an individual showing the other member, the factors for the two characters meet in the hybrid, and that *when the hybrid forms germ-cells the factors segregate from each other without having been contaminated one by the other.* In consequence, half the germ-cells contain one

member of the pair and the other half the other member. When two such hybrid individuals are bred together the combinations of the pure germ-cells give three classes of offspring, namely, two hybrids to one of each of the pure forms. Since the hybrids usually can not be distinguished from one of the pure forms, the observed ratio is 3 of one kind (the dominant) to 1 of the other kind (the recessive).

There is another discovery that is generally included as a part of Mendel's Law. We may refer to this as the *assortment* in the germ-cells of the products of the segregation of two or more pairs of factors. If assortment takes place according to chance, then definite F_2 ratios result, such as 9:3:3:1 (for two pairs) and 27:9:9:9:3:3:3:1 (for three pairs), etc. Mendel obtained such ratios in peas, and until quite recently it has been generally supposed that free assortment is the rule when several pairs of characters are involved. But, as we shall try to show, the emphasis that has been laid on these ratios has obscured the really important part of Mendel's discovery, namely, *segregation*; for with the discovery in 1906 of the fact of linkage the ratios based on free assortment were seen to hold only for combinations of certain pairs of characters, not for other combinations. But the principle of segregation still holds for each pair of characters. Hence segregation remains the cardinal point of Mendelism. Segregation is to-day Mendel's Law.

LINKAGE AND CHROMOSOMES.

It has been found that when *certain* characters enter a cross together (*i. e.*, from the same parent) their factors tend to pass into the same gamete of the hybrid, with the result that other ratios than the

chance ratios described by Mendel are found in the F_2 generation. Such cases of linkage have been described in several forms, but nowhere on so extensive a scale as in the pomace fly, *Drosophila ampelophila*. Here, over a hundred characters that have been investigated as to their linkage relations are found to fall into four groups, the members of each group being linked, in the sense that they tend to be transmitted to the gametes in the same combinations in which they entered from the parents. The members of each group give free assortment with the members of any of the other three groups. A most significant fact in regard to the linkage shown by the *Drosophila* mutants is that *the number of linked groups corresponds to the number of pairs of the chromosomes.* If the gens for the Mendelian characters are carried by the chromosomes we should expect to find demonstrated in *Drosophila* that there are as many groups of characters that are inherited together as there are pairs of chromosomes, provided the chromosomes retain their individuality. The evidence that the chromosomes are structural elements of the cell that perpetuate themselves at every division has continually grown stronger. That factors have the same distribution as the chromosomes is clearly seen in the case of sex-linked characters, where it can be shown that any character of this type appears in those individuals which from the known distribution of the X chromosomes must also contain the chromosome in question. For example, in *Drosophila*, as in many other insects, there are two X chromosomes in the cells of the female and one X chromosome in the cells of the male. There is in the male, in addition to the X, also a Y chromosome, which acts as its mate in synapsis and reduction.

After reduction each egg carries an X chromosome. In the male there are two classes of sperm, one carrying the X chromosome and the other carrying the Y chromosome. Any egg fertilized by an X sperm produces a female; any egg fertilized by a Y sperm produces a male. The scheme of inheritance is as follows.

Eggs	X—X
Sperm	X—Y
Daughter	XX
Son	XY

The sons get their single X chromosome from their mother, and should therefore show any character whose gen is carried by such a chromosome. In sex-linked inheritance all sons show the characters of their mother. A male transmits his sex-linked character to his daughters, who show it if dominant and conceal it if recessive. But any daughter will transmit such a character, whether dominant or recessive, to half of her sons. The path of transmission of the gen is the same as the path followed by the X chromosome, received here from the male. Many other combinations show the same relations. In the case of non-disjunction, to be given later, there is direct experimental evidence of such a nature that there can no longer be any doubt that the X chromosomes are the carriers of certain gens that we speak of as sex-linked. This term (sex-linked) is intended to mean that such characters are carried by the X chromosome. It has been objected that this use of the term implies a knowledge of a factor for sex in the X chromosome to which the other factors in that chromosome are linked; but in fact we have as much knowledge in regard to the occurrence of a sex factor

or sex factors in the X chromosome as we have for other factors. It is true we do not know whether there is more than one sex-factor, because there is no crossing-over in the male (the heterozygous sex), and crossing-over in the female does not influence the distribution of sex, since like parts are simply interchanged. It follows from this that we are unable as yet to locate the sex factor or factors in the X chromosome. The fact that we can not detect crossing-over under this condition is not an argument against the occurrence of linkage. We are justified, therefore, in speaking of the factors carried by the X chromosome as sex-linked.

CROSSING-OVER.

When two or more sex-linked factors are present in a male they are always transmitted together to his daughters, as must necessarily be the case if they are carried by the unpaired X chromosome. If such a male carrying, let us say, two sex-linked factors, is mated to a wild female, his daughters will have one X chromosome containing the factors for both characters, derived from the father, and another X chromosome that contains the factors that are normal for these two factors (the normal allelomorphs). The sons of such a female will get one or the other of these two kinds of chromosomes, and should be expected to be like the one or the other grandparent. In fact, most of the sons are of these two kinds. But, in addition, there are sons that show one only of the two original mutant characters. Clearly an interchange has taken place between the two X chromosomes in the female in such a way that a piece of one chromosome has been exchanged for the homologous piece of the other. The same conclusion is reached if the cross is made in such a

way that the same two sex-linked characters enter, but, one from the mother and the other from the father. The daughter gets one of her sex chromosomes from her mother and the other from her father. She should produce, then, two kinds of sons, one like her mother and one like her father. In fact, the majority of her sons are of these two kinds, but, in addition, there are two other kinds of sons, one kind showing both mutant characters, the other kind showing normal characters. Here again the results must be due to interchange between the two X's in the hybrid female. *The number of the sons due to exchange in the two foregoing crosses is always the same, although they are of contrary classes.* Clearly, then, the interchange takes place irrespective of the way in which the factors enter the cross. We call those classes that arise through interchange between the chromosomes "cross-over classes" or merely "cross-overs." The phenomenon of holding together we speak of as linkage.

By taking a number of factors into consideration at the same time it has been shown that *crossing-over involves large pieces of the chromosomes*. The X chromosomes undergo crossing-over in about 60 per cent of the cases, and the crossing-over may occur at any point along the chromosome. When it occurs once, whole ends (or halves even) go over together and the exchange is always equivalent. If crossing-over occurs twice at the same time a middle piece of one chromosome is intercalated between the ends of the other chromosome. This process is called double crossing-over. It occurs not oftener than in about 10 per cent of cases for the total length of the X chromosome. Triple crossing-over in the X chromosome is extremely rare and has been observed only about a half dozen times.

While the genetic evidence forces one to accept crossing-over between the sex chromosomes in the female, that evidence gives no clue as to how such a process is brought about. There are, however, certain facts familiar to the cytologist that furnish a clue as to how such an interchange might take place. When the homologous chromosomes come together at synapsis it has been demonstrated, in some forms at least, that they twist about each other so that one chromosome comes to lie now on the one side now on the other of its partner. If at some points the chromosomes break and the pieces on the same side unite and pass to the same pole of the karyokinetic spindle, the necessary condition for crossing-over will have been fulfilled.

THE Y CHROMOSOME AND NON-DISJUNCTION.

Following Wilson's nomenclature, we speak of both X and Y as sex chromosomes. Both the cytological and the genetic evidence shows that when two X chromosomes are present a female is produced, when one, a male. This conclusion leaves the Y chromosome without any observed relation to sex-determination, despite the fact that the Y is normally present in every male and is confined to the male line. The question may be asked, and in fact has been asked, why may not the presence of the Y chromosome determine that a male develop and its absence that a female appear? The only answer that has yet been given, outside of the work on *Drosophila*, is that since in some insects there is no Y chromosome, there is no need to make such an assumption. But in *Drosophila* direct proof that Y has no such function is furnished by the evidence discovered by Bridges in the case of non-disjunction. (Bridges, 1913, 1914, 1916, and unpublished

results.)

Ordinarily all the sons and none of the daughters show the recessive sex-linked characters of the mother when the father carries the dominant allelomorph. The peculiarity of non-disjunction is that sometimes a female produces a daughter like herself or a son like the father, although the rest of the offspring are perfectly regular. For example, a vermilion female mated to a wild male produces vermilion sons and wild-type daughters, but rarely also a vermilion daughter or a wild-type son. The production of these exceptions (primary exceptions) by a normal XX female must be due to an aberrant reduction division at which the two X chromosomes fail to disjoin from each other. In consequence both remain in the egg or both pass into the polar body. In the latter case an egg without an X chromosome is produced. Such an egg fertilized by an X sperm produces a male with the constitution XO. These males received their single X from their father and therefore show the father's characters. While these XO males are exceptions to sex-linked inheritance, the characters that they do show are perfectly normal, that is, the miniature or the bar or other sex-linked characters that the XO male has are like those of an XY male, showing that the Y normally has no effect upon the development of these characters. But that the Y does play some positive rôle is proved by the fact that all the XO males have been found to be absolutely sterile.

While the presence of the Y is necessary for the fertility of the male, it has no effect upon sex itself. This is shown even more strikingly by the phenomenon known as secondary non-disjunction. If the two X chromosomes that fail to disjoin remain in

the egg, and this egg is fertilized by a Y sperm, an XXY individual results. This is a female which is like her mother in all sex-linked characters (a matroclinous exception), since she received both her X chromosomes from her mother and none from her father. As far as sex is concerned this is a perfectly normal female. The extra Y has no effect upon the appearance of the characters, even in the case of eosin, where the female is much darker than the male. The only effect which the extra Y has is as an extra wheel in the machinery of synapsis and reduction; for, on account of the presence of the Y, both X's of the XXY female are sometimes left within the ripe egg, a process called secondary non-disjunction. In consequence, an XXY female regularly produces exceptions (to the extent of about 4 per cent). A small percentage of reductions are of this XX-Y type; the majority are X-XY. The XY eggs, produced by the X-XY reductions, when fertilized by Y sperm, give XYY males, which show no influence of the extra Y except at synapsis and reduction. By mating an XXY female to an XYY male, XXYY females have been produced and these are perfectly normal in appearance. We may conclude from the fact that visibly indistinguishable males have been produced with the formulas XO, XY, and XYY, and likewise females with the formulas XX, XXY, and XXYY, that the Y is without effect either on the sex or on the visible characters (other than fertility) of the individual.

The evidence is equally positive that sex is quantitatively determined by the X chromosome—that two X's determine a female and one a male. For in the case of non-disjunction, a zero or a Y egg fertilized by an X sperm produces a male, while conversely an XX egg fertilized by a Y sperm

produces a female. It is thus impossible to assume that the X sperms are normally female-producing because of something else than the X or that the Y sperm produce males for any other reason than that they normally fertilize X eggs. Both the X and the Y sperm have been shown to produce the sex opposite to that which they normally produce when they fertilize eggs that are normal in every respect, except that of their X chromosome content. These facts establish experimentally that sex is determined by the combinations of the X chromosomes, and that the male and female combinations are the causes of sex differentiation and are not simply the results of maleness and femaleness already determined by some other agent.

Cytological examination has demonstrated the existence of one XXYY female, and has checked up the occurrence in the proper classes and proportions of the XXY females. Numerous and extensive breeding-tests have been made upon the other points discussed. The evidence leaves no escape from the conclusion that the genetic exceptions are produced as a consequence of the exceptional distribution of the X chromosomes and that the gens for the sex-linked characters are carried by those chromosomes.

MUTATION IN DROSOPHILA AMPELOPHILA.

The first mutants were found in the spring of 1910. Since then an ever-increasing series of new types has been appearing. An immense number of flies have come under the scrutiny of those who are working in the Zoological Laboratory of Columbia University, and the discovery of so many mutant types is undoubtedly due to this fact. But that mutation is more frequent in *Drosophila ampelophila* than in some

of the other species of *Drosophila* seems not improbable from an extensive examination of other types. It is true a few mutants have been found in other *Drosophilas*, but relatively few as compared with the number in *D. ampelophila*. Whether *ampelophila* is more prone to mutate, or whether the conditions under which it is kept are such as to favor this process, we have no knowledge. Several attempts that we have made to produce mutations have led to no conclusive results.

The mutants of *Drosophila* have been referred to by Baur as "mutations through loss," but inasmuch as they differ in no respect that we can discover from other mutants in domesticated animals and plants, there is no particular reason for putting them into this category unless to imply that new characters have not appeared, or that those that have appeared must be due to loss in the sense of absence of something from the germ-plasm.

In regard to the first point, several of the mutants are characterized by what seem to be additions. For example, the eye-color sepia is darker than the ordinary red. At least three new markings have been added to the thorax. A speck has appeared at the base of the wing, etc. These are recessive characters, it is true, but the character "streak," which consists of a dark band added to the thorax, is a dominant. If dominance is supposed to be a criterion as to "presence," then it should be pointed out that among the mutants of *Drosophila* a number of dominant types occur. But clearly we are not justified by these criteria in inferring anything whatever in regard to the nature of the change that takes place in the germ-plasm. Probably the only data which give a basis for attempting to decide the nature of the

change in the germ-plasm are from cases where multiple allelomorphs are found. Several such cases are known to us, and two of these are found in the X chromosome group, namely, a quadruple system (white, eosin, cherry, red), and a triple system (yellow, spot, gray). In such cases each member acts as the allelomorph of any other member, and only two can occur in any one female, and only one in any male. If the normal allelomorph is thought of as the positive character, which one of the mutants is due to its loss or to its absence? If each is produced by a loss it must be a different loss that acts as an allelomorph to the other loss. This is obviously absurd unless a different idea from the one usually promulgated in regard to "absence" is held.

MULTIPLE ALLELOMORPHS.

It appears that Cuénot was the first to find a case (in mice) in which the results could be explained on the basis that more than two factors may stand in the relation of allelomorphs to each other. In other words, a given factor may become the partner of more than one other factor, although, in any one individual, no more than two factors stand in this relation. While it appears that his evidence as published was not demonstrative, and that, at the time he wrote, the possibility of such results being due to very close linkage could not have been appreciated as an alternative explanation, nevertheless it remains that Cuénot was right in his interpretation of his results and that the factors for yellow, gray, gray white-belly, and black in mice form a system of quadruple allelomorphs.

There are at least two such systems among the factors in the first chromosome in *Drosophila*. The

first of these includes the factor for white eyes, that for eosin eyes, and that for cherry eyes, and of course that allelomorph of these factors present in the wild fly and which when present gives the red color. In this instance the normal allelomorph dominates all the other three, but in mice the mutant factor for yellow dominates the wild or "normal" allelomorph.

The other system of multiple allelomorphs in the first chromosome is a triple system made up of yellow (body-color), spot (on abdomen), and their normal allelomorph—the factor in the normal fly that stands for "gray."

In general it may be said that there are two principal ways in which it is possible to show that certain factors (more than two) are the allelomorphs of each other. First, if they are allelomorphs only two can exist in the same individual; and, in the case of sex-linked characters, while two may exist in the same female, only one can exist in the male, for he contains but one X chromosome. Second, all the allelomorphs should give the same percentages of crossing-over with each other factor in the same chromosome.

It is a question of considerable theoretical importance whether these cases of multiple allelomorphs are only extreme cases of linkage or whether they form a system quite apart from linkage and in relation to normal allelomorphism. It may be worth while, therefore, to discuss this question more at length, especially because *Drosophila* is one of the best cases known for such a discussion.

The factors in the first chromosome are linked to each other in various degrees. When they are as closely linked as yellow body-color and white eyes

crossing-over takes place only once in a hundred times. If two factors were still nearer together it is thinkable that crossing-over might be such a rare occurrence that it would require an enormous number of individuals to demonstrate its occurrence. In such a case the factors might be said to be completely linked, yet each would be supposed to have its normal allelomorph in the homologous chromosome of the wild type. Imagine, then, a situation in which one of these two mutant factors (a) enters from one parent and the other mutant factor (b) from the other parent. The normal allelomorph of a may be called A. It enters the combination with b, while the normal allelomorph B of b enters the combination with a. Since b is completely linked to A and a to B, the result will be the same as though a and b were the allelomorphs of each other, for in the germ-cells of the hybrid aBAb the assortment will be into aB and Ab, which is the same as though a and b acted as segregating allelomorphs.

There is no way from Mendelian data by which this difference between a true case of multiple allelomorphs and one of complete linkage (as just illustrated) can be determined. There is, however, a different line of attack which, in a case like that of *Drosophila*, will give an answer to this question. The answer is found in the way in which the mutant factors arise. This argument has been fully developed in the book entitled "The Mechanism of Mendelian Inheritance," and will therefore not be repeated here. It must suffice to say that if two mutant types that behave as allelomorphs of each other arise separately from the wild form, one of them must have arisen as a double mutation of two factors so close to each other as to be completely linked—a highly

improbable occurrence when the infrequency of mutations is taken into consideration.[1] The evidence opposed to such an interpretation is now so strong that there can be little doubt that multiple allelomorphs have actually appeared.

On *a priori* grounds there is no reason why several mutative changes might not take place in the same locus of a chromosome. If we think of a chromosome as made up of a chain of chemical particles, there may be a number of possible recombinations or rearrangements within each particle. Any change might make a difference in the end-product of the activity of the cell, and give rise to a new mutant type. It is only when one arbitrarily supposes that the only possible change in a factor is its loss that any serious difficulty arises in the interpretation of multiple allelomorphs.

One of the most striking facts connected with the subject of multiple allelomorphs is that the same kind of change is effected in the same organ. Thus, in the quadruple system mentioned above, the color of the eye is affected. In the yellow-spot system the color of the body is involved. In mice it is the coat-color that is different in each member of the series. While this is undoubtedly a striking relation and one which seems to fit well with the idea that such effects are due to mutative changes in the same fundamental element that affects the character in question, yet on the other hand it would be dangerous to lay too much emphasis on this point, because any given organ may be affected by other factors in a similar manner, and also because a factor frequently produces more than a single effect. For instance, the factor that when present gives a white eye affects also the general yellowish pigment of the

body. If red-eyed and white-eyed flies are put for several hours into alcohol, the yellowish body-color of the white-eyed flies is freely extracted, but not that of the red-eyed flies. In the living condition the difference between the body-colors of the red- and of the white-eyed flies is too slight to be visible, but after extraction in alcohol the difference is striking. There are other effects also that follow in the wake of the white factor. Now, it is quite conceivable that in some specific case one of the effects might be more striking than the one produced in that organ more markedly affected by the other factor of the allelomorphic series. In such a case the relation mentioned above might seemingly disappear. For this reason it is well not to insist too strongly on the idea that multiple allelomorphs affect the same part in the same way, even although at present that appears to be the rule for all known cases.

SEX-LINKED LETHALS AND THE SEX RATIO.

Most of the mutant types of *Drosophila* show characteristics that may be regarded as superficial in so far as they do not prevent the animal from living in the protected life that our cultures afford. Were they thrown into open competition with wild forms, or, better said, were they left to shift for themselves under natural conditions, many or most of the types would no doubt soon die out. So far as we can see, there is no reason to suppose that the mutations which can be described as superficial are disproportionally more likely to occur than others. Of course, superficial mutations are more likely to survive and hence to be seen; while if mutations took place in important organs some of them would be expected to affect injuriously parts essential to the

life of the individual and in consequence such an individual perishes. The "lethal factors" of *Drosophila* may be supposed to be mutations of some such nature; but as yet we have not studied this side of the question sufficiently, and this supposed method of action of the lethals is purely speculative. Whatever the nature of the lethals' action, it can be shown that from among the offspring obtained from certain stocks expected classes are missing, and the absence of these classes can be accounted for on the assumption that there are present mutant factors that follow the Mendelian rule of segregation and which show normal linkage to other factors, but whose only recognizable difference from the normal is the death of those individuals which receive them. The numerical results can be handled in precisely the same way as are other linkage results.

There are some general relations that concern the lethals that may be mentioned here, while the details are left for the special part or are found in the special papers dealing with these lethals. A factor of this kind carried by the X chromosome would be transmitted in the female line because the female, having two X chromosomes, would have one of them with the normal allelomorph (dominant) of the lethal factor carried by the other X chromosome. Half of her sons would get one of her X's, the other half the other. Those sons that get the lethal X will die, since the male having only one X lacks the power of containing both the lethal and its normal allelomorph. The other half of the sons will survive, but will not transmit the lethal factor. In all lethal stocks there are only half as many sons as daughters. The heterozygous lethal-bearing female, fertilized by a normal male, will give rise to two kinds of daughters; one normal in both X's, the other with a

normal X and a lethal-bearing X chromosome. The former are always normal in behavior, and the latter repeat in their descendants the 2:1 sex-ratio.

Whether a female bearing the same lethal twice (*i.e.*, one homozygous for a given lethal) would die, can not be stated, for no such females are obtainable, because the lethal males, which alone could bring about such a condition, do not exist. The presumption is that a female of this kind would also die if the lethal acts injuriously on some vital function or structure.

Since only half of the daughters of the lethal-bearing females carry the lethal, the stock can be maintained by breeding daughters separately in each generation to insure obtaining one which repeats the 2:1 ratio. There is, however, a much more advantageous way of carrying on the stock—one that also confirms the sufficiency of the theory.

In carrying on a stock of a lethal, advantage can be taken of linkage. A lethal factor has a definite locus in the chromosome; if, then, a lethal-bearing female is crossed to a male of another stock with a recessive character whose factor lies in the X chromosome very close to the lethal factor, half the daughters will have lethal in one X and the recessive in the other. The lethal-bearing females can be picked out from their sisters by the fact that they give a 2:1 sex-ratio, and by the fact that nearly all the sons that do survive show the recessive character. If such females are tested by breeding to the recessive males, then the daughters which do not show the recessive carry the lethal, except in the few cases of crossing-over. Thus in each generation the normal females are crossed to the recessive males with the assurance

that the lethal will not be lost. If instead of the single recessive used in this fashion, a double recessive of such a sort that one recessive lies on each side of the lethal is used, then in each generation the females which show neither recessive will almost invariably contain the lethal, since a double cross-over is required to remove the lethal.

It is true that females carrying two *different* lethals might arise and not die, because the injurious effect of each lethal would be dominated by its allelomorph in the other X chromosome. Such females can not be obtained by combining two existing lethals, since lethal males do not survive. They can occur only through a new lethal arising through mutation in the homologous chromosome of a female that already carries one lethal. Rare as such an event must be, it has occurred in our cultures thrice. The presence of a female of this kind will be at once noticed by the fact that she produces no sons, or very rarely one, giving in consequence extraordinary sex-ratios. The rare appearance of a son from such a female can be accounted for in the following way: If crossing-over occurs between her X chromosomes the result will be that one X will sometimes contain two lethals, the other none. The latter, if it passes into a male, will lead to the development of a normal individual. The number of such males depends on the distance apart of the two lethals in the chromosome. There is a crucial test of this hypothesis of two lethals in females giving extraordinary ratios. This test has been applied to the cases in which such females were found, by Rawls (1913), by Morgan (1914*c*), and again by Stark (1915), and it has been found to confirm the explanation. The daughters of such a female should all (excepting a rare one due to crossing-over) give 2:1 ratios, because each daughter

must get one or the other X chromosome of her mother, that is, one or the other lethal. Although the mother was fertilized by a normal male, every daughter is heterozygous for one or the other of the lethal factors. The daughters of the two-lethal females differ from the daughters of the one-lethal female in that the former mother, as just stated, gives all lethal-bearing daughters; the latter transmits her lethal to only half of her daughters.

INFLUENCE OF THE ENVIRONMENT ON THE REALIZATION OF TWO SEX-LINKED CHARACTERS.

The need of a special environment in order that certain mutant characters may express themselves has been shown for abnormal abdomen (Morgan, 1912*d*, 1915*b*) and for reduplication of the legs (Hoge, 1915). In a third type, club, described here (page 69), the failure of the unfolding of the wing which occurs in about 20 per cent of the flies is also without much doubt an environmental effect, but as yet the particular influence that causes the change is unknown.

A very extensive series of observations has been made on the character called abnormal abdomen. In pure cultures kept moist with abundance of fresh food all the flies that hatch for the first few days have the black bands of the abdomen obliterated or made faint and irregular. As the bottles get dry and the food becomes scarce the flies become more and more normal, until at last they are indistinguishable from the normal flies. Nevertheless these normal-looking flies will give rise in a suitable environment to the same kind of flies as the very abnormal flies first hatched. By breeding from the last flies of each culture, and in dry cultures, flies can be bred from

normal ancestors for several generations, and then by making the conditions favorable for the appearance of the abnormal condition, the flies will be as abnormal as though their ancestors had always been abnormal. Here, then, is a character that is susceptible to the variations in the environment, yet whatever the realized condition of the soma may be, that condition has no effect whatever on the nature of the germ-plasm. A more striking disproof of the theory of the inheritance of acquired characters would be hard to find.

A demonstration is given in this instance of the interaction between a given genotypic constitution and a special environment. The character abnormal is a sex-linked dominant. Therefore, if an abnormal male is mated to a wild female the daughters are heterozygous for abnormal, while the sons, getting their X chromosome from their mother, are entirely normal. In a wet environment all the daughters are abnormal and the sons normal. As the culture dries out the daughters' color becomes normal in appearance. But while the sons will never transmit abnormality to any of their descendants in any environment, the daughters will transmit (if bred to normal males) in a suitable environment their peculiarity to half of their daughters and to half of their sons. The experiment shows convincingly that the abnormal abdomen appears in a special environment only in those flies that have a given genotypic constitution.

As the cultures dry out the abnormal males are the first to change over to normal, then the heterozygous females, and lastly the homozygous females. It is doubtful if any far-reaching conclusion can be drawn from this series, because the first and second classes

differ from each other not only in the presence of one or of two factors for abnormal, but also by the absence in the first case (male) of an entire X chromosome with its contained factors. The second and third classes differ from each other only by the abnormal factor.

Similar results were found in the mutant type called reduplicated legs, which is a sex-linked recessive character that appears best when the cultures are kept at about 10° C. As Miss M. A. Hoge has shown, this character then becomes realized in nearly all of the flies that have the proper constitution, but not in flies of normal constitution placed in the same environment. Here the effect is produced by cold.

SEXUAL POLYMORPHISM.

Outside the primary and secondary sexual differences between the male and the female, there is a considerable number of species of animals with more than one kind of female or male. Darwin and his followers have tried to explain such cases on the grounds that more than one kind of female (or male) might arise through natural selection, in consequence of some individuals mimicking a protected species. It is needless to point out here how involved and intricate such a process would be, because the mutation theory has cut the Gordian knot and given a simpler solution of the origin of such diandromorphic and digynomorphic conditions.

In *Drosophila* a mutant, eosin eye-color, appeared in which the female has darker eyes than the male. If such stock is crossed with cherry (another sex-linked recessive mutant, allelomorphic to eosin) the females in the F_2 generation are alike (for the pure eosin and the eosin-cherry compound are not separable), but

the cherry males and the eosin males are quite different in appearance. Here we have a simulation, at least, of a diandromorphic species. Such a group perpetuates itself, giving one type of female (inasmuch as eosin and cherry females are very closely similar) and two types of males, only one of which is like the females. A population of this kind is very directly comparable to certain polymorphic types that occur in nature. In *Colias philodice* there is one type of male, yellow, and two types of females, yellow and white. In *Colias eurydice* the male is orange and the females are orange or white. In *Papilio turnus* the male is yellow and the females either yellow or black. Those cases are directly comparable to an eosin-cherry population, except that in Lepidoptera the female is heterozygous for the sex differential, in Diptera the male.

Since in *Drosophila* the results are explicable on a sex-linked basis, a similar explanation may apply to polymorphism in butterflies. By suitable combinations of eosin and cherry most of the cases of polymorphism in butterflies may be simulated. To simulate the more complex cases, such as that of *Papilio polytes* and *memnon*, another allelomorph like eosin would have to be introduced. A population of mixed cherry and white would give three somatic types of females (cherry, cherry-white, and white) and two of males (cherry and white).

FERTILITY AND STERILITY IN THE MUTANTS.

Aside from the decrease in fertility that occurs in certain stocks (a question that need not be treated here), there are among the types described in the text two cases that call for special comment. When the mutant type called "rudimentary" was first

discovered, it was found that the females were sterile but the males were fully fertile. Later work has revealed the nature of the sterility of the female. The ovaries are present and in the young flies appear normal, but while in the normal flies the eggs in the posterior portion enlarge rapidly during the first few days after hatching, in the rudimentary females only a very few (about 15) eggs enlarge. The other eggs in the ovary remain at a lower stage of their development. Rarely the female lays a few eggs; when she does so some of the eggs hatch, and if she has been mated to a rudimentary male, the offspring are rudimentary females and males. The rudimentary females mate in the normal time with rudimentary or with normal males, and their sexual behavior is normal. Their sterility is therefore due to the failure of the eggs to develop properly. Whether in addition to this there is some incompatibility between the sperm and the eggs of this type (as supposed to be the case at one time) is not conclusively disproved, but is not probable from the evidence now available.

In the mutant called "fused" the females are sterile both with wild males and with males from their own stock. An examination of the ovaries of these females, made by Mr. C. McEwen, shows clearly that there are fewer than the normal number of mature eggs, recalling the case of rudimentary.

It should be noticed that there is no apparent relation between the sterility of these two types and the occurrence of the mutation in the X chromosome, because other mutations in the X do not cause sterility, and there is sterility in other mutant types that are due to factors in other chromosomes.

BALANCED INVIABILITY.

The determination of the cross-over values of the factors was at first hindered because of the poor viability of some of the mutants. If the viability of each mutant type could be determined in relation to the viability of the normal, "coefficients of viability" could serve as corrections in working with the various mutant characters. But it was found (Bridges and Sturtevant, 1914) that viability was so erratic that coefficients might mislead. At the same time it was becoming more apparent that poor viability is no necessary attribute of a character, but depends very largely on the condition of culture. Competition among larvæ was found to be the chief factor in viability. Mass cultures almost invariably have extremely poor viability, even though an attempt is made to supply an abundance of food. Special tests (Morgan and Tice, 1914) showed that even those mutants which were considered the very poorest in viability were produced in proportions fairly close to the theoretical when only one female was used for each large culture bottle and the amount and quality of food was carefully adjusted.

For the majority of mutants which did well even under heavy competition in mass cultures the pair-breeding method reduced the disturbances due to viability to a point where they were negligible.

Later a method was devised (Bridges, 1915) whereby mutations of poor viability could be worked with in linkage experiments fairly accurately and whereby the residual inviability of the ordinary characters could be largely canceled. This method consists in balancing the data of a certain class with poor viability by means of an equivalent amount of data in which the same class occurs as the other member of the ratio. Thus in obtaining data upon any linkage

case it is best to have the total number of individuals made up of approximately equal numbers derived from each of the possible ways in which the experiment may be conducted. In the simplest case, in which the results are of the form AB:Ab:aB:ab, let us suppose that the class ab has a disproportionately low viability. If, then, ab occurs in an experiment as a cross-over class, that class will be too small and a false linkage value will be calculated. The remedy is to balance the preceding data by an equal amount of data in which ab occurs as a non-cross-over. In these latter the error will be the opposite of the previous one, and by combining the two experiments the errors should be balanced to give a better approximation to the true value. When equal amounts of data, secured in these two ways, are combined, all four classes will be balanced in the required manner by occurring both as non-cross-overs and as cross-overs. The error, therefore, should be very small. For three pairs of gens there are eight classes, and in order that each of them may appear as a non-cross-over, as each single cross-over, and as the double cross-over, four experiments must be made.

HOW THE FACTORS ARE LOCATED IN THE CHROMOSOMES.

A character is in the first chromosome if it is transmitted by the grandfather to half of his grandsons, while, in the reciprocal cross, the mother transmits her character to all her sons (criss-cross inheritance) and to half of her granddaughters and to half of her grandsons; in other words, if the factor that differentiates the character has the same distribution as the X chromosome. If, however, a new mutant type does not show this sex-linked

inheritance, its chromosome is determined by taking advantage of the fact that in *Drosophila* there is no crossing-over in the male between factors in the same chromosome. For instance, if a new mutant type is found not to be sex-linked, its group is determined by the following tests: It is crossed to black, whose factor is known to be in the second chromosome, and to pink, whose factor lies in the third chromosome. If the factor of the new form should happen to be in the second chromosome, then, in the cross with black, no double recessive can appear, so that the F_2 proportion is 2:1:1:0; but with pink, the mutant type should give the proportion 9:3:3:1, typical of free assortment.

If, however, the factor of the new form is in the third chromosome, then, when crossed to black, the double recessive and the 9:3:3:1 proportion appear in F_2. But when crossed to pink no double recessive appears in F_2, and the proportion 2:1:1:0 occurs.

If these tests show that the new mutant does not belong to either the second or third chromosome, that is, if both with black and with pink the 9:3:3:1 ratio is obtained, then by exclusion the factor lies in the fourth chromosome, in which as yet only two factors have been found.

We propose to give in a series of papers an account of the mutant races of *Drosophila* and the linkage shown in their inheritance. In this paper we shall consider only the members of the first chromosome, describing a large number of new mutants with their linkage relations and summarizing to date all the linkage data relating to the first chromosome. In later papers we propose to consider the members of the second, third, and fourth chromosomes.

The list at the top of page 21 gives the names of the factors dealt with in this paper. They stand in the order of their discovery, the mutant forms reported here for the first time being starred.

In each experiment the percentage of crossing-over is found by dividing the number of the cross-overs by the sum of the non-cross-overs and the cross-overs, and multiplying this quotient by 100. The resulting percentages, or cross-over values, are used as measures of the distances between loci. Thus if the experiments give a cross-over value of 5 per cent for white and bifid, we say that white and bifid lie 5 units apart in the X chromosome. Other experiments show that yellow and white are about 1 unit apart, and that yellow and bifid are about 6 units apart. We can therefore construct a diagram with yellow as the zero, with white at 1, and with bifid at 6. If we know the cross-over values given by a new mutant with any two mutants of the same chromosome whose positions are already determined, then we can locate the new factor with accuracy, and be able to predict the cross-over value which the new factor will give with any other factor whose position is plotted.

The sex-linked factors of Drosophila.

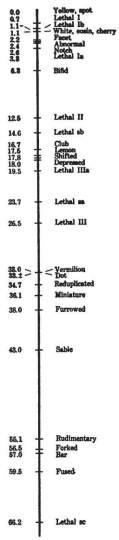
Gen.	Part affected.	Figure.	Symbol.	Locus.	D
White	Eye-color	11	w	1.1	M
Rudimentary	Wings	A	r	55.1	Ju
Miniature	Wings	7-8	m	36.1	Au
Vermilion	Eye-color	10	v	33.0	N
Yellow	Body-color	5	y	0.0	Ja
Abnormal	Abdomen	4	A′	2.4	Ju

Eosin	Eye-color	7-8	w^e	1.1	Au
Bifid	Wings	B	b_i	6.3	No
Reduplicated	Legs			34.7	No
Lethal 1	Life		l_1	0.7	Fe
Lethal 1*a**	Life		l_{1a}	3.3	Ma
Spot*	Body-color	14-17	y^s	0.0	Ap
Sable*	Body-color	2	s	43.0	Ju
Dot*	Thorax			33 ±	Ju
Bow*	Wings	C			Au
Lemon*	Body-color	3	l_m	17.5	Au
Lethal 2	Life		l_2	12.5 ±	Se
Cherry	Eye-color	9	w^c	1.1	Oc
Fused*	Venation	D	f_u	59.5	No
Forked*	Bristles	E	f	56.5	No
Shifted*	Venation	F	s_h	17.8	Ja
Lethal sa	Life		l_{sa}	23.7	Ja
Bar	Eye-shape	12-13	B′	57.0	Fe
Notch	Wing		N′	2.6	Ma
Depressed*	Wing	G	d_p	18.0	Ap
Lethal sb	Life		l_{sb}	16.7	Ap
Club*	Wings	H	c_l	14.6	Ma
Green*	Body-color				Ma
Chrome*	Body-color				Se
Lethal 3	Life		l_3	26.5	De
Lethal 3*a*	Life		l_{3a}	19.5	Ja
Lethal 1*b**	Life		l_{1b}	1.1-	Fe

Facet*	Eye		f_a	2.2	Fe
Lethal *sc*	Life		l_{sc}	66.2	Ap
Lethal *sd*	Life		l_{sd}		M
Furrowed	Eye		f_w	38.0	No

The factors are located preferably by short distances (*i.e.*, by those cases in which the amount of crossing-over is small), because when the amount of crossing-over is large a correction must be made for double crossing-over, and the correction can be best found through breaking up the long distances into short ones, by using intermediate points.

Conversely, when a long distance is indicated on the chromosome diagram, the actual cross-over value found by experiment (*i.e.*, the percentage of cross-overs) will be less than the diagram indicates, because the diagram has been corrected for double crossing-over.



DIAGRAM

I.

Diagram I has been constructed upon the basis of all the data summarized in table 65 (p. 84) for the first or X chromosome. It shows the relative positions of the gens of the sex-linked characters of *Drosophila*. One unit of distance corresponds to 1 per cent of crossing-over. Since all distances are corrected for double crossing-over and for coincidence, the values represent the *total* of crossing-over between the loci. The uncorrected value obtained in any experiment with two loci widely separated will be smaller than the value given in the map.

It may be asked what will happen when two factors whose loci are more than 50 units apart in the same chromosome are used in the same experiment? One might expect to get more than 50 per cent of cross-overs with such an experiment, but double crossing-over becomes disproportionately greater the longer the distance involved, so that in experiments the observed percentage of crossing-over does not rise above 50 per cent. For example, if eosin is tested against bar, somewhat under 50 per cent of cross-overs are obtained, but if the distance of bar from eosin is found by summation of the component distances the interval for eosin bar is 56 units.

In calculating the loci of the first chromosome, a system of weighting was used which allowed each case to influence the positions of the loci in proportion to the amount of the data. In this way advantage was taken of the entire mass of data.

The factors (lethal 1, white, facet, abnormal, notch, and bifid) which lie close to yellow were the first to be calculated and plotted. The next step was to

determine very accurately the position of vermilion with respect to yellow. There are many separate experiments which influence this calculation and all were proportionately weighted. Then, using vermilion as the fixed point the factors (dot, reduplicated, miniature, and sable) which lie close to vermilion were plotted. The same process was repeated in locating bar with respect to vermilion and the factors about bar with reference to bar. The last step was to interpolate the factors (club, lethal 2, lemon, depressed, and shifted), which form a group about midway between yellow and vermilion. Of these, club is the only one whose location is accurate. The apparent closeness of the grouping of these loci is not to be taken as significant, for they have been placed only with reference to the distant points yellow and vermilion and not with respect to each other; furthermore, the data available in the cases of lemon and depressed are very meager.

The factors which are most important and are most accurately located are yellow, white (eosin), bifid, club, vermilion, miniature, sable, forked, and bar. Of these again, white (eosin), vermilion, and bar are of prime importance and will probably continue to claim first rank. Of the three allelomorphs, white, eosin, and cherry, eosin is the most useful.

NOMENCLATURE.

The system of symbols used in the diagrams and table headings is as follows: The factor or gen for a recessive mutant character is represented by a lower-case letter, as v for vermilion and m for miniature. The symbols for the dominant mutant characters bar, abnormal, and notch are B′, A′, and N′. There are now so many characters that it is impossible to

represent all of them by a single letter. We therefore add a subletter in such cases, as bifid (b_i), fused (f_u), and lethal 2 (l_2). In the case of multiple allelomorphs we usually use as the base of the symbol the symbol of that member of the system which was first found and add a letter as an exponent to indicate the particular member, as y^s for spot, w^e for eosin, and w^c for cherry. The normal allelomorphs of the mutant gens are indicated by the converse letter, as V for not-vermilion, B_i for not-bifid, and b′ for not-bar. In the table headings the normal allelomorphs are indicated by position alone without the use of a symbol.

Thus the symbol $\frac{w^e \qquad\qquad B'}{\qquad\quad v}$ indicates that the female in question carried eosin, not-vermilion, and bar in one chromosome and not-eosin, vermilion, and not-bar in the other. The symbol $\frac{w^e \quad v}{\qquad\quad B'}$ when used in the heading of a column in a table indicates that the flies classified under this heading are the result of single crossing-over between eosin and vermilion in a mother which was the composition $\frac{w^e \qquad\qquad B'}{\qquad\quad v}$; the symbol tells at the same time that the flies that result from a single cross-over between eosin and vermilion in the mother are of the two contrary classes, eosin vermilion and bar. When a fly shows two or more non-allelomorphic characters the names are written from left to right in the order of their positions from the zero end of the map.

PART II. NEW DATA.

WHITE.

(Plate II, figure 11.)

The recessive character white eye-color, which appeared in May 1910, was the first sex-linked mutation in *Drosophila* (Morgan, 1910*a*, 1910*b*). Soon afterwards (June 1910) rudimentary appeared, and the two types were crossed (Morgan, 1910*c*). Under the conditions of culture the viability of rudimentary was extremely poor, but the data demonstrated the occurrence of recombination of the factors in the ovogenesis so that white and rudimentary, though both sex-linked, were brought together into the same individual. The results were not fully recognized as linkage, because white and rudimentary are so far apart in the chromosome that they seemed to assort freely from each other.

Owing to the excellent viability and the perfect sharpness of separation, white was extensively used in linkage experiments, especially with miniature and yellow (Morgan, 1911*a*; Morgan and Cattell, 1912 and 1913). White has been more extensively used than any other character in *Drosophila*, though it is now being used very little because of the fact that the double recessives of white with other sex-linked eye-colors, such as vermilion, are white, and consequently a separation into the true genetic classes is impossible. The place of white has been taken by eosin, which is an allelomorph of white and which can be readily used with any other eye-color.

The locus of white and its allelomorphs is only 1.1 units from that of yellow, which is the zero of the chromosome. Yellow and white are very closely linked, therefore giving only about one cross-over per 100 flies.

All the published data upon the linkage of white with other sex-linked characters have been collected into table 65.

RUDIMENTARY.

Rudimentary, which appeared in June 1910, was the second sex-linked character in *Drosophila* (Morgan, 1910*c*). Its viability has always been very poor; in this respect it is one of the very poorest of the sex-linked characters. The early linkage data (Morgan, 1911*a*) derived from mass cultures have all been discarded. By breeding from a single F_1 female in each large culture bottle it has been possible to obtain results which are fairly trustworthy (Morgan, 1912*g*; Morgan and Tice, 1914). These data appear in table 65, which summarizes all the published data.

The locus of rudimentary is at 55.1, for a long time the extreme right end of the known chromosome, though recently several mutants have been found to lie somewhat beyond it.

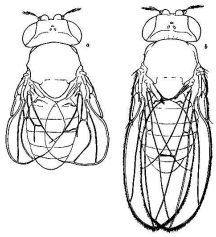


Fig. A. *a.* rudimentary wing; *b.* the wild fly for comparison.

The rudimentary males are perfectly fertile, but the rudimentary females rarely produce any offspring at all, and then only a very few. The reason for this is

that most of the germ-cells cease their development in the early growth stage of the eggs (Morgan, 1915*a*).

MINIATURE.

(Plate II. figures 7 and 8.)

The recessive sex-linked mutant miniature wings appeared in August 1910 (Morgan, 1911b and 1912a). The viability of miniature is fair, and this stock has been used in linkage experiments more than any other, with the single exception of white. While the wings of miniature usually extend backwards, they are sometimes held out at right angles to the body, and especially in acid bottles the miniature flies easily become stuck to the food or the wings become stringy, so that other wing characters are not easy to distinguish in those flies which are also miniature. At present vermilion, whose locus is at 33, in being used more frequently in linkage work. The locus of miniature at 36.1 is slightly beyond the middle of the chromosome.

VERMILION.

(Plate II. figure 10.)

The recessive sex-linked mutant vermilion eye-color (Morgan, 1911*c* and 1912*a*) appeared in November 1910, and has appeared at least twice since then (Morgan and Plough, 1915). This is one of the best of the sex-linked characters, on account of its excellent viability, its sharp distinction from normal with very little variability, its value as a double recessive in combination with other sex-linked eye-colors, and because of its location at 33.0, very near to the middle of the known chromosome.

YELLOW.

(Plate I. figure 5.)

The recessive sex-linked mutant yellow body and wing-color appeared in January 1911 (Morgan, 1911*c* and 1912*a*). Its first appearance was in black stock; hence the fly was a double recessive, then called brown. Later the same mutation has appeared independently from gray stock. Yellow was found to be at the end of the X chromosome, and this end was arbitrarily chosen as the zero or the "left end," while the other gens are spoken of as lying at various distances to the right of yellow. Recently a lethal gen has been located less than one-tenth of a unit (-0.04) to the left of yellow, but yellow is still retained as the zero-point.

The viability of yellow is fairly good and the character can be separated from gray with great facility, and in consequence yellow has been used extensively, although at present it is being used less than formerly, since eosin lies only 1.1 units distant from yellow and is generally preferred.

ABNORMAL ABDOMEN.

(Plate I. figure 4.)

The dominant sex-linked character abnormal abdomen appeared in July 1911 (Morgan, 1911*d*). It was soon found that the realization of the abnormal condition depended greatly upon the nature of the environment (Morgan, 1912). Recently a very extensive study of this character has been published (Morgan, 1915). As this case has been reviewed in the introduction, there is little further to be said here. Because of the change that takes place as the

culture grows older (the abnormal changing to normal), this character is not of much value in linkage work. The location of the factor in the X chromosome at 2.4 has been made out from the data given by Morgan (1915*b*). These data, which in general include only the abnormal classes, are summarized in table 1.

TABLE 1.—*Linkage data, from Morgan, 1915b.*

Gens.	Total.	Cross-overs.	Cross-over values.
Yellow white	28,018	334	1.2
Yellow abnormal	15,314	299	2.0
White abnormal	16,300	277	1.7

EOSIN.

(Plate II, figures 7 and 8.)

The recessive sex-linked mutation eosin eye-color appeared in August 1911 in a culture of white-eyed flies (Morgan 1912*a*). The eye-color is different in the male and female, the male being a light pinkish yellow, while the female is a rather dark yellowish pink. Eosin is allelomorphic to white and the white-eosin compound or heterozygote has the color of the eosin male. There is probably no special significance in this coincidence of color, since similar dilutions to various degrees have been demonstrated for all the other eye-colors tested (Morgan and Bridges, 1913). Since eosin is allelomorphic to white, its locus is also at 1.1. Eosin is the most useful character among all those in the left end of the chromosome.

BIFID.

The sex-linked wing mutant bifid, which appeared in November 1911, is characterized by the fusion of all the longitudinal veins into a heavy stalk at the base of the wing. The wing stands out from the body at a wide angle, so that the fusion is easily seen. At the tip of the wing the third longitudinal vein spreads out into a delta which reaches to the marginal vein. The fourth longitudinal vein reaches the margin only rarely. There is very often opposite this vein a great bay in the margin, or the whole wing is irregularly truncated.

The stock of bifid was at first extremely varied in the amount of this truncation. By selection a stock was secured which showed only very greatly reduced wings like those shown in figures *a*, *b*. Another stock (figs. *c*, *d*) was secured by outcrossing and selection which showed wings of nearly normal size and shape, which always had the bifid stalk, generally the spread positions (not as extreme), and often the delta and the shortened fourth longitudinal vein. We believe that the extreme reduction in size seen in the one stock was due to an added modifier of the nature of beaded, since this could be eliminated by outcrossing and selection.

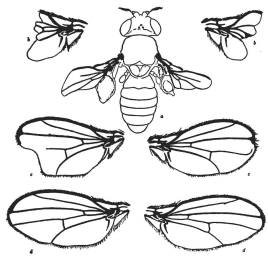


FIG. B.—Bifid wing. *c* and *d* show the typical condition of bifid wings. All the

longitudinal veins are fused into a heavy stalk at the base of the wing. *a* shows the typical position in which the bifid wings are held. The small size of the wings in *a* and *b* is due to the action of a modifier of the nature of "beaded" which has been eliminated in *c*, *d*.

LINKAGE OF BIFID WITH YELLOW, WITH WHITE, AND WITH VERMILION.

The stock of the normal (not-beaded) bifid was used by Dr. R. Chambers, Jr., for determining the chromosome locus of bifid by means of its linkage relations to vermilion, white, and yellow (Chambers, 1913). We have attempted to bring together in table 2 the complete data and to calculate the locus of bifid.

TABLE 2.—*Linkage data, from Chambers, 1913.*

Gens.	Total.	Cross-overs.	Cross-over values.
Yellow bifid	3,175	182	5.8
White bifid	20,800	1,127	5.3
Bifid vermilion	2,509	806	32.1

In the crosses between white and bifid there were 1,127 cross-overs in a total of 20,800 available individuals, which gives a cross-over value of 5.3. In the crosses between yellow and bifid there were 182 cross-overs in a total of 3,175 available individuals,

which gives a cross-over value of 5.8. In crosses between bifid and vermilion there were 806 cross-overs in a total of 2,509, which gives a cross-over value of 32.1. On the basis of all the data summarized in table 65, bifid is located at 6.3 to the right of yellow.

LINKAGE OF CHERRY, BIFID, AND VERMILION.

In a small experiment of our own, three factors were involved—cherry, bifid, and vermilion. A cherry vermilion female was crossed to a bifid male. Two daughters were back-crossed singly to white bifid males. The female offspring will then give data for the linkage of cherry white with bifid, while the sons will show the linkage of the three gens, cherry, bifid, and vermilion. The results are shown in table 3.

TABLE 3.—*P_1 cherry vermilion ♀ ♀ × bifid ♂ ♂. B. C.*[2] *F_1 wild-type ♀ × white bifid ♂ ♂.*

Reference.	F_2 females.					
	Non-cross-overs.		Cross-overs.			
	White-cherry	Bifid.	White-cherry bifid.	Wild-type.	Cherry vermilion.	Bifid.
262	40	46	1	2	45	38
263	47	45	3	3	30	50
Total.	87	91	4	5	75	88

Both males and females give a cross-over value of 5 units for cherry bifid, which is the value determined by Chambers. The order of the factors, viz, cherry, bifid, vermilion, is established by taking advantage of the double cross-over classes in the males. The

male classes give a cross-over value of 20 for bifid vermilion and 24 for cherry vermilion, which are low compared with values given by other experiments. The locus of bifid at 6.3 is convenient for many linkage problems, but this advantage is largely offset by the liability of the bifid flies to become stuck in the food and against the sides of the bottle. Bifid flies can be separated from the normal with certainty and with great ease.

REDUPLICATED LEGS.

In November 1912 Miss Mildred Hoge found that a certain stock was giving some males whose legs were reduplicated, either completely or only with respect to the terminal segments (described and figured, Hoge, 1915). Subsequent work by Miss Hoge showed that the condition was due to a sex-linked gen, but that at room temperature not all the flies that were genetically reduplicated showed reduplication. However, if the flies were raised through the pupa stage in the ice-box at a temperature of about 10° to 12° a majority of the flies which were expected to show reduplication did so. The most extremely reduplicated individual showed parts of 14 legs.

In studying the cross-over values of reduplicated, only those flies that have abnormal legs are to be used in calculation, as in the case of abnormal abdomen where the phenotypically normal individuals are partly genetically abnormal. Table 4 gives a summary of the data secured by Miss Hoge.

TABLE 4.—*Summary of linkage data upon reduplicated legs, from Hoge, 1915.*



Gens.	Total.	Cross-overs.	Cross-over values.
White reduplicated	418	121	29.0
Reduplicated vermilion	667	11	1.7
Reduplicated bar	583	120	20.6

The most accurate data, those upon the value for reduplicated and vermilion, give for reduplicated a distance of 1.7 from vermilion, either to the right or to the left. The distance from white is 29, which would place the locus for reduplication to the left of vermilion, which is at 33. The data for bar give a distance of 21, but since bar is itself 24 units from vermilion, this distance of 21 would seem to place the locus to the right of vermilion. The evidence is slightly in favor of this position to the right of vermilion at 34.7, where reduplicated may be located provisionally. In any case the locus is so near to that of vermilion that final decision must come from data involving double crossing-over, *i. e.*, from a three-locus experiment.

LETHAL 1.

In February 1912 Miss E. Rawls found that certain females from a wild stock were giving only about half as many sons as daughters. Tests continuing through five generations showed that the sons that appeared were entirely normal, but that half of the daughters gave again 2 : 1 sex-ratios, while the other half gave normal 1 : 1 sex-ratios.

The explanation of this mode of transmission became clear when it was found that the cause of the death of half of the males was a particular factor that had

as definite a locus in the X chromosome as have other sex-linked factors (Morgan, 1912*e*). Morgan mated females (from the stock sent to him by Miss Rawls) to white-eyed males. Half of the females, as expected, gave 2 : 1 sex-ratios, and daughters from these were again mated to white males. Here once more half of the daughters gave 2 : 1 sex-ratios, but in such cases the sons were nearly all white-eyed and only rarely a red-eyed son appeared, when under ordinary circumstances there should be just as many red sons as white sons. The total output for 11 such females was as follows (Morgan, 1914*b*): white ♀, 457; red ♀, 433; white ♂, 370; red ♂, 2. It is evident from these data that there must be present in the sex-chromosome a gen that causes the death of every male that receives this chromosome, and that this lethal factor lies very close to the factor for white eyes. The linkage of this lethal (now called lethal 1) to various other sex-linked gens was determined (Morgan 1914*b*), and is summarized in table 5. On the basis of these data it is found that the gen lethal 1 lies 0.4 unit to the left of white, or at 0.7.

TABLE 5.—*Summary of linkage data upon lethal 1, from Morgan, 1914b, pp. 81-92.*

Gens.	Total.	Cross-overs.	Cross-over values.
Yellow lethal 1	131	1	0.8
Yellow miniature	131	45	34.4
Lethal 1 white	1,763	7	0.4
Lethal 1 miniature	814	323	39.7
White miniature	994	397	39.9

LETHAL 1a.

In the second generation of the flies bred by Miss Rawls, one female gave (March 1912) only 3 sons, although she gave 312 daughters. It was not known for some time (see lethals 3 and 3*a*) what was the cause of this extreme rarity of sons. It is now apparent, however, that this mother carried lethal 1 in one X and in the other X a new lethal which had arisen by mutation. The new lethal was very close to lethal 1, as shown by the rarity of the surviving sons, which are cross-overs between lethal 1 and the new lethal that we may call lethal 1*a*. There is another class of cross-overs, namely, those which have lethal 1 and get lethal 1*a* by crossing-over. These doubly lethal males must also die, but since they are theoretically as numerous as the males (3) free from both lethals, we must double this number (3 × 2) to get the total number of cross-overs. There were 312 daughters, but as the sons are normally about 96 per cent of the number of the females, we may take 300 as the number of the males which died. There must have been, then, about 2 per cent of crossing-over, which makes lethal 1*a* lie about 2 units from lethal 1. This location of lethal 1*a* is confirmed by a test that Miss Rawls made of the daughters of the high-ratio female. Out of 98 of these daughters none repeated the high sex-ratio and only 2 gave 1 ♀ : 1 ♂ ratios. The two daughters which gave 1 : 1 ratios are cross-overs. There should be an equal number of cross-overs which contain both lethals. These latter would not be distinguishable from the non-cross-over females, each of which carries one or the other lethal. In calculation, allowance can be made for them by doubling the number of observed cross-overs (2 × 2) and taking 98 - 2 as the number of non-cross-overs. The cross-over fraction {6 + 4}/{300 + 96} gives 2.6 as the distance between the

two lethals. Lethal 1*a* is probably to the right of lethal 1 at 0.7 + 2.6 = 3.3.

SPOT.

(Plate II, figures 14 to 17.)

In April 1912 there was found in the stock of yellow flies a male that differed from yellow in that it had a conspicuous light spot on the upper surface of the abdomen (Morgan, 1914*a*). In yellow flies this region is dark brown in color. In crosses with wild flies the spot remained with the yellow, and although some 30,000 flies were raised, none of the gray offspring showed the spot, which should have occurred had crossing-over taken place. The most probable interpretation of spot is that it was due to another mutation in the yellow factor, the first mutation being from gray to yellow and the second from yellow to spot.

Spot behaves as an allelomorph to yellow in all crosses where the two are involved and is completely recessive to yellow, *i. e.*, the yellow-spot hybrid is exactly like yellow. A yellow-spot female, back-crossed to a spot male, produces yellows and spots in equal numbers.

In a cross of spot to black it was found that the double recessive, spot black, flies that appear in F_2 have, in addition to the spot on the abdomen, another spot on the scutellum and a light streak on the thorax. These two latter characters ("dot and dash") are very sharply marked and conspicuous when the flies are young, but they are only juvenile characters and disappear as the flies become older. The spot flies never show the "dot and dash" clearly, and it only comes out when black acts as a

developer. These characters furnish a good illustration of the fact that mutant gens ordinarily affect many parts of the body, though these secondary effects often pass unnoticed.

In the F_2 of the cross of spot by black one yellow black fly appeared, although none are expected, on the assumption that spot and yellow are allelomorphic. Unless due to crossing-over it must have been a mutation from spot back to yellow. Improbable as this may seem to those who look upon mutations as due to losses from the germ-plasm, yet we have records of several other cases where similar mutations "backwards" have taken place, notably in the case of eosin to white, under conditions where the alternative interpretation of crossing-over is excluded.

SABLE.

(Plate I, figure 2.)

In an experiment involving black body-color[3] a fly appeared (July 19, 1912) whose body-color differed slightly from ordinary black in that the trident mark on the thorax was sharper and the color itself was brighter and clearer. This fly, a male, was mated to black females and gave some black males and females, but also some gray (wild body-color) males and females, showing not only that he was heterozygous for ordinary recessive black, but at the same time that his dark color must be due to another kind of black. The gray F_1 flies when mated together gave a series of gray and dark flies in F_2 about as follows: In the females 3 grays to 1 dark; in the males 3 grays to 5 dark in color. The result indicated that the new black color, which we call sable, was

due to a sex-linked factor. It was difficult to discover which of the heterogeneous F_2 males were the new blacks. Suspected males were bred (singly) to wild females, and the F_2 dark males, from those cultures that gave the closest approach to a 2 gray ♀ : 1 gray ♂ : 1 dark ♂, were bred to their sisters in pairs in order to obtain sable females and males. Thus stock homozygous for sable but still containing black as an impurity was obtained. It became necessary to free it from black by successive individual out-crossings to wild flies and extractions.

This account of how sable was purified shows how difficult it is to separate two recessive factors that give closely similar somatic effects. If a character like sable should be present in any other black stock, or if a character like black should be present in sable, very erratic results would be obtained if such stocks were used in experiments, before such a population had been separated into its component races.

Sable males of the purified stock were mated to wild females and gave wild-type (gray) males and females. These inbred gave the results shown in table 6.

No sable females appeared in F_2, as seen in table 6. The reciprocal cross gave the results shown in table 7.

The F_1 males were sable like their mother. The evidence thus shows that sable is a sex-linked recessive character. Our next step was to determine the linkage relations of sable to certain other sex-linked gens, namely, yellow, eosin, cherry, vermilion, miniature, and bar.

TABLE 6.—*P_1 wild* ♀ ♀ × *sable* ♂. *F_1 wild-type* ♀ ♀ × *F_1 wild-type* ♂ ♂.

Reference. [4]	Wild-type ♀.	Wild-type ♂.	Sable ♂.
88 C	218	100	70
143 C	245	108	72
146 C	200	115	82
Total	663	323	224

TABLE 7.—*P_1 sable* ♀ × *wild* ♂ ♂. *F_1 wild-type* ♀ × *F_1 sable* ♂.

Reference.	Wild-type ♀.	Wild-type ♂.	Sable ♀.	Sable ♂.
4 I	10	10	6	10

LINKAGE OF YELLOW AND SABLE.

The factor for yellow body-color lies at one end of the known series of sex-linked gens. As already stated, we speak of this end as the left end of the diagram, and yellow as the zero in locating factors.

When yellow (not-sable) females were mated to (not-yellow) sable males they gave wild-type (gray) daughters and yellow sons. These inbred gave in F_2 two classes of females, namely, yellow and gray, and four classes of males, namely, yellow and sable (non-cross-overs), wild type and the double recessive yellow sable (cross-overs). From off-spring (F_3) of the F_2 yellow sable males by F_2 yellow females, pure stock of the double recessive yellow sable was made up and used in the crosses to test linkage.

In color the yellow sable is quite similar to yellow black, that is, a rich brown with a very dark brown

trident pattern on the thorax. Yellow sable is easier to distinguish from yellow than is yellow black, even when the flies have not yet acquired their adult body-color.

Yellow sable males were bred to wild females and F_1 consisted of wild-type males and females. These inbred gave the results shown in table 8.

TABLE 8.—*P_1 wild ♀ ♀ × yellow sable ♂ ♂. F_1 wild-type ♀ ♀ × F_1 wild-type ♂ ♂.*

Reference.	Wild-type ♀.	Non-cross-over ♂.		Cross-over ♂.		To ma
		Yellow sable.	Wild-type.	Yellow.	Sable.	
44 I	292	110	43	75	36	2
45 I	384	104	58	71	60	2
Total	676	214	101	146	96	5

Some of the F_1 females were back-crossed to yellow sable males and gave the data for table 9.

TABLE 9.—*P_1 wild-type ♀ ♀ × yellow sable ♂ ♂. B. C. F_1 wild-type ♀ × yellow sable ♂ ♂.*

Reference.	Non-cross-overs.		Cross-overs.		Total.	Cr o va
	Wild-type.	Yellow sable.	Yellow.	Sable.		
31 I	108	51	58	56	273	
49 I	265	175	161	169	770	
Total	373	226	219	225	1,043	

In these tables the last column (to the right) shows for each culture the amount of crossing-over between yellow and sable. These values are found by dividing the number of cross-overs by the total number of individuals which might show crossing-over, that is, males only or both males and females, as the case may be. Free assortment would give 50 per cent of cross-overs and absolute linkage 0 per cent of cross-overs. Except where the percentage of crossing-over is very small these values are expressed to the nearest unit, since the experimental error might make a closer calculation misleading.

The combined data of tables 8 and 9 give 686 cross-overs in a total of 1,600 individuals in which crossing-over might occur. The females of table 8 are all of one class (wild type) and are useless for this calculation except as a check upon viability. The cross-over value of 43 per cent shows that crossing-over is very free. We interpret this to mean that sable is far from yellow in the chromosome. Since yellow is at one end of the known series, sable would then occupy a locus somewhere near the opposite end. This can be checked up by finding its linkage relations to the other sex-linked factors.

LINKAGE OF CHERRY AND SABLE.

The origin of cherry eye-color (Plate II, fig. 9) has been given by Safir (Biol. Bull., 1913). From considerations which will be discussed later in this paper we regard cherry as allelomorphic to white in a quadruple allelomorph system composed of white, eosin, cherry, and their normal red allelomorph. Cherry will then occupy the same locus as white, which is one unit to the right of yellow, and will show the same linkage relations to other factors as

does white. A slightly lower cross-over value should be given by cherry and sable than was given by yellow and sable.

When cherry (gray) females were crossed to (red) sable males the daughters were wild type and the sons cherry. Inbred these gave the results shown in table 10.

TABLE 10.—*P_1 cherry ♀♀ × sable ♂♂. F_1 wild-type ♀ × F_1 cherry ♂ ♂.*

Reference.	Wild-type ♀.	Cherry ♀.	Non-cross-over ♂.		Cross-ov ♂.	
			Cherry.	Sable.	Cherry sable.	W t
24 I	94	105	51	42	20	
55 I	101	131	63	52	38	
55′ I	96	94	52	31	29	
Total	291	330	166	125	87	

The percentage of crossing-over between cherry and sable is 42. Since cherry is one point from yellow, this result agrees extremely well with the value 43 for yellow and sable. Since yellow and eosin lie at the left end of the first chromosome, the high values, namely, 43 and 42, agree in making it very probable that sable lies near the other end (*i. e.*, to the right). Sable will lie farther to the right than vermilion, for vermilion has been shown elsewhere to give 33 per cent of crossing-over with eosin. The location of sable to the right of vermilion has in fact been substantiated by all later work.

LINKAGE OF EOSIN, VERMILION, AND SABLE.

Three loci are involved in the next experiment. Since eosin is an allelomorph of cherry, it should be expected to give with sable the same cross-over value as did cherry. When eosin (red) sable females were crossed to (red) vermilion (gray) males, the daughters were wild type and the males were eosin sable. Inbred these gave the classes shown in table 11.

TABLE 11.—P_1 *eosin sable* ♀ × *vermilion* ♂♂. F_1 *wild-type* ♀♀ × F_1 *eosin sable* ♂♂.

Reference.	F_2 females.					
	w^e s		w^e		w^e s	
	Eosin sable.	Wild-type.	Eosin.	Sable.	Eosin sable.	Ver milic
26 I	132	171	113	109	127	163
26′I	96	146	86	78	74	128
Total.	228	317	199	187	201	291

If we consider the male classes of table 11, we find that the smallest classes are eosin vermilion sable and wild type, which are the expected double cross-over classes if sable lies to the right of vermilion, as indicated by the crosses with eosin and with yellow. The classes which represent single crossing-over between eosin and vermilion are eosin vermilion, and sable, and those which represent single crossing-over between vermilion and sable are eosin and vermilion sable. These relations are seen in diagram II.

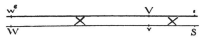
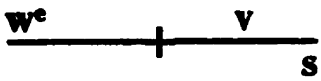


DIAGRAM II.—The upper line represents an X chromosome, the lower line its mate. The cross connecting lines indicate crossing-over between pairs of factors.

Non-cross-overs

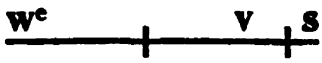


Single cross-overs





Double cross-overs



If we consider the female classes of table 11, we get information as to the cross-over value of eosin and sable, namely, 42 units. The male classes will be considered in connection with the cross that follows.

The next experiment involves the same three gens which now enter in different relations. A double

recessive, eosin vermilion (gray) female was mated to (red red) sable males and gave 202 wild-type[5] females and 184 eosin vermilion males. Two F_1 pairs gave the results shown in table 12 (the four classes of females not being separated).

TABLE 12.—*P_1 eosin vermilion F_1 wild-type ♀ × F_1 eosin vermilion ♂ ♂.*

Reference.	F_2 females.	F_2			
		w^e v		w^e s	
		Eosin Vermilion ♂.	Sable ♂.	Eosin sable ♂.	Vermilion. ♂.
59 C	133	40	33	7	16
61 C	101	34	26	8	11
Total	234	74	59	15	27

If we combine the data for males given in table 12 with those of table 11, we get the following cross-over values. Eosin vermilion, 32; vermilion sable, 12; eosin sable, 41.

LINKAGE OF MINIATURE AND SABLE.

The miniature wing has been described (Morgan, Science, 1911) and the wing figured (Morgan, Jour. Exp. Zool., 1911). The gen for miniature lies about 3 units to the right of vermilion, so that it is still closer to sable than is vermilion. The double recessive, miniature sable, was made up, and males of this stock were bred to wild females (long gray). The

wild-type daughters were back-crossed to double recessive males and gave the results (mass cultures) shown in table 13.

TABLE 13.—*P_1 wild* ♀ ♀ × *miniature sable* ♂ ♂. *B. C. F_1 wild-type* ♀ ♀ × *miniature sable* ♂ ♂.

Reference.	Non-cross-overs.		Cross-overs.		Tota
	Miniature sable.	Wild-type.	Miniature.	Sable.	
38 I	245	283	15	17	56
43 I	191	236	13	18	45
46 I	232	274	24	21	55
Total	668	793	52	56	1,56

Since the results for the male and the female classes are expected to be the same, the sexes were not separated. The combined data give 7 per cent of crossing-over between miniature and sable.

LINKAGE OF VERMILION, SABLE, AND BAR.

Bar eye has been described by Mrs. S. C. Tice (1914). It is a dominant sex-linked character, whose locus, lying beyond vermilion and sable, is near the right end of the chromosome series, that is, at the end opposite yellow.

In the first cross of a balanced series of experiments for the gens vermilion, sable, and bar, vermilion (gray not-bar) entered from one side (♀) and (red) sable bar from the other (♂). The daughters were bar and the sons vermilion. The daughters were back-crossed singly to the triple recessive males vermilion sable (not-bar), and gave the data included

in table 14.

In the second cross, vermilion sable (not-bar) went in from one side (♀) and (red, gray) bar from the other. The daughters were bar and the sons were vermilion sable. Since these sons have the three recessive factors, inbreeding of F_1 is equivalent to a triple back-cross. The results are given by pairs in table 15.

TABLE 14.—*P_1 vermilion ♀ ♀ × sable bar ♂ ♂. B. C. F_1 bar ♀ × vermilion sable ♂ ♂.*

Reference.	v / s B′		v s / B′		v / s B′	
	Ver-milion.	Sable bar.	Ver-milion sable bar.	Wild-type.	Ver-milion bar.	Sable
147 I	81	66	12	15	15	1
148 I	103	108	4	19	11	1
149 I	97	88	10	8	17	1
150 I	95	75	10	11	21	2
151 I	116	96	11	15	23	2
89	89	94	10	19	15	1
90	49	50	4	8	15	1
91	104	88	13	15	12	1
Total.	734	665	74	110	129	13

TABLE 15.—*P_1 vermilion sable ♀ ♀ × bar ♂ ♂. B. C. F_1 bar ♀ × vermilion sable ♂ ♂.*

Reference.	v s / B′	v / s B′	v s / B′

	Ver-milion sable.	Bar	Ver-milion bar.	Sable.	Ver-milion sable bar.	Wild type
105 I	41	75	10	4	5	11
106 I	59	122	16	13	11	17
107 I	92	98	8	12	16	10
116 I	111	149	19	16	20	19
117 I	92	117	16	14	15	18
126 I	96	160	13	13	17	35
127 I	117	124	13	25	24	30
Total	608	845	95	97	108	140

In the third cross, vermilion (gray) bar entered from one side (♀) and (red) sable (not-bar) from the other (♂). The daughters are bar and the sons vermilion bar. The daughters were back-crossed singly to vermilion sable males and gave the data in table 16.

TABLE 16.—*P_1 vermilion bar ♀ ♀ × sable ♂ ♂. B. C. F_1 bar ♀ × vermilion sable ♂ ♂.*

Reference.	v B′ / s	Sable.	v s / B′	Bar.	v / s B′	Sable bar
	Ver-milion bar.		Ver-milion sable.		Ver-milion.	
129 I	132	147	15	15	19	2
130 I	194	168	21	17	28	2
131 I	121	89	10	20	26	1
137 I	139	113	19	12	33	1
138 I	131	128	11	11	28	2

139 I	83	79	4	12	17	1
Total.	800	724	80	87	151	10

In the fourth cross, vermilion sable bar entered from one side, and (red gray not-bar) wild type from the other. The daughters were bar and the sons vermilion sable bar. The daughters were back-crossed singly to vermilion sable males, with the results shown in table 17.

TABLE 17.—P_1 *vermilion sable bar* ♀ ♀ × *wild* ♂ ♂. *B. C.* F_1 *bar* ♀ × *vermilion sable* ♂ ♂.

Reference.	v s B′		v / s B′		v s / B′	
	Vermilion sable bar.	Wild-type	Vermilion.	Sable bar.	Vermilion sable.	Bar
132 I	95	108	10	13	24	22
133 I	112	150	18	16	26	16
134 I	84	95	14	7	15	16
135 I	100	86	16	17	19	22
152 I	73	88	12	8	14	18
153 I	114	138	12	12	17	17
154 I	63	90	10	8	8	15
Total.	641	755	92	81	123	12

In tables 14 to 17 the calculations for the three cross-over values for vermilion, sable, and bar are given for the separate cultures and for the totals. The latter are here repeated.

From—	Vermilion sable.	Sable bar.	Vermilion bar.
Table 14	10	14	24
15	10	13	23
16	9	14	22
17	10	14	23

The results of the different experiments are remarkably uniform. There can be no doubt that the cross-over value is independent of the way in which the experiment is made, whether any two recessives enter from the same or from opposite sides.

TABLE 18.—*Linkage of vermilion, sable, and bar with balanced viability.*

	—	+	— +
Wild-type	755	110	140
Vermilion	734	92	151
Sable	724	97	131
Bar	845	87	126
Vermilion sable	608	80	123
Vermilion bar	800	95	129
Sable bar	665	81	107
Vermilion sable bar	641	74	108
Total	5,772	716	1,015
Percentage	76.7	9.53	13.49

In table 18 the data from each of the four separate experiments have been combined in the manner explained, so that viability is canceled to the greatest

extent. The amount of each kind of cross-over appears at the bottom of the table. The total amount of crossing-over between vermilion and sable is the sum of the single (9.53) and of the double (0.28) cross-overs, which value is 9.8. Likewise the cross-over value for sable bar is 13.49 + 0.28 (= 14), and for vermilion bar is 9.53 + 13.49 (= 23). By means of these cross-over values we may calculate the coincidence involved, which is in this case

$$\frac{0.0028 \times 100}{0.0953 + 0.0028 \times 0.1349 + 0.0028} = 20.8$$

This value shows that there actually occurs only about 21 per cent of the double cross-overs which from the values of the single cross-overs are expected to occur in this section of the chromosome. This is the result which is to be anticipated upon the chromosome view, for if crossing-over is connected with loops of the chromosomes, and if these loops have an average length, then if the chromosomes cross over at one point it is unlikely they will cross over again at another point nearer than the average length of the loop.

The calculation of the locus for sable gives 43.0.

DOT.

In the F_2, from a cross of a double recessive (white vermilion) female by a triple recessive (eosin vermilion pink) male, there appeared, July 21, 1912, three white-eyed females which had two small, symmetrically placed, black, granular masses upon the thorax. These "dots" appeared to be dried exudations from pores. It did not seem possible that such an effect could be inherited, but as this

condition had never been observed before, it seemed worth while to mate the three females to their brothers. In the next generation about 1 per cent of the males were dotted. From these females and males a stock was made up which in subsequent generations showed from 10 to 50 per cent of dot. Selection seemed to have no effect upon the percentage of dot. Although the stock never showed more than 50 per cent of dot, yet it was found that the normal individuals from the stock threw about the same per cent as did those that were dotted, so that the stock was probably genetically pure. The number of males which showed the character was always much smaller than the number of dotted females; in the hatches which produced nearly 50 per cent of dot, nearly all the females but very few of the males were dotted. Quite often the character showed on only one side of the thorax.

Since this character arose in an experiment involving several eye-colors an effort was made by crossing to wild and extracting to transfer the dot to flies normal in all other respects. This effort succeeded only partly, for a stock was obtained which differed from the wild type only in that it bore dot (about 30 per cent) and in that the eyes were vermilion. Several attempts to get the dot separated from vermilion failed. Since this was only part of the preliminary routine work necessary to get a mutant stock in shape for exact experimentation, no extensive records were kept.

LINKAGE OF VERMILION AND DOT.

When a dot male with vermilion eyes was bred to a wild female the offspring were wild-type males and females. These inbred gave the data shown in table

19.

TABLE 19.—*P_1 vermilion dot ♂ × wild ♀ ♀. F_1 wild-type ♀ ♀ × F_1 wild-type ♂ ♂.*

Reference.	F_2 females.	Wild-type ♂.	Vermilion ♂.	Vermilion dot ♂.	Do ♂
7	345	151	130	0	0
8	524	245	220	3	0
Total.	869	396	350	3	0

Only three dot individuals appeared in F_2, but since these were males the result indicates that the dot character is due to a sex-linked gen. These three males had also vermilion eyes, indicating linkage of dot and vermilion. The males show no deficiency in numbers, therefore the non-appearance of the dot can not be due to its being semi-lethal. It appears, therefore, that the expression of the character must depend on the presence of an intensifying factor in one of the autosomes, or more probably, like club, it appears only in a small percentage of flies that are genetically pure for the character.

The reciprocal cross (dot female with vermilion eyes by wild male) was made (table 20). The daughters were wild type and the sons vermilion. Not one of the 272 sons showed dot. If the gen is sex-linked the non-appearance of dot in the F_1 males can be explained on the ground that males that are genetically dot show dot very rarely, or that its appearance is dependent upon the intensification by an autosomal factor of the effect produced by the sex-linked factor for dot.

TABLE 20.—P_1 *vermilion dot* ♀ × *wild* ♂.

First generation.			Se			
Reference.	Wild-type ♀.	Ver-milion ♂.	Reference.	Wild-type ♂.	Wild-type ♀.	1
137 C.	44	45	19	211	198	
138 C.	77	62	22	266	220	
	124	124	28	143	149	
	57	41	Total.	620	567	
Total.	291	272				

The F_2 generation is given in table 20. The dot reappeared in F_2 both in females and in males, but instead of appearing in 50 per cent of both sexes, as expected if it is simply sex-linked, it appeared in 4.0 per cent in the females and in only 0.4 per cent in the males. The failure of the character to be fully realized is again apparent, but here, where it is possible for it to be realized equally in males and females, we find that there are 50 females with dot to only 4 dot males. This would indicate that the character is partially "*sex-limited*" (Morgan, 1914*d*) in its realization. The dot appeared only in flies with vermilion eyes, indicating extremely strong linkage between vermilion and dot.

The evidence from the history of the stock, together with these experiments, shows that the character resembles club (wing) in that it is not expressed somatically in all the flies which are homozygous for it. In the case of club we were fortunate enough to find a constant feature which we could use as an index, but, so far as we have been able to see, there is no such constant accessory character in the case of

the dot. Unlike club, dot is markedly sex-limited in its effect; that is, there is a difference of expression of the gen in the male and female. This difference recalls the sexual dimorphism of the eosin eye.

BOW.

In an F_2 generation from rudimentary males by wild females there appeared, August 15, 1912, a single male whose wings instead of being flat were turned down over the abdomen (fig. c). The curvature was uniform throughout the length of the wing. A previous mutation, arc, of this same type had been found to be a recessive character in the second group. The new mutation, bow, is less extreme than arc and is more variable in the amount of curvature. When the bow male was mated to wild females the offspring had straight wings.

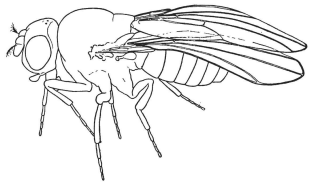


FIG. C.—Bow wing.

TABLE 21.—*P_1 bow* ♂♂ × *wild* ♀♀.

First generation.			Second generation.			
Reference.	Wild-type ♀♀.	Wild-type	Reference.	Wild-type ♀♀.	Wild-type ♂♂.	B ○
169 C.	17	17	18 I.	193	145	
			21 I	182	100	
			Total.	375	245	1

The F_2 ratio in table 21 is evidently the 2:1:1 ratio typical of sex-linkage, but with the bow males running behind expectation. This deficiency is due in part to viability but more to a failure to recognize all the bow-winged individuals, so that some of them were classified among the not-bow or straight wings. In favor of the view that the classification was not strict is the fact that the sum of the two male classes about equals the number of the females.

BOW BY ARC.

When this mutant first appeared its similarity to arc led us to suspect that it might be arc itself or an allelomorph of arc. It was bred, therefore, to arc. The bow male by arc females gave straight (normal) winged males and females. The appearance of straight wings shows that bow is not arc nor allelomorphic to arc. When made later, the reciprocal cross of bow female by arc male gave in F_1 straight-winged females but bow males. This result is in accordance with the interpretation that bow is a sex-linked recessive. Further details of these last two experiments may now be given. The F_1 (wild-type) flies from bow male by arc female were inbred. The data are given in table 22.

TABLE 22.—*P_1 bow* ♂ × *arc* ♀.

First generation.			Second generation.		
Reference.	Wild-type ♀ ♀.	Wild-type ♂ ♂.	Reference.	Straight.	Not-straigł
71 C.	48	43	71 C.	179	133
75 C.	28	27			

Total.	76	70			

Bow and arc are so much alike that they give a single rather variable phenotypic class in F_2. Therefore the F_2 generation is made up of only two separable classes—flies with straight wings and flies with not-straight wings. The ratio of the two should be theoretically 9:7, which is approximately realized in 179:133.

If the distribution of the characters according to sex is ignored, the case is similar to the case of the two white races of sweet peas, which bred together gave wild-type or purple peas in F_1 and in F_2 gave 9 colored to 7 white. If sex is taken into account, the theoretical expectation for the F_2 females is 6 straight to 2 arc, and for the F_2 males 3 straight to 1 arc to 3 bow to 1 bow-arc.

The F_1 from bow females by arc male and their F_2 offspring are given in table 23.

TABLE 23.—*P_1 bow* ♀ × *arc* ♂.

First generation.			Second generation.		
Reference.	Wild-type ♀ ♀.	Bow ♂ ♂.	Reference.	Straight.	Not-straight
72 C.	22	19	3 I.	56	69
73 C.	12	10	3.1 I.	46	62
5 I.	22	21	5 I.	56	68
74 C.	56	52	5.1 I.	90	108
Total.	112	102	Total.	248	307

In this case the F_2 expectation is 6 straight to 10 not-

straight. Since the sex-linked gen bow entered from the female, half the F_2 males and females are bow. The half that are not-bow consist of 3 straight to 1 arc, so that both in the female classes and in the male classes there are 3 straight to 5 not-straight or in all 6 straight to 10 not-straight. The realized result, 248 straight to 307 not-straight, is more nearly a 3:4 ratio, due probably to a wrong classification of some of the bow as straight.

LEMON BODY-COLOR.

(Plate I, figure 3.)

A few males of a new mutant with a lemon-colored body and wings appeared in August 1912. The lemon flies (Plate II, fig. 3) resemble quite closely the yellow flies (Plate II, fig. 4). They are paler and the bristles, instead of being brown, are black. These flies are so weak that despite most careful attention they get stuck to the food, so that they die before mating. The stock was at first maintained in mass from those cultures that gave the greatest percentage of lemon flies. In a few cases lemon males mated with their gray sisters left offspring, but the stock obtained in this way had still to be maintained by breeding heterozygotes, as stated above. But from the gray sisters heterozygous for lemon (bred to lemon males) some lemon females were also produced.

LINKAGE OF CHERRY, LEMON, AND VERMILION.

In order to study the linkage of lemon, the following experiment was carried out. Since it was impracticable to breed directly from the lemon flies, virgin females were taken from stock throwing

lemon, and were mated singly to cherry vermilion males. Only a few of the females showed themselves heterozygous for lemon by producing lemon as well as gray sons. Half the daughters of such a pair are expected to be heterozygous for lemon and also for cherry and vermilion, which went in from the father. These daughters were mated singly to cherry vermilion males, and those that gave some lemon sons were continued, and are recorded in table 24. The four classes of females were not separated from each other, but the total of females is given in the table.

TABLE 24.—*P_1 lemon (het.)* ♀ × *cherry vermilion* ♂ ♂. *F_1 wild-type* ♀ × *cherry vermilion* ♂ ♂.

Females.	$\frac{w^c \quad v}{l_m}$		$\frac{w^c}{+}$ $\frac{l_m}{v}$		$\frac{w^c}{l_m}$	
	Cherry ver-milion.	Lemon.	Cherry lemon.	Ver-milion.	Cherry	
71	42	19	2	6	3	
88	26	19	2	8	8	
36	28	7	0	2	1	
51	12	22	0	4	4	
98	29	35	0	8	5	
47	17	11	0	1	3	
46	23	20	1	6	5	
437	177	133	5	35	29	

There are three loci involved in this cross, namely, cherry, lemon, and vermilion. Of these loci two were known, cherry and vermilion. The data are consistent with the assumption that the lemon locus is between

cherry and vermilion, for the double cross-over classes (the smallest classes) are cherry lemon vermilion and wild type. The number of single cross-overs between cherry and lemon and between lemon and vermilion are also consistent with this assumption. Since lemon flies fail to emerge successfully, depending in part upon the condition of the bottle, the classes involving lemon are worthless in calculating crossing-over and are here ignored. In other words, lemon may be treated as though it did not appear at all, *i. e.*, as a lethal. The not-lemon classes—cherry, vermilion, cherry vermilion, and wild type—give the following approximate cross-over values for the three loci involved: Cherry lemon, 15; lemon vermilion, 12; cherry vermilion, 27. The locus of lemon, calculated by interpolation, is at about 17.5.

LETHAL 2.

In September 1912 a certain wild female produced 78 daughters and only 16 sons (Morgan, 1914*b*); 63 of these daughters were tested and 31 of them gave 2 females to 1 male, while 32 of them gave 1:1 sex-ratios. This shows that the mother of the original high sex-ratio was heterozygous for a recessive sex-linked lethal. In order to determine the position of this lethal, a lethal-bearing female was bred to an eosin (or white) miniature male, and those daughters that were heterozygous for eosin, lethal, and miniature were then back-crossed to eosin miniature males. The daughters that result from such a cross give only the amount of crossing-over between eosin and miniature (as 29.7), but the males give the cross-over values for eosin lethal (9.9), lethal miniature (15.4), and eosin miniature (25.1). The data for this cross are given in table 25.

TABLE 25.—*Total data upon linkage of eosin, lethal 2, and miniature, from Morgan, 1914b.*

Females.					
Total.	Cross-overs.	Cross-over value.	$\frac{w^e \quad m}{l_2}$	$\frac{w^e \; l_2}{m}$	$\frac{w^e}{l}$
15,904	4,736	29.7	5,045	653	1,

A similar experiment, in which eosin and vermilion were used instead of eosin and miniature, is summarized in table 26.

TABLE 26.—*Total data upon the linkage of eosin, lethal 2, and vermilion, from Morgan, 1914b.*

Females.					
Total.	Cross-overs.	Cross-over value.	$\frac{w^e \quad v}{l_2}$	$\frac{w^e \; l_2}{v}$	$\frac{v}{}$
2,656	729	27.5	902	124	

Considerable data in which lethal was not involved were also obtained in the course of these experiments and are included in the summary of the total data given in table 27.

TABLE 27.—*Summary of all data upon lethal 2, from Morgan, 1914b.*

Gens.	Total.	Cross-overs.	Cross-over values.
White lethal 2	8,011	767	9.6
White vermilion	6,023	1,612	26.8
White miniature	36,021	11,048	30.7
Lethal 2 vermilion	1,400	248	17.7
Lethal 2 miniature	6,752	1,054	15.4

The amount of crossing-over between eosin and lethal is about 10 per cent and the amount of crossing-over between lethal and miniature is about 18 per cent. Since the amount of crossing-over between eosin and miniature is over 30 per cent, the lethal factor must lie between eosin and miniature, somewhat nearer to eosin. It is impossible at present to locate lethal 2 accurately because of a real discrepancy in the data, which makes it appear that lethal 2 extends for a distance of about 5 units along the chromosome from about 10 to about 15. Work is being done which it is hoped will make clear the reason for this. For the present we may locate lethal 2 at the midpoint of its range, or at 12.5.

CHERRY.

(Plate II, figure 9.)

The origin of the eye-color cherry has been given by Safir (Biol. Bull., 1913).

Cherry appeared (October 1912) in an experiment involving vermilion eye-color and miniature wings.

This is the only time the mutant has ever come up, and although several of this mutant (males) appeared in Safir's experiment, they may have all come from the same mother. It is probable that the mutation occurred in the vermilion stock only a generation or so before the experiment was made, for otherwise cherry would be expected to be found also in the vermilion stock from which the mothers were taken; however, it was not found.

A SYSTEM OF QUADRUPLE ALLELOMORPHS.

Safir has described crosses between this eye-color and red, white, eosin, and vermilion. We conclude for reasons similar to those given by Morgan and Bridges (Jour. Exp. Zool., 1913) for the case of white and eosin, that cherry is an allelomorph of white and of eosin. This is not the interpretation followed in Safir's paper, where cherry is treated as though absolutely linked to white or to eosin. Both interpretations give, however, the same numerical result for each cross considered by itself. Safir's data and those which appear in this paper show that white, eosin, cherry, and a normal (red) allelomorph form a system of quadruple allelomorphs. If this interpretation is correct, then the linkage relations of cherry should be identical with those of white or of eosin.

LINKAGE OF CHERRY AND VERMILION.

The cross-over value for white (eosin) and vermilion, based on a very large amount of data, is about 31 units. An experiment of our own in which cherry was used with vermilion gave a cross-over value of 31 units, which is a close approximation to the cross-over value of white and vermilion. The cross which

gave this data was that of a cherry vermilion (double recessive) male by wild females. The F_1 wild-type flies inbred gave a single class of females (wild-type) and the males in four classes which show by the deviation from a 1:1:1:1 ratio the amount of crossing-over involved.

In one of the F_2 male classes of table 28 the simple eye-color cherry appeared for the first time (since the original mutant was vermilion as well as cherry). Safir has recorded a similar cross with like results.

TABLE 28.—*P_1 cherry vermilion* ♂ ♂ × *wild* ♀ ♀. *F_1 wild-type* ♀ ♀ × *F_1 wild-type* ♂ ♂.

Reference.	Wild-type ♀♀.	Non-cross-over ♂.		Cross-over ♂.	
		Cherry vermilion.	Wild-type.	Cherry.	Ver-milion.
160 C	188	57	61	32	34
161 C	256	85	93	40	52
162 C	251	78	78	20	37
163 C	229	76	95	34	33
Total	924	296	327	126	156

Some cherry males were bred to wild females. The F_1 wild-type males and females inbred gave the results shown in table 29. Some of the cherry males thus produced were bred to their sisters. Cherry females as well as males resulted; and it was seen that the eye-color is the same in the males and females, in contradistinction to the allelomorph eosin, where there is a marked bicolorism (figs. 7, 8, Plate II). The cherry eye-color is almost identical with that of the eosin female, but is perhaps slightly more translucent

and brighter.

TABLE 29.—*P_1 cherry* ♂ ♂ × *wild* ♀ ♀. *F_1 wild-type* ♀ ♀ × *F_1 wild-type* ♂ ♂.

Reference.	Wild-type ♀.	Wild-type ♂.	Cherry ♂.
15 I	266	120	100

COMPOUNDS OF CHERRY.

In order to examine the effect of the interaction of cherry and white in the same individual (*i. e.*, white-cherry compound) cherry females were crossed to white males. This cross should give white-cherry females and cherry males. These white-cherry females were found (table 30) to be very much lighter than their brothers, the cherry males. The color of the pure cherry females and males is the same, but the substitution of one white for one cherry lowers the eye-color of the female below that of the cherry male. In eosin the white also lowers the eye-color of the compound female about in the same proportion as in the case of cherry. In the eosin the female starts at a higher degree of pigmentation than the male and dilution seems to bring her down to the level of the male. But this coincidence of color between eosin male and white-eosin compound female is probably without significance, as shown by the results with cherry.

TABLE 30.—*P_1 cherry* ♀♀ × *white* ♂♂.

Reference.	First generation.	
	White-cherry compound ♀.	Cherry ♂.

9 M	321	302

Eosin-cherry compound was also made. An eosin female was mated to a cherry male. The eosin-cherry daughters were darker than their eosin brothers. Inbred they gave the results shown in table 31.

TABLE 31.—*P_1 eosin* ♀ × *cherry* ♂.

First generation.			Second genera	
Reference.	Eosin-cherry compound ♀♀.	Eosin ♂♂.	Reference.	Eosin and eosin-cherry compound ♀♀.
43C	71	58	1I	154
			2I	174
				328

Although in the F_2 results there are two genotypic classes of females, namely, pure eosin and eosin-cherry compound, the eye-colors are so nearly the same that they can not be separated. The two classes of males can be readily distinguished; of these, one class, cherry, has the same color as the females, while the other class, eosin, is much lighter. Such an F_2 group will perpetuate itself, giving one type of female (of three possible genotypic compositions, but somatically practically homogeneous) and two types of males, only one of which is like the females.

FUSED.

In a cross between purple-eyed[6] males and black females there appeared in F_2 (Nov. 4, 1912) a male having the veins of the wing arranged as shown in text-figure D *b*. It will be seen that the third and the

fourth longitudinal veins are fused from the base to and beyond the point at which in normal flies the anterior cross-vein lies. The cross-vein and the cell normally cut off by it are absent. There are a number of other features (see fig. D *c*) characteristic of this mutation: the wings are held out at a wide angle from the body, the ocelli are very much reduced in size or entirely absent, the bristles around the ocelli are usually small. The females are absolutely sterile, not only with their own, but with any males.

Fused males by wild females gave wild-type males and females. Inbred these gave the results shown in table 32. The fused character reappeared only in the F_2 males, showing that it is a recessive sex-linked character.

TABLE 32.—P_1 *fused* ♂ × *wild* ♀♀.

First generation.			Second generation.			
Reference.	Wild-type ♀♀.	Wild-type ♂♂.	Reference.	Wild-type ♀♀.	Wild-type ♂♂.	F ♂
4I	66	43	190C	258	96	1
			14I	239	105	
			Total	497	201	2

The reciprocal cross was tried many times, but is impossible, owing to the sterility of the females. Since the fused females are sterile to fused males, the stock is kept up by breeding heterozygous females to fused males.

By means of the following experiments the position of fused in the X chromosome was determined. A preliminary test was made by mating with eosin, whose factor lies near the left end of the X

chromosome series.

LINKAGE OF EOSIN AND FUSED.

Fused (red-eyed) males mated to eosin (not-fused) females gave wild-type daughters and eosin sons, which inbred gave the classes shown in table 33.

TABLE 33.—*P_1 eosin* ♀♀ × *fused* ♂♂. *F_1 wild-type* ♀♀ × *F_1 eosin* ♂♂.

Reference.	Females.	Non-cross-over ♂♂.		Cross-over ♂♂.		T n
		Eosin.	Fused.	Eosin fused.	Wild-type.	
56I	496	131	113	82	104	

The data give 43 per cent of crossing-over, which places fused far to the right or to the left of eosin. The latter position is improbable, since eosin already lies very near the extreme left end of the known series. Therefore, since 43 per cent would place the factor nearly at the right end of the series, the next step was to test its relation to a factor like bar that lies at the right end of the chromosome. By mating to bar alone we could only get the linkage to bar without discovering on which side of bar the new factor lies, but by mating to a fly that carries still another sex-linked factor, known to lie to the left of bar, the information gained should show the relative order of the factors involved. Furthermore, since, by making a back-cross, both males and females give the same kind of data (and need not be separated), the experiment was made in this way. In order to have material for such an experiment double mutant

stocks of vermilion fused and also of bar fused were made up.

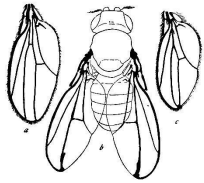


Fig. D.—*a*, normal wing; *b* and *c*, fused wings. *c* shows a typical fused wing. The most striking feature is the closure of the cell between the third and fourth longitudinal veins with the elimination of the cross-vein; the veins at the base of the wing differ from those in the normal shown in *a*. *b* shows the normal position in which the fused wings are held. The fusion of the veins in *b* is unusually complete.

LINKAGE OF VERMILION, BAR, AND FUSED.

Males from the stock of (red) bar fused were mated to vermilion (not-bar, not-fused) females, and

produced bar females and vermilion males. The bar F_1 daughters were back-crossed to vermilion fused males and produced the classes of offspring shown in table 34.

TABLE 34.—P_1 *vermilion* ♀ ♀ × *bar fused* ♂ ♂. *B. C.* F_1 *bar* ♀ × *vermilion fused* ♂ ♂.

Reference.	v / B′ f		v + B′ f		v f / + B′	
	Ver-milion.	Bar fused.	Ver-milion bar fused.	Wild-type.	Ver milion fused.	Ba
140 I	137	130	35	40	5	8
141 I	144	137	38	41	4	2
142 I	153	120	43	58	6	7
143 I	153	92	44	41	3	7
145 I	69	62	29	19	1	.
146 I	96	103	30	34	7	3
156 I	62	45	25	27	1	4
157 I	93	57	11	31	2	2
Total.	907	746	255	291	29	33

The data show that the factor for fused lies about 3 units to the right of bar. This is the furthest point yet obtained to the right. The reasons for locating fused to the right of bar are that, if it occupies such a position, then the double cross-over classes (which are expected to be the smallest classes) should be vermilion bar and fused, and these are, in fact, the smallest classes. The order of factors is, then, vermilion, bar, fused. This order is confirmed by the result that the number of cross-overs between fused

and vermilion is greater than that between bar and vermilion.

In order to obtain data to balance viability effects, the following experiment was made:

Vermilion (not-bar) fused males were bred to (red) bar (not-fused) females. The daughters and sons were bar. The daughters were back-crossed, singly, to vermilion fused males and gave the results shown in table 35. Each female was also transferred to a second culture bottle, so that for each female there are two broods given consecutively (82, 82′, etc.) in table 35.

The results given by the two broods of the same female are similar. The values are very near to those given in the last experiment, and confirm the conclusions there drawn. The combined data give the results shown in table 36.

TABLE 35.—*P_1 bar ♀ ♀ × vermilion fused ♂ ♂. B. C. F_1 bar ♀ × vermilion fused ♂ ♂.*

Reference.	v f$_u$ / B′		v B′ / f$_{sd}$		v / B′	f
	Ver-milion fused.	Bar.	Ver-milion bar.	Fused.	Ver-milion.	
82	165	165	63	57	8	
82′	104	87	26	24	..	
83	128	164	51	39	6	
83′	100	94	28	30	4	
89	85	105	23	24	5	
89′	78	91	21	27	1	

90	86	85	30	28	5
90′	33	38	22	14	4
91	125	107	41	31	1
91′	91	95	31	25	5
92	109	136	41	24	4
92′	100	105	29	29	..
93	75	67	19	20	..
93′	68	94	31	17	1
94	84	96	31	35	8
94′	61	73	20	22	5
95	84	102	27	26	3
96	144	148	43	34	1
97	81	96	25	20	5
98	107	112	39	33	1
Firsts	1,273	1,383	433	371	47
Seconds	635	677	208	188	20
Total.	1,908	2,060	641	559	67

TABLE 36.—*Linkage of vermilion, bar, and fused with balanced viability.*

	$\frac{v\ B'\ f_u}{+\ +\ +}$	$\frac{v}{+\ B'\ f_u}$	$\frac{v\ B'}{+\ +\ f_u}$
	5,621	1,756	175
Percentage	74.3	23.19	2.31

Some additional data bearing on the linkage of vermilion and fused were obtained. Males of (red) fused stock were bred to vermilion (not-fused) females, and gave wild-type females and vermilion

males, which inbred gave the results shown in table 37.

The percentage of cross-overs between vermilion and fused is here 27, which is in agreement with the 26 per cent of the preceding experiment.

The converse experiment, namely, red (not-fused) females by vermilion fused males also gave, when the wild-type daughters were back-crossed to vermilion fused males, a linkage value of 27 units. Two 10-day broods were reared from each female. The data given in table 38 show that the percentage of crossing-over does not change as the flies get older. The locus of fused on the basis of all of the data is at 59.5.

TABLE 37.—P_1 vermilion ♀ ♀ × fused ♂ ♂. F_1 wild-type ♀ ♀ × F_1 vermilion ♂ ♂.

Reference.	Females.	Non-cross-over ♂ ♂.		Cross-over ♂
		Vermilion.	Fused.	Vermilion fused.
79 I	299	93	96	37
80 I	245	93	60	28
81 I	263	101	63	22
Total.	807	287	219	87

TABLE 38.—P_1 wild ♀ ♀ × vermilion fused ♂ ♂. F_1 wild-type ♀ × F_1 wild-type ♂ ♂.

Reference.	Females.	Non-cross-over ♂ ♂.	Cross-over ♂

		Vermilion fused.	Wild-type.	Vermilion.	F
52	96	25	30	16	
52′	176	59	64	24	
53	60	20	22	9	
53′	76	21	27	11	
54	88	35	38	14	
54′	60	22	20	8	
57	61	22	20	7	
57′	170	47	54	24	
58	128	37	55	14	
58′	144	38	64	16	
Firsts	433	139	165	60	
Seconds	626	187	229	83	
Total	1,059	326	394	143	1

FORKED.

On November 19, 1912 there appeared in a stock of a double recessive eye-color, vermilion maroon, a few males which showed a novel form of the large bristles (macrochætæ) upon the head and thorax. In this mutation (text-fig. E) the first of several which affect the shape and distribution of the bristles, the macrochætæ, instead of being long, slender, and tapered (see Plate 1, fig. I), are greatly shortened and crinkled as though scorched. The ends are forked or branched, bent sharply, or merely thickened. The bristles which are most distorted are those upon the scutellum, where they are sometimes curled together into balls.

LINKAGE OF VERMILION AND FORKED.



FIG. E.—Forked bristles.

Since forked arose in vermilion stock, the double recessive for these two sex-linked factors could be used in testing the linkage relations of the mutation. Vermilion forked males were crossed to wild females and gave wild-type males and females, which inbred gave in F_2 the results shown in table 39. Forked reappeared only in the males in the following proportion: not-forked ♀, 742; not-forked ♂, 346; forked ♂, 301. The result shows that the character is a sex-linked recessive.

TABLE 39.—*P_1 wild* ♀ ♀ × *vermilion-forked* ♂ ♂. *F_1 wild-type* ♀ ♀ × *F_1 wild-type* ♂ ♂.

Reference.	Wild-type ♀♀.	Non-cross-over ♂ ♂.		Cross-over ♂ ♂	
		Vermilion forked.	Wild-type.	Vermilion.	Fork
9 I	366	113	123	49	41
11 I	376	116	150	42	31
Total.	742	229	273	91	72

In table 39 vermilion forked and wild-type are non-

cross-overs, and vermilion and forked are cross-overs, giving a cross-over value of 25 units. The locus, therefore, is 25 units to the right or to the left of vermilion, that is, either about 58 or 8 units from the yellow locus.

LINKAGE OF CHERRY AND FORKED.

Forked males were crossed to cherry females (cherry has the same locus as white, which is about 1 unit from yellow) and gave wild-type females and cherry males. These gave in F_2 the results shown in table 40. The non-cross-overs (cherry and forked) plus the cross-overs (cherry forked and wild type) divided into the cross-overs give a cross-over value of 46 units, which shows that the locus lies to the right of vermilion, because if it had been to the left, the value would have been 8 (*i. e.*, 33-25) instead of $33+25=58$. The difference between 58 and 46 is due to the expected amount of double crossing-over. In fact, for a distance as long as 58 an almost independent behavior of linked gens is to be expected.

TABLE 40.—*P_1 cherry ♀ ♀ × forked ♂ ♂. F_1 wild-type ♀ ♀ × F_1 cherry ♂ ♂.*

Reference.	Females.		Non-cross-over ♂ ♂.		Cross-o ♂
	Cherry.	Wild-type.	Cherry.	Forked.	Cherry forked.
25	129	145	73	70	65
25′	167	148	74	82	66
36	96	88	52	52	35
36′	57	76	41	32	24

84	76	86	40	34	38
84′	62	71	24	39	25
85	114	86	43	78	41
85′	98	95	48	63	52
86	307	323	152	144	118
87	351	341	183	213	160
88	244	246	142	142	107
Total.	1,701	1,705	872	949	731

LINKAGE OF FORKED, BAR, AND FUSED.

This value of 58 gave the furthest locus to the right obtained up to that time, since forked is slightly beyond rudimentary. Later, the locus for bar-eye was found still farther to the right, and the locus for fused even farther to the right than bar. A cross was made involving these three gens. A forked (not-bar) fused male was bred to a (not-forked) bar (not-fused) female and gave bar females and males. The F_1 females were back-crossed singly to forked fused males with the result shown in table 41.

TABLE 41.—*P_1 bar* ♀ ♀ × *forked fused* ♂ ♂. *B. C. F_1 bar* ♀ × *forked fused* ♂ ♂.

Reference.	Forked fused.	Bar.	Forked bar.	Fused.	Forked.	fu
163	45	55	..	1	4	
164	71	90	..	..	4	
165	97	106	..	..	2	

11	21	35	..	..	1
33	15	23	..	..	..
Total.	250	309	..	1	11

The same three points were combined in a different way, namely, by mating forked females to bar fused males. The bar daughters were back-crossed to forked fused males and gave the results shown in table 42.

TABLE 42.—*P_1 forked ♀ ♀ × bar fused ♂ ♂. B.C. F_1 bar ♀ × forked fused ♂ ♂.*

Reference.	f B′		f B′ f_u		f B′	
	Forked.	Fused bar.	Forked bar fused.	Wild-type.	Forked fused.	B
158	131	124	1	..	3	
159	31	45	..	..	..	
160	29	23	..	..	1	
161	24	11	1	..	..	
162	96	91	2	..	1	
Total.	311	294	4	..	5	

By combining the results of tables 41 and 42 data are obtained for cross-over values from which (by balancing the inviable classes, as explained in table 43) the element of inviability is reduced to a minimum.

TABLE 43.

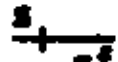
				
	1,164	5	32	0
Per cent.	96.9	0.42	2.7	0

The linkages involved in these data are very strong. The cross-overs between forked and bar number only 5 in a total of 1,201, which gives less than 0.5 per cent of crossing-over. There are 32 cross-overs or 2.7 per cent between bar and fused. The value for forked fused is the sum of the two other values, or 3.1 per cent.

LINKAGE OF SABLE, RUDIMENTARY, AND FORKED.

Rudimentary, forked, bar, and fused form a rather compact group at the right end of the chromosome, as do yellow, lethal 1, white, abnormal, etc., at the zero end. The following two experiments were made to determine more accurately the interval between rudimentary and the other members of this group. A sable rudimentary forked male mated to a wild female gave wild-type sons and daughters. These inbred give the results shown in table 44.

TABLE 44.—*P_1 sable rudimentary forked* ♂ × *wild* ♀. *F_1 wild-type* ♀ × *F_1 wild-type* ♂ ♂.

Reference.	Wild-type ♀♀.				
		Sable rudimentary forked.	Wild-type.	Sable.	Rudimentary forked.

264	98	28	17	2	5
265	97	29	54	4	9
266	114	42	49	11	11
Total	309	99	120	17	25

There were 265 males, of which 42 were cross-overs between sable and rudimentary and 4 between rudimentary and forked. The values found are: sable rudimentary, 16; rudimentary forked, 1.5; sable forked, 17.

LINKAGE OF RUDIMENTARY, FORKED, AND BAR.

The three gens, rudimentary, forked, and bar, form a very compact group. A rudimentary forked male was crossed to bar females and the daughters (bar) were back-crossed singly to rudimentary forked males, the results being shown in table 45.

TABLE 45.—*P_1 rudimentary forked ♂ × bar ♀. B.C. F_1 bar ♀ × rudimentary forked ♂ ♂.*

Reference.	$\frac{r\ f}{B'}$		$\frac{r\ B'}{+\ f}$		$\frac{r\ f}{\ }$
	Rudimentary forked.	Bar.	Rudimentary bar.	Forked.	Rudimentary forked bar.
267	56	104	..	2	1
268	82	86	1	2	..
269	68	101	..	..	..
Total	206	291	1	4	1

The cross-over values are: rudimentary forked, 1; forked bar, 0.6; rudimentary bar, 1.6. The order of

factors is rudimentary, forked, bar. On the basis of the total data the locus of forked is at 56.5.

SHIFTED.

Shifted appeared (January 1913) in a stock culture of vermilion dot. The chief characteristic of this mutant is that the third longitudinal vein (see text-fig. F) does not reach the margin as it does in the normal fly. The vein is displaced toward the fourth throughout its length, and only very rarely does it extend far enough to join the marginal vein. The cross-vein between the third and the fourth veins is often absent because of the shifting. The flies themselves are smaller than normal. The wings are held out from the body at a wide angle. The two posterior bristles of the scutellum are much reduced in size and stick straight up—a useful landmark by which just-hatched shifted flies may be recognized, even though the wings are not expanded.

LINKAGE OF SHIFTED AND VERMILION.

Since shifted arose in vermilion, the double recessive shifted vermilion was available for the following linkage experiment: shifted vermilion males by wild females gave wild-type males and females which inbred gave the data shown in table 46.

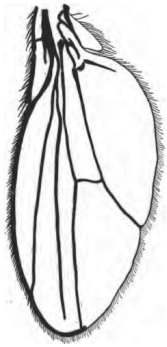


FIG. F.—Shifted venation. The third longitudinal vein is shifted toward the fourth and fails to reach the margin. Cross-vein between third and fourth longitudinal veins is lacking.

Disregarding the eye-color, the following is a summary of the preceding results: wild-type ♀, 1,001; wild-type ♂, 437; shifted ♂, 328. The result shows that shifted is a sex-linked recessive. The data of table 46 show that the locus of shifted lies about 15 units on one side or the other of vermilion, which from the calculated position of vermilion at 33 would give a position for shifted at either 18 or 48 from yellow.

TABLE 46.—*P_1 shifted vermilion* ♂ ♂ × *wild* ♀ ♀. *F_1 wild-type* ♀ × *F_1 wild-type* ♂ ♂.

Reference.	Females.	Non-cross-over ♂ ♂.		Cross-over ♂	
		Shifted vermilion.	Wild-type.	Shifted.	Verr
13	345	79	115	8	
29	68	20	32	3	
30	191	37	54	5	
31	151	41	65	17	
33	133	49	40	4	
34	113	56	59	9	
Total.	1,001	282	365	46	

LINKAGE OF SHIFTED, VERMILION, AND BAR.

In order to determine on which side of vermilion shifted lies, a shifted vermilion (not-bar) female was crossed to a (not-shifted red) bar male. Three factors are involved, of which one, bar, is dominant. The shifted vermilion (not-bar) stock is a triple recessive, and a three-point back-cross was therefore possible. The daughters were bar and the sons were shifted vermilion (the triple recessive). Inbred these gave the results shown in table 46. The smallest classes (double cross-overs) are shifted and vermilion bar, which places shifted to the left of vermilion at approximately 17.8 units from yellow.

TABLE 47.—*P_1 shifted vermilion ♀ × bar ♂ ♂. F_1 bar ♀ × F_1 shifted vermillion ♂ ♂.*

Reference.	$\frac{s_h \ v}{B'}$	$\frac{s_h \ B'}{v}$	$s_h \ v \ B$

	Shifted vermilion.	Bar.	Shifted bar.	Vermilion	Shifted vermilion bar.	W ty
65	56	108	15	20	8	3

The stock of shifted has been thrown away, since too great difficulty was encountered in maintaining it, because, apparently, of sterility in the females.

LETHALS SA AND SB.

The first lethal found by Miss Rawls was in a stock that had been bred for about 3 years. While there was no *a priori* reason that could be given to support the view that lethal mutations would occur more frequently among flies inbred in confinement, nevertheless a hundred females from each of several newly caught and from each of several confined stocks were examined for lethals (Stark, 1915). No lethals were found among the wild stocks, but 4 were found among the confined stocks. Whether this difference is significant is perhaps open to question. The first lethal was found in January 1913, in a stock that had been caught at Falmouth, Massachusetts, in 1911, and had been inbred for 18 months, *i.e.*, for about 50 generations. This lethal, lethal *sa*, was recessive and behaved like the former lethals, being transmitted by half the females and causing the death of half the sons. The position of this lethal to the X chromosome was found as follows, by means of the cross-over value white lethal *sa*. Lethal-bearing females were mated to white males and the lethal-bearing daughters were again mated to white males. The white sons (894) were non-cross-overs and the red sons (256) were cross-overs. The percentage of crossing-over is 22.2. A correction of 0.4 unit should

be added for double crossing-over, indicating that the locus is 22.6 units from white, or at 23.7.

When the work on lethal *sa* had been continued for 3 months, the second lethal, lethal *sb*, was found (April 1913) to be present in a female which was already heterozygous for lethal *sa*. It is probable that this second lethal arose as a mutation in the father, and that a sperm whose X carried lethal *sb* fertilized an egg whose X carried lethal *sa*. As in the cases of lethals 1 and 1*a* and lethals 3 and 3*a*, this lethal, lethal *sb*, was discovered from the fact that only a very few sons were produced, there being 82 daughters and only 3 sons. If, as in the other cases, the number of daughters is taken as the number of non-cross-overs and twice the number of sons as the cross-overs, it is found that the two lethals are about 7 units apart. Since the two lethals were in different X chromosomes, all the daughters should receive one or the other lethal, except in those few cases in which crossing over had taken place. Of the daughters 19 were tested and every one was found to carry a lethal. Again, if the cross-over values of the lethals with some other character, such as white eyes, be found and plotted, the curve should show two modes corresponding to the two lethals. This test was applied, but the curve failed to show two modes clearly,[7] the two lethals being too close together to be differentiated by the small number of determinations that were made. It seems probable that lethal *sa* and lethal *sb* are about 5 units apart.

The position of lethal *sb* was accurately found by continuing the determinations with a white lethal cross-over. A white female was found which had only one of the two lethals and the linkage of this lethal with eosin and miniature was found as follows: A

female carrying white and lethal in one chromosome and no mutant factor in the homologous chromosome was bred to an eosin miniature male. The white eosin daughters carried lethal, and their sons show the amount of crossing-over between white and lethal (15.6), between lethal and miniature (19.9), and between white and miniature (32.9). The data on which these calculations are based are given in table 48.

TABLE 48.—*Data on the linkage of white, lethal sb, and miniature, from Stark, 1915.*

$\frac{w^e \quad m}{w \quad l_{sb}}$ Eosin miniature.	$\frac{w^e \; l_{sb}}{w \; m}$ White miniature.	$\frac{w^e}{w \; l_{sb} \; m}$ Eosin.	$\frac{w^e \; l_{sb} \; m}{w}$ White.
2,421	524	685	48

The locus of this lethal is at 16.7; the locus of lethal *sa* was found to be at 23.7, so that the lethal at 16.7 is evidently the second lethal or lethal *sb* whose advent gave rise to the high sex-ratio. This interpretation is in accord with the curve which Miss Stark published, for although the mode which corresponds to lethal *sa* is weak, the mode at 15-16 is well marked.

The two other lethals, lethals *sc* and *sd*, which came up in the course of these experiments by Miss Stark, are treated in other sections of this paper.

BAR.

(Plate II, figures 12 and 13.)

The dominant sex-linked mutant called bar-eye (formerly called barred) appeared in February 1913 in an experiment involving rudimentary and long-winged flies (Tice, 1914). A female that is heterozygous for bar has an eye that is intermediate between the rounded eye of the wild fly and the narrow band of the bar stock. This heterozygous bar female is always readily distinguishable from the normal, but can not always be separated from the pure bar. Bar is therefore nearly always used as a dominant and back-crosses are made with normal males.

Bar is the most useful sex-linked character so far discovered, on account of its dominance, the certainty of its classification, and its position near the right end of the X chromosome. The locus of bar at 57 was determined on the basis of the data of table 65.

NOTCH.

A sex-linked dominant factor that brings about a notch at the ends of the wings appeared in March 1913, and has been described and figured by Dexter (1914, p. 753, and fig. 13, p. 730). The factor acts as a lethal for the male. Consequently a female heterozygous for notch bred to a wild male gives a 2:1 sex-ratio; half of her daughters are notch and half normal; the sons are only normal. The actual figures obtained by Dexter were 235 notch females, 270 normal females, and 235 normal males.

The location of notch in the X chromosome was not determined by Dexter, but the mutant has appeared anew three or four times and the position has been found by Bridges to be approximately at 2.6.

DEPRESSED.

Several mutations have appeared in which the wings are not flat. Of these the first that appeared was curved (second chromosome), in which the wings are curved downward throughout their length, but are elevated and held out sidewise from the body; the texture is thinner than normal. The second of these wing mutants to appear was jaunty (second chromosome), in which the wings turn up sharply at the tip; they lie in the normal position. The third mutant, arc (second chromosome), has, as its name implies, its wings curved like the arc of a circle. The fourth mutant, bow (first chromosome, fig. C), is like arc, but the amount of curvature is slightly less. The fifth mutant, depressed (first chromosome, fig. G), has the tip of its wings turned down instead of up, as in jaunty, but, as in jaunty, the wing is straight, except near the tip, where it bends suddenly. These stocks have been kept separate since their origin, and flies from them have seldom been crossed to each other, because in the succeeding generations it would be almost impossible to make a satisfactory classification of the various types. But that they are genetically different mutations is at once shown on crossing any two, when wild-type offspring are produced. For instance, bow and arc are the two most nearly alike. Mated together (bow ♂ by arc ♀), they give in F_1 straight-winged flies which inbred give in F_2 9 straight to 7 not-straight (*i.e.*, bow, arc, and bow arc together).

Depressed wings first appeared (April 1913) among the males of a culture of black flies. They were mated to their sisters and from subsequent generations both males and females with depressed wings were obtained which gave a pure stock. This

new character proved to be another sex-linked recessive.

LINKAGE OF DEPRESSED AND BAR.

Depressed (not-bar) males mated to (not-depressed) bar females gave bar daughters. Two of these were back-crossed singly to depressed males and gave the results shown in table 49. Males and females were not separated, since they should give the same result.

TABLE 49.—*P_1 depressed ♀ ♀ × bar ♀ ♀. B.C. F_1 bar ♀ × depressed ♂ ♂.*

Reference.	Non-cross-overs.		Cross-overs.		Total.
	Depressed.	Bar.	Depressed bar.	Wild-type.	
66 I	48	51	21	41	161
67 I	85	104	44	70	303
Total.	133	155	65	111	464

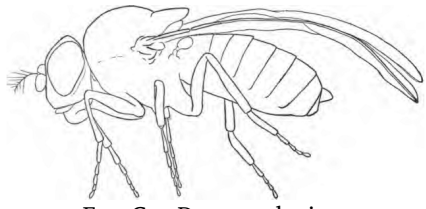


FIG. G.—Depressed wing.

LINKAGE OF CHERRY, DEPRESSED, AND VERMILION.

The linkage value 38 (see table 49) indicates that depressed is somewhere near the opposite end of the series of sex-linked factors from bar. The locus could be more accurately determined by finding the linkage relations of depressed with gens at its end of the chromosome. Accordingly, depressed females were crossed to cherry vermilion males. F_1 gave wild-type females and depressed males. The daughters bred again to cherry vermilion males gave the results shown in table 50. The data only suffice to show that the locus of depressed is about midway between cherry and vermilion, or at about 15 units from yellow.

The F_1 males in the last experiment did not have their wings as much depressed as is the condition in stock males, and in F_2 most of the depressed winged males were of the F_1 type, although a few were like those of stock. This result suggests that the stock is a double recessive, *i. e.*, one that contains, in addition to the sex-linked depressed, an autosomal factor that intensifies the effect of the primary sex-linked factor.

TABLE 50.—*P_1 depressed* ♀ × *cherry vermilion* ♂♂.

First generation.		Sec				
		Ref-erence.	♀♀.	$\frac{w^c \quad v}{d \quad p}$		
Wild-type ♀♀.	Depressed ♂♂.			Cherry ver-milion ♂.	De-pressed ♂.	Cl pr
21	31	19 I	59	23	24	

CLUB.

In May 1913 there were observed in a certain stock some flies which, although mature, did not unfold their wings (text-fig. H*a*). This condition was at first found only in males and suspicion was aroused that the character might be sex-linked. When these males were bred to wild females the club-shaped wings reappeared only in the F_2 males, but in smaller number than expected for a recessive sex-linked character. The result led to the further suspicion that not all those individuals that are genetically club show club somatically. These points are best illustrated and proven by the following history of the stock:

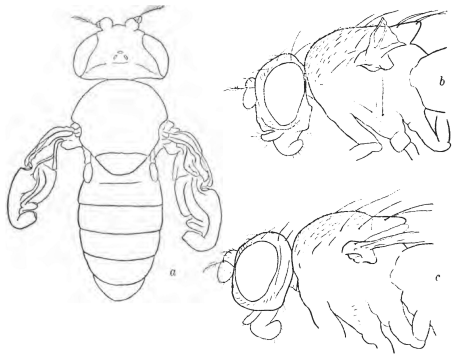


FIG. H.—Club wing. *a* shows the unexpanded wings of club flies; *c* shows the absence of the two large bristles from the side of the thorax present in the normal condition of the wild, *b*.

Club females were obtained by breeding F_2 club males to their F_2 long-winged sisters, half of which should be heterozygous for club. 5,352; wild-type ♂, 4,181; club ♂, 236. The wild-type males include, of

course, those club males that have expanded wings (potential clubs).

Club females by wild males gave in the F_2 generation (mass cultures): wild-type ♀, 1,131; wild-type ♂, 897; club ♀, 57; club ♂, 131.

It is noticeable that there were fewer club females than club males, equality being expected, which might appear to indicate that the club condition is more often realized by the male than by the female, but later crosses show that the difference here is not a constant feature of the cross.

Long-winged males from club stock (potential clubs) bred to wild females gave in F_2 the following: wild-type ♀, 521; wild-type (and potential club) ♂, 403; club ♂, 82.

Club females by club males of club stock gave in F_2: potential club ♀, 126; potential club ♂, 78; club ♀, 95; club ♂, 81. These results are from 8 pairs. The high proportion of club is noticeable.

Potential club females and males from pure club stock (*i. e.*, stock derived originally from a pair of club) gave in F_2 the following: potential club ♀, 1,049; potential club ♂, 666; club ♀, 450; club ♂, 453.

GENOTYPIC CLUB.

Accurate work with the club character was made possible by the discovery of a character that is a constant index of the presence of homozygous club. This character is the absence of the two large bristles (text-fig. H*c*) that are present on each side of the thorax of the wild fly as shown in figure H*b*. All club flies are now classified by this character and no

attention is paid to whether the wings remain as pads or become expanded.

LINKAGE OF CLUB AND VERMILION.

The linkage of club and vermilion is shown by the cultures listed in table 51, which were obtained as controls in working with lethal III. The cross-over value is shown in the male classes by the cross-over fraction $^{276}/_{1463}$ or 19 per cent.

LINKAGE OF YELLOW, CLUB, AND VERMILION.

The data just given in table 51 show that club is 19 units from vermilion, but in order to determine in which direction from vermilion it lies, the crossing-over of club to one other gen must be tested. For this test we used yellow, which lies at the extreme left of the chromosome series. At the same time we included vermilion, so that a three-point experiment was made.

Females that were (gray) club vermilion were bred to yellow (not-club red) and gave wild-type daughters and club vermilion sons. These inbred gave the results of table 52.

The data from the males show that the locus of club is about midway between yellow and vermilion. This conclusion is based on the evidence that yellow and club give 18 per cent of crossing-over, club and vermilion 20 per cent, and yellow and vermilion 35 per cent. The double cross-overs on this view are yellow club (3) and vermilion (3). The females furnish additional data for the linkage of club and vermilion. The value calculated from the female classes alone is 20 units, which is the same value as that given by the males.

TABLE 51.—*P_1 club ♀ ♀ × vermilion ♂ ♂. F_1 wild-type ♀ × F_1 club ♂.*

Reference.	Females.	Non-cross-over ♂ ♂.		Cross-over ♂ ♂.	
		Club.	Ver-milion.	Club Vermilion.	Wild type
137	75	17	39	6	11
138	64	24	32	6	8
139	56	10	31	4	3
140	74	13	39	3	5
144	97	30	40	10	13
145	63	15	29	4	6
146	126	44	46	9	9
106	92	33	34	6	10
107	55	31	25	7	3
108	86	29	32	7	10
109	103	25	36	4	9
	83	30	34	6	9
	77	18	26	7	8
	67	20	21	6	7
	126	32	60	15	13
	63	21	28	7	10
	114	45	71	9	7
	46	18	18	3	3
	111	35	56	6	7
Total.	1,578	490	697	125	151

TABLE 52.—*P_1 club vermilion ♀ ♀ × yellow ♂ ♂. F_1 wild-type ♀ ♀ × F_1 club vermilion ♂ ♂.*

Reference.	F_2 females.					
	Non-cross-overs.		Cross-overs.		y	
	Club ver-milion.	Wild-type.	Club.	Ver-milion.	Yellow.	cl m
99	44	52	13	7	35	
100	38	58	6	12	43	
101	30	32	6	12	19	
102	44	55	20	13	48	
103	...	...	...	...	43	
Total.	156	197	45	44	188	

LINKAGE OF CHERRY, CLUB, AND VERMILION.

The need for a readily workable character whose gen should lie in the long space between cherry and vermilion has long been felt. Cherry and vermilion are so far apart that there must be considerable double crossing-over between them. But with no favorably placed character which is at the same time viable and clearly and rapidly distinguishable, we were unable to find the exact amount of double crossing-over, and hence could not make a proper correction in plotting the chromosome. Club occupies just this favorable position nearly midway between cherry and vermilion. The distances from cherry to club and from club to vermilion are short enough so that no error would be introduced if we ignored the small amount of double crossing-over within each of these distances.

It thus becomes important to know very exactly the

cross-over values for cherry club and club vermilion. The experiment has the form of the yellow club vermilion cross of table 52, except that cherry is used instead of yellow. Cherry is better than yellow because it is slightly nearer club than is yellow and because the bristles of yellow flies are very inconspicuous. In yellow flies the bristles on the side of the thorax are yellowish brown against a yellow background, while in gray-bodied flies the bristles are very black against a light yellowish-gray background.

For the time being we are able to present only incomplete results upon this cross. In the first experiment cherry females were crossed to club vermilion males and the wild-type daughters were back-crossed to cherry club vermilion, which triple recessive had been secured for this purpose. Table 53 gives the results.

TABLE 53.—*P_1 cherry ♀ ♀ × club vermilion ♂ ♂. B. C. F_1 wild-type ♀ × cherry club vermilion ♂ ♂.*

Reference.	w^c		w^c c_l v		w^c v	
	Cherry.	c_l Club vermilion.	Cherry club vermilion.	Wild-type.	Cherry vermilion.	c_l Club
163	68	68	4	10	21	13
164	99	67	13	21	21	12
165	23	37	9	7	15	2
166	107	86	14	28	31	43
167	42	49	7	11	12	11
168	40	30	6	15	16	8

Total.	379	337	53	92	116	89

A complementary experiment was made by crossing cherry club vermilion females to wild males and inbreeding the F_1 in pairs. Table 54 gives the results of this cross.

TABLE 54.—*P_1 cherry club vermilion* ♂ ♂. ♀ ♀ × *wild* ♂ ♂. *F_1 wild-type* ♀ × *F_1 cherry club vermilion* ♂ ♂.

Reference.	w^c c_l v		w^c + / c_l v		w^c c_l + /	
	Cherry club vermilion.	Wild-type.	Cherry.	Club vermilion.	Cherry club.	Ver milio
188	60	76	12	8	12	29
189	228	314	48	44	50	60
197	68	81	23	13	9	22
Total.	356	471	83	65	71	111

The combined data of tables 53 and 54 give 14.2 as the value for cherry club. All the data thus far presented upon club vermilion (886 cross-overs in a total of 4,681), give 19.2 as the value for club vermilion. The locus of club on the basis of the total data available is at 14.6.

GREEN.

In May 1913 there appeared in a culture of flies with gray body-color a few males with a greenish-black

tinge to the body and legs. The trident pattern on the thorax, which is almost invisible in many wild flies, was here quite marked. A green male was mated to wild females and gave in F_2 a close approach to a 2:1:1 ratio. The green reappeared only in the F_2 males, but the separation of green from gray was not as easy or complete as desirable. From subsequent generations a pure stock of green was made. A green female by wild male gave 138 wild-type females and 127 males which were greenish. This green color varies somewhat in depth, so that some of these F_1 males could not have been separated with certainty from a mixed culture of green and gray males.

The results of these two experiments show that green is a sex-linked melanistic character like sable, but the somatic difference produced is much less than in the case of sable, so that the new mutation, although genetically definite, is of little practical value. We have found several eye-colors which differed from the red color of the wild fly by very small differences. With some of these we have worked successfully by using another eye-color as a developer. For example, the double recessive vermilion "clear" is far more easily distinguished from vermilion than is clear from red. But it is no small task to make up the stocks necessary for such a special study. In the case of green we might perhaps have employed a similar method, performing all experiments with a common difference from the gray in all flies used.

CHROME.

In a stock of forked fused there appeared, September 15, 1913, three males of a brownish-yellow body-color. They were uniform in color, without any of the

abdominal banding so striking in other body-colors. Even the tip of the abdomen lacked the heavy pigmentation which is a marked secondary sexual character of the male. About 20 or more of these males appeared in the same culture. This appearance of many males showing a mutant character and the non-appearance of corresponding females is usual for sex-linked characters. In such cases females appear in the next generation, as they did in this case when the chrome males were mated to their sisters in mass cultures. Since both females and males of chrome were on hand, it should have been an easy matter to continue the stock, but many matings failed, and it was necessary to resort to breeding in heterozygous form. The chrome, however, gradually disappeared from the stock. Such a difficult sex-linked mutation as this could be successfully handled (like a lethal) if it could be mated to a double recessive whose members lie one on each side of the mutant, but in the case of chrome this was not attempted soon enough to save the stock.

LETHAL 3.

In the repetition of a cross between a white miniature male and a vermilion pink male (December 1913), the F_2 ratios among the males were seen to be very much distorted because of the partial absence of certain classes (Morgan 1914*c*). While it was suspected that the disturbance was due to a lethal, the data were useless for determining the position of such a lethal, from the fact that more than one mother had been used in each culture. From an F_2 culture that gave practically a 2:1 sex-ratio, vermilion females were bred to club males. Several such females gave sex-ratios. Their daughters were again mated to vermilion males. Half of these

daughters gave high female sex-ratios and showed the linkage relations given in table 55.

TABLE 55.—*Linkage data on club, lethal 3, and vermilion, from Morgan, 1914c.*

Females.	Males.			
	$\frac{c_l}{\text{club. } v}$	$\frac{c_l \; l_3 \; v}{+}$ Wild-type.	$\frac{c_l \quad v}{l_3 \quad +}$ Club vermilion.	
588	182	28	11	

Lethal 3 proved to lie between club and vermilion, 13 units from club and 5 from vermilion. The same locus was indicated by the data from the cross of vermilion lethal-bearing females by eosin miniature males. The complete data bearing on the position of lethal 3 is summarized in table 56. On the basis of this data lethal 3 is located at 26.5.

TABLE 56.—*Summary of linkage data on lethal 3, from Morgan, 1914c.*

Gens.	Total.	Cross-overs.	Cross-over values.
Eosin lethal 3	1,327	268	20.2
Eosin vermilion	1,327	357	27.0
Eosin miniature	3,374	967	29.0
Club lethal 3	222	29	13.0
Club vermilion	877	161	18.4
Lethal 3 vermilion	1,549	105	6.8
Lethal 3 miniature	1,481	138	9.3
Vermilion miniature	1,327	31	2.3

LETHAL 3a.

In January 1914 a vermilion female from a lethal 3 culture when bred to a vermilion male gave 71 daughters and only 3 sons; 34 of these daughters were tested, and every one of them gave a 2:1 sex-ratio. The explanation advanced (Morgan 1914*c*) was that the mother of the high ratio was heterozygous for lethal 3, and also for another lethal that had arisen by mutation in the X chromosome brought in by the sperm. On this interpretation the few males that survived were those that had arisen through crossing-over. The rarity of the sons shows that the two lethals were in loci near together, although here of course in different chromosomes, except when one of them crossed over to the other. As explained in the section on lethal 1 and 1*a* the distance between the two lethals can be found by taking twice the number of the surviving males (2 + 3) as the cross-overs and the number of the females as the non-cross-overs. But the 34 daughters tested were also non-cross-overs, since none of them failed to carry a lethal. The fractions (6 + 0)/(71 + 34) = 6/105 give 5.7 as the distance between the lethals in question. In the case of lethals 3 and 3*a* another test was applied which showed graphically that two lethals were present. Each of the daughters tested showed, by the classes of her sons, the amount of crossing-over between white and that lethal of the two that she carried. These cross-over values were plotted and gave a bimodal curve with modes 7 units apart. It had already been shown that the locus of one of the two lethals was at 26.5, and since the higher of the two modes was at about 23, it corresponds to lethal 3. The data and the curve show that the lethals 3 and 3*a* are about 7 units apart, *i. e.*, lethal 3*a* lies at about 19.5.

LETHAL 1b.

A cross between yellow white males and abnormal abdomen females gave (February 1914) regular results in 10 F_2 cultures, but three cultures gave 2 ♀ : 1 ♂ sex-ratios (Morgan, 1914*b*, p. 92). The yellow white class, which was a non-cross-over class in these 10 cultures, had disappeared in the 3 cultures. Subsequent work gave the data summarized in table 57. At the time when the results of table 57 were obtained it did not seem possible that two different lethals could be present in the space of about 1 unit between yellow and white, and this lethal was thought to be a reappearance of lethal 1 (Morgan, 1912*b*, p. 92). Since then a large number of lethals have arisen, one of them less than 0.1 unit from yellow, and at least one other mutation has taken place between yellow and white, so that the supposition is now rather that the lethal in question was not lethal 1. Indeed, the linkage data show that this lethal, which may be called lethal 1*b*, lies extraordinarily close to white, for the distance from yellow was 0.8 unit and of white from yellow on the basis of the same data 0.8. There was also a total absence of cross-overs between lethal 1*b* and white in the total of 846 flies which could have shown such crossing-over. On the basis of this linkage data alone we should be obliged to locate lethal 1*b* at the point at which white itself is situated, namely, 1.1, but on *a priori* grounds it seems improbable that a lethal mutation has occurred at the same locus as the factor for white eye-color. Farther evidence against this supposition is that females that have one X chromosome with both yellow and white and the other X chromosome with yellow, lethal, and white are exactly like regular stock yellow white flies. The lethal must have appeared in a chromosome which

was already carrying white and yet did not affect the character of the white. We prefer, therefore, to locate lethal 1*b* at 1.1-.

TABLE 57.—*Summary of all linkage data upon lethal 1b, from Morgan, 1914b.*

Gens.	Total.	Cross-overs.	Cross-over values.
Yellow lethal 1*b*	744	6	0.81
Yellow white	2,787	23	0.82
Lethal 1*b* white	846	0	0.0

FACET.

Several autosomal mutations had been found in which the facets of the compound eye are disarranged. One that was sex-linked appeared in February 1914. Under the low power of the binocular microscope the facets are seen to be irregular in arrangement, instead of being arranged in a strictly regular pattern. The ommatidia are more nearly circular than hexagonal in outline, and are variable in size, some being considerably larger than normal. The large ones are also darker than the smaller, giving a blotched appearance to the eye. The short hairs between the facets point in all directions instead of radially, as in the normal eye. The irregular reflection breaks up the dark fleck which is characteristic of the normal eye. The shape of the eye differs somewhat from the normal; it is more convex, smaller, and is encircled by a narrow rim destitute of ommatidia.

Facet arose in a back-cross to test the independence of speck (second chromosome) and maroon (third chromosome). One of the cultures produced, among

the first males to hatch, some males which showed the facet disarrangement. None of the females showed this character. The complete output was that typical of a female heterozygous for a recessive sex-linked character: not-facet ♀ ♀ (2), 112; not-facet ♂ ♂ (1), 57; facet ♂ ♂ (1), 51.

Of the three characters which were shown by the F_2 males, one, facet, is sex-linked, another, speck, is in the second chromosome, and maroon is in the third chromosome. All eight F_2 classes are therefore expected to be equal in size, and each pair of characters should show free assortment, that is, 50 per cent. The assortment value for facet speck is 48, for speck maroon 52, and for facet maroon 48, as calculated from the F_2 males of table 58.

TABLE 58.—*P_1 speck maroon* ♂ × *wild* ♀ ♀. *B.C. F_1 wild-type* ♀ × *speck maroon* ♂.

Reference.	F_2 females.				
	Speck maroon.	Wild-type.	Speck.	Maroon.	Facet.
66	31	30	26	25	14

LINKAGE OF FACET, VERMILION AND SABLE.

In order to determine the location of facet in the first chromosome, one of the facet males which appeared in culture 66 was crossed out to vermilion sable females. Three of the wild-type daughters were back-crossed to vermilion sable males. The females of the next generation should give data upon the linkage of vermilion and sable, while the males should show the linkage of all three gens, facet, vermilion, and sable. The offspring of these three females are

classified in table 59.

The cross-over fraction for vermilion sable as calculated from the females is $^{19}/_{194}$. The cross-over value corresponding to this fraction is 10 units, which was the value found in the more extensive experiments given in the section on sable.

It will be noticed that the results in the males of culture 150 are markedly different from those of the other two pairs. While the sable males are fully represented, their opposite classes, the gray males, are entirely absent. This result is due to a lethal factor, lethal 5, which appeared in this culture for the first time.

The males of the two cultures 149 and 151 give the order of gens as facet, vermilion, sable; that is, facet lies to the left of vermilion and toward yellow. The cross-over values are: facet vermilion 40; vermilion sable 12; facet sable 42. Since yellow and vermilion usually give but 34 per cent of crossing-over, this large value of 40 for facet vermilion shows that facet must lie very near to yellow.

TABLE 59.—*P_1 facet ♂ × vermilion sable ♀ ♀. B.C. F_1 wild-type ♀ × vermilion sable ♂ ♂.*

Reference.	F_2 females.					
	Non-cross-overs.		Cross-overs.			
	Vermilion sable.	Wild-type.	Vermilion.	Sable.	Facet.	V mi sal
149	16	29	3	3	17	1

150	13	17	2	2	..	1
151	37	63	7	2	38	2
Total.	66	109	12	8	55	4

LINKAGE OF EOSIN, FACET, AND VERMILION.

In order to obtain more accurate information on the location of facet, a facet male was mated to an eosin vermilion female. The F_1 females were mated singly to wild males and they gave the results shown in table 60. The F_2 females were not counted, since they do not furnish any information. The evidence of table 60 places facet at 1.1 units to the right of eosin, or at 2.2.

TABLE 60.—*P_1 eosin vermilion ♀ × facet ♂. F_1 wild-type ♀ × wild ♂.*

Reference.	$\frac{w^e \quad v}{f_a}$		$\frac{w^e \; f_a}{v}$		$\frac{w^e}{f_a}$	
	Eosin ver-milion.	Facet.	Eosin facet.	Ver-milion.	Eosin.	F v mi
512	43	43	..	1	13	
513	28	35	..	2	19	
514	18	31	1	..	17	
515	18	60	..	..	20	
516	10	31	..	..	7	
517	24	34	..	..	10	
518	44	38	1	1	23	
Total.	185	272	2	4	109	

LETHAL SC.

The third of the lethals which Miss Stark found (Stark, 1915) while she was testing the relative frequency of occurrence of lethals in fresh and inbred wild stocks arose in April 1914 in stock caught in 1910. Females heterozygous for this lethal, lethal *sc*, were mated to white males and the daughters were back-crossed to white males. Half of the daughters gave lethal sex-ratio, and these gave 1,405 cross-overs in a total of 3,053 males, from which the amount of crossing-over between white and lethal *sc* has been calculated as 46 per cent.

By reference to table 65 it is seen that white and bar normally give only about 44 per cent of crossing-over in a two-locus experiment; lethal *sc* then is expected to be situated at least as far to the right as bar. Females heterozygous for lethal *sc* were therefore crossed to bar males, and their daughters were tested. The lethal-bearing daughters gave 144 cross-overs in a total of 1,734 males, that is, bar and lethal *sc* gave 8.3 per cent of crossing-over. Lethal *sc* therefore lies 8.3 units beyond bar or at about 66.5. The cross-over value sable lethal *sc* was found to be 23.5 (387 cross-overs in a total of 1,641 males) which places the lethal at 43 + 23.5, or at 66.5. We know from other data that there is enough double crossing-over in the distance which gives an experimental value of 23.5 per cent, so that the true distance is a half unit longer or the locus at 67.0 is indicated by the 1,641 males of the sable lethal experiment. In a distance so short that the experimental value is only 8.3 per cent there is, as far as we have been able to determine, no double crossing-over at all, or at most an amount that is entirely negligible, so that a locus at 57 + 8.3 or 65.3 is indicated by the 1,734 males of the bar lethal experiment. To get the value indicated by the total

data the cases may be weighted, that is, the value 65.3 may be multiplied by 1,734, and 67.0 may be multiplied by 1,641. The sum of these two numbers divided by the sum of 1,734 and 1,641 gives 66.2 as the locus indicated by all the data available. This method has been used in every case where more than one experiment furnishes data upon the location of a factor. In constructing the map given in diagram I rather complex balancings were necessary.

LETHAL SD.

The fourth lethal which Miss Stark found (May 1914) in the inbred stocks of *Drosophila* has not been located by means of linkage experiments. It is interesting in that the males which receive the lethal factor sometimes live long enough to hatch. These males are extremely feeble and never live more than two days. There is, as far as can be seen, no anatomical defect to which their extreme feebleness and early death can be attributed.

FURROWED.

In studying the effect of hybridization upon the production of mutations in *Drosophila*, F. N. Duncan found a sex-linked mutation which he called "furrowed eye" (Duncan 1915). The furrowed flies are characterized by a foreshortening of the head, which causes the surface of the eye to be thrown into irregular folds with furrows between. The spines of the scutellum are stumpy, a character which is of importance in classification, since quite often flies occur which have no noticeable disturbance of the eyes.

The locus of furrowed was determined to be at 38.0 on the basis of the data given in table 61.

TABLE 61.—*Data on the linkage of furrowed, from Duncan, 1915.*

Gens.	F_2 males.		
	$\frac{w^e \; m}{f_w}$	$\frac{w^e \quad f_w}{m}$	$\frac{w^e \; m \quad f_w}{\quad}$
Eosin, miniature, furrowed.	142	59	4
	$\frac{f_w \quad \quad}{s \quad f}$	$\frac{f_w \; s \quad f}{\quad}$	$\frac{f_w \quad \quad f}{s \quad \quad}$
Furrowed, sable, forked.	166	9	31
	$\frac{v \quad B'}{f_w}$	$\frac{v \; f_w}{B'}$	$\frac{v \quad \quad}{f_w \; B'}$
Vermilion, furrowed, bar.	188	9	43

ADDITIONAL DATA FOR YELLOW, WHITE, VERMILION, AND MINIATURE.

Considerable new work has been done by various students upon the linkage of the older mutant characters, namely, yellow, white, vermilion, and miniature. We have summarized these new data, and they give values very close to those already

published. We have included in the white miniature data those published by P. W. Whiting (Whiting 1913).

TABLE 62.—*Data upon the linkage of yellow, white, vermilion, and miniature* (*contributed by students*).

Gens.	Non-cross-overs.	Cross-overs.	
White miniature.	w m 6,219[8] 7,378	w 3,754 3,3[illegible]	2(
	w 1,651 1,1[illegible]	w m 671 1,047	4
Yellow miniature.	y 761 9[illegible]	y m 421 653	2
Vermilion miniature.	v 1,685 1,4[illegible]	v m 32 36	3
Yellow white.	y w 1,600 1,807	y 10 w	3

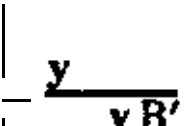
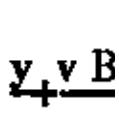
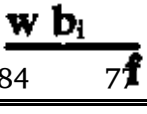
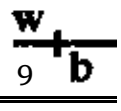
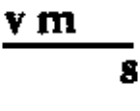
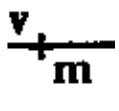
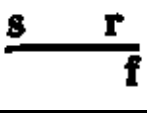
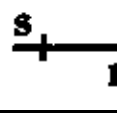
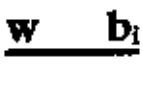
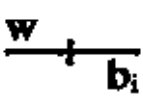
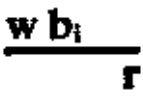
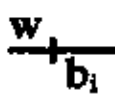
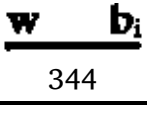
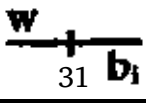
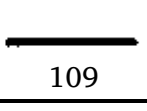
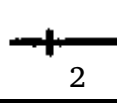
Yellow vermilion.	y	v	509	587	328	284	1
White bar.	w	B′	198	272	168	166	
Bifid rudimentary.	b_1	r	142	15	12	116	
Rudimentary forked.	r	f	73	21	...	4	

NEW DATA CONTRIBUTED BY A. H. STURTEVANT AND H. J. MULLER.

Data from several experiments upon sex-linked characters described in this paper have been contributed by Dr. A. H. Sturtevant and Mr. H. J. Muller, and are given in table 63.

TABLE 63.—*Data contributed by A. H. Sturtevant and H. J. Muller.*

Gens.				
Yellow white × bifid.	y w	b_1	233	25	y	w	1	

				
Yellow × vermilion bar.	99	101	60	5
				
White bifid × forked.	84	71	9	
				
Vermilion miniature × sable.	152	111	4	
				
Sable rudimentary × forked.	143	195	26	2
				WHITE
F_2 females.				
				
228 335	15 11	150 66	2	1
				WHITE BIFID
				
344	31	109	2	

SUMMARY OF THE PREVIOUSLY DETERMINED CROSS-OVER VALUES.

The data of the earlier papers, namely, Dexter, 1912; Morgan, 1910*c*, 1911*a*, 1911*f*, 1912*f*, 1912*g*; Morgan and Bridges, 1913; Morgan and Cattell, 1912 and 1913; Safir, 1913; Sturtevant, 1913 and 1915; and Tice, 1914, have been summarized in a recent paper by Sturtevant (Sturtevant, 1915) and are given here in table 64. Our summary combines three summaries of Sturtevant, viz, that of single crossing-over and two of double crossing-over.

TABLE 64.—*Previously published data summarized from Sturtevant, 1915*.

Factors.	Total.	Cross-overs.	Cross-over values.
Yellow white.	46,564	498	1.07
Yellow vermilion.	10,603	3,644	33.4
Yellow miniature.	18,797	6,440	34.3
Yellow rudimentary.	2,563	1,100	42.9
Yellow bar.	191	88	46.1
White vermilion.	15,257	4,910	32.1
White miniature.	41,034	13,513	32.8
White rudimentary.	5,847	2,461	42.1
White bar.	5,151	2,267	44.0
Vermilion miniature.	5,329	212	4.0

Vermilion rudimentary.	1,554	376	24.1
Vermilion bar.	7,514	1,895	25.2
Miniature rudimentary.	12,567	2,236	17.8
Miniature bar.	3,112	636	20.4
Rudimentary bar.	159	7	4.4

SUMMARY OF ALL DATA UPON LINKAGE OF GENS IN CHROMOSOME I.

In table 65 all data so far secured upon the sex-linked characters are summarized. These data include the experiments previously published in the papers given in the bibliography and the experiments given here. The data from experiments involving three or more loci are calculated separately for each value and included in the totals.

TABLE 65.—*A summary of all linkage data upon chromosome I.*

Gens.	Total.	Cross-overs.	Cross-over values.
Yellow lethal 1.	131	1	0.8
Yellow lethal 1*b*.	744	6	0.8
Yellow white.	81,299	875	1.1
Yellow abnormal.	15,314	299	2.0
Yellow bifid.	3,681	201	5.5
Yellow club.	525	93	17.7

Yellow vermilion.	13,271	4,581	34.5
Yellow miniature.	21,686	7,559	34.3
Yellow sable.	1,600	686	42.9
Yellow rudimentary.	2,563	1,100	42.9
Yellow bar.	626	300	47.9
Lethal 1 white.	1,763	7	0.4
Lethal 1 miniature.	814	323	39.7
Lethal 1*b* white.	846	0	0.0
White facet.	666	7	1.1
White abnormal.	16,300	277	1.7
White bifid.	23,595	1,260	5.3
White lethal 2.	8,011	767	9.6
White club.	2,251	321	14.3
White lethal *sb*.	3,678	572	15.6
White lemon.	241	35	14.5
White depressed.	59	12	20.3
White lethal *sa*.	1,150	256	22.2
White vermilion.	27,962	8,532	30.5
White reduplicated.	418	121	28.9
White miniature.	110,701	31,071	33.2
White furrowed.	208	63	30.3
White sable.	2,511	1,032	41.2
White rudimentary.	6,461	2,739	42.4

White forked.	3,664	1,676	45.7
White bar.	5,955	2,601	43.6
White fused.	430	186	43.3
White lethal *sc*.	3,053	1,406	46.0
Facet vermilion.	852	278	32.6
Facet sable.	186	80	43.0
Bifid vermilion.	2,724	849	31.1
Bifid miniature.	219	67	30.6
Bifid rudimentary.	899	384	42.7
Bifid forked.	306	130	42.5
Lethal 2 vermilion.	1,400	248	17.7
Lethal 2 miniature.	6,752	1,054	15.4
Club lethal 3.	222	29	13.0
Club vermilion.	5,558	1,047	18.8
Lethal *sb* miniature.	3,678	733	19.9
Lemon vermilion.	241	29	12.0
Shifted vermilion.	1,007	155	15.5
Shifted bar.	242	76	31.4
Depressed vermilion.	59	10	17.0
Depressed bar.	464	176	38.0
Lethal 3 vermilion.	1,549	105	6.8
Lethal 3 miniature.	1,481	138	9.3
Vermilion dot.	57	0	0.0

Vermilion reduplicated.	667	11	1.7
Vermilion miniature.	10,155	317	3.1
Vermilion furrowed.	240	9	3.8
Vermilion sable.	9,209	929	10.1
Vermilion rudimentary.	1,554	376	24.1
Vermilion forked.	665	163	24.5
Vermilion bar.	23,522	5,612	23.9
Vermilion fused.	9,252	2,390	25.8
Reduplicated bar.	583	120	20.6
Miniature furrowed.	208	7	3.4
Miniature sable.	1,855	125	6.7
Miniature rudimentary.	12,786	2,284	17.9
Miniature bar.	3,112	636	20.5
Furrowed sable.	209	12	5.7
Furrowed forked.	209	40	19.1
Furrowed bar.	240	43	17.9
Sable rudimentary.	663	95	14.3
Sable forked.	872	140	16.0
Sable bar.	7,524	1,036	13.8
Sable lethal *sc*.	1,641	387	23.6
Rudimentary forked.	1,456	20	1.4

Rudimentary bar.	664	15	2.3
Forked bar.	1,706	8	0.5
Forked fused.	1,201	37	3.1
Bar fused.	8,768	222	2.5
Bar lethal *sc*.	1,734	144	8.3

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DESCRIPTIONS OF PLATES.

PLATE I.

FIG. 1. Normal ♀.

FIG. 2. Sable ♀.

FIG. 3. Lemon ♂.

FIG. 4. Abnormal abdomen ♀.

FIG. 5. Abnormal abdomen ♀.

FIG. 6. Yellow ♀.

PLATE II.

FIG. 7. Eosin, miniature, black ♂.

FIG. 8. Eosin, miniature, black ♀.

FIG. 9. Cherry.

FIG. 10. Vermilion.

FIG. 11. White.

FIG. 12. Bar (from above).

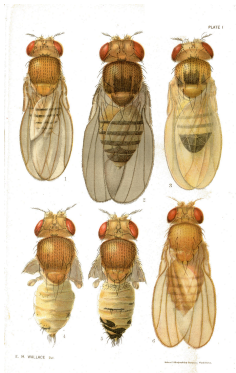
FIG. 13. Bar (from side).

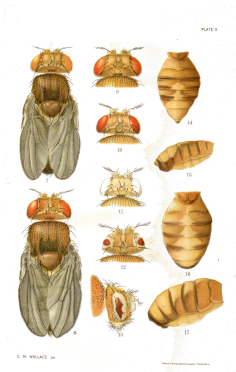
FIG. 14. Spot ♀ (abdomen from above).

FIG. 15. Spot ♀ (abdomen from side).

FIG. 16. Spot ♂ (abdomen from above).

FIG. 17. Spot ♂ (abdomen from side).





Notes

[1] For a fuller discussion see "The Mechanism of Mendelian Heredity" by Morgan, Sturtevant, Muller, and Bridges. Henry Holt & Co., 1915.

[2] *B. C.* here and throughout stands for back-cross.

[3] The first dark body-color mutation "black" (see plate II, figs. 7, 8) had appeared much earlier (Morgan 1911*b*, 1912*c*). It is an autosomal character, a member of the second group of linked gens. Still another dark mutant, "ebony," had also appeared, which was found to be a member of the third group of gens.

[4] Wherever reference numbers are given, these denote the pages in the note-books of Bridges upon which the original entries for each culture are to be found.

[5] In addition to these expected F_1 wild-type females there occurred 13 females of an eye-color like that of the mutant pink. So far as was seen none of the F_1 males differed in eye-color from the expected eosin vermilion. Since the eosin vermilion and sable stocks were unrelated and neither was known to contain a "pink" as an impurity, these "pinks" must be due to mutation of an unusual kind. That these "pinks" were really products of the cross is proven by the result of crossing one of them to one of her eosin vermilion brothers, for she showed herself to be heterozygous for eosin, vermilion, and sable.

F_1 "pink" (Ref. 51 C) ♀ × *F_1 eosin vermilion* ♂.

Reference.	Wild-type.		Eosin vermilion.		Eosin.		Vermilio	
	♀	♂	♀	♂	♀	♂	♀	♂
59 C	59	38	43	40	15	9	16	1

In addition to the combinations of eosin and vermilion, sable also appeared in its proper distribution though no counts were made. The four smaller classes are cross-overs between eosin and vermilion. Since no "pinks" appeared the color is recessive, and the brother was not heterozygous for it.

Two other "pink" females mated to wild males gave similar results in their sons.

F_1 "pink" ♀ × *wild* ♂.

Reference.	Wild-type ♀.	Wild-type ♂.	Eosin vermilion ♂.	Eosin ♂.	Vermi ♂
61 C	101	33	37	9	11

These F_1 flies should all be heterozygous for "pink." A pair of wild-type flies which were mated gave a 3 : 1 ratio—wild type 51 to "pink" 18. From the "pinks" which appeared in this cross a stock was made which was lost through sterility. Females tested to males of true pink were also sterile, so that no solution can be given of the case.

[6] Purple is an eye-color whose gen is in the second chromosome.

[7] The curve published by Miss Stark included by mistake 6 cultures from the succeeding generations, and these coming from only one of the lethals (lethal *sb*) increase its mode so that the mode of the other lethal (lethal *sa*) becomes submerged. If these cultures are taken out the curve shows two modes more clearly.

[8] The figures to the left in each double column correspond to the symbols above the heavy line, as, in the first example 6,219 white miniature. The similar figure to the right corresponds to the symbol below the heavy line. If no symbols are present below, as in the first example, the column to the right should be read wild-type.

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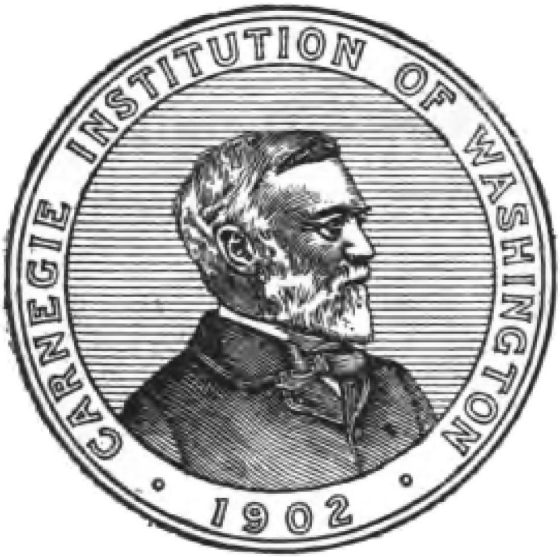
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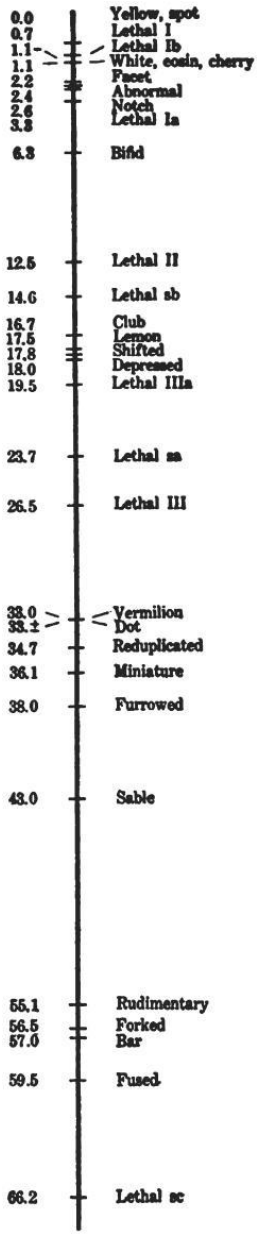
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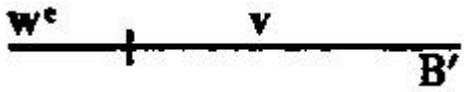
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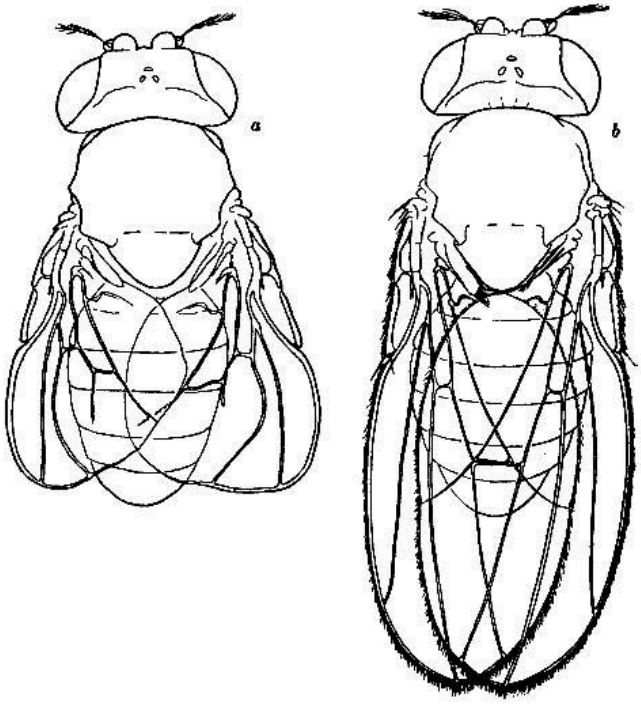
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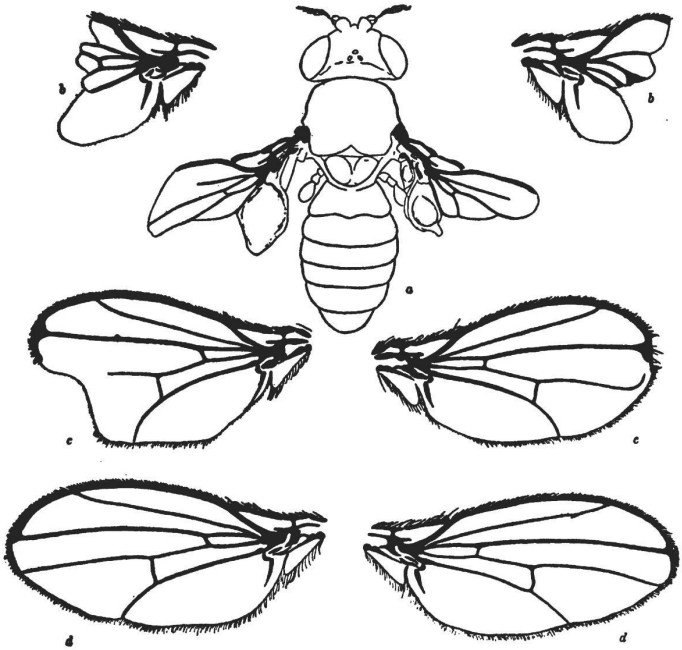
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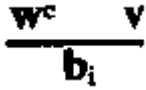
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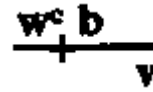
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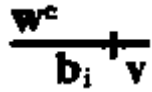
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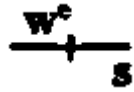
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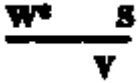
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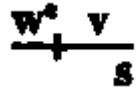
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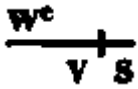
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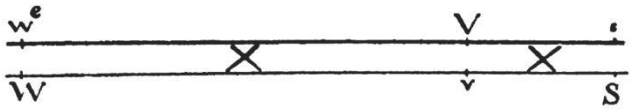
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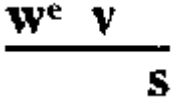
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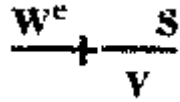
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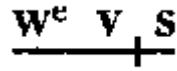
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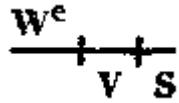
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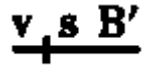
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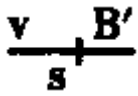
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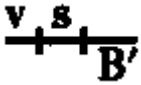
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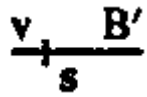
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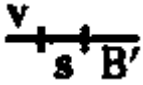
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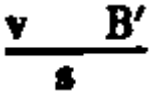
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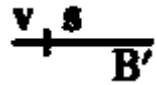
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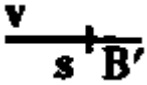
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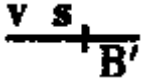
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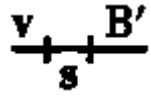
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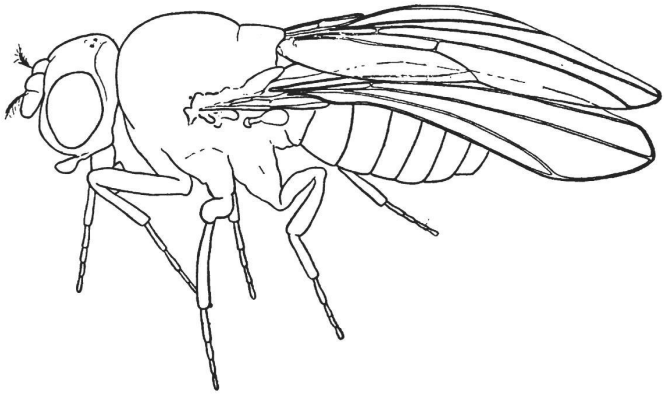
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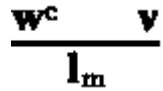
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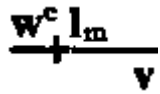
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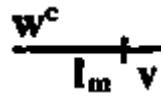
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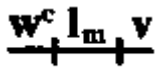
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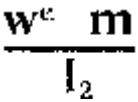
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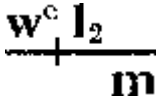
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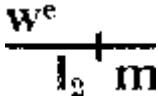
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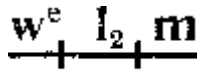
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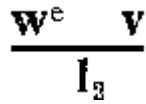
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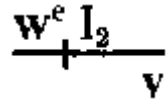
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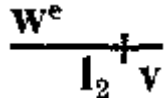
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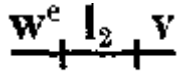
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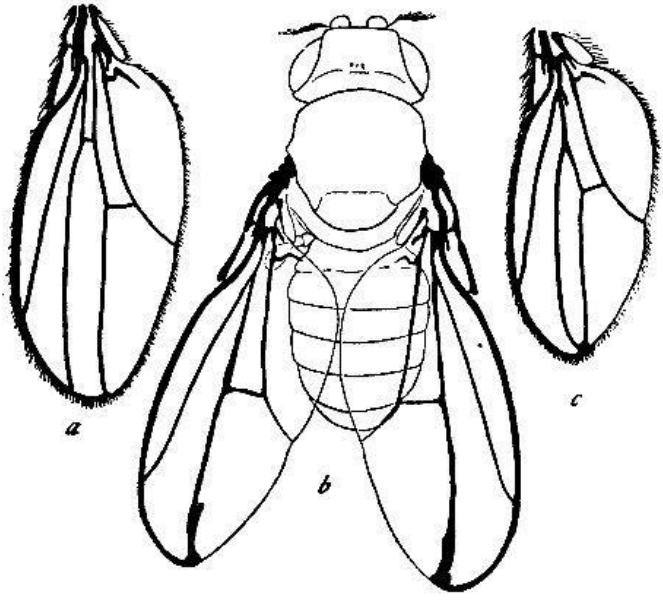
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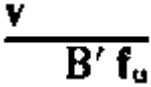
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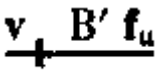
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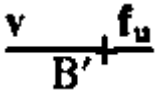
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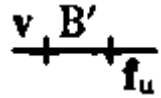
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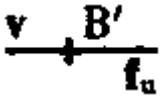
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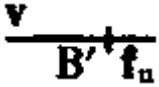
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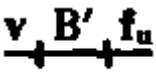
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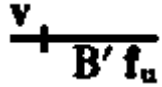
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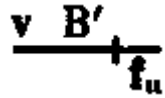
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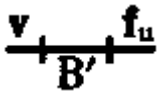
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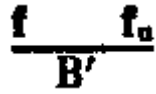
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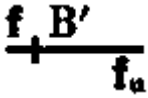
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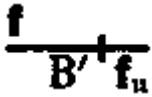
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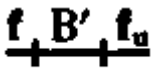
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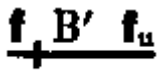
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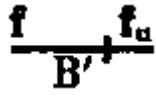
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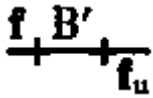
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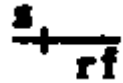
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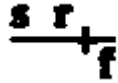
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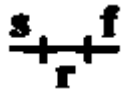
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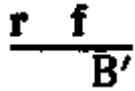
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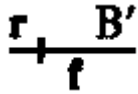
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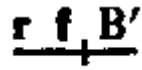
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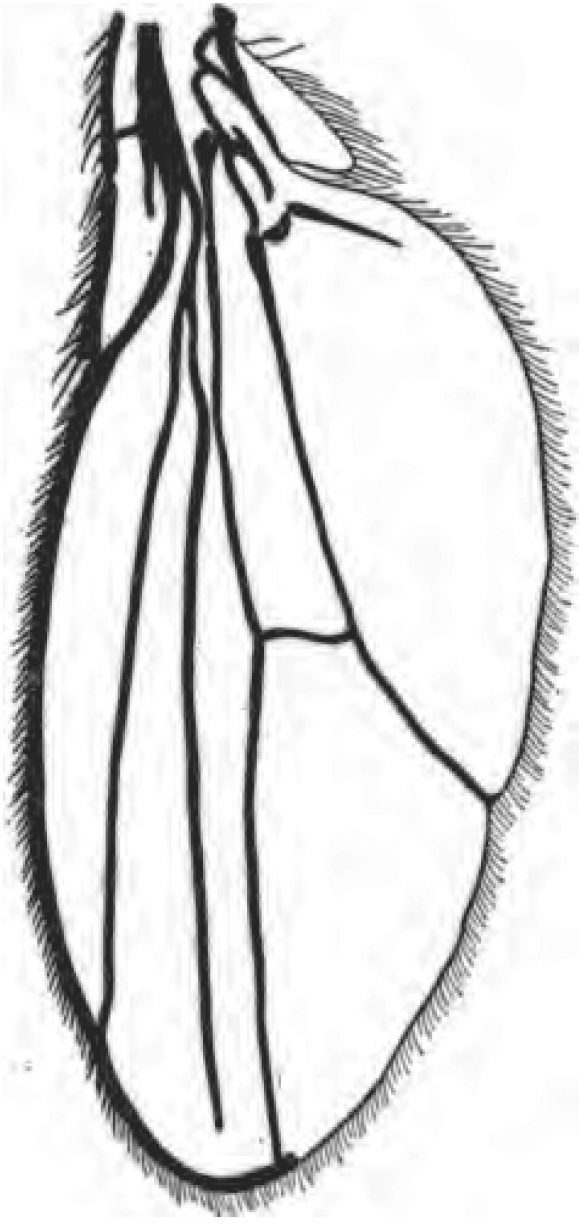
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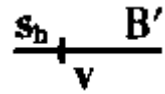
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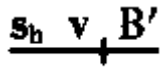
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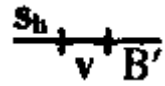
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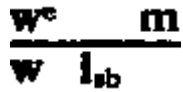
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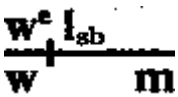
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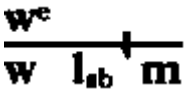
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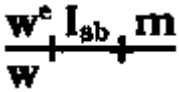
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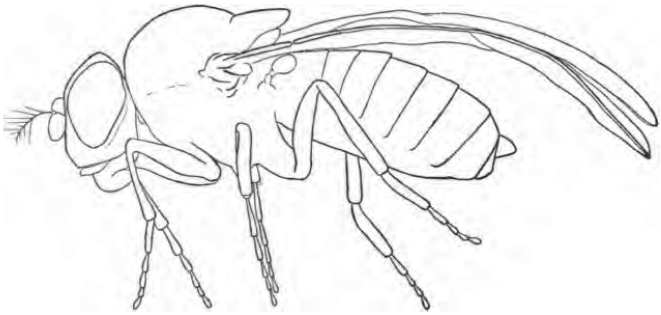
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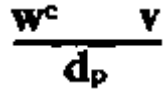
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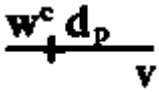
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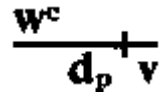
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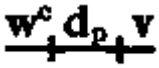
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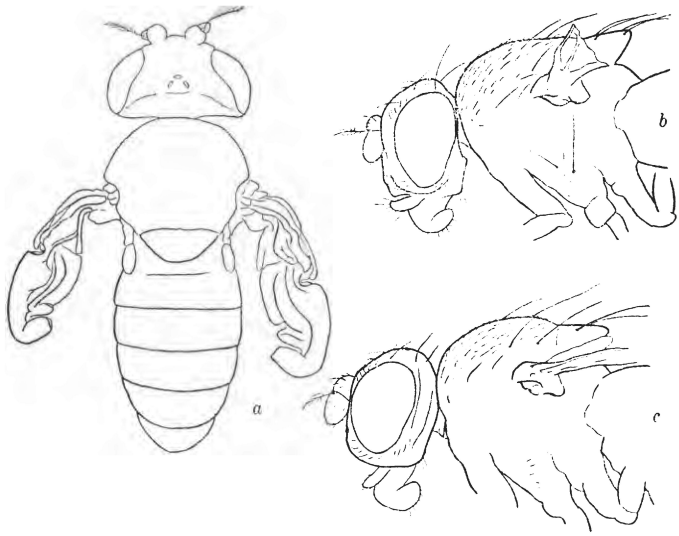
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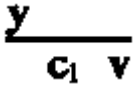
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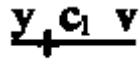
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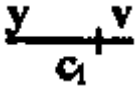
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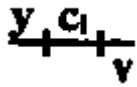
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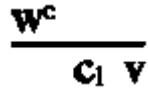
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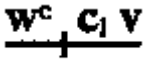
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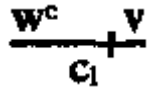
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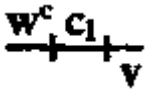
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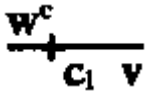
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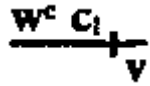
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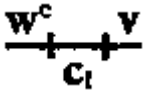
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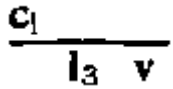
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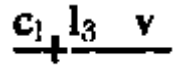
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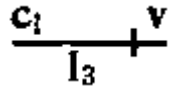
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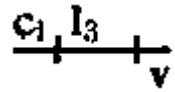
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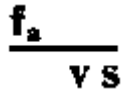
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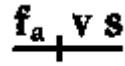
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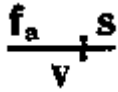
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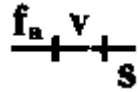
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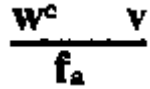
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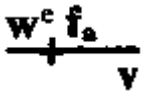
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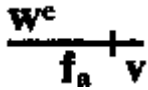
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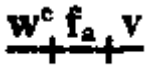
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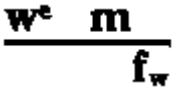
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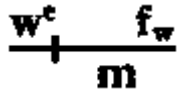
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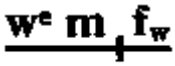
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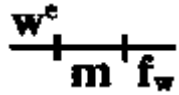
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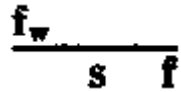
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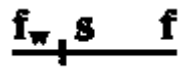
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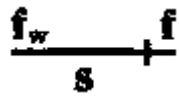
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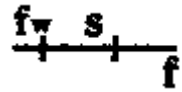
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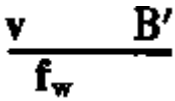
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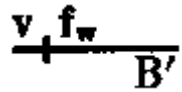
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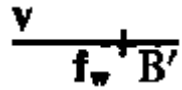
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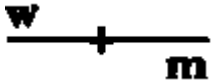
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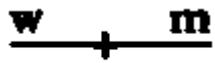
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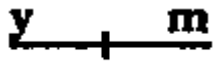
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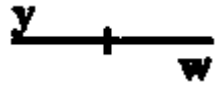
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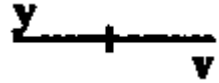
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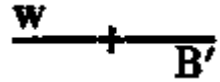
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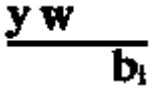
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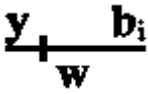
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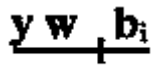
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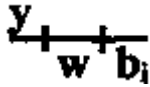
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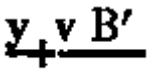
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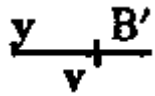
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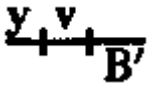
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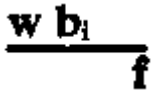
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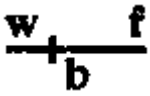
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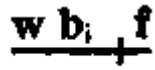
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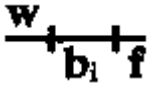
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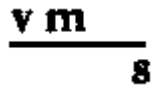
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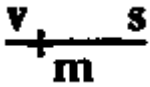
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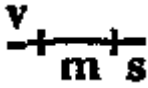
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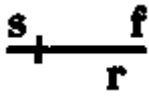
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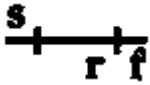
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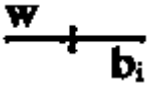
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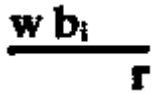
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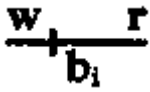
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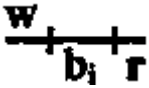
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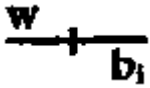
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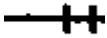
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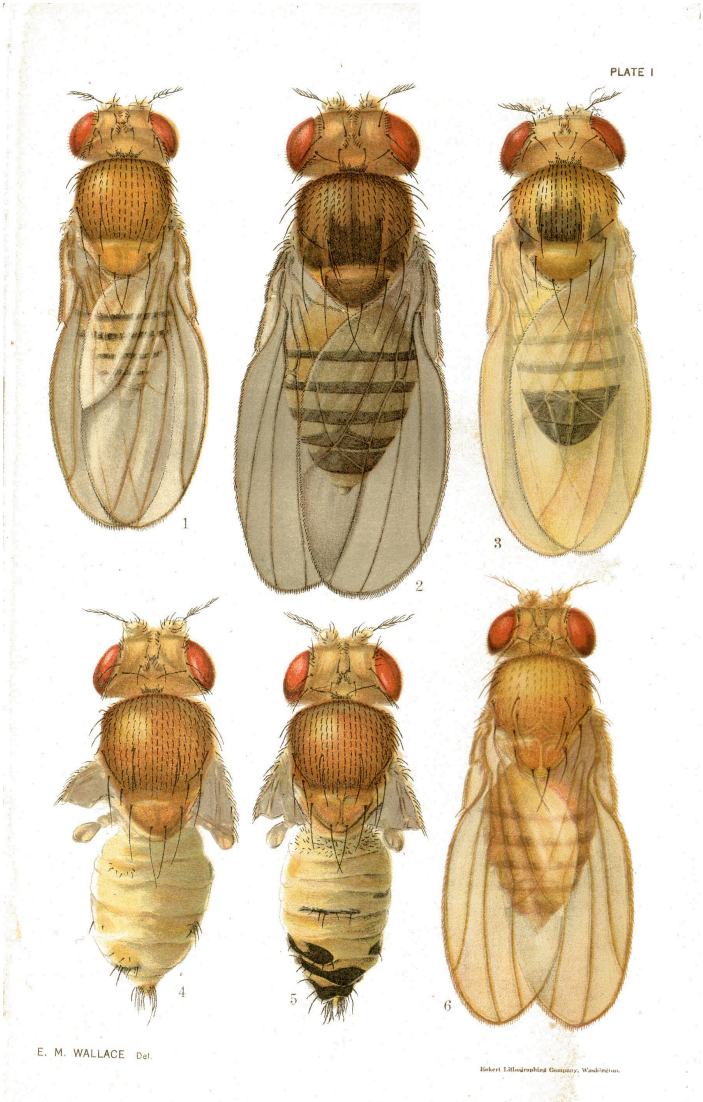
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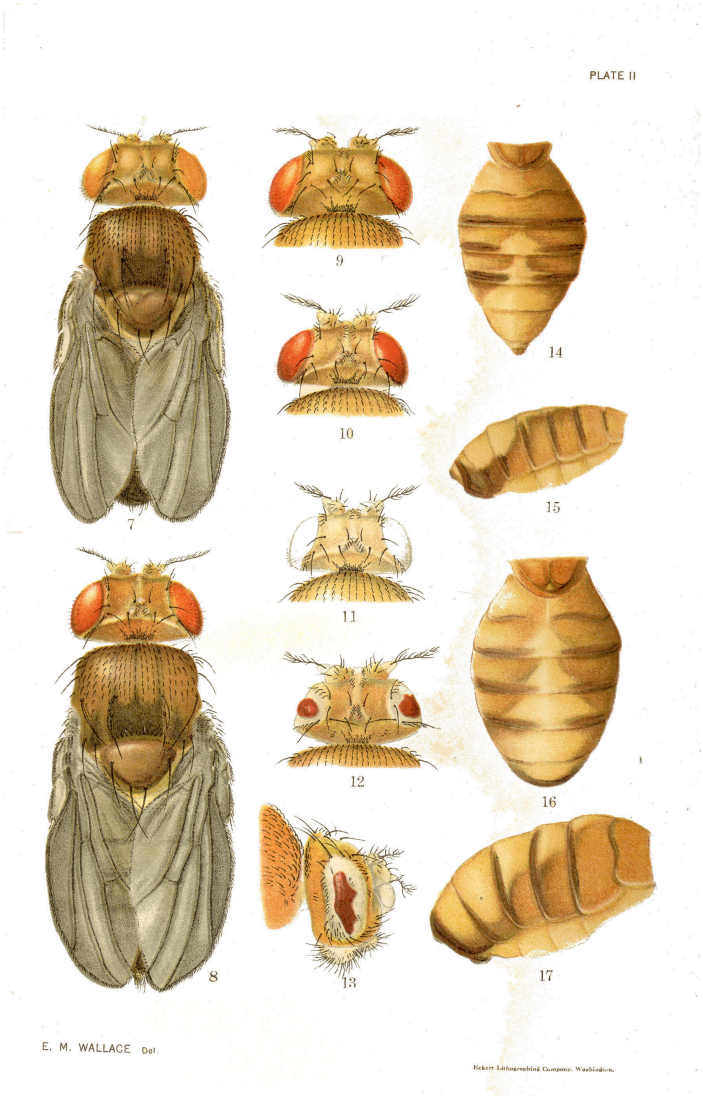
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