GENETIC STUDIES ON DROSOPHILA VIRILIS

WITH CONSIDERATIONS ON

THE GENETICS OF OTHER SPECIES OF DROSOPHILA

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I. INTRODUCTORY.

GENERAL INTRODUCTION.

In most groups of animals and plants, including those susceptible to genetic study through intensive breeding, the chromosome groups of related species show a high degree of uniformity. The different members of a genus, for instance, usually differ relatively little in this regard. In some cases the uniformity may extend even to subfamilies or families, as, for example, in the Acrididæ among the Orthoptera, where all of approximately 40 genera studied agree in having essentially the same chromosome group (cf. McClung, 1914; Harvey, 1916). It would seem probable, *a priori*, that where many related species exhibit such a constancy in chromosome groups, the apparent homology of chromosomes is real, i. e., similar chromosomes in different species are essentially alike in genetic make-up. On the other hand, there are various exceptions to the general rule of constancy, and a number of cases are known in which closely related species have very dissimilar chromosome groups. Hence it may be argued that even where a constancy exists it may be superficial and not dependent upon, or significant of, a likeness in genetic constitution of similar chromosomes. In fact, very little is known as to how far morphological criteria are trustworthy as indications of homology between chromosomes. In one case recently investigated by Lancefield and Metz (1921, 1922), the results indicate that genetic homology does not correspond to morphological similarity as regards two pairs of chromosomes in *Drosophila willistoni* compared with two similar pairs in *D. melanogaster*.

These and other considerations serve to emphasize the necessity of learning something of the genetic constitution of chromosomes before they can safely be compared from the evolutionary standpoint. It is believed that the only method of obtaining reliable information on chromosome evolution is by means of genetic analysis combined with cytological observation.

Ideal material for such a study would be provided by a group of species satisfying the following four requirements: In the first place, it should exhibit among its members a series of different chromosome groups; secondly, the species should be susceptible to intensive breeding under controlled conditions; in the third place, one or more of the species should be favorable for genetic analysis through the study of mutant races; and lastly, the species should hybridize with one another and give fertile hybrids.

Many cases of species hybrids are known, and some have been studied extensively. Those involving domestic or semidomestic animals, e. g., the mule, ducks, pheasants, etc., are too well known to need more than a mention, as are also those of numerous cultivated plants. Likewise, various kinds of fish hybrids have long been familiar. The work of Federley (1914, 1915) and Harrison and Doncaster (1914) has revealed the fact that hybridization is readily obtained in some families of Lepidoptera. That of de Vries, Davis, Bartlett, and others on *Oenothera* and of East and others on *Nicotiana* has demonstrated the same thing for these groups. The list might be continued at length, but the examples given include many of the most thoroughly studied cases. None of the groups known to be favorable for hybridization, however, fulfils the other requirements necessary for a detailed study of chromosome relationships, such as we are considering here.

The genus *Drosophila* has long been known to include species that are excellent for breeding purposes, and the pioneer work of Morgan and others on *D. melanogaster* indicated that this species, at least, mutates frequently enough to provide ample material for genetic analysis. Consequently, when it was found (Metz, 1914) that other species of *Drosophila* differed from *melanogaster* and from one another in respect to their chromosomes, it was recognized that the material offered unusual possibilities for a study of chromosome relationships and chromosome evolution. The only uncertainty was with regard to the possibility of hybridization. If favorable in that respect, all of the above requirements would be fulfilled. With this in mind, an extensive series of tests was carried out cooperatively by Dr. A. H. Sturtevant and one of us (Metz) during 1914 and 1915, involving most of the species obtainable in the United States and Cuba, save those that were not at all amenable to laboratory treatment. The results of these tests were all negative, however. This presented a serious difficulty, since it indicated that if such a comparative study were undertaken with this material it would be necessary to make separate genetic studies of selected species and then compare the results.

However, an excellent foundation for such an investigation was provided by the well-known observations on *D. melanogaster;* and since a study of this kind promised to be of interest in several additional respects, it was undertaken.

It should be noted at this point that Dr. Sturtevant has recently succeeded in hybridizing *D. melanogaster* and *D. simulans* (Sturtevant, 1920) with very interesting results. For the purposes outlined above, however, the possibilities here are limited. The two species are almost identical and appear to have identical chromosome groups, and in addition the F_1 hybrids are sterile, so that only mutant

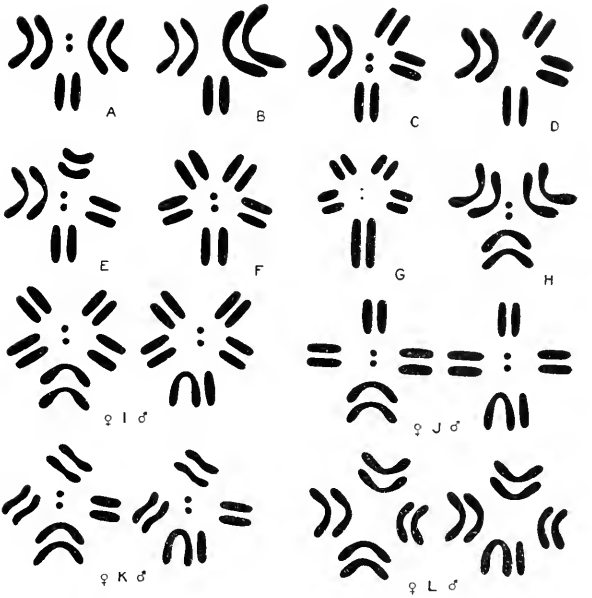


FIG. 1.—Types of *Drosophila* chromosome groups. (From Metz, 1916*b*). All but type H are found in the genus *Drosophila*. H is from *Cladochaeta nebulosa* Coq.

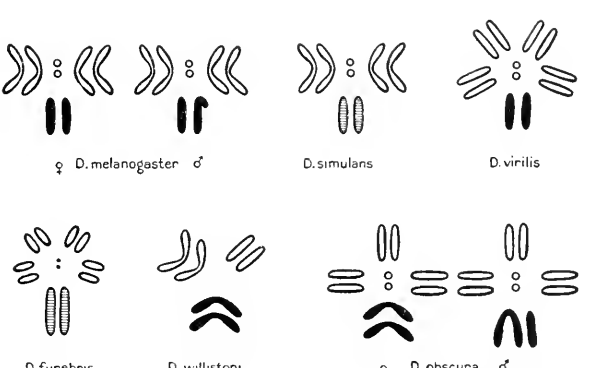


FIG. 2.—Chromosome groups of species of *Drosophila* which are being studied genetically.

genes obtained in both species can be used for comparison. Further details concerning this case are given in a later section.

Owing to the fact that the material for the present work, and for other investigations of a similar kind, has been selected largely on the basis of apparent chromosome relationships, these may be considered briefly here.

CHROMOSOME RELATIONSHIPS.

The known types of chromosome groups found in the genus *Drosophila*, with the addition of one type from the related genus *Cladochæta*, are represented in figure 1 (from Metz, 1916*b*). A detailed comparison of the various types is given in the paper just cited, and we may limit ourselves to features concerning the species under genetic observation. The types represented by the latter are shown in figure 2.[1] In this figure the sex chromosomes, where identified are represented in solid black, and where not definitely known, the ones presumed to be the sex chromosomes are cross-ruled. Considering first the sex chromosomes, it may be noted that two main kinds are involved—the short, rod-like form found in *D. melanogaster, simulans,* and *virilis*, and the long V-shaped form found in *willistoni* and *obscura*. In *funebris* the sex chromosomes have not been identified, although the behavior of the longest pair suggests that it represents the sex chromosomes.

Comparing the autosomes, it is seen that the same two sorts are represented—short rods and long V's—in addition to the small, dot-like pair common to all save possibly *D. willistoni*. In both the autosomes and the sex chromosomes, it is to be noted that the V-shaped members are approximately twice the size of the rod-like ones (with the exception of one pair in *D. funebris*) and that each has a constriction in the middle. This suggests a possible relationship between the types which may best be appreciated, perhaps, by imagining all of the V-shaped chromosomes broken in the middle, at the point of constriction. With this alteration all of the groups conform essentially to one type, that represented by *D. virilis*.

For the present purposes, this series of chromosome groups represents an almost ideal condition. There are clear-cut differences between the types, yet the differences do not appear to be purely at random, and it is possible to compare the individual types, chromosome for chromosome.

The relations between the types suggest the hypothesis that the latter have arisen by a process involving the breaking up of large V-shaped chromosomes into rods or, vice versa, by the fusion of rods to form V's. If this hypothesis is correct, genetic analysis should reveal the fact through the resemblance between groups of linked

[1] Exclusive of two or three species which have only been studied slightly.

characters, or portions of such groups, in the different species. For instance, each of the large non-sex-linked groups of characters in *D. melanogaster* should resemble two of the groups in *virilis* combined, while the sex-linked groups should correspond in the two species. This is only one of the possible hypotheses to cover the case, but it will serve to illustrate the mode of attack.

FIG. 3.—Camera lucida drawings of chromosomes of *Drosophila virilis*. 1 and 2 from ovarian cells, 3 from a spermatogonial cell.

Such considerations are, of course, based on the assumption that homologous mutant characters may be found in the species concerned. The validity of this assumption is becoming more and more probable as the work progresses (see below), and the question now hinges mainly on whether or not a *sufficient number* of homologous characters may be obtained for the purpose.

CHROMOSOMES OF DROSOPHILA VIRILIS.

The chromosome group of *D. virilis*, as noted above, consists of 6 pairs, 5 of which are rod-like and of approximately the same size, and 1 of which is small and spherical. The small pair normally lies in the center of the figure during metaphase, as shown in the accompanying figures (fig. 3). In size, position, and behavior this pair agrees with the similar pair in most other species of *Drosophila* (Metz, 1916*b*).

The five pairs of rod-like chromosomes have a terminal spindle-fiber attachment and hence are usually arranged radially in metaphase (figs. 1 and 2, Metz, 1916*a*). As in other species of Diptera, homologous chromosomes are normally associated in pairs in the somatic cells, as well as in the germ cells.[1]

In some figures one of the five rod-like pairs appears to be slightly longer than the others, suggesting that it may represent the sex chromosomes. But since no pair is conspicuously dimorphic in the male, this view has not been corroborated. It seems practically certain, however, from both cytological and genetic evidence, that one of the rod-like pairs, and not the small spherical pair, is the sex-chromosome pair.

[1] For a discussion of this feature see Metz, 1916*a*.

PREVIOUS WORK ON DROSOPHILA VIRILIS.

In earlier papers on *Drosophila virilis* (Metz and Metz, 1915; Metz, 1916*c*, 1916*d*, 1918, 1920; Weinstein, 1920) it has been shown that the genetic behavior of this species agrees in a general way with that of the well-known *D. melanogaster* and that some of its mutant characters bear a striking resemblance to those of *melanogaster*. In genetic behavior, for instance, the two species agree, (1) in that "crossing-over" occurs only in the female, (2) in that the Y chromosome appears to be functionless as far as the ordinary Mendelian characters are concerned, and (3) in that the number of groups of linked characters agrees with, or at least does not exceed, the haploid number of chromosomes. In regard to the resemblance between mutant characters, it has been found that the four characters confluent, yellow, forked, and crossveinless are sufficiently similar in the two species to give some ground for believing them to be homologous, and that the likeness between certain others suggests a similar relation.

PRESENT AIM OF THE WORK.

With the completion of the preliminary tests, concerning the general genetic behavior of *D. virilis*, attention was directed particularly to the genetic analysis of the chromosomes by means of mutant characters, and a detailed comparison of the results with those obtained in other species of *Drosophila*. The latter feature, and the work of the different investigators involved, is considered in detail in later sections. It may be stated at the outset that the studies have not yet progressed to the point of giving final answers to the main questions toward which they are directed. The aim of the present paper, therefore, is primarily to bring together the data and to indicate the trend of the results thus far obtained. For this reason it is largely descriptive. The descriptive part is also emphasized, necessarily, because of the fact that detailed information concerning both the appearance and the genetic behavior of mutant characters is necessary before those of different species can be compared satisfactorily.

DESCRIPTION OF DROSOPHILA VIRILIS.

The following taxonomic description of *D. virilis* Sturtevant is taken from Sturtevant's (1921*c*) "The North American species of *Drosophila*," p. 97:

"♂, ♀. Arista with about five branches above and two below. Antennæ brown, third joint dark opaque reddish-brown. Front over one-third width of head, wider above; dull coffee-brown, ocellar dot black. Second orbital one-third other two. Second oral bristle three-quarters length of first. Only one long bristle on each palpus. Carina broad, slightly sulcate, nose-like; face somewhat shiny, brown. Cheeks yellowish brown; their greatest width over one-fourth greatest diameter of eyes. Eyes pilose.

"Achrostichal hairs in six rows; no prescutellars. Mesonotum and scutellum dark dull-brown. Pleuræ and abdomen dull brown, somewhat darker. Legs pale brown. Apical and preapical bristles on first and second tibiæ, preapicals on third.

"Wings clear, veins brown. Costal index about 2.8; fourth-vein index about 1.8; 5*x* index about 1.2; 4*c* index about 0.9.

"Length body 2.8 mm.; wing 3.0 mm.

"The eggs have four filaments. The females do not ordinarily begin to lay until they are 4 or 5 days old. About 3 weeks are required for development.

"The small eyes and broad cheeks make this species obviously distinct from such types as *D. robusta* that resemble it superficially."

Supplementary to the above, especial attention may be called to certain characteristics that are particularly noticeable in living specimens or that need to be kept in mind in considering the comparison of mutant characters with those of other species: The dark dull-brown body-color and large size of *D. virilis* contrast sharply with the yellowish gray color and small size of such species as *D. melanogaster*, *D. simulans*, and *D. willistoni*. The color more nearly resembles that of *D. obscura*, but is duller and lighter. It is duller and darker than that of *D. funebris* and lacks the olive tone of the latter. The eyes of *D. virilis* are dark, dull, reddish brown, more opaque than those of *melanogaster*, *simulans*, *willistoni*, or *obscura*. *Virilis* males do not possess the tarsal "sex-combs" found in *melanogaster*, *simulans*, and *obscura*. In this respect they agree with the males of *willistoni* and *funebris*. A wild-type or normal male of *D. virilis* is shown in figure 1 of plate 1.

SOURCE OF MATERIAL.

The original stock of *Drosophila virilis* Sturtevant, used in our experiments, was derived from a single pair hatched from a pineapple exposed at Columbia University, in November, 1913, by Dr. A. H. Sturtevant. Nearly all of our work has been based on descendants of this one pair, which have been kept in the laboratory, in bottles, for 8 years, or approximately 136 generations. In 1919 a second stock collected at Terre Haute, Indiana, was obtained from Dr. Roscoe Hyde. One mutant character (hump) was found in this stock soon after it was secured and others appeared subsequently. The two stocks have been more or less intercrossed in the course of the experiments. They appear to be identical in all respects and we have made no effort to keep them separated.

Since no other records of this species are known save one from Los Angeles, California, and one from a doubtful specimen taken at Chattanooga, Tennessee (Sturtevant, l. c., p. 97), it is practically certain that our stocks have never been contaminated from sources outside the laboratory.

It may be noted in this connection that no decrease in fertility has been observed in the stocks during their 8 years' confinement in the laboratory.

METHODS EMPLOYED.

Detailed methods of treatment of the data are given under the respective headings below, but the following general features may be noted at this point.

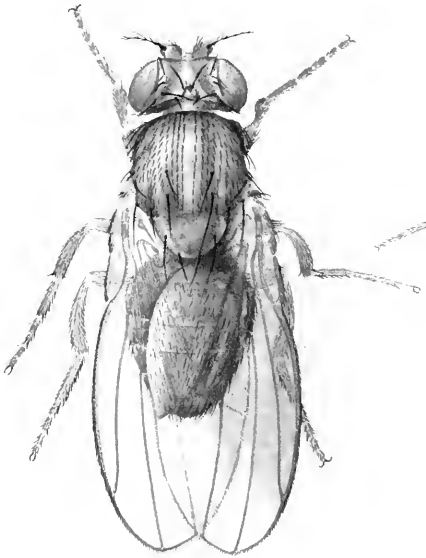
For the sake of convenience, a description of each mutant type is given in the present paper, whether it has been published previously or not. Some of these include features that have previously been overlooked or omitted. In connection with the descriptions brief notes are added (under "Comparison"), indicating resemblances to characters in the other species, if such exist. The absence of such comparison indicates that no similar characters are known to us. These comparisons are given very briefly, for a full consideration of such relationships is included in later sections.

The terminology used is that commonly employed at the present time in animal genetics. Symbols have been avoided as far as is practicable in the tables and text, although they have necessarily been used extensively. Recessive mutant characters, or genes, are designated by small letters and dominants by capitals. Superscripts are employed only in the case of multiple allelomorphs.

In order to simplify treatment of the experimental data, the name of a mutant type is frequently used to designate either the character itself or the gene responsible for the character or the locus of the gene, without distinction. Although this usage is possibly open to some criticism, its great convenience justifies its adoption, we believe, at least when care is taken to qualify the expression where clarity demands.

Since the purpose of this study is comparative, the linkage experiments have been carried only far enough to indicate the relative order of the genes and their approximate "locations" on the chromosome map. No corrections have been made for differential viability or double crossing-over in constructing the maps. Likewise, map values have in nearly all cases been given in whole numbers. It is believed that any attempt to make a more refined calculation or to express values in decimals would in most cases give a false impression of accuracy. It is for this reason, for instance, that the method suggested by Fisher (1922) has not been used. For certain types of work the latter method promises to be useful, but, as indicated by Fisher himself, when applied to cases like the present it gives values only slightly different from those obtained by the more simple method of calculation used here.

Several characters have been included which overlap normal to such an extent as to make them unsatisfactory for detailed linkage studies, but which are valuable for comparative studies. On the other hand, sex-linked lethals have been omitted, since they are of little value for purposes of comparison.



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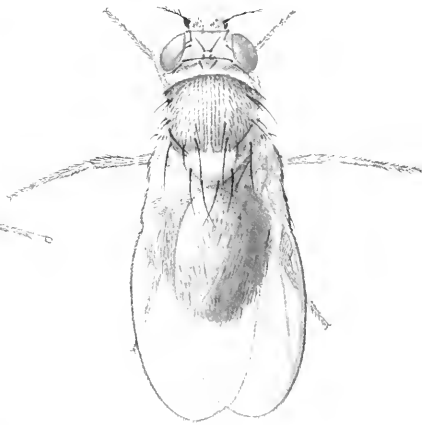

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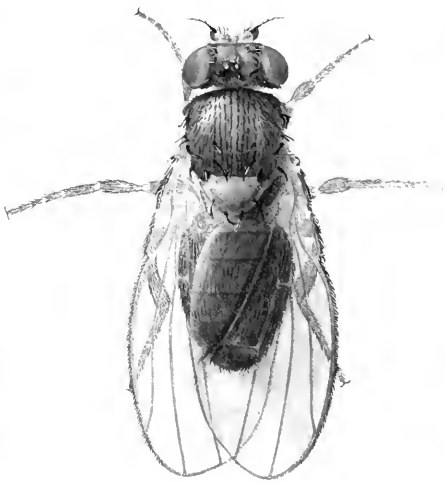

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E. M. Wallace Pinx.

SEX-LINKED MUTANT CHARACTERS IN DROSOPHILA VIRILIS

In a study of this kind, in which new characters are appearing from time to time, there are always some on hand which have not been fully studied in respect to linkage. This is true of several in the present case. These have been included for the sake of completeness, although in some instances little can be given beyond the description of the character and its mode of origin.

The method of detecting linkage among non-sex-linked characters, and thus of assorting them into linkage groups, has been by means of F_2 counts, and back-crosses of heterozygous males. In the earlier experiments each new character was tested with representatives of all known linkage groups, and most of the characters have been so tested; but more recently the tests have been discontinued as soon as a character was found to be linked to one of the test characters. The data from these purely test experiments are not included, except in the cases showing linkage.

In considering each linkage group, the data from the test experiments are all given first; then follow the experiments from which crossover values are taken. This method of treatment facilitates examination of the linkage data.

The order of the genes on the maps has been determined in the usual manner, mainly by means of three-point crosses. In the latter case the smallest cross-over class has been assumed to represent the double cross-overs and the order has been arranged accordingly. In a few cases the order has been determined by "locating" a gene with reference to two others independently.

The records of matings given in the text and tables refer to the original laboratory notes. Those not prefixed, or prefixed by V, L, or M are records of C. W. Metz, those prefixed by E are records of E. D. Mason, and those prefixed by P are records of M. S. Moses.

ACKNOWLEDGMENTS.

We are indebted to Professor T. H. Morgan and to Doctors A. H. Sturtevant, C. B. Bridges, and D. E. Lancefield for the loan of specimens and for information concerning mutant characters in other species of *Drosophila*, and also for suggestions as to their possible relationships to characters in *D. virilis*. Dr. Bridges has furnished information on *D. melanogaster*, Dr. Sturtevant on *melanogaster* and *simulans*, and Dr. Lancefield on *obscura*. Our indebtedness is particularly great to Dr. Sturtevant, whose interest and cooperation have added materially to the progress of the work from its inception. We likewise acknowledge with gratitude the assistance of the following persons, who made the drawings and photographs for the accompanying figures: Miss E. M. Wallace, figures 5 and 12 and plate 1; Miss G. Ruth Lincks, figures 4 and 6; Miss E. M. Lord, plates 2 to 4.

II. LINKAGE GROUP I. SEX-LINKED CHARACTERS.

The sex-linked group consists of 18 characters. These are listed in table 1 in chronological order. The first 10 have been described previously (Nos. 1 to 4, Metz, 1916*d*; Nos. 5 to 8, Metz, 1918; No. 9, Metz, 1920*b*; No. 10, Weinstein, 1920). In the accompanying descriptions the order of treatment is not chronological, but conforms to the order of the genes on the chromosome map. Under each heading is given a description of the character, an account of its origin, and a comparison with similar characters in other species where such are known.

TABLE 1.—*Chronological list of sex-linked characters in Drosophila virilis.*

Character.	Symbol.	Parts affected.	First observed.	Found by—	Record.
Yellow	y	Body-color	Jan. 1916	B. S. Metz	2127.
Magenta	m	Eye-color	June 1916	C. W. Metz.	ac stock.
Glazed	r^g	Eyes	Do.	Do.	stock.
Forked	f	Bristles	Do.	Do.	C stock.
Rugose	r	Eyes	Do.	Do.	V 611.
Vesiculated	vs	Wings	July 1916	Do.	V 290.
Frayed	fd	Abdomen	Sept. 1916	Do.	V 590.
Hairy	ha	Eyes	Nov. 1916	Do.	V 745.
Wax	r^w	Eyes	May 1917	Do.	V 1095.
Crossveinless	c	Wing veins	Nov. 1917	Weinstein	Weinstein, 1920.
Triangle	T	Wing veins.			
Vermilion	v	Eye-color	Oct. 1919	Mason	E 1.
Sepia	se	Eye-color	Do.	Metz	L 404.
Droop	dp	Wings	Mar. 1920	Mason	E 780.
Singed	si	Bristles and hairs	Oct. 1920	Moses	P 220.
Short	s	Wing veins	Nov. 1920	Do.	P 384.
Oblique	o	Wings	June 1922	Metz	M 47
Cut	ct	Wings	Do.	Do.	M 102.

DESCRIPTION, ORIGIN AND COMPARISON OF SEX-LINKED CHARACTERS.

SEPIA (se). (Plate 1, Figure 6.)

Description.—The only visible effect of sepia is on the eyes, which are deep opaque brown, almost lacking in red. The character is readily recognized in both young and old flies, but is most striking in young ones.

Origin.—(L404) 8 sepia males were obtained from a mating of 2 heterozygous pinched females with one mosaic (or deformed) male. (The male may have been a true mosaic or merely deformed by injury. Its left wing was short and the scutellar bristles on the left side were forked. Evidently its germ-cells were not affected, however, for the character did not appear again in its descendants.)

Comparison.—Sepia bears a general resemblance to various dark eye-colors in other species (e. g., prune, ruby, purple in *Drosophila melanogaster*, and prune and plum in *D. simulans*), and also to magenta and garnet in *D. virilis*. The flat or opaque nature of the color, with a minimum of red in its composition, particularly suggests "prune" in *melanogaster* and *simulans*.

YELLOW (y). (Plate 1, Figure 2.)

Description.—Yellow changes the ground-color of the entire fly from dark brown to yellow (compare figs. 1 and 2, plate 1). The change is especially noticeable in the wings, although it is readily observable in body and legs, especially in young flies. Very old flies are darkened, so that the body-color approaches that of pale specimens of non-yellow stocks. The color of the hairs and bristles in yellow flies is not noticeably different from normal. They may be faintly tinged with bronze, but if so the change is very slight. Yellow averages slightly later than normal flies in hatching, and has somewhat lowered viability.

Origin.—(1281, 2127.) Several males appeared in a mass culture. (See Metz. 1916*d*, p. 599.)

Comparison.—Yellow resembles the "yellow" of *D. melanogaster*, *D. simulans*, *D. willistoni*, and *D. obscura*, except for its brown instead of bronze or yellow bristles and hairs.[1] In each of these species the character is sex-linked, and it is possible that they are all homologous.

FRAYED (fd).

Description.—In frayed flies the dorsal bands of the pigment on the abdomen are frayed out or irregularly broken at the ends as they extend down the sides of the body. Accompanying this are various other modifications. Almost the entire fly is affected in some way (see figs. 3 and 6, Metz, 1918); the thoracic bristles are reduced to little more than hairs; some of the bristles on the head are entirely gone; frequently the aristæ, and sometimes the entire antennæ, are abortive or wanting; the wings are frequently broken and disarranged in various ways; and finally, development is retarded several days, so that frayed flies hatch several days later than normal. Frayed is recessive to wild-type. The stock was lost soon after the character first appeared, owing to the sterility of the females.

Origin.—(V 590.) Several males appeared in a mass culture (see Metz, 1918, p. 110).

CROSSVEINLESS (c). (Plate 1, Figure 2.)

Description.—This character is distinguished by the absence of the posterior cross-vein and sometimes part or all of the anterior cross-vein.

Origin.—(See Weinstein, 1920.)

Comparison.—Crossveinless resembles the crossveinless of *D. melanogaster* and non-sex-linked characters of the same general type in *D. obscura* and *D. willistoni* (unpublished data).

VERMILION (v). (Plate 1, Figure 5.)

Description.—Vermilion, like sepia, is an eye-color character. The color is near Ridgeway's scarlet, but slightly darker and more yellowish. Vermilion is also characterized by the presence of the dark fleck in the eye, which is absent in the other stocks of *virilis*. It bears a close resemblance to the eye-color of the wild type *D. melanogaster*, with perhaps a darker tinge. It can be distinguished from normal in flies of any age.

Origin.—(E 1.) One male was found in a stock bottle.

Comparison.—In appearance vermilion suggests the characters of the same name in *D. melanogaster*, *obscura*, and *willistoni* (unpublished data of Miss Ruth Ferry), although the actual color is considerably darker than in these species.

VESICULATED (vs). (Plate 2, Figure 2.)

Description.—Vesiculated is characterized by the presence of vesicles or blisters in the wings. Occasionally the entire wing may be swollen into a single large vesicle

[1] In the latter respect it suggests "lemon" in *D. melanogaster* (Morgan and Bridges, 1916). In lemon, however, the males are infertile and have low viability, and the females are unknown.

filled with liquid, but usually there is only a small blister, or perhaps two near the center of the wing. Frequently only one wing is affected, and ordinarily in from 1 to 5 per cent of the cases both wings appear to be normal. The viability of vesiculated stock is good, and aside from the inconstancy just mentioned the character is good for linkage studies.

Origin.—(V 290.) Several males were obtained from a mass culture (see Metz, 1918, p. 107).

Comparison.—Vesiculated suggests "inflated" in *D. melanogaster* (Weinstein, 1918), "bubble" in *D. simulans* (Sturtevant unpublished data), and "inflated" in *D. funebris* (Sturtevant, unpublished data).

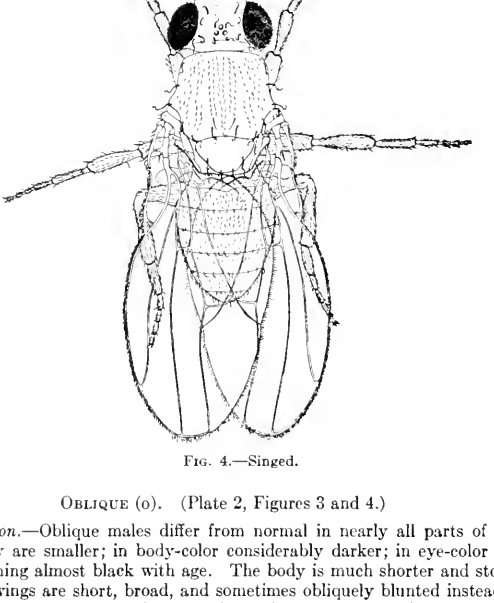


FIG. 4.—Singed.

OBLIQUE (o). (Plate 2, Figures 3 and 4.)

Description.—Oblique males differ from normal in nearly all parts of the body. In size they are smaller; in body-color considerably darker; in eye-color extremely dark, becoming almost black with age. The body is much shorter and stouter than usual, the wings are short, broad, and sometimes obliquely blunted instead of being rounded (fig. 3, plate 2), and usually hang down over the sides of the abdomen, roof-like, instead of being held horizontally. The fifth vein is often short and the posterior crossvein is often broken or wanting. Oblique females are sterile and consequently pure stock has not been obtained. The name of this character was taken from its appearance in combination with short. In this combination both characters are exaggerated; the wings are frequently very short and cut off obliquely at the tips (fig. 4, plate 2), and the veins are shortened more than in ordinary "short" flies.

Origin.—(M 47.) 16 oblique males were found among the offspring of 2 females heterozygous for vermilion and short.

SINGED (si). (FIGURE 4.)

Description.—Singed affects the bristles and hairs, particularly on the body and legs. The bristles are shortened and depressed and are twisted and curled, as if singed. The hairs are likewise depressed and sometimes curled. The hairs in the wings are affected slightly, if at all. Those on the costa lie in approximately a normal position, instead of standing out at an angle from the wing, as they tend to do in forked flies. The eggs and the body-color are normal, or very near normal. The character is ordinarily used as a recessive, and is the same in males and in homozygous females. It is possible to distinguish heterozygous females from the wild type, however, by their shorter, less tapering bristles. Singed flies have good viability, and both sexes are fertile, making the character one of the most useful for linkage studies.

Origin.—(P. 220.) A single male was obtained from glazed stock.

Comparison.—(See page 60.)

HAIRY (ha).

Description.—Superficially hairy resembles "rugose," but it lacks the light color of the latter and has a sprinkling of heavy black hairs over the eye-surface, giving it a peculiar bushy appearance entirely wanting in rugose. Typical specimens of hairy are readily recognized, but the character varies considerably and is not always readily distinguished. The stock was discarded after a few linkage experiments were completed.

Origin.—(V 745.) One male was found among the offspring of a single pair. (See Metz, 1918, p. 60.)

MAGENTA (m). (Plate 1, Figure 7.)

Description.—Magenta is very similar to sepia, but is slightly more reddish in tone and is a "deeper" or more "liquid" color instead of being "flat," as in the case of sepia. The character is more marked in the males than in the females, but is usually readily recognizable in either sex. It is almost, if not quite, indistinguishable from the third chromosome dominant "garnet." The viability of magenta flies is excellent and the character is one of the best for linkage studies.

Origin.—Magenta was first observed in half of the sons of an "acute" female. (Metz, 1918, p. 599.)

Comparison.—Magenta suggests "garnet" in *D. melanogaster* and "carmine" in *D. simulans*.

FORKED (f). (Plate 1, Figure 3.)

Description.—In forked flies the bristles on the head, thorax, and legs are shorter and stouter than usual, are often irregularly twisted, or bent at sharp angles, and a few are usually forked. The hairs are not greatly affected, but are somewhat stouter and less tapering than usual. The thorax is darkened and has a characteristic glossy appearance. Males and homozygous females are similar; heterozygous females, like those of singed, have the bristles slightly shortened. The eggs appear to be normal.

Forked resembles singed in its affect on the bristles and hairs, but is much less extreme than the latter. The bristles and hairs are not flattened down or tightly twisted as in singed. On the legs they are only slightly affected in forked, while they are markedly affected in singed flies. The marginal hairs on the costal vein of the wing stand out at a greater angle than usual, especially toward the back of the wing.

In singed the hairs on the abdomen are twisted and depressed, while in forked they are almost normal. In the double recessive forked-singed males the hairs and

bristles resemble singed, but the presence of forked is revealed by the dark, glossy color of the thorax. Both sexes are fertile, but have poor viability.

Origin.—A single male from a mating in which only one female parent was used. (See Metz, 1916, p. 600.)

Comparison.—(See p. 60.)

TRIANGLE (T). (Plate 2, Figures 5 and 6.)

Description.—Triangle flies usually have an extra cross-vein between the costal and second veins near their junction, and have the anterior cross-vein thickened at its junction with the third vein (fig. 6, plate 2). The latter characteristic can usually be detected in the few flies that fail to show the former. Sometimes the character resembles the non-sex-linked dominant confluent. Triangle is a dominant character, but is not lethal when homozygous.

Origin.—The origin of triangle is not definitely known, since it was for a time confused with branched, a non-sex-linked character. The separation of triangle from branched was accomplished by Dr. Alexander Weinstein.

SHORT (s). (Plate 2, Figure 7.)

Description.—Short is more extreme in the males than in the females. In the former the fifth vein is greatly shortened. Usually it does not extend much beyond the posterior cross-vein, and frequently does not reach this vein. Approximately half of the flies have the fourth vein slightly shortened also. In extreme cases the cross-vein curves back to meet the fifth vein, or is curved back toward it, instead of being straight. In the females the fifth vein is usually slightly shortened, but the fourth is seldom affected, and often the wings appear to be normal.

Origin.—(P. 384.) One male was obtained from a pair mating.

Comparison.—Short resembles the character of the same name in *D. willistoni* (Lancefield and Metz, 1922) and in *D. obscura* (D. E. Lancefield, 1922).

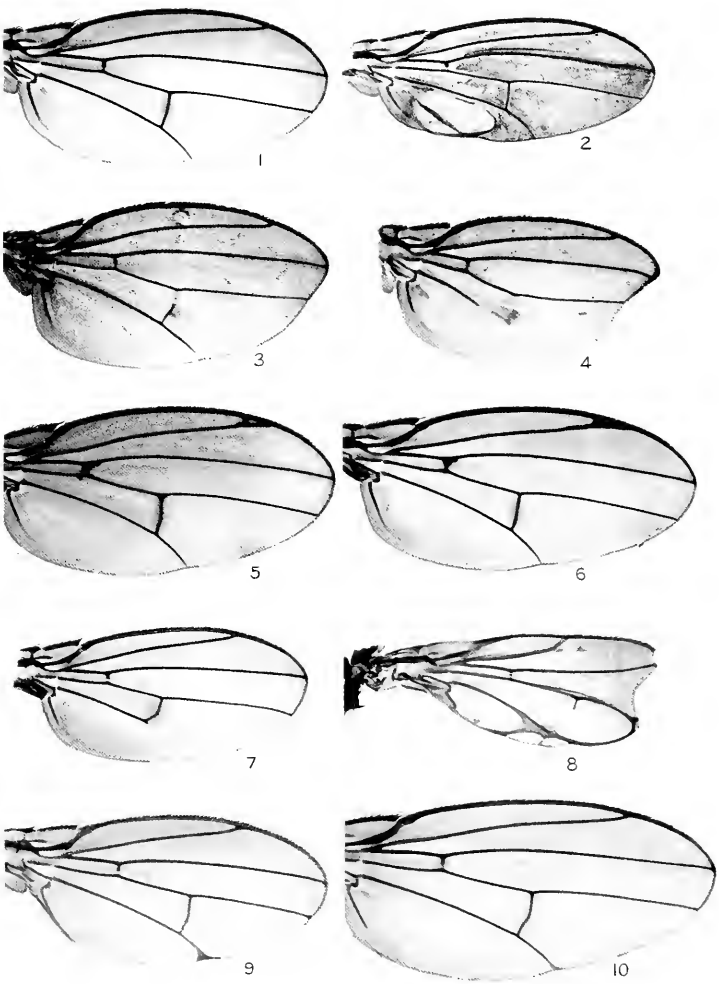
CUT (ct). (Plate 2, Figures 8 to 10.)

Description.—It should be noted in connection with the following description that the gene for cut, if not allelomorphic to that for short, may be accompanied by short in the same chromosome, and hence the effects described may be due to the combination and not to cut alone. Cut flies, of both sexes, have short, narrow wings, held at an angle from the body, and cut in at the apex, between the longitudinal veins (fig. 8, plate 2). The cuts vary in depth from slight indentations to deep incisions. The venation is irregular; the costal vein ends between the second and third veins; the tips of the fifth, and sometimes of the other veins, are swollen, delta-like; the second vein occasionally fails to reach the margin, and may fork at the tip or send off a branch toward the third vein; the posterior cross-vein is usually gone or broken; the anterior cross-vein is thickened, and lateral branches or swellings frequently project from the longitudinal veins. The more common positions for the latter are down from the second vein and from the fourth vein near the apex. Frequently the wings are very small and are swollen or blistered. The anterior scutellar bristles are usually gone, or small and slender, and the posterior scutellars are often erect, or in abnormal positions, while the scutellum itself is shorter than usual.

Cut flies do not breed readily, but both sexes are fertile to some extent and it is possible to keep pure stock.

In some (and possibly all) females heterozygous for cut, the tip of the fifth vein is slightly thickened or delta-like (fig. 10, plate 2). This feature was overlooked at first, hence we are not certain that it is constant.

In females heterozygous for cut, and carrying short in the opposite X chromosome (possibly homozygous for short), the wings are smaller than usual, are held at an angle from the body, and usually droop down over the sides; the tips of the fifth



SEX-LINKED MUTANT CHARACTERS IN DROSOPHILA VIRILIS.

1, Wild-type; 2, Vesiculated; 3, Oblique; 4, Oblique short; 5, Triangle; 6, Triangle; 7, Short; 8, Cut; 9, Heterozygous short cut ♀; 10, Heterozygous cut ♀.

veins, and sometimes of the third, are delta-like (fig. 9, plate 2); the posterior cross-vein is sometimes broken, and occasionally the entire wing is soft in texture.

The origin and behavior of cut are such that we are unable to tell, as yet, whether the character is an allelomorph of short or is due to a dominant modifier closely linked to short. The character itself seems to be of the opposite nature from that of short, increasing instead of diminishing the size of the veins, which argues somewhat against its being an allelomorph. On the other hand, it should be noted that in females heterozygous for cut the same vein (fifth) is affected as is affected by short. The absence of cross-overs between the two genes (thus far) indicates that if not allelomorphic they must be very closely linked.

Origin.—(M 102.) From a mating (M 40) of a female heterozygous for short and vermilion, by 2 short garnet brothers, approximately 200 offspring of the expected classes were obtained, and in addition one female with the wings slightly spread and the end of each fifth vein thickened. This female proved to be heterozygous for cut. Her daughters were all normal, but her sons were of two classes, approximately half (19) short and half (16) cut. The data in this case show that the mother of this exceptional female was not heterozygous for cut, else cut sons and additional heterozygous daughters should have appeared. The mutation evidently occurred in one of the parents or in the egg that gave rise to this female.

Comparison.—Cut shows a slight resemblance to "bifid" in *D. melanogaster* (Morgan and Bridges, 1916, p. 29), but not enough to make homology probable.

RUGOSE (r).

Description.—This character derives its name from the roughening of the eye due to disarrangement of the ommatidia (fig. 4, Metz, 1918). The color of the eye is also affected, being considerably lighter than normal and having a more yellowish tinge. The eye is full-sized, however, and the ommatidia are not coalescent, as they tend to be in the two following characters glazed and wax. Rugose is sex-limited, appearing only in the males. Its viability is excellent.

Origin.—(V 611.) One male from a pair mating of a confluent male by normal female (Metz, 1918, p. 110).

GLAZED (r^g).

Description.—Glazed is a more extreme eye modification than its allelomorph rugose. The ommatidia show greater disarrangement, many are lacking, leaving smooth spaces on the eye-surface, and others tend to coalesce. The whole eye has a glazed or varnished appearance, but lacks the lighter color shown by rugose. It appears in both sexes. Glazed females are usually sterile and the males have poor viability, making the character less useful than rugose.

Origin.—Glazed appeared slightly before, and independently of, rugose. One male was found in a mass culture (see Metz, 1916*d*, p. 599).

Comparison.—(See under wax, below.)

WAX (r^w).

Description.—Wax flies resemble glazed, but the eyes are more extremely affected. They are of a pale yellowish, uneven color, and the ommatidia are fused together, or absent, so that the surface of the eye has a waxy appearance. The eyes are considerably reduced in size and are narrowed, leaving a white zone much broader than usual around the margin. In the eye itself on the posterior side there is often a white or cream-colored patch resembling a vesicle. Wax, like glazed, appears in both sexes and has sterile females.

Origin.—(V 1095.) Three males were found in a stock bottle carrying fused.

Comparison.—In appearance wax and glazed both resemble the sex-linked character "lozenge" in *D. melanogaster*. The eye of lozenge more nearly approaches

glazed in structure, but it is more like wax in shape, and has a bushy appearance, due to heavy black hairs or clusters of hairs on the surface. Lozenge females appear to be partly sterile, but do not show such a high degree of sterility as do those of glazed and wax. An allelomorph of lozenge—lozenge-2—bears a close resemblance to wax in appearance, and probably had sterile females, according to information

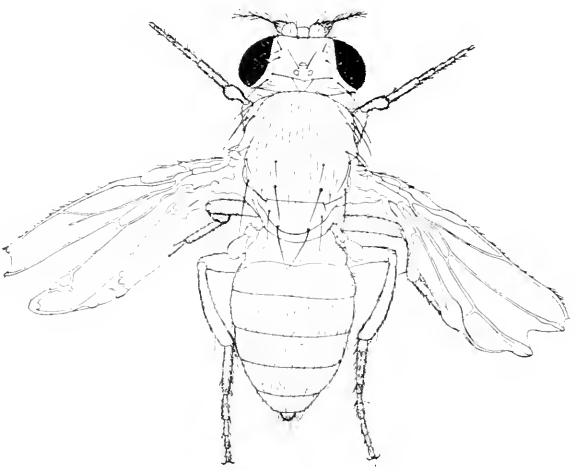


FIG. 5.—Cut.

DROOP (d). (Figure 6.)

furnished us by Dr. Sturtevant and Dr. Bridges. The stock of lozenge-2 has been lost, however, and we have not been able to compare specimens with those of wax.

Description.—The wings of droop flies curve downward or droop at the ends. The character usually appears in both wings, but sometimes appears only in one or fails to appear at all.

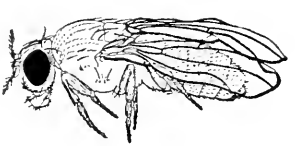


FIG. 6.—Droop. (Legs are normal, not short, as indicated.)

Origin.—(E 780.) 14 droop males were obtained from a pair mating of scaly flies, indicating that the mother was heterozygous for droop.

Comparison.—In appearance droop resembles the sex-linked character "depressed" in *D. melanogaster* (Morgan and Bridges, 1916, p. 67), but differs from the latter in being inconstant.

LINKAGE IN GROUP I, AND CONSTRUCTION OF X-CHROMOSOME MAP.

(Figure 7.)

In a previous paper (Metz, 1918) the linkage of the 8 characters yellow, frayed, vesiculated, hairy, magenta, forked, rugose, and glazed was considered, and a "chromosome map" constructed with the genes placed in the order given. Two of the genes were "located" only provisionally—frayed because the stock was lost, and hairy because of insufficient data. The position of frayed (with reference to yellow) remains uncertain; but that of hairy is now known to be to the "left" (i. e.,above) instead of to the right of magenta (Weinstein, 1920, and present data). Weinstein (l. c.) has "located" the gene for the character crossveinless at 17.6, or about 2 units to the left of vesiculated.

In the present paper the genes for the new characters are "located" with reference to those already known, and additional data are given on several of the latter. Unless otherwise specified the new data in the tables include only the male offspring from the various matings.

In this connection we would emphasize the fact that we have made no attempt to carry out a detailed and exhaustive study of linkage, even in the sex-linked group of characters. This would represent a separate study, aside from the purpose of the present work, and one which can be carried out much better after more mutant characters are obtained. It will be noted, therefore, that numerous experiments which would be of value for a critical study have not yet been made.

Since chromosome "maps" are now usually placed vertically, instead of horizontally, on the page, the terms "above" and "below" are here used in place of "left" and "right," respectively.

The data from linkage experiments on sex-linked characters are given in full on pages 78 to 88 (experiments 1 to 53) and are summarized in table 2. These are arranged according to the number of genes concerned and the order of the loci on the chromosome map, beginning with the "zero end." Thus the first experiments are those involving 2 pairs of genes, then those involving 3 pairs, and so on; and in each series the uppermost loci are considered first. The summary in table 2 includes the calculated cross-over percentages for successive regions in each experiment.

The present section deals separately with the linkage data on each successive gene, and indicates the method and data used in "locating" the genes and constructing the map. The data are included, in summary form, in table 3, although not all of the data in this table are used in constructing the map. For the latter purpose, an effort has been made to use the experiments considered most reliable, and particularly those involving adjacent loci. By

consulting tables 2 and 3 in connection with the following considerations, the data on each locus may be evaluated as they are taken up for treatment. Table 3 gives the data for each gene in the order of treatment, together with the experiment number and the number of flies involved. The latter indicates the relative value of the experiments in respect to numbers, and the experiment number permits reference to table 2, which indicates the number of genes involved in the experiment and other details that aid in evaluating it.

SEPIA.

In previous papers yellow has been placed at the zero-point on the map; but sepia, as shown by experiment 19 (table 2) occupies a position "above" that of yellow, and thus becomes the terminal gene. Sepia and yellow give approximately 5.6 per cent crossing-over, placing yellow at about 6.

YELLOW.

Yellow is one of the most frequently used characters, and its locus has served as a base in numerous experiments, as shown by table 3. Its relation to sepia has been considered under sepia (experiment 19). This placed yellow at 5.6 units from sepia. With crossveinless it averaged 18.7 per cent crossing-over, with vermilion 19.6 per cent and with vesiculated 18.8 per cent. All of the latter three values should be increased slightly by correction for double crossing-over.

FRAYED.

Frayed was only used in three experiments before the stock was accidentally lost. One of these (experiment 2) was with forked. It gave almost 48 per cent of crossing-over, showing that the frayed locus is remote from that of forked. Another was with yellow (experiment 1, Metz, 1918) and indicated very close linkage (1.3 per cent crossing-over). The third was with vesiculated and magenta (experiment 14, Metz, 1918) and indicated a locus about 18 units to the left of vesiculated. On the basis of these, frayed is tentatively placed 1 unit below yellow. That it is close to yellow is clear, but it is possible that the position should be above rather than below that of yellow.

CROSSVEINLESS.

Weinstein (1920) has placed crossveinless at 17.6 units to the right of (or below) yellow. Our data, summarized in table 3, give a value of 19.6 units for this "region," based on 3,093 flies, without correction for double crossing-over. The value of 18.7 per cent used for calculating map length is based on the combined data (5,450 flies). By adding this 18.7 per cent to the 5.6 per cent given by sepia and yellow, the value 24.3 per cent is obtained. Expressed in round numbers, this gives crossveinless a locus at 24 on the map.

VERMILION.

Preliminary tests indicated that vermilion was very closely linked to crossveinless, and experiments 20, 36, and 46, involving yellow, crossveinless, and vermilion, placed vermilion slightly below crossveinless. The average of all data (table 3) gives a cross-over value of about 0.47 per cent between the two. This would place vermilion between crossveinless and vesiculated, although the sum of our crossveinless-vermilion and vermilion-vesiculated values does not agree very closely with the crossveinless-vesiculated value (1.2 per cent) obtained by Weinstein (1920). Our tests of vermilion with vesiculated (table 3) give a value of approximately 2 units.

The exact value depends upon how the data are treated. If all the flies are counted the result is 2 per cent. But since vesiculated occasionally fails to appear

(i. e., overlaps normal), this value is probably not accurate. When only vesiculated flies are considered the value becomes 1.7 per cent.

In either case this value, plus the crossveinless-vermilion value of 0.47 unit, considerably exceeds the crossveinless-vesiculated value of 1.2 units obtained by Weinstein, which suggests that the above sequence of loci may be incorrect. To test this possibility an experiment involving all three genes (crossveinless, vermilion, and vesiculated) together was carried out.

VESICULATED.

The results of this experiment (see last paragraph) make it practically certain that the sequence is as given above, i. e., crossveinless-vermilion-vesiculated (see experiment 36, p. 81). The conclusion is warranted in spite of the fact that two of the cross-over classes contain only one fly each, for one of these is critical. It is the one in the crossveinless-vermilion-vesiculated class. The presence of this fly rules out the order vermilion-crossveinless-vesiculated because it would involve a double cross-over within a "distance" of less than 3 units. Likewise the order crossveinless-vesiculated-vermilion is ruled out by the large number of vermilion flies and of yellow-crossveinless-vesiculated flies, which would also require double cross-overs in this short region. The proper order, therefore, appears to be crossveinless, vermilion, vesiculated, unless an error was made in classification, which seems very unlikely.

The map locus of vesiculated is calculated by using that of crossveinless as a base and adding the crossveinless-vermilion and vermilion-vesiculated values. These are, respectively, 0.5, and 1.7, giving a total of 2.2, of a map locus of 26.

SINGED.

Singed has been tested with vermilion, crossveinless, and yellow in the one direction, and with magenta, forked, triangle, and others in the opposite direction (table 3). Experiment 21, involving yellow, crossveinless, and singed, gives singed a position about 17 units below crossveinless and makes clear the order of the genes. This is verified by experiments 25 and 41, involving yellow, singed, and short in the one case, and vermilion, singed, magenta, and forked in the other. The best available data for locating singed are provided by experiments involving vermilion or crossveinless on the one side (experiments 6, 21, 34, 41, 48) and magenta forked on the other (experiments 41, 45, 48). The crossveinless-singed value is 15.7, and the vermilion-singed value is 17.9. The former value is probably too low, due to the inclusion of experiment 48, which appears to give low values in the upper part of the map (i. e., the sepia-crossveinless value is only 18.7, and the crossveinless-singed value only 14). On this account, and also because the vermilion-singed value is based on a larger count, the latter is used in constructing the map. It places singed at 43.0. Tests with magenta and forked are considered in the discussion of the latter characters.

OBLIQUE.

Oblique was obtained too late to permit of the data on its linkage relations being included in the tables of summaries, hence they will be considered fully here. The approximate location of oblique on the chromosome map was determined by means of two small experiments involving, respectively, magenta, forked, oblique, and short (experiment 49) and sepia, crossveinless, oblique, and short (experiment 50). In the latter only the not-oblique flies are used in the calculation, because oblique interferes with the classification of both sepia and crossveinless. The values obtained in these two experiments indicated that oblique was between crossveinless and forked, so matings were made to test its linkage with singed, which has a locus intermediate between these two. The results of the tests with singed are given in experiments 51, 52, and 53. The first of these shows that oblique falls very close to singed (2 cross-

overs in 48 flies), and the other two agree in giving it a position approximately 6 units above that of singed. In both of the latter a difficulty in classification arises through the presence of oblique and sepia together. This necessitates omitting the oblique flies from the calculation or else apportioning them between the oblique and the oblique sepia classes. Both methods are used, and the results are in such close agreement as to cause no difficulty in estimating the approximate values.

The map location of oblique has been calculated from the average of the three experiments just considered. When only the not-oblique flies are used (in the last two cases) the result is 11 cross-overs in 186 flies, or a value of 5.9 per cent. When all flies are used the result is 15 cross-overs in 263 flies, or a value of 5.7 per cent; 6 per cent is therefore used as the approximate value in constructing the map, and oblique is placed 6 units above singed. It should be noted, however, that in both of the experiments involving sepia, the sepia-singed value is unusually low, ranging around 19 instead of about 40, as it should. The singed-short value, on the other hand, agrees approximately with expectation. This suggests that in these experiments a factor was present which reduced crossing-over in the "upper end" of the chromosome. If so, the locus of oblique may be placed too close to that of singed.

HAIRY.

Hairy has been used very little in linkage tests because of its unsatisfactory nature. In a test with forked (Metz, 1918) it gave about 3 per cent crossing-over. Weinstein (1920) found it to be at the "left" of (above) magenta, and obtained a cross-over value of 5.4 per cent with magenta. Our experiments 26, 28, 29, 37, and 42 indicate the same sequence of genes and give very nearly the same cross-over value with magenta (5 per cent). The combined data give a value of 5.3 per cent, placing it at about 62 of the map.

MAGENTA AND FORKED.

Since magenta and forked have been used in combination almost exclusively, they may be considered together. They were among the first sex-linked characters obtained and have been used extensively ever since. The order of their genes with reference to the other principal loci is indicated by previously published data and by experiments 27, 29, 30, 31, 37, and 40 to 48. The cross-over value of the magenta-forked region is the best known one in *D. virilis*. The data of Metz (1918) give a value of 3.7 units, based on 2,529 flies and those of Weinstein (1920) give a value of 4 per cent based on 1,642 flies. Data in the present paper (table 3) give 3.4 units, based on 6,208 flies. Combined these give a value of 3.6 units, which is used in constructing the present map.

Magenta and forked are located with reference to singed by using the singed-magenta value of 25.1 units given by experiments 41, 45, and 48 (table 3). This places magenta at about 67 and forked at about 71 units from the zero end of the map. These loci should be placed more accurately by obtaining large numbers in an experiment involving vermilion (or crossveinless), singed, magenta, and forked simultaneously. Our experiments 41 and 48 are of this nature, but the counts only include 718 flies.

TRIANGLE AND SHORT.

Triangle is shown by experiments 13 and 32 to be closely linked to short. The latter character appeared later, chronologically, than triangle, but is much better for linkage studies and consequently is used more than triangle. The average cross-over value between the two (table 3) is 5.1 per cent. Experiment 32 shows that the position of short is between that of triangle and droop, and experiment 33 shows that it is above rugose.

In locating triangle and short on the map, four different lines of evidence have been considered, as summarized on the following page.

I.	II.	III.	IV.
f 71.1	.....	.....	f 71.1
f–T 10.7 (269)	si 42.4	f 71.1	f–r 26.3 (3,727)
T 81.8			r 97.4
T–s 5.1 (607)	si–s 42.9 (1,442)	f–s 18.5 (577)	s–r 15.9
s 86.9	s 85.3	s 89.6	s 81.5
s–r 15.9 (1,564)	T–s 5.1	T–s 5.1	T–s 5.1
r 102.8	T 80.2	T 84.5	T 76.4
	s 85.3		
r–d 7.2 (470)	s–r 15.9		
d 110	r 101.2		

By adding the successive values from forked (i. e., f-T+T-s), triangle comes at 81.8 and short at 86.9. Neither of these is based on large numbers, however, and consequently they are open to question. The second method involves the use of the singed-short value, which is based on 1,442 flies. This would place short at 85.3, which differs by less than 2 units from the other value. By working back from this, triangle would be placed at 80.2. In contrast to these two lines of evidence, which give essentially the same results, the other two deviate considerably, and in opposite directions. The first is based on the forked-short value as given by experiments 45 and 48 (577 flies). These experiments are particularly significant, because both involve singed, magenta, forked, and short simultaneously. According to these, the forked-short distance is 18.5, placing short at 89.6, or 3 units beyond the more extreme of the two values given above.

The fourth method considered is that of using the forked-rugose value to locate rugose (at 97.4) and then working backward to locate short and triangle. This places short at 81.5 and triangle at 76.4, about 4 units less than the least extreme value given above. Since the forked-rugose value, upon which these depend, is probably too short by about this amount, due to undetected double crossing-over, it seems probable that the first two methods give approximately correct results. They also represent roughly the average of the other values, and hence they are used in constructing the map. Triangle is thus placed at 81 (intermediate between 80.2 and 81.8) and short at 86 (intermediate between 85.3 and 86.9).

CUT.

As noted above, cut appeared in a culture carrying short, and has behaved like an allelomorph of short. The original female, heterozygous for cut, and either heterozygous or homozygous for short, gave 23 cut and 26 short sons, with no wild-type or cut short sons. The daughters were all wild-type. Nine of these were tested individually and proved to be of two types; 4 of them gave short sons and sons with normal wings, but no cut, and 5 of them gave cut sons and sons with normal wings, but no short (M 182, 197, 204, 206–209, 232, 234). Females heterozygous for cut and carrying short in the opposite X-chromosome have been used in keeping the stock of cut, and their sons have thus far been of the two types short and cut.

RUGOSE, GLAZED, AND WAX.

Since rugose is the best of these three allelomorphs for use in linkage experiments, the present data are nearly all based on this character. These are summarized under experiments 9, 14, 16, 18, 33, 35, 38, 39, 43, 44, and 47. The locus of rugose is placed on the map on the basis of the short-rugose value of 15.9, which gives rugose a position at 102, based on 1,564 flies. This is about 4 units beyond the position given by using the forked-rugose value, but is believed to be more accurate than the latter, since it eliminates most of the undetected double cross-overs.

DROOP.

Droop has been used in experiments with singed, magenta, forked, triangle, short, and rugose (table 3). These agree in indicating that its locus is in the lower part of the map, and experiments 32 and 33 show that it falls beyond rugose, which has previously marked the extreme end of the map. Its position is determined with reference to rugose by experiments 18 and 33, which place it 7.2 units from rugose, or at approximately 109.

TABLE 2.—*Summary of linkage experiments on sex-linked characters.*

Experiment No.	Genes involved.	Cross-over percentage.	Total flies.
1	se–v	se–v 23.5	545
2	fd–f	fd–f 47.6	254
3	y–c	y–c 21.2	406
4	y–v	y–v 20.6	432
5	v–vs	v–vs 2.4, counting all flies	967
5	v–vs	v–vs 1.9, counting only vs flies	472
6	v–si	v–si 18.6	802
7	v–s	v–s 43.2	1653
8	v–T	v–T 38.9	167
9	v–r^g	v–r^g 42.5	200
10	si–T	si–T 39 7	136
11	si–s	si–s 39.2	551
12	si–d	si–d 46.2, counting all flies	80
12	si–d	si–d 41.3, counting only d flies	29
13	T–s	T–s 5.5	292
14	T–r	T–r 8.9	168
15	T–d	T–d 23.6, counting only d flies	72
16	s–r	s–r 18 2	730
17	s–d	s–d 28.0, counting all flies	196
17	s–d	s–d 14.3, counting only d flies	56
18	r–d	r–d 13.2, counting all flies	688
18	r–d	r–d 7.5, counting only d flies	306
19	se–y–c	se–y 5 6, y–c 20 8	548
20	y–c–v	y–c 20.3, c–v 0.4	472
21	y–c–si	y–c 17.0, c–si 16 8	417
22	y–c–s	y–c 17.5, c–s 44.5	137
23	y–c–d	y–c 20.2, c–d 39 2	79
24	y–v–s	y–v 14 2, v–s 37.3	225
25	y–si–s	y–si 34.1, si–s 33.5	173
26	y–ha–m	y–ha 41.3, ha–m 4.8	63
27	v–m–f	v–m 31.5, m–f 3 6	165
28	vs–ha–m	vs–ha 39.6, ha–m 3.3, counting all flies	121
		vs–ha 41.8, counting only vs flies	55
29	ha–m–f	ha–m 3.6, m–f 1.8	166
30	m–f–T	m–f 0.7, f–T 10 7	269
		f–T 3.7, counting only T flies	135
31	m–f–d	m–f 2 5, f–d 38.5, counting all flies	161
		f–d 25 0, counting only d flies	64
32	T–s–d	T–s 4.8, s–d 20 6	315
33	s–r–d	s–r 13.2, r–d 21.3, counting all flies	409
		r–d 6 7, counting only d flies	164
34	se–c–si–s	se–c 21.9, c–si 17.7, si–s 39 0	141
35	se–c–s–r	se–c 20.0, c–s 44.2, s–r 14.8	425
36	y–c–v–vs	y–c 20.7, c–v 0.5, v–vs 1.0, counting all flies	395
		v–vs 1.1, counting only vs flies	176
37	y–ha–m–f	y–ha 48.8, ha–m 5 4, m–f 4.9	223
38	y–vs–f–r	y–vs 21.1, vs–f 40.1, f–r 28.8, counting all flies	142
		y–vs 7.1, vs–f 47.1, counting only vs flies	70
39	y–vs–f–r^g	y–vs 17.9, vs–f 32.4, f–r^g 35.5, counting all flies	478
		y–vs 18.3, vs–f 45.9, counting only vs flies	207
40	c–v–m–f	c–v 0.4, v–m 36.9, m–f 1.9	1411
41	v–si–m–f	v–si 16.3, si–m 19 2, m–f 5 1	312
42	vs–ha–m–f	vs–ha 30.9, ha–m 6.9, m–f 2 3, counting all flies	217
		vs–ha 19.8, counting only vs flies	96
43	vs–m–f–r	vs–m 33.7, m–f 5.2, f–r 26 0, counting all flies	1708
44		vs–m 32.8, counting only vs flies	830
45	si–m–f–s	si–m 28.6, m–f 4 1, f–s 19 8	171
46	y–c–v–m–f	y–c 18 3, c–v 0.6, v–m 35 0, m–f 2.0	639
47	y–vs–m–f–r	y–vs 20.8, vs–m 31.6, m–f 4.7, f–r 27.2, counting all flies	360
		y–vs 21.2, vs–m 43 2, counting only vs flies	141
48	se–c–si–m–f–s	se–c 18 7, c–si 14 0, si–m 28.0, m–f 3 2, f–s 17.9	406

TABLE 3.—*Summary of linkage data on sex-linked genes arranged according to map order.*

Region.	Experiment No.[1]	Total flies.	Cross-overs.	Average per cent.
se–y	19	548	31	5.6
y–fd	1 (Metz, 1918)	308	4	1.3
y–c	1, 2, 3 (Weinstein, 1920)	2,357	415	
	3	406	86	
	19	548	114	
	20	472	96	
	21	417	71	
	22	137	24	
	23	79	16	
	36	395	82	
	46	639	117	
	Total	3,093	606	
	Grand total	5,450	1,021	18.7
y–v	4	432	89	
	20	472	98	
	24	225	32	
	36	395	84	
	46	639	121	
	Total	2,163	424	19.6
y–vs	2 (Metz, 1918)	151	35	
	6 (Metz, 1918)	187	41	
	7 (Metz, 1918)	187	32	
	9 (Metz, 1918)	579	92	
	16 (Metz, 1918)	1,086	183	
	17 (Metz, 1918)	298	47	
	18 (Metz, 1918)	699	120	
	19 (Metz, 1918)	361	71	
	1, 4, (Weinstein, 1920)	2,473	495	
	Total	6,021	1,116	
	36	395, counting all flies (176, counting only vs flies)	88 (36)	
	38	142, counting all flies (70, counting only vs flies)	30 (5)	
	39	478, counting all flies (207, counting only vs flies)	86 (38)	
	47	360, counting all flies (141, counting only vs flies)	75 (30)	
	Total	1,375, counting all flies	279	
	Grand total	7,396, counting all flies	1,395	18.8
fd–vs	14 (Metz, 1918)	296	55	18.5

[1] Except where otherwise specified the experiment numbers refer to experiments in the present paper.

TABLE 3.—*Summary of linkage data on sex-linked genes arranged according to map order*—Continued.

Region.	Experiment No.	Total flies.	Cross-overs.	Average per cent.
c–v	20	472	2	
	36	395	2	
	40	1,411	6	
	46	639	4	
	Total	2,917	14	0.47
c–vs	1 (Weinstein, 1920)	1,560	18	
	36	395, counting all flies	6	
		(176, counting only vs flies)	(3)	
	Grand total	1,955, counting all flies	24	1.2
v–vs	5	(967, counting all flies)	(23)	
		472, counting only vs flies	9	
	36	(395, counting all flies)	(4)	
		176, counting only vs flies	2	
	Total	648, counting only vs flies	11	1.7
c–si	21	417	70	
	34	141	25	
	48	406	57	
	Total	964	152	15.7
v–si	6	802	149	
	41	312	51	
	Total	1,114	200	17.9
si–m	41	312	60	
	45	171	49	
	48	406	114	25.1
	Total	889	223	
si–f	41	312	76	
	45	171	56	
	48	406	127	
	Total	889	259	29.1
si–T	10	136	54	39.7
si–s	11	551	216	
	25	173	58	
	34	141	55	
	45	171	90	
	48	406	200	
	Total	1,442	619	42.9
vs–m	3 (Metz, 1918)	263	85	
	7 (Metz, 1918)	187	57	
	11 (Metz, 1918)	463	138	
	12 (Metz, 1918)	504	190	
	14 (Metz, 1918)	296	106	
	16 (Metz, 1918)	1,086	368	
	19 (Metz, 1918)	361	107	
	Total	3,160	1,051	

TABLE 3.—*Summary of linkage data on sex-linked genes arranged according to map order*—Continued.

Region.	Experiment No.	Total flies.	Cross-overs.	Average per cent.
	28	121, counting all flies	52	
		(55, counting only vs flies)	(24)	
	42	217, counting all flies	82	
		(96, counting only vs flies)	(21)	
	43	1,708, counting all flies	576	
	44	(830, counting only vs flies)	(275)	
	47	360, counting all flies	114	
		(141, counting only vs flies)	(61)	
	Total	2,406, counting all flies	824	
	Grand total	5,566	1,875	33.6
ha–m	3, 4, 5 (Weinstein, 1920)	1,388	76	
	26	63	3	
	28	121	4	
	29	166	6	
	37	223	12	
	42	217	15	
	Total	790	40	
	Grand total	2,178	116	5.3
m–f	3 (Metz, 1918)	262	13	
	5 (Metz, 1918)	677	17	
	12 (Metz, 1918)	504	23	
	16 (Metz, 1918)	1,086	42	
	2, 4 (Weinstein, 1920)	1,642	66	
	Total	4,171	161	
	27	165	6	
	29	166	3	
	30	269	2	
	31	161	4	
	37	223	11	
	40	1,411	28	
	41	312	16	
	42	217	5	
	43	1,708	89	
	44			
	45	171	7	
	46	639	13	
	47	360	17	
	48	405	13	
	Total	6,208	214	
	Grand total	10,379	375	3.6
f–T	30	269, counting all flies	29	10.7
		(135, counting only T flies)	(5)	

TABLE 3.—*Summary of linkage data on sex-linked genes arranged according to map order*—Continued.

Region.	Experiment No.	Total flies.	Cross-overs.	Average per cent.
f–s	45	171	34	
	48	406	73	
	Total	577	107	18.5
f–r	4 (Metz, 1918)	286	81	
	13 (Metz, 1918)	173	47	
	18 (Metz, 1918)	699	193	
	2 (Weinstein, 1920)	359	74	
	Total	1,517	395	
	38	142	41	
	43, 44	1,708	445	
	47	360	98	
	Total	2,210	584	
	Grand total	3,727	979	26.3
f–d	31	(161, counting all flies)	(62)	
		64, counting only d flies	16	25.0
T–s	13	292	16	
	32	315	15	
	Total	607	31	5.1
T–r	14	168	15	8.9
T–d	15	72, counting only d flies	17	
	32	(315, counting all flies)	(80)	
		157, counting only d flies	42	
	Total	229, counting only d flies	59	25.7
s–r	16	730	133	
	33	409	54	
	35	425	63	
	Total	1,564	250	15.9
s–d	17	(196, counting all flies)	(55)	
		56, counting only d flies	8	
	32	(315, counting all flies)	(65)	
		157, counting only d flies	33	
	33	(409, counting all flies)	(141)	
		164, counting only d flies	26	
	Total	377, counting only d flies	67	17.7
r–d	18	306, counting only d flies	23	
	33	164, counting only d flies	11	
	Total	470, counting only d flies	34	7.2

III. LINKAGE GROUP II.

Since confluent was the first non-sex-linked character found in *D. virilis*, the group to which it belongs is designated Group II. It consists of the four characters *confluent*, *concave*, *double*, and *broken*. The first two are excellent characters and have been used extensively; the third is very poor for linkage work and has been used relatively little; while the last, although a good character, appeared so recently that it has been possible to use it only in preliminary experiments.

DESCRIPTION, ORIGIN, AND COMPARISON OF CHARACTERS IN GROUP II.

CONFLUENT (C). (Plate 3, Figure 1.)

Description.—Confluent derives its name from the fact that the second vein is confluent with the costal vein for a short distance near the tip of the latter, as shown in the figure (also Metz, 1916, fig. 2). The fly appears to be unaffected otherwise, save for a thickening of the outer ends of the two cross-veins, and a slight roughening of the eyes in most cases. Confluent resembles the extreme form of the sex-linked character triangle, and like the latter is dominant. Unlike triangle, however, it is lethal in the homozygous condition and pure stock can not be obtained. In combination with the other dominant wing characters, branched, net, and extra, confluent is exaggerated, the confluence of the second and costal veins being more extended. It is likewise exaggerated by capsule, as noted under the description of the latter.

Origin.—Confluent was one of the first characters found in *D. virilis* (see Metz, 1916, p. 593).

Comparison.—Confluent resembles the "confluent" of *D. melanogaster* in appearance and in being a dominant. It is probable that they agree also in being lethal when homozygous (see Metz, 1916, p. 591, and Morgan, Bridges, and Sturtevant, 1919, p. 257).

CONCAVE (cc). (Plate 3, Figures 3 to 7.)

Description.—The principal diagnostic characters of concave are the curled, instead of straight, hairs on the arista (fig. 4, plate 3), and the heavy, somewhat wavy bristles on the scutellum. The former is constant and definite and the latter is usually evident. In addition the scutellar bristles frequently stand erect or point in various directions, the dorso-central bristles sometimes are similarly affected, the posterior scutellar bristles extend nearly parallel instead of crossing, and often the wings are abnormal. The latter effect is very irregular. Sometimes both wings are very small, or narrow, or short and nearly circular (a common type), or concave instead of convex on the inner margin. Often only one wing is affected, or the two may be differently affected. Two typical wing forms are shown in an earlier paper (Metz, 1916, figs. 5 and 6).

Origin.—The origin of concave is given in the paper just cited.

Comparison.—Concave is paralleled very closely by the third chromosome recessive character "crumpled" in *D. melanogaster*. Both have the curled hairs on the arista, and the same type of abnormal scutellar bristles and both exhibit a series of wing modifications, of which the most frequent types are similar in the two species.

DOUBLE (dc).

Description.—Double is characterized by an occasional doubling of part of the fourth vein or fifth vein, especially near the posterior cross-vein, by the presence of a tubercle on the first vein in some individuals, and frequently by a broadening and

arching of the wing as well as by the angular position in which the wing is held out from the body. None of these characters is constant, and for this reason considerable difficulty is experienced in classifying the flies. Owing to this and to the fact that double flies have very poor viability, the stock has been discarded.

Origin.—(V 1169.) Double first appeared in a pair mating, both parents evidently having been heterozygous; the offspring were 57 double (28 ♀ ♀ : 29 ♂ ♂), and 190 not double (89 ♀ ♀ : 101 ♂ ♂).

TABLE 4.—*Chronological list of autosomal characters in Drosophila virilis.*

Character.	Symbol.	Parts affected.	Linkage group	First observed.	Found by—	Record.
Confluent	C	Wing veins	II	July, 1914	Metz	Metz, 1916, p. 593.
Concave	cc	Bristles and wings	II	Sept., 1915	Metz	Metz, 1916, p. 597.
Steel	st	Eyes	III	Feb., 1916	Metz	Metz, 1916, p. 598.
Acute	ac	Wings	IV	Do	Metz	c stock.
Branched	B	Wing veins	V	Sept., 1916	Metz	V 601, 606.
Fused	fu	Wing veins	V	Nov., 1916	Metz	V 778.
Telescoped	t	Thorax	III	Feb., 1917	Metz	V 974.
Scaly	S	Eyes	III	July, 1917	Metz	V 1128.
Double	de	Wing veins	II	Do	Metz	V 1169.
Hump	hp	Thorax	IV	Mar., 1919	Metz	Hyde stock.
Minus	mi	Bristles	?	Do	Metz	L 22.
Capsule	cp	Wings	?	Apr., 1919	Metz	L 92.
Hunch	h	Thorax	III	May, 1919	Metz	L 176.
Pinched	P	Wing veins	IV	June, 1919	Metz	L 252.
Interrupted	i	Wing vein	V	Sept., 1919	Mason	E 15.
Approximated	a	Wing vein	V	Do	Mason	E 15.
Net	Nt	Wing veins and bristles	?	Do	Metz	L 462.
Spine	sn	Wing vein	?	June, 1920	M. Demerec	P stock.
Spread	sp	Wings	III	Mar., 1921	Moses	P 577.
Broken	b	Wing vein	II	May, 1922	Moses	M 66.
Garnet	G	Eye color	III	Do	Metz	M 13.
Extra	E	Wing vein	?	June, 1922	Metz	M 24.
Ruffled	ru	Thoracic hairs and bristles	V	Do	Metz	M 113.

BROKEN (b). (Plate 3, Figures 8 and 9.)

Description.—The character takes its name from the break in the cross-veins. The posterior cross-veins are usually lacking, but may be broken, or, in rare cases, one may be intact but thin in the middle. The anterior cross-veins are sometimes absent or broken, but not constantly so. Frequently, the distal end of the third and fourth veins is thin, and occasionally these veins fail to reach the wing-margin. In addition to the effects on the veins, a characteristic soft, wavy, and glossy appearance of the wing as a whole may usually be noticed. In most of the flies the posterior cross-veins are entirely gone, as they are in crossveinless flies. When this is not the case, the end of the vein nearest the fourth vein is usually gone, resulting in a condition almost indistinguishable from that found in interrupted flies (fifth chromosome). The frequency of these types may be judged roughly from the following count of 50 flies taken from a stock bottle: in 46 specimens both posterior cross-veins were entirely gone, in 3 both posterior cross-veins were broken (end next to fourth vein gone), and in 1 one posterior cross-vein was gone while the other was intact, but thin in the middle.

In addition to modifying the wings, broken also affects the legs. The tibia on the hind leg is strongly curved, or arched, with the concave side next to the femur, and frequently the tarsi are shorter and swollen.

Origin.—(M 66.) Broken appeared in acute stock. Only one broken fly was observed, but others may have appeared.

Comparison.—Superficially broken resembles the sex-linked character "crossveinless" in *D. virilis* and *D. melanogaster* (as noted above), and also a non-sex-linked character in *obscura*, the stock of which has been lost (unpublished data of D. E. Lancefield). It is not known how close the resemblance is in the latter case.

LINKAGE DATA.

DETECTION OF LINKAGE IN GROUP II.

Confluent and concave.—Four back-cross matings (V 675, 730, 740, 741) of males heterozygous for confluent and concave (in opposite chromosomes) to homozygous concave females gave the following counts: confluent 213, concave 213, confluent concave 0, wild-type 0. A similar back-cross (V 752) using a male heterozygous for confluent and concave, but this time in the same chromosome, gave: confluent 0, concave 0, confluent concave 46, wild-type 44. These experiments show that confluent and concave are linked.

Double with concave and confluent.—Double has proved to be such an unsatisfactory character to work with, on account of its tendency to grade into normal, and its effect on viability, that only a few tests were made for linkage before the stock was discarded. These are summarized below. Linkage between double and concave was indicated by the F_2 count from a cross of concave by double. This consisted of 118 wild-type, 33 concave, 33 double, without any concave doubles (P 19, 30, 31). Similarly, linkage between double and confluent was indicated by the progeny of matings (E 998, E 1001) between confluent and double, using double females and males heterozygous for confluent (dominant) and double. These gave: confluent 142, double 113, wild-type 5, confluent double 0. The 5 wild-type flies in the latter case are assumed to be genetically double.

Confluent and broken.—Linkage between these two characters was shown by the usual back-cross test, using heterozygous males. Two such matings (M 291, M 292) gave: 23 confluent, 27 broken, and no wild-type or confluent broken flies.

CROSS-OVER VALUES IN GROUP II.

Confluent and concave.—Two back-cross matings (experiment 54), using females heterozygous for the two genes in opposite chromosomes, gave 123 non-cross-over flies, and 90 cross-overs. This gives a cross-over value of approximately 42 per cent, without any correction for double crossing-over.

Confluent and double.—Six back-crosses (E 931, E 947, E 948, E 1032, E 1033, E 1034), using heterozygous females from confluent

by double, gave: confluent 343, double 113, confluent double 83, wild-type 435. Counting only the double flies (to avoid errors due to viability and to inability to exclude all double flies from the other two classes), this gives a cross-over value of 42 per cent, which is reliable at least to the extent of showing that confluent and double are not closely linked. No attempt was made to determine the amount of crossing-over between double and concave, because of the difficulty of distinguishing the two characters.

Confluent and broken.—Two back-crosses of heterozygous females (experiment 55) gave 139 non-cross-over flies and 93 cross-overs, from which we obtain a cross-over value of 40 per cent, showing very loose linkage.

CONSTRUCTION OF SECOND-CHROMOSOME MAP.

(Figure 7).

Unfortunately, broken appeared so recently that it has only been possible to secure counts from the one type of mating given above; hence broken can not yet be located on the map.

Since the "position" of double is likewise uncertain, only the genes for confluent and concave can be located. These are probably at least 50 units apart, and perhaps much farther, since double crossing-over would probably prevent the detection of more than about 42 per cent of crossing-over, even if more occurred.

IV. LINKAGE GROUP III.

This group consists of the five characters scaly, spread, hunch, telescoped, and garnet. A sixth character, steel (for description see Metz, 1916*d*), also belongs in this group, but it proved to be so difficult to classify that the stock was discarded.

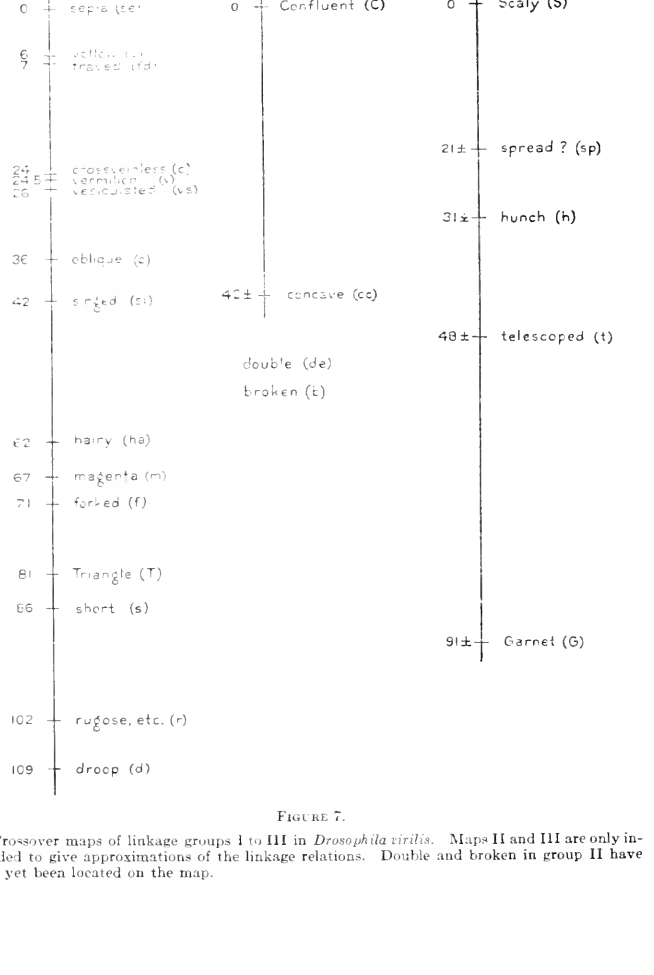


FIGURE 7.

Crossover maps of linkage groups I to III in *Drosophila virilis*. Maps II and III are only intended to give approximations of the linkage relations. Double and broken in group II have not yet been located on the map.

DESCRIPTION, ORIGIN, AND COMPARISON OF CHARACTERS IN GROUP III.

SCALY (S).

Description.—Scaly is a dominant, characterized by flattened, scale-like ommatidia. The eye usually has a moist appearance also. The expression of this character seems to be influenced by environmental conditions. In some cultures it appears in all flies heterozygous for the gene; in others many such flies have eyes normal in appearance, although breeding tests show them to carry the gene. It is probable that this irregularity applies even to homozygous flies, although we have not tested this point thoroughly. Scaly is not lethal when homozygous and pure stock is easily maintained.

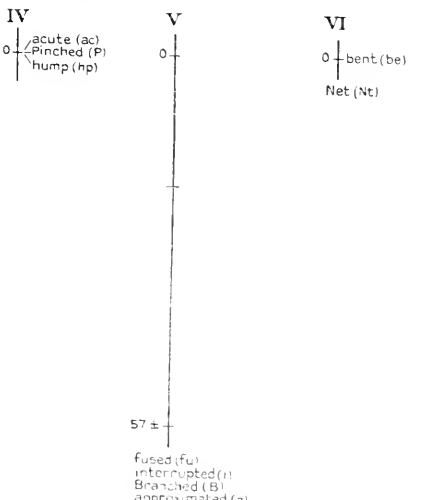


FIGURE 8.
Crossover maps of linkage groups IV to VI in *Drosophila virilis*.
The genes are not placed on the map in group V, for
reasons given in the text (p. 50).

Origin.—(V 112S.) Scaly was first observed among the offspring of 3 females from one stock mated to males from another stock. The mating gave 86 wild-type and 23 scaly individuals, suggesting that one of the parent flies was heterozygous for scaly.

SPREAD (sp).

Description.—In spread flies the wings are held out from the body at varying angles, usually between 60° and 90°. Otherwise the flies appear to be normal. Their viability is poor, however, making the character a difficult one to use in linkage experiments. It can not be classified accurately in combination with the third-chromosome character hunch, because in the latter the wings are often held out at an angle also.

Origin.—(P 577.) One female was found in a bottle of droop stock.

Comparison.—Spread resembles the third-chromosome recessive "spread" in *D. melanogaster* (Dexter, 1914) and also the second-chromosome recessive "spread" in *D. simulans* (Sturtevant, 1921*b*, p. 186). It differs from the former in that the wings are not uniformly held at an angle of 90°. In this respect it agrees more closely with "spread" of *simulans*.

HUNCH (h). (Figure 9.)

Description.—Hunch flies lack the usual depression between the mesonotum and scutellum on the dorsal side, giving a hunch-back appearance. They frequently show an exudation on each side of the thorax near the junction of mesonotum and scutellum. The wings are usually soft and "moist" in texture, and sometimes are only partially expanded and are held out at an acute angle from the body.

Origin.—(L 176.) Hunch arose from a mating of a single female by two males, all from the same mass culture. The offspring were 35 not-hunch and 12 hunch. Evidently the female and at least one of the males were heterozygous for the hunch gene.

Comparison.—Hunch agrees in its main characteristics with the third-chromosome recessive "ascute" in *D. melanogaster* and with two similar characters in *D. obscura*, one sex-linked and one non-sex-linked. The latter one we have not seen, owing to the stock having been lost, but Dr. Lancefield informs us that it does not differ noticeably from the other.

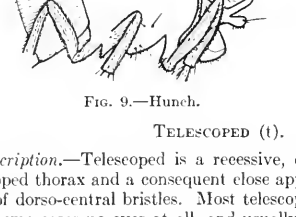


FIG. 9.—Hunch.

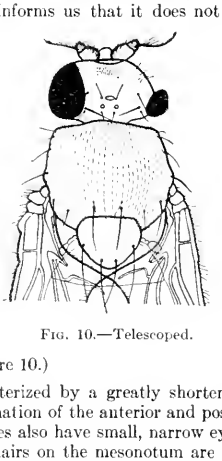


FIG. 10.—Telescoped.

TELESCOPED (t). (Figure 10.)

Description.—Telescoped is a recessive, characterized by a greatly shortened or telescoped thorax and a consequent close approximation of the anterior and posterior pairs of dorso-central bristles. Most telescoped flies also have small, narrow eyes, or in extreme cases no eyes at all, and usually the hairs on the mesonotum are sparse and irregular in distribution, and the anterior dorso-central bristles are small.

Origin.—(V 974.) A female found in confluent stock and segregated because she had "groove eyes" was mated to normal-eyed males from the same bottle. Among the offspring was one female with very narrow eyes, which, when bred to normal-eyed brothers (or half brothers), gave 225 not-telescoped and 48 telescoped progeny. At first the telescoped flies were distinguished merely by their narrow eyes, and it is probable that among the 225 flies recorded as "not-telescoped" many telescoped were present. Indeed, it is probable that the original female from confluent stock was telescoped and one or more of the males to which she was mated were at least heterozygous for telescoped.

Comparison.—Dr. Lancefield informs us that the sex-linked character "compressed" in *D. obscura* resembled telescoped, but unfortunately the stock of com-

pressed has been lost and we are unable to make a detailed comparison. The description of telescoped suggests that of the character "furrowed" in *D. melanogaster* (Morgan and Bridges, 1916). This is not borne out by a detailed comparison, however, for the modifications are not alike in the two cases.

GARNET (G).

Description.—Garnet is an eye-color character in which the color is very close to Ridgeway's garnet-brown. It is almost indistinguishable from the sex-linked character magenta, but differs in being a dominant. It is uniform and regular in appearance, and promises to be a very useful character. Pure stock has not yet been obtained, but from one mating of garnet by garnet (M 101) all of the 51 offspring were garnet, indicating that one parent was probably homozygous. Tests are now under way to determine whether or not garnet is lethal in the homozygous condition. Its viability is excellent. Heterozygous flies outcrossed gave 231 garnet to 240 not-garnet offspring (M 13, 18, 19, 42, 99).

Origin.—(M 13.) The origin of the garnet is not definitely known. It was found in a bottle of mixed stock carrying the sex-linked characters vermilion and singed, and supposedly magenta also. Tests revealed the presence of a dominant eye-color resembling magenta, but no actual magenta. How long this character (garnet) had been present is not known.

Comparison.—So far as we are aware, this is the only dominant mutant eye-color character of this sort known in any species of *Drosophila*.

LINKAGE DATA.

DETECTION OF LINKAGE IN GROUP III.

Scaly and telescoped.—Scaly and telescoped were shown to belong to the same group by back-crossing males heterozygous for the respective genes (in opposite chromosomes) to telescoped females. The following count was obtained (V 1220, 1244, 1252): scaly 116, telescoped 110, wild-type 0, telescoped scaly 0. (See also under scaly, hunch, and telescoped.)

Steel and telescoped.—The linkage of these two characters was detected when a heterozygous male was back-crossed to a double recessive female. This mating (V 1191) gave: telescoped 12, steel 13, wild-type 1, telescoped steel 0. The one wild-type fly doubtless belongs in the steel class, but failed to show the spot in the eyes. F_2 counts also indicated linkage by the absence of the double recessive class.

Hunch and telescoped.—Both F_2 and back-cross counts indicate linkage between these characters. Four F_1 matings (L 376, 388, 394, 400) gave the following total of F_2 individuals: telescoped 67, hunch 74, wild-type 162, telescoped hunch 0. The back-cross data are given in the following paragraph.

Scaly, hunch, and telescoped.—Two back-cross matings using heterozygous males, with scaly in one chromosome and hunch telescoped in the other, by homozygous hunch telescoped females gave the following totals: hunch telescoped 132, scaly 202, wild-type 58, hunch 0, telescoped 0, scaly hunch 0, scaly telescoped 0, scaly hunch tel-

escoped 0. The 58 wild-type flies here should be in the scaly class but do not show the eye modification. The double-recessive class is small, as usual, on account of low viability.

Scaly and garnet.—Linkage between scaly and garnet was shown by the usual back-cross test. This gave (M 289, 311) 42 scaly, 49 garnet, 3 wild-type (probably genetically scaly), and no scaly garnet.

Hunch, telescoped, and spread.—The following F_2 counts from a mating of hunch telescoped by spread indicate that spread probably belongs in the third linkage group; hunch telescoped 86, spread 110, wild-type 227, hunch 9, telescoped 22, hunch telescoped spread (4?), hunch spread 0, telescoped spread 0. The four doubtful hunch telescoped flies had wings slightly spread, but this condition is occasionally found in hunch telescoped flies, and the present cases are probably due to hunch. Tests of spread with members of groups II and IV show no linkage, and the same is probably true in the case of group V, although the data are not conclusive as yet.

CROSS-OVER VALUES IN GROUP III.

Scaly and hunch.—Two back-crosses using heterozygous females gave 35 cross-over flies and 99 non-cross-overs (experiment 57). The wild-type and hunch classes are probably enlarged at the expense of the other two through the occasional failure of scaly to manifest itself, but the error due to this is probably not as great as that due to viability. As they stand, the data indicate approximately 26 per cent crossing-over.

Scaly and telescoped.—Two back-crosses (experiment 58), using heterozygous females by telescoped males, gave 237 cross-overs to 313 non-cross-overs. These counts, like those in the preceding case, are subject to some error due to viability and possibly to errors in classifying scaly flies, but they leave no doubt that the cross-over value is high (43 per cent here).

Scaly and spread.—Spread has only been tested with scaly and with garnet, and hence its locus is not yet accurately placed. Five back-crosses of females heterozygous for scaly and spread are summarized under experiment 56. These give a cross-over value of approximately 21 per cent (counting only scaly flies). This is subject to considerable error, but the value is smaller than that given by any of the other three characters when used with scaly and indicates that the locus of spread is probably between scaly and hunch, or else above scaly.

Scaly, hunch, telescoped.—Under experiment 60 are given the results of 8 back-crosses of heterozygous females with hunch and telescoped in one chromosome and scaly in the other. The cross-over values here are approximately 41 units between scaly and hunch and 19 units between scaly and telescoped. These values are only approxi-

mate, but they are probably reliable to the extent of indicating that the serial order of the genes is scaly-hunch-telescoped and in showing that hunch and telescoped are more closely linked than are scaly and hunch. The former value is probably reasonably accurate.

Scaly, hunch, telescoped, and garnet.—The relative "location" of garnet was determined by a back-cross involving garnet on one side and scaly hunch telescoped on the other. This is summarized in experiment 61. It gives garnet a position on the opposite end of the map from scaly. The numbers are not large enough to give accurate cross-over data, but they support the preceding experiment in indicating that the loci of hunch and telescoped are relatively close together, while that of scaly is remote from both. That of garnet is likewise remote, but in the opposite direction. As indicated by the table, two sets of values may be considered, one based on the total count and the other on only the flies showing scaly. In either case the telescoped-garnet value is so large as to indicate that these two loci are probably 50 or more units apart. As a result of the remoteness of scaly and garnet from the other two loci, double crossing-over is high. In fact the single cross-overs in region 2 are not as numerous as either type of doubles involving this region. Even the triples appear to exceed this class of singles, but this is probably due in part to the failure of scaly to appear in some of the flies classified as hunch. Taken at their face value, the data suggest that hunch and telescoped may be in the reverse order from that given. This should be kept in mind as a possibility, although it is opposed by the more extensive data from experiment 60, which are the ones used here for the tentative determination of serial order.

Spread and garnet.—Two back-crosses involving these two genes (in opposite chromosomes) gave 59 cross-over flies and 82 non-cross-overs. This gives a cross-over value of 41.8 per cent (experiment 59), indicating that spread is remote from garnet, thus agreeing with the experiment involving scaly and spread, which placed spread near the zero end of the map.

CONSTRUCTION OF THE THIRD-CHROMOSOME MAP.

(Figure 7.)

The data available for constructing a map of the third chromosome are given in tables 5 and 6. For reasons given above, only a rough map can be constructed at present. In table 5 the data are arranged according to experiments, while in table 6 they are arranged according to the map regions involved. In both tables two sets of values are given for some of the experiments. The upper value in these cases is based on all of the flies, and the lower value on only those showing scaly. In the experiment involving scaly and hunch alone the two values, thus obtained, differ markedly. But the numbers are small

in this case, and since these two genes are involved in two other experiments, giving larger counts, the latter are used for calculating the map distance.

The probable order of the genes in group III has been considered above and it remains to estimate the length of the map regions.

With the locus of scaly as the zero-point, the distance to spread is estimated as about 21 units on the basis of experiment 56. Since spread and hunch can not be used together satisfactorily, hunch is located with reference to scaly rather than spread. The value believed to be most reliable is that obtained from experiments 60 and 61, counting only the scaly flies. This is approximately 31 units. The hunch-telescoped value is also taken from these two experiments, giving an average of approximately 17 units. Telescoped is accordingly placed at 48± on the map. The telescoped-garnet value of 43 units is taken from experiment 61. This places garnet at 91 on the map, and it seems probable that subsequent data will increase this to well over 100.

V. LINKAGE GROUP IV.

In group IV only three mutant characters are known, *acute*, *pinched*, and *hump*. The first is sometimes difficult to classify, but the other two are excellent. Their linkage relations may be summarized by saying that up to the present time no crossing-over has been detected between any two of the three, although fairly large counts have been obtained.

TABLE 5.—*Summary of cross-over experiments in group III.*

Experiment No.	Mating.	Cross-over percentage.	Total flies.
60	S × h t....	Counting all: S–h 40.8, h–t 18.8.....	1,137
		Counting only S: S–h 31.3.....	479
57	S × h.....	Counting all: S–h 26.1.....	134
		Counting only S: S–h 14.0.....	64
58	S × t.....	Counting all: S–t 43.0.....	550
		Counting only S: S–t 39.6.....	240
56	S × sp.....	Counting all: S–sp 23.8.....	227
		Counting only S: S–sp 21.1.....	109
61	S h t × G..	Counting all: S–h 32.8, h–t 9.1, t–G 42.9.....	219
		Counting only S: S–h 30.9.....	84
59	sp × G....	Counting all: sp–G 41.8.....	141

TABLE 6.—*Summary of cross-over data on group III, arranged according to regions.*

Region.	Exp. No.	Total flies.	Cross-overs.	Per cent.
S–sp	56	227, counting all flies.....	54	23.8
	56	109, counting only S flies.....	23	21.1
S–h	60	1,137, counting all flies.....	465	40.8
	60	479, counting only S flies.....	150	31.3
	57	134, counting all flies.....	35	26.1
	57	64, counting only S flies.....	9	14.0
	61	219, counting all flies.....	72	32.8
h–t	60	1,137.....	214	18.8
	61	219.....	20	9.1
t–G	61	219.....	94	42.9
sp–G	59	141.....	59	41.8

DESCRIPTION AND ORIGIN OF CHARACTERS IN GROUP IV.

ACUTE (ac). (Plate 3, Figure 10.)

Description.—Acute is characterized by short, pointed wings and small anterior dorso-central bristles. The posterior and often the anterior sterno-pleural bristles are reduced to hairs, the anterior and posterior scutellar bristles are close together, and one or more of the orbital bristles are frequently absent. In addition the fifth vein, and less often the second vein, is slightly shortened. The flies tend to be small and to have short legs, but they can not be classified accurately on this basis.

Origin.—(See Metz, 1916, p. 597.) Acute arose in concave stock and was at first thought to be a form of concave.

PINCHED (P). (Plate 3, Figure 11.)

Description.—Pinched is a dominant. In heterozygous flies the anterior cross-vein is shortened, so that the third and fourth longitudinal veins are almost pinched together, and a characteristic short branch projects from the fourth vein below the first basal cell. Homozygous flies exhibit these same features, and in addition the effect often extends to other veins; the posterior cross-vein may be shortened and may lie diagonally between the fourth and fifth longitudinal veins and the latter may be broken or shortened. No difficulty is experienced in classifying pinched flies, but considerable variation is exhibited in both heterozygous and homozygous individuals, and it is not possible to separate them in a mixed culture. The pinched factor does not have the completely lethal effect frequently exhibited by dominants when homozygous. It does, however, have a very detrimental effect on the viability and fertility.

Origin.—(L 252.) Pinched appeared in a culture carrying hump, and the pinched factor shows complete linkage to that for hump. Evidently the mutation occurred in the chromosome carrying the hump factors, for the two have remained inseparable; consequently all homozygous pinched flies are hump. It should be noted that although pinched is always accompanied by hump, the converse is not true, for hump arose independently some months before the appearance of pinched and the original hump stock is free from pinched. The two mutations may have occurred in the same locus, producing allelomorphic characters, but the characters bear no relation to each other, one affecting the thorax, the other the wings, and probably merely constitute a case of complete linkage. This is made all the more probable by the apparent absence of crossing-over between either of these characters and acute (see below).

HUMP (hp). (Figure 11.)

Description.—Hump is characterized by an unusually arched and shortened thorax and a dark, glossy body-color somewhat like that of forked. The males may also be distinguished by the absence of color in the testes, which in normal flies are orange red. It has excellent viability and fertility.

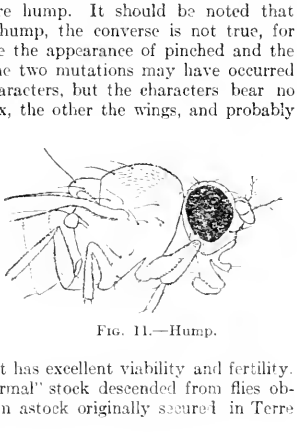


FIG. 11.—Hump.

Origin.—Hump was first observed in a "normal" stock descended from flies obtained from Dr. Roscoe Hyde, and taken from a stock originally secured in Terre Haute, Indiana.

LINKAGE DATA.

DETECTION OF LINKAGE IN GROUP IV.

Acute and pinched.—Since pinched is a dominant character, males heterozygous for acute and pinched were back-crossed to acute females. Two such matings (L 497, L 505) gave the following count: acute 84, pinched 100, wild-type 0, acute pinched 0, which shows that acute and pinched are linked.

Acute and hump.—In this case the preliminary indications of linkage were obtained from the F_2 of a mating between acute and hump. This gave (L 561): wild-type 68, acute 27, hump 16, without any acute hump flies.

Pinched and hump.—The linkage of pinched and hump was verified by both F_2 counts and back-crosses. In the latter, males heterozygous for pinched and hump, in the same chromosome, were back-crossed to hump females and gave (L 338, L 344): 99 wild-type, 77 pinched hump, no pinched, and no hump offspring.

COMPLETE LINKAGE OF ACUTE, PINCHED, AND HUMP.

Further matings involving acute, pinched, and hump have indicated an extremely close, if not complete, linkage between them. Up to the present time no certain case of crossing-over has been obtained among 151 flies in back-crosses involving pinched and hump (experiment 62) and 978 flies involving acute and pinched (experiment 63), where heterozygous females were used and cross-overs would be expected to appear. In one culture a single fly with abnormal wing venation was found which was recorded as possibly pinched, and may have represented a cross-over. Unfortunately it died without giving any progeny.

The dissimilarity of the three characters involved makes it improbable that they are allelomorphs, as does also the fact that no effect has been observed on the heterozygotes involving hump and acute, or pinched, hump, and acute. It should be noted that these flies were not examined specifically with this point in mind, but it is unlikely that any appreciable effect of either gene would have been overlooked. Since pinched appeared in connection with hump, and no cross-overs have been detected, the gene for pinched has always been accompanied by that for hump, and it is not known whether pinched would be altered if the gene for hump were eliminated.

The complete linkage involved here suggests at once that the genes might be in the small spherical *m*-chromosome that resembles the "fourth" chromosome of *D. melanogaster*, in which there appears to be very little crossing-over (see p. 76).

VI. LINKAGE GROUP V.

Group V includes five characters, thus equaling the number of the workable characters in group III, the largest of the other autosomal groups (leaving steel out of account in the latter). It also presents the same difficulties as does group III in the way of irregular characters and characters that can not be used satisfactorily in combination.

DESCRIPTION, ORIGIN, AND COMPARISON OF CHARACTERS IN GROUP V.

FUSED (fu). (Plate 4, Figure 4.)

Description.—Fused is ordinarily used as a recessive, but may often be distinguished in heterozygous flies. In homozygous flies the third and fourth longitudinal veins are fused or lie very close together from the base to the anterior cross-vein; the wings are held at an angle from the body; the ocelli and surrounding bristles on top of the head are entirely gone; and usually some or all of the bristles on the scutellum are lacking. In addition, the mutant is considerably weaker than the normal and usually gives a deficient ratio in crosses. In heterozygous flies the wings appear to be normal, but some or all the bristles on top of the head, and sometimes the ocelli also, may be lacking. The effect of fused is exaggerated by net. Flies heterozygous for fused and net, on the average, lack more bristles on the head than those heterozygous for fused without net. The heads in this case are almost completely bald.

Origin.—(V 778.) Fused, like many of the other non-sex-linked characters, was first observed in a mass culture.

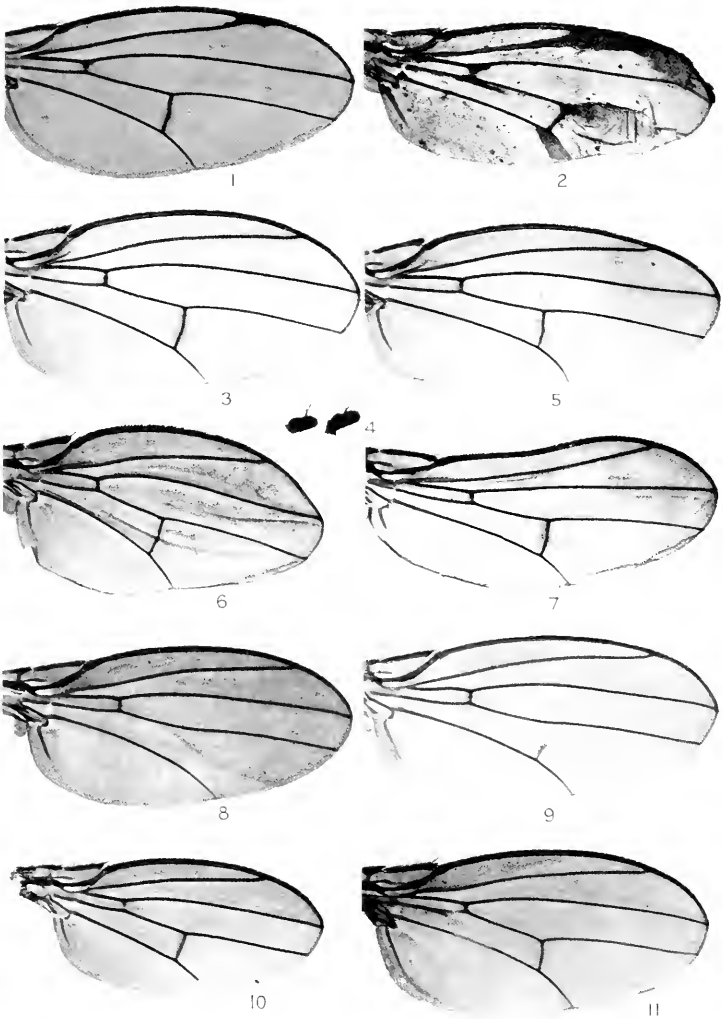
Comparison.—Fused bears a slight resemblance to the sex-linked "fused" of *D. melanogaster*, but not enough to indicate any probability of homology between the two.

INTERRUPTED (i). (Plate 4, Figures 6 to 8.)

Description.—Interrupted is a variable character grading into normal and frequently not distinguishable. In extreme cases, the posterior cross-vein is broken or almost gone (fig. 6, plate 4). The break may be near the middle, but is more often near the fourth vein, or at the junction with this vein. It seems probable that interrupted is exaggerated by approximated, for it seems to be distinguishable more often in the presence of approximated than in its absence. It is difficult to make certain of this without extensive tests, however, for environmental conditions appear to be an important factor, and these may have been more favorable in the former case. Large, well-fed flies tend to show the interrupted character more often than small, under-fed ones. For instance, in one count of 130 flies (M 1) from stock every fly was interrupted, while in others, especially old bottles, many appear normal.

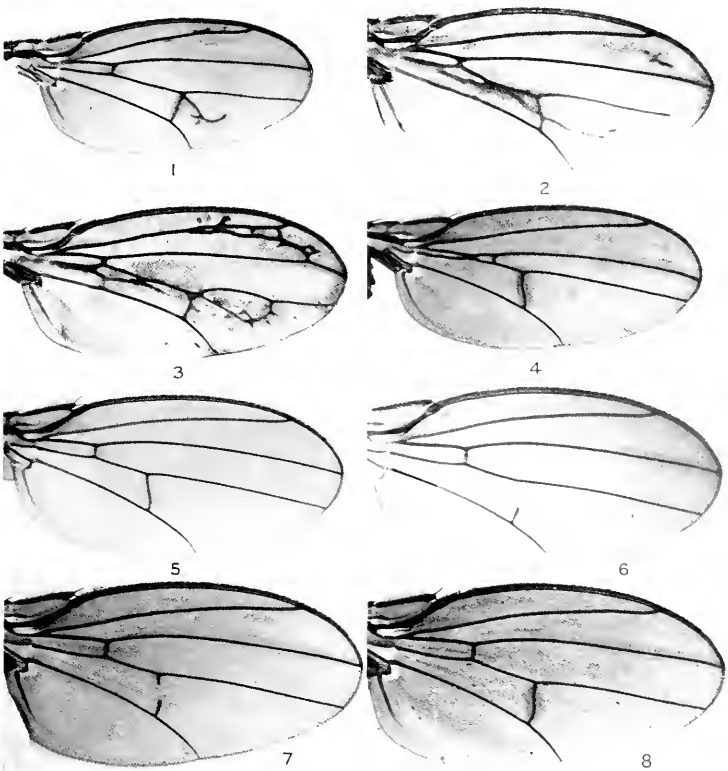
Origin.—(E 15.) From a pair mating in which both parents were heterozygous for hunch and fused, 178 offspring were obtained, of which 28 lacked posterior cross-veins. It subsequently developed that two mutant characters, interrupted and approximated, were involved here, and since their distinguishing features were not known at the time, the records do not tell the exact number of each in this culture. Since they are both recessives, however, it is apparent that each parent must have been heterozygous for them. Subsequent tests showed that the fused stock carried approximated (concealed by the fused character); hence the mutation responsible for this character probably occurred earlier than that for interrupted.

Comparison.—Characters similar to interrupted are known in *D. melanogaster* and in *D. willistoni*. We have tested two such characters in the former species, but neither resembles interrupted sufficiently to be considered as a homologue.



AUTOSOMAL MUTANT CHARACTERS IN DROSOPHILA VIRILIS.

1, Confluent; 2, Heterozygous confluent capsule; 3, and 5 to 7, Different types of wings from concave flies; 4, Wild-type (right) and concave (left) antennæ; 8 and 9, Broken; 10, Acute; 11, Pinched.



AUTOSOMAL MUTANT CHARACTERS IN DROSOPHILA VIRILIS.

1, Branched; 2, Branched Pinched; 3, Branched Pinched Extra; 4, Fused approximated; 5, Approximated; 6, Interrupted; 7, Interrupted approximated; 8, Heterozygous interrupted approximated.

BRANCHED (B). (Plate 4, Figures 1, 2, and 3.)

Description.—Branched is a dominant, irregular in its manifestation and inconstant in its appearance. It is usually characterized by a branch extending distally from the posterior cross-vein. This is often accompanied by slight protuberances or branches above the second vein, near its tip, in the region affected by confluent, triangle, and extra. The branch from the posterior cross-vein may be long or short, or may not connect with the cross-vein. When this happens a short vein lies free in the cell beyond the posterior cross-vein. Sometimes only a vestige of this is present, and frequently no extra veins appear. Homozygous flies are more extremely affected, on the average, than heterozygous ones, but the two types over-lap and can not be differentiated. Homozygous branched flies are viable and fertile and breed readily in pure stock.

Origin.—(V 601, V 606.) Several branched flies were found in a stock bottle. From these, two males were out-crossed and gave respectively (V 601) 60 branched, 79 wild-type, and (V 606) 33 branched, 67 wild-type, showing the dominance of branched.

APPROXIMATED (a). (Plate 4, Figures 5, 7, and 8.)

Description.—The nature of this character may best be appreciated by an examination of figure 5, plate 4, and a comparison of the wild-type wing shown in figure 1 of plate 2. The name is derived from the fact that the two cross-veins are closer together than usual. This is apparently due almost entirely to a modification of the posterior cross-vein. The junction of this vein and the fifth is slightly nearer the base of the wing than usual, but is not moved much. The junction with the fourth vein, however, is shifted considerably toward the base, making the distance between the cross-veins along the fourth vein about two-thirds as long as usual. In wild-type flies the segment of the fourth vein between the two cross-veins is considerably longer than the apical segment of the fifth vein. In approximated flies it is shorter. In the latter the posterior cross-vein is also usually bent in an S shape instead of being straight.

In flies heterozygous for approximated the condition is somewhat intermediate (plate 4, fig. 8), but nearer wild-type than homozygous approximated. Such flies are readily distinguished from approximated, but it is difficult to separate them from wild-type. The curved cross-vein is frequently found in heterozygous flies. It is not a definite enough characteristic, however, to permit the use of approximated as a dominant.

Origin.—See under interrupted (p. 46).

RUFFLED (ru). (Figure 12.)

FIG. 12.—Ruffled.

Description.—In ruffled flies the tips of the dorsocentral bristles and the hairs near them are curved forward and toward the midline of the thorax, as if they had been brushed back toward the head and in from the sides. This gives the thorax a ruffled appearance. The viability of ruffled flies is very good, making the character one of the best for linkage studies.

Origin.—(M 113.) 24 ruffled flies (both sexes) appeared in the progeny of two pairs from a previous mating of two pairs. At least one male and one female of the former must have been heterozygous for the new character.

LINKAGE DATA.

Considerable difficulty is encountered in using the characters of this group in combination for linkage tests, because some are irregular in appearance, and all but ruffled affect the wings. Branched is unsatisfactory because it does not always manifest itself; interrupted causes difficulty for the same reason, and also because it prevents the detection of approximated, in some cases, by removing most of the posterior cross-vein; and finally fused often interferes with the identification of approximated by eliminating the anterior cross-vein. For these reasons it is usually necessary to classify some of the flies as doubtful, with the result that cross-over values are not accurate.

The new character "ruffled" was obtained too recently to permit of extensive use in linkage tests, but it promises to be very valuable for this purpose, since it does not affect the wings.

DETECTION OF LINKAGE IN GROUP V.

Branched and fused.—The linkage of these two characters was revealed when heterozygous males were back-crossed to fused females (branched being a dominant). This type of mating gave (E 581, E 607, E 615): 140 fused, 199 branched, and 5 (somatically) wild-type offspring—the latter almost certainly being genetically branched. (See above under "branched.")

Branched and approximated.—Linkage in this case was likewise detected by back-crossing heterozygous males (E 1123, E 1139), from which the following offspring were obtained: branched 115, approximated 162, branched approximated 0, and wild-type 9 (the latter presumably genetically branched).

Fused and interrupted.—Linkage in this case was indicated by the F_2 results following a cross of fused and interrupted. The counts here were (E 560, E 569): wild-type 148, fused 62, and interrupted 84, with the double recessive class lacking.

Interrupted and approximated.—These characters were shown to be linked by the following back-cross, a heterozygous male, which had received both mutant genes from one parent, mated to a double recessive female, gave 51 interrupted approximated flies, 49 wild-type, two approximated (genetically interrupted also), and no interrupted.

Branched and ruffled.—Back-crosses of heterozygous males were used to detect the linkage in this case also. Two of these (M 325 and M 327) gave 67 branched, 38 ruffled, 4 wild-type (presumably genetically branched), and no branched ruffled.

CROSS-OVER VALUES.

Fused and interrupted.—Data involving these two characters are subject to error, due to the irregularity of interrupted and the low viability of fused. The results of 6 back-crosses are given under experiment 64. It is evident that a large proportion of the genetically

interrupted flies here appear to be normal, hence it is unsafe to use the total count. Using only the interrupted flies, a cross-over value of 19 per cent is obtained.

Fused and branched.—Back-crosses of females heterozygous for these two characters, in opposite chromosomes gave 49 cross-overs in a total of 271 flies, a cross-over value of approximately 18 per cent (experiment 65).

Fused and approximated.—Experiment 66 gives the results from back-crosses involving these two characters alone. Owing to the difficulty of classifying approximated in the presence of fused, only the not-fused flies are used in calculating the cross-over value. These give a value of 35 per cent. Breeding tests of flies in both the approximated, and the fused (not approximated) classes, were made to verify the classification.

Interrupted and branched.—Experiment 67 gives the results of 6 back-crosses involving these two characters. The data are very unsatisfactory, for both characters are irregular in appearance, making the wild-type class very large, at the expense of the two non-cross-over classes. Using only the interrupted flies a cross-over value of 2.4 per cent is obtained. This seems to indicate close linkage between the two, but it needs to be checked by the opposite type of mating, using both mutant genes in one chromosome, to make sure that branched does not tend to conceal interrupted.

Interrupted and approximated.—The regularity in appearance of interrupted varies considerably in different bottles (see description), and for this reason many of the data can not be used for linkage calculations. Furthermore, it is often difficult to classify approximated in the presence of interrupted. Experiment 68 gives the results of 6 back-crosses involving interrupted and approximated (both genes in the same chromosome). In the first part of this experiment, the flies were all put in the four regular classes, the doubtful ones being classified as accurately as possible. Values have been calculated here by using (1) only the not-interrupted flies, (2) only the interrupted flies, and (3) all flies. These are respectively 21, 13 and 17 per cent. The second part of the experiment is from counts in which especial attention was paid to separating the interrupted flies into three classes—those that were approximated, those that were not approximated, and those that were doubtful. When only the not-interrupted flies are counted, a cross-over value of 16 per cent is obtained.

Another method of handling the data in the second part of the experiment has been used to obtain the value given. This permits the use of all flies by dividing the doubtful flies between the interrupted and the interrupted approximated classes in proportion to the sizes of the latter. On this basis 16.2 per cent (35) are added to the

interrupted class and the remainder to the interrupted approximated class. A calculation of the totals thus obtained, using all of the flies, gives 16.9 per cent crossing-over. Using only the interrupted flies it gives 17.5 per cent crossing-over. When all of the data in both parts of the experiment are used, a value of 17 per cent is obtained. The agreement between these various values is sufficient to indicate that 17 per cent is probably not far from the correct value.

Branched and ruffled.—Ruffled has thus far only been tested with branched. Four back-crosses (experiment 69), in which the mutant genes were in opposite chromosomes, gave 200 non-cross-over flies and 198 cross-overs. This gives a value of approximately 50 per cent, showing that ruffled is remote from branched.

DISCUSSION.

On the basis of the experiments involving two genes at a time, the following (approximate) values are obtained: branched-fused 18 per cent, branched-interrupted 2.4 per cent, fused-approximated 35 per cent, interrupted-approximated 17 per cent, fused-interrupted 19 per cent, branched-ruffled 50 per cent. Since interrupted is placed here with reference to both fused and approximated, it is possible to arrange the three genes in a series, in which interrupted comes about midway between the other two. Since branched and interrupted appear to be closely linked, and give nearly the same cross-over value with fused, branched should fall near interrupted.

It should be possible to check these values by means of three-point crosses, but we have not been able to do so, thus far. Since branched and interrupted are both irregular, it is unsafe to use them in the same experiment, and it is unsafe to use fused with interrupted and approximated for reasons mentioned above. This leaves only the combination branched, fused, approximated with which to make the test. And in the results obtained from this (experiment 70) the two smallest cross-over classes are so nearly equal that it is impossible to determine which represents the double cross-overs. The order should be either fused-branched-approximated, or branched-fused-approximated, with a value of about 19 per cent for the first region and 38 per cent for the second, in either case. If the former order is correct, the fused approximated value (60 per cent) is much greater than that (35 per cent) obtained when these two characters were used alone. On the other hand this agrees better with the two-point experiments involving interrupted, because it places branched near interrupted and between the other two.

The location of the genes on a map may be postponed until the loci are determined more accurately. For this reason the characters are merely listed in figure 8 below a map of 57 units length, which is the length indicated by experiment 70.

VII. LINKAGE GROUP VI.

After much of the present paper had been written, a new mutant character appeared which bears considerable resemblance to the fourth-chromosome character "bent" in *D. melanogaster*. On account of this resemblance it is also called bent. It has not been studied fully, but, as indicated below, it does not appear to be in any of the preceding linkage groups.

BENT (be). (Plate 5, Figure 2.)

Description.—Bent appears to involve modifications in three separate parts of the fly—legs, wings, and eyes. None of these is absolutely constant, however. The legs vary from normal to a condition in which they are very much shortened and more or less distorted. The first part affected seems to be the basal tarsal joint on the hind legs, which is often greatly shortened and may be thickened, when the legs are otherwise nearly normal. Different degrees of modification of the hind legs are shown in figure 2 of plate 5. The leg on the left in this figure is from a fly from normal stock, those on the right are from bent stock. The effect on the wings is less marked and is seldom observed. Usually only one wing is affected. The modification resembles the short wing types in concave (plate 3, fig. 6), and frequently involves a partial spreading of the wings. The sharp bend near the base of the wing characteristic of bent in *melanogaster* is lacking, or at least is much less marked.

The eye modification may be described as speckled. Small dark specks appear here and there over the eye surface, due apparently to irregularities in the small hairs between the ommatidia. The speckling of the eye is practically constant, although very slight in some individuals.

It is possible that the speckling of the eye is a distinct mutant character, due to a different gene from that responsible for the other two modifications, but this seems highly improbable. It arose with bent and appears to be inseparable from bent.

Bent is greatly influenced by environmental conditions. Some bottles of pure stock give mostly normal flies, with the "bent" ones appearing mainly toward the end of the hatch. Preliminary experiments indicate that crowding, dryness, or poor food conditions favor the development of the leg and wing modifications. When mass cultures and pair matings were carried on side by side, the mass cultures gave a higher percentage of flies exhibiting the leg modification. The flies from the pair matings were considerably larger and better fed than those in the mass cultures.

Origin.—(M 346.) From a pair mating made to test for a possible short bristle character, the P_1 female was removed and put in a fresh bottle with an F_1 male. The small-bristle character failed to materialize, but in the latter culture several flies were found which had short tarsi on the hind legs. These were especially marked among the last flies that hatched. Altogether 15 females and 10 males with short hind legs were obtained, together with 57 females and 40 males that were not noticeably affected. The separation was made on the basis of the legs alone, as the eye modification was not noticed until afterwards. The P_1 female and the male used in the second bottle had normal legs.

Comparison.—Bent appears to correspond closely to the bent of *melanogaster* in its effect on the legs. The wing modification is somewhat similar to, but is not so nearly a duplicate of, that in *melanogaster*. In both species the character is very variable and dependent on environment. The same stock may give at one time almost all normal appearing flies and at another time almost all bent flies. We have reared one culture of bent *melanogaster* in a small vial under crowded conditions and found that practically all exhibited the leg modification, which suggests that crowding may have the same effect here as in *virilis*. In these respects, then, the

two mutant races seem to agree. The eye modification, however, is absent or inconspicuous in *melanogaster* bent.

LINKAGE TESTS WITH BENT.

The origin of bent indicated that it was an autosomal recessive, and this is borne out by subsequent tests. Since bent was not always recognized at first, it is impossible to tell just how many flies in the original culture were bent. Two matings of normal flies from this bottle both gave bent. Likewise matings of bent flies gave bent, apparently pure stocks. Several out-crosses were also made from this bottle and no bent flies were found in F_1 in any of these. In F_2, however, bent appeared in every bottle. All of these results indicate that bent is a recessive.

Bent flies from the original culture were out-crossed to confluent garnet pinched flies, to branched flies, and to concave telescoped acute flies. The first four are dominants representing groups II, III, IV, and V respectively, and the last three are recessives from groups II, III, and IV respectively. From the former crosses heterozygous males were back-crossed to bent females, and from the others pairs were mated to secure F_2 counts. Unfortunately, when this was done it was not known that bent appeared best in crowded bottles, hence most of the offspring appeared normal when the leg modification was used for classifying. However, several cultures of each type were made up and a sufficient number of unquestionable bent flies have appeared to give conclusive results. These experiments are being repeated and the counts need not be given here in detail, but they may be summarized by saying that recombinations were obtained with all of the above characters. Since these included two representatives of groups II, III, and IV, and one from group V, the results seem to show conclusively that bent is in an independent linkage group (group VI) unless some unusual genetic behavior is involved, of which there is no evidence.

Reasons have already been given for considering linkage groups I to V as representing the five large chromosomes. Bent, therefore, appears to represent the small *m*-chromosome.

This fact, together with the resemblance of bent to the bent of *melanogaster*, which is a fourth, or *m*-chromosome character, provides evidence for considering the two characters homologous, and for considering the *m*-chromosomes of the two species homologous. In the case of the large chromosomes such resemblances as those shown by the two bents might well be due to accidental mimicry, but in the minute *m*-chromosomes the chance of such mimicry is reduced to a minimum.

NET (Nt). (Plate 5, Figure 1.)

Description.—Net is characterized primarily by its small, slender bristles and by the frequent absence of many of the head bristles. Associated with these are a whole series of minor modifications affecting nearly all parts of the fly. The name is derived from the network of veins in extreme specimens. Extra veins or bits of veins appear frequently between the costa and second vein, resembling those of triangle and extra; others appear occasionally between the second and third veins near the apex, and more often in the neighborhood of the posterior cross-veins. The latter resemble those of the character branched. In some specimens no extra veins are present and the wings appear to be normal, while in others the wing is a network of veins. Between the two extremes practically all intermediates appear. Among the other characteristics of net may be mentioned its somewhat smaller size and paler color, the occasional speckling of the eyes like that found in bent, but less extreme, the absence or disarrangement of some of the hairs on the thorax and head, the paler bands on the abdomen and the frequent appearance of abnormalities of the abdominal segments. In some cases the head is denuded of hairs and bristles over the entire interocular region. Rarely a specimen appears in which the eyes and legs are like

those of bent, described above. It is thought that these may be homozygous, but the few found thus far have failed to breed.

Net exhibits as many peculiarities in behavior as it does in appearance. It is a dominant and is lethal, or nearly so, in a homozygous condition. No fertile homozygous flies have been obtained. The viability of net flies is very poor; their developmental period is longer than that of most races; they begin hatching from two to four days later than their normal sibs, and they usually fall far behind expectation in number.

Origin.—(L 462.) Net was first recognized among the offspring of a pair mating in which both parents were heterozygous for telescoped and hump and one parent was heterozygous for pinched. Only one fly was observed to be net, but it is possible that other net flies would have appeared if the culture had been a good one.

The peculiarities of net suggest that it is a "deficiency" instead of an ordinary gene mutation, and that it may be analogous to Bridges' (1921) "diminished" in *D. melanogaster*, with which it agrees fairly closely in appearance and behavior. Diminished is due to the absence of one of the two small *m*-chromosomes. In our material (of net), however, cytological examination has shown that all of the chromosomes are present. But crosses with bent support the conclusion that net is a deficiency and that it is probably due to the absence or inactivation of a part of a chromosome containing genes homologous to those in the *m*-chromosomes ("fourth chromosome") of *melanagoster*.

When net and bent are crossed the F_1 net flies are all bent. When F_1 net bent males are back-crossed to bent females the offspring are of only two classes, net bent and bent. This indicates that net and bent are in the same linkage group (chromosome) and also that net is a deficiency for bent. Corroborative evidence is furnished by the fact that both net and bent show independent segregation with characters in the other five linkage groups. F_1 net bent females have not been back-crossed, because all that have been tested (about a dozen) have been sterile.

VIII. ADDITIONAL CHARACTERS.

In addition to the above characters whose linkage relations are known to some extent, the following characters have been found, but have not yet been placed with certainty in any linkage group. These are characters that are difficult to test for linkage, because of poor viability, irregularity of appearance, or interference with the classification of other characters. Since the linkage tests have not been completed, none of the data are included here.

EXTRA (E). (Plate 5, Figure 3.)

Description.—Extra is a dominant character somewhat like the sex-linked dominant triangle. It is not uniform in appearance, but usually takes the form of a V-shaped branch above the second vein near its apex. Occasionally it is lacking and the fly appears normal. In combination with the other wing characters, concave, confluent, pinched, or branched, extreme effects are produced. In the first case the wing is apt to be crinkled and the costal vein thick around the end of the wing. In the others more extra veins appear than would come from the sum of the two characters acting alone. With confluent the effect of both characters is exaggerated; an irregular network of veins is apt to be present, and thickenings appear at the junction of cross-veins and longitudinal veins. With pinched, extra veins appear not only above the second vein, but also between the third and fourth (the region affected by pinched). With branched a cluster of veins usually appears in both the region normally affected by extra and in that normally affected by branched. When all three characters—pinched, branched and extra—are combined, the three corresponding clusters of veins appear (plate 4, fig. 3).

Origin.—(M 21.) Among the offspring of a spine female by confluent (dominant) concave males one confluent female appeared with net-like wings. When mated to normal-appearing brothers this female produced the following classes of offspring: confluent 16, extreme confluent (net-like) 39, wild-type 39, and extra vein 19. This and subsequent matings indicate that the net-like condition in the confluent flies and the extra-vein condition in part of the others is due to the same gene—that for "extra."

SPINE (sn). (Plate 5, Figure 4.)

Description.—The only distinguishing characteristic that we have been able to detect in spine is the presence of a small bristle arising from one of the sense-organs on the third vein opposite the posterior cross-vein. It is very inconstant in appearance, frequently being absent or present in only one wing. It ordinarily behaves as a recessive, but in at least one case it was manifest in an F_1 fly from an out-cross, which suggests that it may occasionally act as a dominant.

Origin.—(E 1286.) One male from pinched stock, found by Mr. M. Demerec.

CAPSULE (cp).

Description.—Capsule is a recessive character affecting the wings. As the name implies, the wing is swollen and cylindrical like a capsule. All trace of venation is gone. Both wings are bladder-like and stand out at right angles from the thorax. The viability and fertility of capsule flies are very poor and the stock was lost before linkage tests were made. The males appeared to be sterile, although only a few were tested. In the heterozygous condition capsule has an exaggerating effect on confluent, as shown in figure 2 of plate 3. All of the confluent flies from a cross of confluent by a capsule were of this extreme type.

AUTOSOMAL MUTANT CHARACTERS IN DROSOPHILA VIRILIS.

1, Net; 2, Hind legs from wild-type (left) and 3 bent flies; 3, Extra; 4, Spine.

Origin.—(L 92.) Two capsule flies, one male and one female, were found among the offspring of a concave female from stock. The capsule female mated to normal brothers gave 24 capsule to 60 not-capsule offspring. Three capsule females from this culture mated to confluent males gave 9 wild-type and 13 exaggerated confluent flies of the type described above; 3 other capsule females mated to wild-type males from stock gave only wild-type offspring (about 20).

MINUS (mi).

Description.—Minus flies frequently lack one or more of the thoracic bristles, particularly the scutellar or dorso-central bristles. Occasionally the effect may be reversed, and one or more bristles may be doubled. The character is very inconstant in appearance and seems to be affected greatly by environmental conditions. In some cases nearly all the flies in the homozygous stock will appear normal. The character is a recessive.

Origin.—(L 22.) Many flies from a stock carrying wax.

IX. COMPARISON OF MUTANT CHARACTERS IN D. VIRILIS WITH THOSE IN OTHER SPECIES OF DROSOPHILA.

Several species of *Drosophila* have now been studied sufficiently to permit a comparison of their genetic behavior. With the exception of *D. virilis* and of the well-known *D. melanogaster*, these are listed in table 7, together with references to the papers dealing with them and a statement as to the number of mutant characters in each. Their chromosomal relations may be determined by reference to figures 1 and 2. By examining the table an estimate may be made of the extent of the published information on the various species.

TABLE 7.

Species.	References.	Mutant characters.				Chromosomes.		Characters mentioned not described.
		Sex-linked.		Autosomal.		Haploid No.	Type.	
		Recessive.	Dominant.	Recessive.	Dominant.			
D. affinis Sturt.	Hyde, R. R., 1915			1		5	K	
D. busckn Coq.	Warren, D. C., 1917			2		4	A	
D. caribbea Sturt.	Sturtevant, 1921c			1		4	L	
D. funebris Fabr.	Sturtevant, A. H., 1918		1			6	G	
	Mohr and Sturtevant, 1919			1				
	Sturtevant, A. H., 1921a	1						
	Sturtevant, A. H., 1921c							2
D. hydei Sturt.	Hyde, R. R., 1915			1		6	I	
	Hyde, R. R., 1922			1				
D. immigrans Sturt.	Metz and Metz, 1915			1		4	D	
	Sturtevant, 1921c							5
D. obscura Fall.	Metz, 1916*d*	1		2		5	J	
	Lancefield, D. E., 1922	28						
	Sturtevant, A. H., 1921c			1				
D. repleta Will.	Sturtevant, A. H., 1915	1				6	I	
	Sturtevant, A. H., 1921c							2
D. similis Will.	Metz, 1916*d*			1		6	F	
D. simulans Sturt.	Sturtevant, A. H., 1921a	7				4	A	
	Sturtevant, A. H., 1921b			11	1			
	Sturtevant, A. H., 1921*d*			1	1			
D. willistoni Sturt.	Lancefield and Metz, 1921					3	See fig. 2	Non-disjunction.
	Lancefield and Metz, 1922	28						

In the following comparisons, unpublished as well as published information has been drawn upon freely, with the consent of the investigators, as mentioned on page 13 under "Acknowledgments."

At the outset of a comparison of this kind, which seeks to detect homologies, it is necessary to inquire as to what evidence is to be considered reliable in the absence of direct hybridization tests. As stated in the introduction, the failure of the above species to hybridize (with one exception noted) presents a serious obstacle to this particular feature of the work.

Direct proof of homology of individual mutant characters can hardly be obtained, except by hybridization. On the other hand, it ought to be possible to obtain evidence very nearly as conclusive by the use of *series* of characters, even without hybridization tests, especially when several related species are being studied. Fortunately, in the case of the drosophilas, deductions from such evidence receive added support from analogy with the one case in which hybridization is possible. For example, we may consider the case discussed below, involving the four sex-linked characters yellow, crossveinless, singed, and forked in *virilis* and those of the same names in *melanogaster*. These characters are morphologically similar in the two species, and in addition they are all sex-linked and their genes come in the same order and at approximately proportional distances on the chromosome maps. This agreement in several respects affords ground for considering them homologous, but the probability is increased still more by analogy with the known cases of homology in *D. simulans* and *melanogaster*. Yellow and forked and three characters whose genes occupy intermediate loci in *D. simulans* have been shown by Sturtevant (1921*a*) to be homologous to corresponding characters in *melanogaster*. The map relations of these are shown in figure 13. To be sure, the two species, *melanogaster* and *simulans*, are so nearly identical that resemblances in genetic behavior would be expected to be closer here than in the other cases, but the analogy between the proven relations here and the apparent relations in the other cases can not but add probability to the latter.

This, however, does not obviate the necessity for extreme caution in considering possible homologies. The dangers in this regard have often been pointed out. It is well known, for instance, that mimic characters may appear in one species, which are somatically identical, or nearly so, but which are due to mutations in different loci or even in different chromosomes. Likewise there is the possibility that identical mutations may give different results in different species. These and other possibilities of error emphasize the need of a relatively large amount of data before cases of homology can be considered as established. In the present paper, therefore, we will confine ourselves to a consideration of the trend of the evidence, recognizing the fact that subsequent data may modify the case.

COMPARISON OF SEX-LINKED CHARACTERS.

THE "FORKED AND SINGED" SERIES.

The most extensive series of similar mutant characters in the drosophilas includes those called "forked," "singed," or "stubby." The most prominent characteristic common to these is the modified thoracic bristles. One or more mutants in this category are known in each of the following species: *D. melanogaster, D. virilis, D. willistoni,*

D. obscura, *D. simulans*, and *D. funebris*. In all of these the characters are sex-linked and with one exception[1] there are no autosomal characters of this kind known. The maximum number of loci involved is two, and two are represented in all but the last two species. In *D. melanogaster* at least five allelomorphs are known in the forked locus, and two in the singed locus (Mohr, 1922, and unpublished data of C. B. Bridges). In each case these express different degrees of modification in the same direction. Similarly in *D. willistoni* two "forked" allelomorphs are known, one being more extreme than the other.

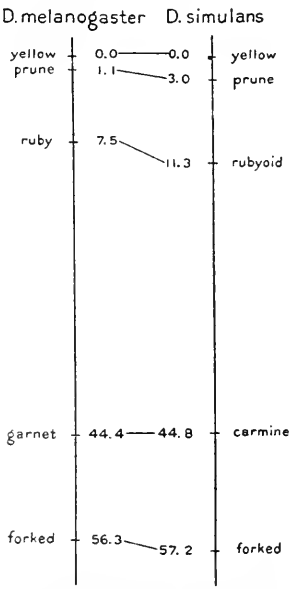


FIG. 13.—X-chromosome maps of *D. melanogaster* and *D. simulans* (from Sturtevant 1921*a*).

The resemblance between these characters in the different species is so obvious as to suggest at once that some homology exists between them. Indeed, homology has been demonstrated in the case of forked *melanogaster* and forked *simulans*, as noted above. But in the species in which two non-allelomorphic characters are concerned it is necessary to find some distinction between the two before a comparison can safely be made. Mohr (1922) has given a detailed account of forked and singed in *D. melanogaster*, and has indicated a series of differences between them. In order to determine whether or not any of these differences will hold constantly between the non-allelomorphic mutants of this type in the other species, we have examined specimens of all of the available mutants. These are included in the list on page 59, together with those (in parenthesis) which we have not been able to examine (due mainly to loss of the stocks).

Before considering the relationships of these we may give brief comparative descriptions of the different characters. These include practically all of the features in which differences have been found. Except where specified to the contrary the descriptions are based on comparisons of male specimens side by side under the microscope.

[1] A recessive, semi-lethal character in *D. simulans* (unpublished data of Dr. A. H. Sturtevant) with stubby bristles, not unlike those of the less extreme stubby or forked mutants.

In most cases there is a moderate range of variability in the character, so the description is made to represent the average condition as nearly as possible.

D. melanogaster:	forked, (forked–2), forked–3, (forked–4), forked–5.
	singed, singed–2.
D. willistoni:	forked–1, (forked–2).
	stubby.
D. virilis:	forked.
	singed.
D. obscura:	singed.
	(stubby).
D. simulans:	forked.
D. funebris:	forked.

DROSOPHILA MELANOGASTER.

Forked.—Effect moderate to extreme. Bristles shortened, twisted, sharply forked; not depressed. Hairs somewhat stubby, not depressed or curled. Both sexes fertile. Eggs normal. Heterozygous females apparently normal.

Forked–2.—(From Mohr, 1922.) Effect slight, variable, more pronounced in females than in males. Bristles long, not crinkled or twisted; one or more usually forked at tip. Head bristles rarely affected. Presumably hairs and bristles not depressed; females fertile; eggs normal. (These features not mentioned in description.)

Forked–3.—Effect slight. Bristles mostly not forked, but only stubby; not depressed; few bristles forked at tip, or bent sharply back, hook-shaped; bristles not wavy. Hairs on thorax, abdomen, legs, and wings normal or nearly so; bristles bordering segments of abdomen curled slightly. Hairs on arista apparently normal. Both sexes fertile; eggs normal. Heterozygous females not examined.

Forked–4.—(From Mohr, 1922.) Effect strikingly like that of singed. Differs only slightly. Bristles and hairs all over the body affected; bristles curled as in singed. "The bristles are slightly thicker in forked–4 than in singed flies, small bifurcations of the bristles are somewhat more frequent in the former, and the alteration of the small hairs all over the body seems to be slightly less pronounced in forked–4 than in singed individuals." Females fertile, eggs presumably normal. Heterozygous females not examined.

Forked–5.—Effect extreme. Bristles heavy, depressed, greatly twisted, knotted and forked, projections sharp, hairs on head, thorax, abdomen and legs depressed and often curled; hairs on costa heavy, stand out at a greater angle than usual. Hairs on arista practically normal. (See also under singed.) Both sexes fertile; eggs normal. Heterozygous females not examined. It is possible that forked–5 and forked–4 are identical.

Singed.—Effect extreme, but not as extreme as forked–5. Very much like forked–5 in most respects. Bristles longer and more slender, but twisted and forked in much the same manner. Hairs on entire fly essentially the same as in forked–5. Females sterile. Eggs abnormal, short filaments (Mohr, 1922). Double recessive singed-forked indistinguishable from singed (Mohr, 1922). Double recessive singed-forked–4 indistinguishable from singed or from forked–4 (Mohr, 1922). Heterozygous females not examined.

Singed–2.—Effect slight to moderate, much less extreme than singed. Bristles wavy, somewhat depressed, a few slightly forked at the tip. Hairs on thorax depressed, those on abdomen, legs and wings practically normal. Arista practically normal. Females fertile; eggs normal. (This is not singed–2 of Mohr, 1922, which was indistinguishable from singed.) Heterozygous females not examined.

DROSOPHILA VIRILIS.

Forked.—Effect moderate. Bristles erect, heavier and shorter than normal, wavy, a few forked sharply at tip. Hairs on entire fly somewhat shortened but not depressed or curled; those on arista very short, those on costa stand out at an angle of about 60°. Body-color darker and glossier than normal. Both sexes fertile; eggs normal. Heterozygous females have short bristles.

Singed.—Effect extreme; probably most extreme of all the characters in the present series. Bristles and hairs much like those of singed and forked–5 *melanogaster*, but more extremely affected. Bristles, especially on scutellum, greatly depressed, short, thick, twisted, curled or knotted, and forked. Hairs on body and legs depressed, curled, and shortened; those on costa affected as much as in forked; those on arista nearly normal, not as short as in forked. Double recessive singed-forked is like singed, but has glossy body like forked. Heterozygous females have short bristles. Females fertile; eggs normal.

DROSOPHILA WILLISTONI.

Stubby.—Effect slight to moderate. Bristles heavy, sharply forked, not depressed. Hairs on thorax, abdomen, head, legs, and wings apparently normal; those on arista apparently normal, not branched. Females fertile; eggs normal. Heterozygous females not examined.

Forked.—(From two alcoholic specimens.) Effect moderate. Bristles depressed, curled, few forked. Hairs on thorax decidedly depressed, somewhat curled; those on abdomen apparently same, those on legs and wings apparently slightly affected. Hairs on arista long, slender, normal or nearly so, not branched. Females sterile; eggs dissected from alcoholic specimen have very short, broad filaments, decidedly abnormal, like those of singed *melanogaster*. Heterozygous females not examined.

Forked–2.—(From Lancefield and Metz, 1922, p. 217.) Effect extreme. Bristles twisted, thickened, forked, depressed. Hairs short, depressed, somewhat curled. Hairs on arista branched. Females sterile; eggs not examined (stock lost). Heterozygous females not examined.

DROSOPHILA OBSCURA.

Stubby.—(From description, D. E. Lancefield, 1922, p. 372.) "Their main characteristic is the shortening of the macrochætæ and a bending or twisting of the bristles that occurs rather infrequently. It does not resemble the forked mutants of other species."

Singed.—Effect slight to moderate. Bristles wavy, some slightly forked at tip, somewhat depressed. Hairs on thorax depressed; those on abdomen and legs not depressed. Hairs on arista slightly shortened, not branched. Body glossy black; females sterile; no eggs have been found, although females have been dissected and attempts have been made to get them to lay eggs. It is possible that eggs do not mature in singed females. Bristles of heterozygous females often shorter than normal (possibly not constant).

DROSOPHILA SIMULANS.

Forked.—Effect moderate to extreme; intermediate between forked and forked–5 (in *D. melanogaster*) to which it is allelomorphic. Some hairs on arista branched, not short and stubby. Females fertile, eggs normal. Resembles most closely forked *melanogaster*. Heterozygous females apparently normal.

DROSOPHILA FUNEBRIS.

Forked.—Effect slight to moderate. Bristles stubby, stout, not wavy; a few forked sharply near tip, not depressed. Hairs on thorax, abdomen, legs, and wings shortened, but not depressed and curled as in singed *virilis*. Some of the bristles on abdomen

forked. Hairs on costa stand out at an angle of about 60°. Females fertile; eggs normal. Resembles most closely forked *virilis*. Heterozygous females not examined.

RELATIONSHIPS.

One of the first points revealed by this comparison is that a similarity in name does not necessarily indicate a close similarity in the appearance of the characters in different species. For instance, forked–1 and forked–2 in *willistoni* suggest singed in *virilis* instead of forked, which is more like stubby in *willistoni*.

Our search for some feature upon which to base a dichotomous separation of the characters in the whole series has been largely unsuccessful. The range of modifications shown by the forked allelomorphs in *melanogaster*, for instance, covers most of the conditions found in any of the "forked," "singed," or "stubby" characters in the other species. No single criterion, therefore, can be used exclusively for determining homology or lack of homology. The best we can do at present is to relate the characters on the basis of the degree of resemblance.

The two singed allelomorphs in *melanogaster*, the two forked allelomorphs in *willistoni*, and singed in *obscura* agree in regard to female sterility and presumably in regard to egg abnormality (see descriptions). This gives good ground for considering them to be parallels. It is supported also by the general appearance of the characters, which are of the type having twisted or curled rather than jagged and sharply bent bristles. Correlated with this are the depressed bristles and curled and depressed hairs on the thorax. We may group these characters together, then, in the "singed" series.

The other character in *willistoni* (stubby) differs in all of these respects and bears a closer resemblance to the forked allelomorphs of *melanogaster*. So we may group these together in the "forked" series. In *obscura* the character stubby represents such a slight modification that it is hard to compare with the others, especially since no specimens are available for examination. Since singed seems to belong to the singed series, however, stubby may tentatively be correlated with the forked series.

These relations are shown schematically in figure 14, in which the chromosome maps are oriented so that the loci of parallels[1] correspond.

In *simulans* forked has been shown by Sturtevant (l. c.) to be allelomorphic to that in *melanogaster*, and consequently the *simulans* map would correspond to that of *melanogaster*, and may be omitted here.

[1] The term parallel is used to indicate a resemblance which suggests homology.

It remains, then, to determine whether or not forked and singed in *virilis* and forked in *funebris* will fit into the above series. The resemblance between the forked characters in the latter two species has been noted under the description of forked (see also Sturtevant, l. c.). The resemblance is very close in nearly all respects, hence these two may tentatively be classed as parallels.

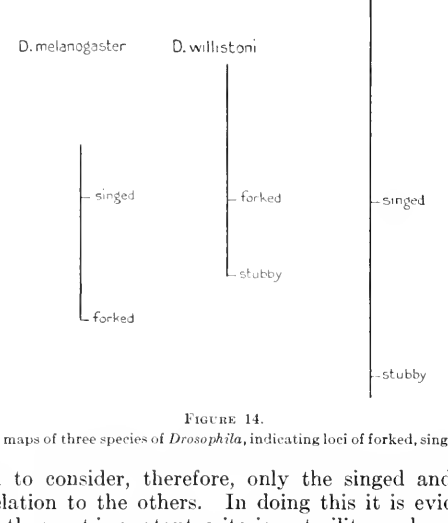


FIGURE 14.
X-chromosome maps of three species of *Drosophila*, indicating loci of forked, singed, and stubby.

We need to consider, therefore, only the singed and forked in *virilis* in relation to the others. In doing this it is evident at the outset that the most important criteria—sterility and egg modifications—can not be used. Fortunately, however, the two characters are well marked (i. e., fairly extreme) and are different in several respects. In singed the bristles are twisted and depressed, so that they lie almost flat, especially on the thorax. The hairs are curled and are also depressed. In forked the bristles and hairs are little if any depressed, and are not noticeably curled. The bristles likewise tend to be of the sharply forked rather than the curled type.

None of these features is diagnostic, but they all tend to put singed with the singed series. If a singed allelomorph with sterile females were present in *virilis* the case would be much stronger, but until some supporting or contradicting evidence is obtained the above relationships may be considered as at least probable.

This view receives considerable support from the relations of other characters and the sequence of the loci on the map, as discussed below.

COMPARISON WITH SEX-LINKED CHARACTERS IN DROSOPHILA MELANOGASTER.

The parallelism between yellow and forked in *D. virilis* and *D. melanogaster* was pointed out in an earlier paper (Metz, 1918). This was extended to include crossveinless by Weinstein (1920); and it may now be enlarged by the addition of singed, as suggested above. When this is done and the X-chromosome maps of the two species are compared, the sequence and relative positions of the four loci agree as closely as would be expected if the characters were known to be homologues. These relations are indicated in figure 15. The two outside maps in this figure are drawn to the same scale; but since the *virilis* map is considerably longer than that of *melanogaster* (due presumably to a greater amount of crossing-over in this species), the *relative* positions of the genes are shown better by making the maps the same length. For this reason the *melanogaster* map is represented twice, the right-hand one being drawn to a different scale, to equal that of *virilis*.

Another case of close resemblance is found in the allelomorphs glazed and wax compared with the allelomorphs lozenge and lozenge–2 in *melanogaster*, as discussed above under wax (p. 19). The map order here is very different, however. The locus of glazed and wax is near the end of the map (102), while that of lozenge is near the middle (28). The third allelomorph, rugose, in *virilis* is not represented in *melanogaster*. Perhaps the resemblance in the two species is accidental, but the similarity in appearance and in the sterility, or tendency toward sterility, of the females, suggests homology, and this in turn suggests a rearrangement of genes.

Of the other sex-linked characters, however, none parallels any in *melanogaster* sufficiently to make homology very probable. Sepia resembles prune in *melanogaster*, and its locus is near that of yellow, as in *melanogaster*, but it is on the opposite side of yellow. If the two are homologous they apparently indicate a rearrangement of genes. The case of magenta in *virilis* and garnet in *melanogaster* is similar. The characters are somewhat alike, but the map location does not correspond very closely, although the order of genes is the same. The great difficulty in both of these cases is that the characters are not sufficiently reliable for comparison. If they were distinguished by a combination of features, instead of merely by the possession of darker eyes than usual, the case would be more plausible. This is especially true in view of the radical difference between the "normal" eye-colors in the two species and the fact that several dark-eyed mutants are known in each.

Much the same argument may be used in the case of vermilion *virilis* and vermilion *melanogaster*, vesiculated *virilis* and inflated *melanogaster* and droop *virilis* and depressed *melanogaster;* hence it seems unnecessary to give a detailed discussion of these. Their

factorial relations are shown on the accompanying chromosome maps (fig. 16), with the exception of depressed, which is an autosomal character.

COMPARISON WITH SEX-LINKED CHARACTERS IN DROSOPHILA SIMULANS.

Turning to the sex-linked characters of other species than *melanogaster*, we find first the parallels yellow and forked in *D. simulans*. Since these are homologous to the yellow and forked in *melanogaster* the above discussion covers their case. A third character, bubble, in *simulans* parallels vesiculated in *virilis* both in appearance and in its map locus. This type of character, like many of the eye-colors, is not very reliable for comparison, but, so far as the evidence goes, it points towards homology.

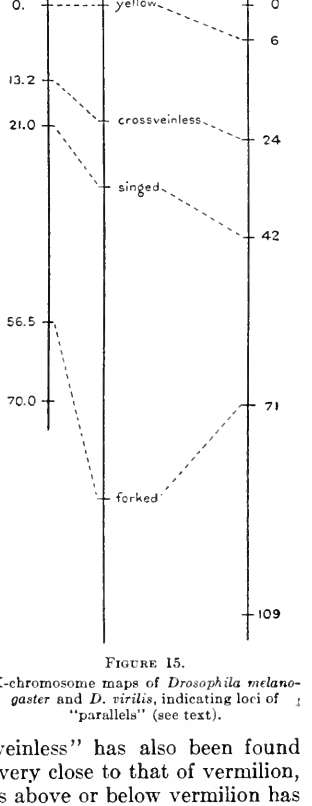


FIGURE 15.
X-chromosome maps of *Drosophila melanogaster* and *D. virilis*, indicating loci of "parallels" (see text).

COMPARISON WITH SEX-LINKED CHARACTERS IN D. WILLISTONI.

In *D. willistoni*, the four characters yellow, vermilion (unpublished), forked, and stubby resemble, respectively, yellow, vermilion, singed, and forked in *virilis*, and the order and relative positions of their loci on the map are similar, except that in *willistoni* the series begins (with yellow) at approximately the middle of the map instead of at the end. The latter fact has suggested (cf. Lancefield and Metz, 1922) that the large, V-shaped X chromosome of *willistoni* may represent the rod-like X of *melanogaster* and *virilis* plus another rod of equal length attached at its end. This is in agreement with the apparent chromosomal relations of these species, and with the interpretation given by D. E. Lancefield for similar conditions in *D. obscura*. A sex-linked "crossveinless" has also been found recently in *willistoni*, and its locus is very close to that of vermilion, as is the case in *virilis*. Whether it is above or below vermilion has not yet been determined. It will be recalled that the vermilion

melanogaster does not agree in position (with respect to yellow, etc.) with the vermilion in *virilis* (see fig. 16). In the former it is between singed and forked, while in the latter it is between crossveinless and singed, at a point very close to crossveinless. The order in *willistoni* agrees with that in *virilis*, suggesting that in these the vermilions may be homologous. If crossveinless in *willistoni* should prove to be "located" between yellow and vermilion, the parallelism would be complete.[1]

The only other case of close resemblance between sex-linked characters in these two species is that of short. Short *virilis* is similar to, but less extreme than, the least extreme of the short allelomorphs in *willistoni* (cf. Lancefield and Metz, 1922, fig. 13). Its locus with respect to the other characters considered above, however, is very different (fig. 16). This indicates that the two are merely mimics or else that a rearrangement of genes is probably involved. The former interpretation seems more probable, for mutants with short veins appear frequently—indeed a second "short" is now known in *willistoni* which is due to a mutation in another locus in the X chromosome (unpublished data).

COMPARISON WITH SEX-LINKED CHARACTERS IN DROSOPHILA OBSCURA.

(Figure 16.)

When the sex-linked characters of *D. obscura* are considered in relation to those of *virilis*, two different comparisons may be made, according to the manner of orientation of the map. These have been discussed by D. E. Lancefield (1922, p. 377), and need only a brief review here. Yellow, vermilion, and singed are fairly similar in the two species and their loci are in the same sequence. It is also the same sequence as that of yellow, vermilion, and forked (probably singed) in *willistoni*. The map-distances in the three species differ considerably, but this appears to be correlated with general differences in crossing-over in the three. The parallelism of these series is suggestive of homology throughout, especially since an additional character, scute, is present and coincides in its locus in *obscura* and *willistoni*. The case for *willistoni* and *obscura* is further strengthened by the fact that both possess V-shaped X chromosomes and that the series begins (with scute and yellow) at approximately the middle of the map.

The alternative comparison of the *virilis* and *obscura* sex-linked groups is based on the resemblance between the two "glazed" characters. Glazed in *obscura* agrees with glazed in *virilis* both in appearance and in the sterility of the females. If these characters are considered as parallels, it is necessary to reorient the maps or to

[1] Subsequent data indicate that this is the case.

postulate some rearrangement of loci, for with the above orientation of the maps glazed lies near the upper end in one case and the lower end in the other.

In both of these comparisons the character "short" has been omitted because it is so unreliable for comparative purposes (see above, under *willistoni*). It is similar in the two species, however, and the sequence of loci is the same when the maps are oriented with respect to yellow, vermilion, and singed. But the short locus is much farther from the others than it is in *virilis*. Stubby in *obscura*, with a locus close to that of short, has also been omitted, although it might be compared with forked in *virilis*. The difficulty here is that stubby does not have forked bristles, and consequently may not be in the same category as the "forked" and "singed" characters. (See special discussion of these above.)

COMPARISON WITH SEX-LINKED CHARACTERS IN DROSOPHILA FUNEBRIS.

Comparison with the remaining species, *D. funebris*, involves only the character forked. As pointed out by Sturtevant (1921*a*, p. 63), and as noted above, forked in *funebris* bears a close resemblance to forked in *virilis*. It might also be compared with singed, however, and since there are no other apparent parallels with which to construct a series, both possibilities must be considered.

COMPARISON OF AUTOSOMAL CHARACTERS.

As might be expected from the small number involved, the autosomal characters of *D. virilis* include too few "parallels," as yet, to permit of a detailed comparison of the linkage groups with those in the other species. Hence the following considerations are given mainly for the sake of completeness.

The resemblance between confluent in *virilis* and *melanogaster* has been pointed out in previous papers (see under description of confluent). The probability of homology here is reduced somewhat by the fact that dominant characters of this type appear to be fairly common. Triangle in *virilis*, for instance, is similar to confluent, although less extreme and not lethal when homozygous. Extra also resembles confluent in some cases. The veins affected by confluent seem to be particularly susceptible to modification in this direction.

In *D. obscura* a dominant, autosomal confluent is known (unpublished data of D. E. Lancefield), but this is much more extreme than those in *virilis* and *melanogaster* and involves other veins. It is improbable that this is homologous to either of the others.

Concave in *virilis* bears a close resemblance to crumpled in *melanogaster*, and gives perhaps the most convincing evidence of homology. Both characters are autosomal recessives; both affect the scutellar bristles and the hairs on the arista in the same fashion; and both

involve an irregular series of wing modifications that ranges from the normal condition through various long, narrow, curved, or shortened forms (see figs. 5 to 7 in plate 3) to a condition in which the wing is very short and broad and is wavy or crumpled. In both cases the wings are frequently asymmetrical and are often held at an angle from the body. Crumpled is in the third-chromosome series in *melanogaster* at approximately 93 (unpublished data of C. B. Bridges), and concave is in the second-chromosome group of *virilis* (fig. 7). If we consider the genes homologous, we would compare the *virilis* second-chromosome group with the third of *melanogaster*. The only other third-chromosome characters that resemble any in *virilis* are ascute (at about the middle of the map) and spread (at about 65). The latter may be left out of consideration for the present, because the nature of the character makes it of little value for comparison, (i. e., spread-wing mutants are too numerous). Ascute resembles hunch in *virilis*, which is in the third-chromosome series. This suggests that chromosome III of *melanogaster* may represent chromosomes II and III in *virilis* combined.

The presence in *D. obscura*, however, of two characters like ascute, in different linkage groups, casts considerable doubt on the reliability of ascute for comparative purposes. Likewise, it should be noted that confluent is in the same linkage group as concave in *virilis*, while the characters resembling them in *melanogaster* are in different groups (II and III). It seems probable that most of the above cases involve mimicry rather than homology.

The other cases of resemblance among the autosomal characters are equally doubtful, except in the case of bent and net, which have been discussed fully above (pp. 51–53). Telescoped resembles furrowed *melanogaster* in its effect on the thorax, but the eyes are affected very differently in the two cases, and the bristles are short in furrowed and not in telescoped, so that the resemblance is probably superficial. A closer resemblance is shown by the sex-linked character compressed in *D. obscura*. It resembles telescoped in nearly all respects (see D. E. Lancefield, 1922). This resemblance recalls the fact that hunch in *virilis* is in the same linkage group (III) as telescoped and that in *obscura* ascute, which resembles hunch, is sex-linked. Thus the two sex-linked characters in the one case resemble the two third-chromosome characters in the other, suggesting that the V-shaped X chromosome of *obscura* represents the rod-like X of *virilis*, plus chromosome III. This is made improbable, however, by the presence in *obscura* of an autosomal character like ascute, and also by the fact that the loci of compressed and ascute are in the part of the map that seems to correspond to the X-chromosome map of *virilis*.

Only two other characters need be noted in this connection. The first of these is approximated. It resembles several characters in

melanogaster, as for example, dachsous and arc, but each of the latter involves additional modifications. The same is true with respect to approximated in *willistoni*, which has short legs like dachsous. The second character is broken. This resembles crossveinless, or characters of this type of which there are several in other species. One such autosomal character is known in *obscura*, two or three are known in *willistoni* (one being sex-linked), and a sex-linked crossveinless is known in *melanogaster* and *virilis*.

X. THE CASE OF VERMILION, AND THE POSSIBILITY OF A REARRANGEMENT OF GENES.

The resemblance between *virilis*, *willistoni*, and *obscura* in respect to the location of vermilion, and their consistent difference from *melanogaster* in this feature, have already been pointed out. They suggest that the vermilion of *melanogaster* is not homologous to any of the others. This view receives some support from the observations of Lancefield (1922, p. 377) on *obscura*, showing that the double-recessive eosin vermilion differs from the eosin vermilion of *melanogaster*. As Dr. Sturtevant has suggested to us, however, the fact that vermilion is a frequently appearing mutant—at least in some species—and that only one such character is known in the sex-linked group of any of the above species supports the opposite view, i. e., that the same gene is involved throughout. This argument may be questioned, perhaps, on the ground that vermilion (in *obscura* and *melanogaster* at least) resembles the autosomal character scarlet in *obscura*, *melanogaster*, and *simulans* (cf. D. E. Lancefield, 1922, p. 377), but such an objection is not serious enough to rule out the hypothesis. There are other cases also (e. g., sepia, magenta, wax, vesiculated, etc.), as noted above, involving similar characters but a different map order. And more striking examples are known in other species. Sturtevant (1921*d*), for instance, has presented evidence that indicates a rearranged map order in the third chromosome of *D. simulans* (as compared with *melanogaster*), where the homology of genes has been tested by hybridization. Lancefield (1922) has observed a similar case in *D. obscura*, although here no hybridization tests are possible. Both of these cases have been discussed by the authors mentioned and the details need not be given here. The most probable interpretation of the results, at least in the case of *D. simulans*, would seem to be on the assumption of a rearrangement of genes, brought about by a transposition of part of a chromosome. And this is the interpretation given by Sturtevant (l. c.).

Recent evidence obtained by Dr. H. J. Muller, however, brings up the possibility of another interpretation for cases of this kind. In a paper presented before the American Naturalists at the Toronto meeting (1921),[1] Muller described the results of experiments with a mutant race of *Drosophila melanogaster* in which crossing-over was greatly reduced by a "cross-over modifier." One of the pecularities of these results was that when treated in the ordinary fashion for constructing a map they gave a reversed order of loci for certain well-known characters. This was apparently due to an excess of double

[1] "A lethal gene which changes the order of the loci in the chromosome map." The title of this paper, without abstract, is printed in the Anatomical Record, Jan. 1922, **23**:129. The present reference is made with Dr. Muller's permission.

cross-overs over singles. In any case, according to Muller, it was not due to a chromosomal reorganization, as was shown by genetic test in cases where the "cross-over modifier" was eliminated.

It is perhaps too early to draw general conclusions from this and other cases involving cross-over modifiers,[1] but it is to be observed that Muller's case gives the appearance of involving a rearrangement of genes, and is analogous in some respects to the case of vermilion just cited and to those in *D. simulans* and *D. obscura*. Until further evidence is obtained, therefore, it is necessary to consider the possibility of an inverted sequence of loci being due to a disturbance in crossing-over rather than to an actual rearrangement of genes.

[1] Cf. especially Muller (1916) and Sturtevant (1919). In Sturtevant's table 17 (p. 320) the three cross-overs involving the region b–pr were all doubles.

XI. COMPARISON OF X-CHROMOSOME MAPS.

Taking into account all, or practically all, of the characters that bear a resemblance to one another, and omitting the remainder, the X-chromosome maps of the six species considered above appear as shown in figure 16. These maps are all drawn to the same scale, based on percentages of crossing-over. The first three represent X chromosomes of the short, rod-like type; the third and fourth are of the long V-shaped type; and the last (*D. funebris*) is rod-like, but uncertain as to length (see p. 7). Three different grades of characters are represented on these maps. Characters that give considerable indication of homology to one or more of the others are represented by words beginning with capitals; those considered as possible but not probable homologues are represented in small type; while the remainder are represented merely by marks to indicate their respective loci.

The alinement of the maps is based on the apparent degree of resemblance of the characters as discussed above. One of the most striking features noticeable in a comparison of the maps is shown by the relations of yellow. In the three species having the rod-like type of X chromosome, yellow comes at or near the end of the map; while in the two possessing long V-shaped X chromosomes it comes near the middle. The probability of homology throughout this series is supported by the presence in three species of a very closely linked character scute (=scutellar). On the basis of this resemblance, the maps are placed so that the locus of yellow corresponds throughout, except in the case of the *funebris* map, where yellow is not represented. The latter has been oriented with respect to notch and forked (see Sturtevant, 1921*a*).

If we compare the total lengths of the different maps (omitting *funebris* on account of the small number of loci), and consider the size relations of the chromosomes involved, we note at once that the maps are not proportional to chromosome length in all cases. If we use the *melanogaster* map as a standard of comparison, we find that the *simulans* map agrees fairly closely, but that the *virilis* map is nearly 50 per cent too long. Likewise, the *obscura* map, which should be approximately twice as long, is actually about three times as long. The *willistoni* map, on the other hand, is much too short. It should be approximately double that of *melanogaster*, and equal to that of *obscura;* but instead it is only slightly longer than that of *melanogaster*.

In each of these cases (excluding *funebris*) the number of characters studied is sufficient to make it probable that most of the chromosome is represented. The difference appears to be due, therefore, to differences in amount of crossing-over in the various species. This interpretation is supported also by the distribution of the loci on the maps. In *willistoni*, where crossing-over is presumed to be low, the

loci are relatively crowded as compared with those of *virilis* and *obscura*, in which almost as many loci are represented. The differences seem to be largely due to *general* increase or decrease in crossing-over, but it is probable that some regions in the chromosomes differ more than others in this respect. This has been shown to be the case in *D. simulans* (Sturtevant, 1921*a*), and is indicated in the

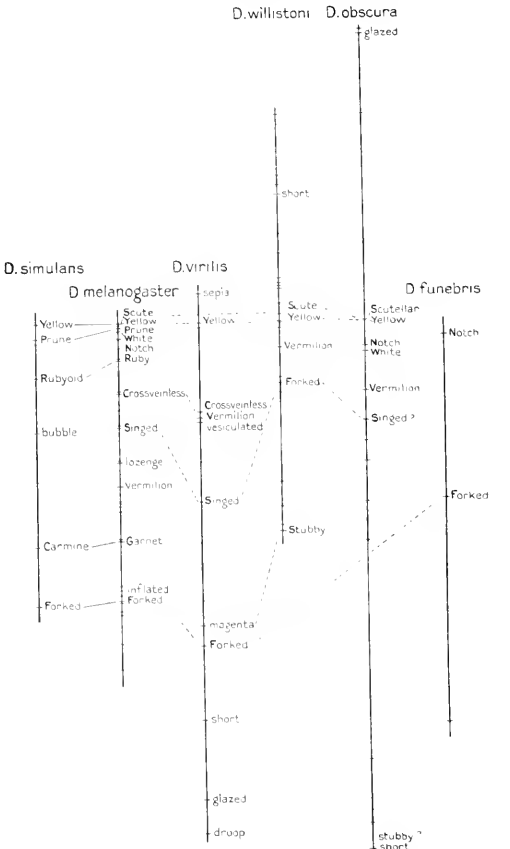


FIGURE 16.—X-chromosome maps of six species of *Drosophila* drawn to scale according to cross-over percentages.

others by the spacing of the loci in clusters, with intermediate regions almost blank. Such regions show relatively little conformity in the different species. If the cases of parallel characters are reliable, they furnish more definite information, but we do not consider it safe to base any detailed comparison on this ground at present. The relations are easily seen by an examination of figure 16.

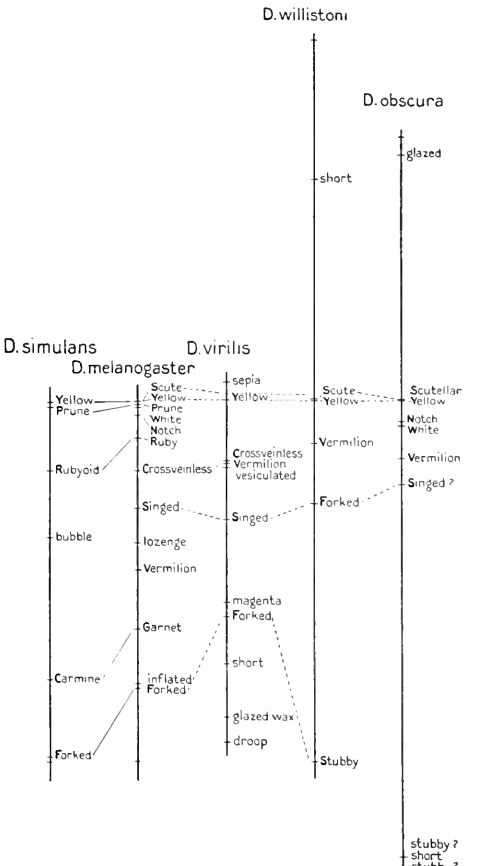


FIGURE 17.—The same maps as those shown in figure 16, but drawn to different scales in accordance with chromosome length.

In figure 17 we have represented the same maps as shown in figure 16, but drawn to different scales, so that they are roughly proportional to the lengths of the respective chromosomes. This tends to eliminate the differences due to any *general* increase or decrease in crossing-over, but of course it does not eliminate differences that affect particular regions.

A comparison of these maps shows a degree of conformity between the loci of possible "parallels" that harmonizes in most cases with the view that they may be homologous. There is, of course, a considerable element of chance entering in here, and some of the resemblances may be accidental, but they can hardly all be accounted for on this basis.

The autosomal maps of *D. virilis* are not yet sufficiently reliable for comparison. In considering rates of crossing-over, however, we may compare the X chromosome map of *virilis* with the autosomal maps of *D. melanogaster* (the only ones available for the purpose). When this is done we find the same sort of difference as noted in the case of the X chromosomes of the two species, i. e., crossing-over is more frequent in *virilis*. The X-chromosome map of *virilis* slightly exceeds both of the long autosomal maps in *melanogaster*, although the autosomes themselves are both of the long V-shaped type, approximately twice as long as the rod-like X chromosome of *virilis*.

XII. COINCIDENCE.

Coincidence in the X chromosome of *D. virilis* appears to resemble that in *D. melanogaster*, as has already been noted by Weinstein (1920). Since this subject is being investigated in detail by Dr. Weinstein, we will confine ourselves to a tabulation of the values obtained from the *new data* in the present paper. In most cases the numbers are not large enough to be satisfactory, but the results agree with previous ones in indicating a resemblance to those obtained from *D. melanogaster*.

TABLE 8.—*Coincidence in Drosophila virilis.*

Experiment.	Regions involved.	Total flies.	Double cross-overs.	Calculated distance.	Map-distance.	Coincidence.
34, 48	se–c–si.....	547	16	35	42	0.997
48	se–c si–m....	406	22	61	67	1.031
48	se–c si–f.....	406	22	64	71	1.004
34, 48	se–c si–s.....	547	34	81	86	0.882
48	se–c f–s.....	406	8	82	86	0.585
34, 35, 48	se–c–s.....	972	81	74	86	1.002
20, 36, 46	y–c–v.....	1,506	2	20	18	1.276
46, 47	y–v(vs)–m...	999	51	53	61	0.777
38, 39, 47	y–vs–f.....	980	61	55	65	0.945
46, 47	y–v(vs) m–f..	999	3	56	65	0.515
38, 39, 47	y–vs f–r.....	980	36	86	96	0.598
40, 46	c–v–m.....	2,050	3	37	43	0.824
40, 46	c–v m–f.....	2,050	0	39	47	0.0
48	c–si–m.....	406	12	42	43	0.749
34, 48	c–si–s.....	547	29	62	62	0.982
48	c–si m–f.....	406	1	45	57	0.548
48	c–si f–s.....	406	9	63	62	0.878
27, 40, 41, 42 43, 44, 46, 47 48	c v vs } –m–f.....	5,218	73	39	46	1.124
43, 44, 47	vs–m f–r....	2,068	168	65	77	0.927
38, 39, 47	vs–f–r.....	980	104	67	77	0.996
45, 48	si–m–f.....	577	7	32	29	1.239
45, 48	si–m f–s.....	577	31	50	44	1.025
45, 48	m–f–s.....	577	9	22	19	2.426
43, 44, 47	m–f–r.....	2,068	29	31	35	1.042
32	t–s–d.....	315	2	25	28	0.646
33	s–r–d.....	409	19	34	23	1.654

In table 8 the data are given in order, according to the map region involved, beginning with the uppermost loci. The cases involving more than 25 double cross-overs and more than 900 flies are summarized separately in table 9, and are arranged in accordance with map-distance rather than map-region. In both tables the column headed "Calculated distance" gives the "distance" between the uppermost and lowermost loci, calculated from the particular experiments involved. Under "Map-distance" is given the corresponding value taken from the final map (fig. 7). The latter is the larger value in most cases.

TABLE 9.—*Coincidence in Drosophila virilis* (selected data from table 8.)

Experiment.	Regions involved.	Total flies.	Double cross-overs.	Calculated distance.	Map-distance.	Coincidence.
43, 44, 47	m–f–r.....	2,068	29	31	35	1.042
27, 40, 41, 42	c v vs	5,218	73	39	46	1.124
43, 44, 46, 47 48	–m–f.....					
46, 47	y–v(vs)–m...	999	51	53	61	0.777
38, 39, 47	y–vs–f.....	980	61	55	65	0.945
43, 44, 47	vs–m f–r....	2,068	168	65	77	0.927
38, 39, 47	vs–f–r	980	104	67	77	0.996
34, 35, 48	se–c–s.....	972	81	74	86	1.002
38, 39, 47	y–vs f–r ...	980	36	86	96	0.598

Since the loci of crossveinless, vermilion, and vesiculated are so close together, data from experiments involving these characters have been lumped together in some cases (e. g., the second case in table 9), in order to secure larger numbers for the calculations. This introduces a slight error, but one that may safely be ignored for present purposes.

XIII. CHROMOSOMES AND LINKAGE GROUPS COMPARED.

On the basis of its chromosomes, *Drosophila virilis* would be expected to possess six groups of linked genes. Five of these, including the sex-linked group, should be of approximately the same size as regards amount of crossing-over, and the sixth should be relatively very small, both in respect to amount of crossing-over and to number of genes. Six groups have been identified, as indicated in the above account. Of these the sex-linked group (group I) includes far more genes than any of the others, as would be anticipated from the fact that sex-linked mutations are more readily detected than autosomal ones. The autosomal linkage groups (II-VI) contain respectively 4, 6, 3, 5, and 2 characters, and do not, as yet, show the expected difference distinguishing one group from the other four. As to amount of crossing-over, it is too early to compare them, except in a general way. Groups II, III, and V show sufficient crossing-over to indicate that they will probably equal the sex-linked group in map-length when more characters are obtained. On this basis, these four groups (I, II, III, and V) are identified with four of the large chromosomes. Groups IV and VI, however, although containing 3 and 2 characters, respectively, give no crossing-over, and the question arises as to which is to be identified with the remaining large chromosome and which with the small *m*-chromosome. This question can not be answered with certainty at present, but the following three lines of evidence favor the view that group VI represents the *m*-chromosome: (1) One of its two characters appears to be a deficiency for the other, indicating that a small "region" is involved. (2) Both characters resemble characters in group IV (representing the *m*-chromosome) of *D. melanogaster* (see above under group VI). (3) The absence of crossing-over in group IV of *virilis* may possibly be due to the fact that the characters involved have arisen in stocks obtained from different localities (see above under group IV). Possibly the "fourth" chromosomes in these stocks are sufficiently different to inhibit crossing-over. An attempt is being made to test this view. Another explanation is that group IV represents a long chromosome, and that crossing-over is infrequent in this chromosome because of the presence of one or more genes reducing crossing-over, analogous to those known to have this effect in certain races of *D. melanogaster* (Muller, 1916; Sturtevant, 1919; Detlefsen, 1920; Gowen and Gowen, 1922).

In the other species of *Drosophila*, exclusive of *melanogaster* and *simulans*, little has been published regarding the autosomal linkage groups. It may be stated, however, that in both *willistoni* and *obscura* the number of such groups agrees with or at least does not

exceed the haploid number of autosomes. In *willistoni*, which has only two pairs of autosomes (unless the *m*-chromosomes are present but are so small as to have escaped detection), only two groups of non-sex-linked characters have been found. One of these contains eight characters and gives a long map; the other contains six characters, but their linkage relations are not yet worked out.

In *obscura* where four pairs of autosomes are represented, two autosomal linkage groups with four or more characters each, are known; and preliminary results indicate that the other two are probably represented by one character each (unpublished data of D. E. Lancefield).

In *D. melanogaster*, as is well known, the four linkage groups show a fairly close correspondence to the four pairs of chromosomes, both as regards number of loci and amount of crossing-over. In the other species (at least *simulans*, *virilis*, and *willistoni*) the evidence points in the same direction.

XIV. TABULATION OF LINKAGE EXPERIMENTS.

LINKAGE EXPERIMENTS ON SEX-LINKED GENES (GROUP I).

(Experiments 1 to 53.)

EXP. 1.—*Sepia vermilion.*

Mating: sepia × vermilion.
6 cultures (E 525–6, 535–6, 545–6).

Non-cross-overs (se 191; v 226)	417
Cross-overs (se v 60; + 68)	128
Total	545

Per cent cross-overs, se–v, 23.5.

EXP. 2.—*Frayed forked.*

Mating: frayed × forked.
3 cultures (V 812, 815, 827).

Non-cross-overs (fd 72; f 61)	133
Cross-overs (fd f 47; + 74)	121
Total	254

Per cent cross-overs, fd–f, 47.6.

EXP. 3.—*Yellow crossveinless.*

Mating: yellow crossveinless × wild-type.
5 cultures (P 833–837).

Non-cross-overs (y c 159; + 161)	320
Cross-overs (y 40; c 46)	86
Total	406

Per cent cross-overs, y–c, 21.2.

EXP. 4.—*Yellow vermilion.*

Mating: yellow × vermilion.
6 cultures (P 656, 681, 693–4, 722, 725).

Non-cross-overs (y 176; v 167)	343
Cross-overs (y v 44; + 45)	89
Total	432

Per cent cross-overs, y–v, 20.6.

EXP. 5.—*Vermilion vesiculated.*

Mating: vermilion × vesiculated.
7 cultures (E 447–8, 473, 735–6, 747–8).

Non-cross-overs (v 481; vs 463)	944
Cross-overs (v vs 9; + 14)	23
Total	967

Per cent cross-overs, v–vs 2.4; counting only vs, 1.9.

EXP. 6.—*Vermilion singed.*

Mating: vermilion × singed.
9 cultures (P 529–532, 538, 553, 682, 736–7).

Non-cross-overs (v 344; si 309)	653
Cross-overs (v si 75; + 74)	149
Total	802

Per cent cross-overs, v–si 18.6.

EXP. 7.—*Vermilion short.*

Mating: vermilion × short.
14 cultures (P 543–7, 551–2, 562–5, M 40, 42, 62).

Non-cross-overs (v 489; s 450)	939
Cross-overs (vs 344; + 370)	714
Total	1,653

Per cent cross-overs, v–s 43.2.

EXP. 8.—*Vermilion triangle.*

Mating: vermilion × triangle.
3 cultures (E 410–11, 446).

Non-cross-overs (v 59; T 43)	102
Cross-overs (v T 13; + 52)	65
Total	167

Per cent cross-overs, v–T 38.9.

EXP. 9.—*Vermilion glazed.*

Mating: vermilion × glazed.
6 cultures (L 541, 541 (1), E 166, 179, 347–8).

Non-cross-overs (v 70; r^g 45)	115
Cross-overs (v r^g 30; + 55)	85
Total	200

Per cent cross-over, v–r^g 42.5.

EXP. 10.—*Singed triangle.*

Mating: singed × triangle.
4 cultures (M 27, 30, 32, 52).

Non-cross-overs (si 38; T 44)	82
Cross-overs (si T 18; + 36)	54
Total	136

Per cent cross-overs, si–T 39.7.

EXP. 11.—*Singed short.*

Mating: singed × short.
8 cultures (P 643–4, 650, 672–3, 704, M 91, 124*b*).

Non-cross-overs (si 176; s 159)	335
Cross-overs (si s 97; + 119)	216
Total	551

Per cent cross-overs, si–s 39.2.

EXP. 12.—*Singed droop.*

Mating: singed × droop.
2 cultures (M 44, 50).

Non-cross-overs (si 26; d 17)	43
Cross-overs (si d 12; + 25)	37
Total	80

Per cent cross-overs, si–d 46.2; counting only d flies 41.3.

EXP. 13.—*Triangle short.*

Mating: triangle × short.
5 cultures (M 41, 51, 64, 122, 198).

Non-cross-overs (T 152; s 124)	276
Cross-overs (T s 8; + 8)	16
Total	292

Per cent cross-overs, T–s 5.5.

EXP. 14.—*Triangle rugose.*

Mating: triangle × rugose.
2 cultures (L 681, 690).

Non-cross-overs (T 72; r 81)	153
Cross-overs (T r 7; + 8)	15
Total	168

Per cent cross-overs, T–r 8.9.

EXP. 15.—*Triangle droop.*

Mating: triangle × droop.
3 cultures (M 43, 45, 63).

Non-cross-overs (T 68; d 55)	123
Cross-overs (T d 17; + 51)	68
Total	191

Per cent cross-overs, T–d 23.6, counting only d flies.

EXP. 16.—*Short rugose.*

Mating: short × rugose.
7 cultures (P 533–4, 539, 555–8).

Non-cross-overs (s 327; r 270)	597
Cross-overs (s r 57; + 76)	133
Total	730

Per cent cross-overs, s–r 18.2.

EXP. 17.—*Short droop.*

Mating: short × droop.
3 cultures (M 38, 96, 100).

Non-cross-overs (s 93; d 48)	141
Cross-overs (s d 8; + 47)	55
Total	196

Per cent cross-overs, s–d 28.0; counting only d flies, 14.3.

EXP. 18.—*Rugose droop.*

Mating: rugose × droop.
8 cultures (E 1260–2, 1307–8, 1349–51).

Non-cross-overs (d 283; r 314)	597
Cross-overs (d r 23; + 68)	91
Total	688

Per cent cross-overs, r–d, counting only d, 7.5.

EXP. 19.—*Sepia yellow crossveinless.*

Mating: sepia × yellow crossveinless.
7 cultures (L 492, 495–6, E 528–9, 547–8).

Non-cross-overs (se 204; y c 206)	410
Co. region 1 (se y c 8; + 16)	24
Co. region 2 (se c 53; y 54)	107
Co. region 1–2 (se y 2; c 5)	7
Total	548

Per cent cross-overs, se–y 5.6; y–c 20.8.

EXP. 20.—*Yellow crossveinless vermilion.*

Mating: yellow crossveinless × vermilion.
3 cultures (E 409, 744, 746).

Non-cross-overs (y c 177; v 197)	374
Co. region 1 (y v 59; c 37)	96
Co. region 2 (y c v 1; + 1)	2
Total	472

Per cent cross-overs, y–c 20.3, c–v 0.4.

EXP. 21.—*Yellow crossveinless singed.*

Mating: yellow crossveinless × singed.
5 cultures (P 498, 508–11).

Non-cross-overs (y c 148; si 135)	283
Co. region 1 (y si 28; c 36)	64
Co. region 2 (y c si 23; + 40)	63
Co. region 1–2 (y 5; c si 2)	7
Total	417

Per cent cross-overs, y–c 17.0; c–si 16.8.

EXP. 22.—*Yellow crossveinless short.*

Mating: yellow crossveinless × short.
1 culture (P 567).

Non-cross-overs (y c 34; s 27)	61
Co. region 1 (y s 7; c 8)	15
Co. region 2 (y c s 26; + 26)	52
Co. region 1–2 (y 4; c s 5)	9
Total	137

Per cent cross-overs, y–c 17.5; c–s 44.5.

EXP. 23.—*Yellow crossveinless droop.*

Mating: yellow crossveinless × droop.
1 culture (E 1314).

Non-cross-overs (y c 28; d 15)	43
Co. region 1 (y d 1; c 4)	5
Co. region 2 (y c d 5; + 15)	20
Co. region 1–2 (y 10; c d 1)	11
Total	79

Per cent cross-overs, y–c 20.2; c–d 39.2.

EXP. 24.—*Yellow vermilion short.*

Mating: yellow short × vermilion.
4 cultures (P 707–8, 710, 712).

Non-cross-overs (y s 56; v 65)	121
Co. region 1 (y v 9; s 11)	20
Co. region 2 (y 43; v s 29)	72
Co. region 1–2 (y v s 5; + 7)	12
Total	225

Per cent cross-overs, y–v 14.2; v–s 37.3.

EXP. 25.—*Yellow singed short.*

Mating: yellow singed × short.
4 cultures (P 649, 674–5, 677).

Non-cross-overs (y s 34; si 40)	74
Co. region 1 (y si 17; s 24)	41
Co. region 2 (y 19; si s 21)	40
Co. region 1–2 (y si s 9; + 9)	18
Total	173

Per cent cross-overs, y–si 34.1; si–s 33.5.

EXP. 26.—*Yellow hairy magenta.*

Mating: yellow hairy × magenta.
1 culture (V 866).

Non-cross-overs (y ha 16; m 19)	35
Co. region 1 (y m 16; ha 9)	25
Co. region 2 (y ha m 1; + 1)	2
Co. region 1–2 (y 0; ha m 1)	1
Total	63

Per cent cross-overs, y–ha 41.3; ha–m 4.8.

EXP. 27.—*Vermilion magenta forked.*

Mating: vermilion × magenta forked.
2 cultures (E 475–6).

Non-cross-overs (v 59; m f 48)	107
Co. region 1 (v m f 24; + 28)	52
Co. region 2 (v f 3; m 3)	6
Total	165

Per cent cross-overs, v–m 31.5; m–f 3.6.

EXP. 28.—*Vesiculated hairy magenta.*

Mating: vesiculated magenta × hairy.
4 cultures (V 1054–55, 1061–62).

Non-cross-overs (vs m 32; ha 39)	71
Co. region 1 (vs ha 22; m 24)	46
Co. region 2 (vs 0; ha m 2)	2
Co. region 1–2 (vs ha m 1; + 1)	2
Total	121

Per cent cross-overs, vs–ha 39.6; ha–m 3.3; counting only vs flies, vs–ha 41.8.

EXP. 29.—*Hairy magenta forked.*

Mating: hairy × magenta forked.
4 cultures (V 1114, 1116, 1119–20).

Non-cross-overs (ha 105; m f 53)	158
Co. region 1 (ha m f 1; + 4)	5
Co. region 2 (ha f 0; m 2)	2
Co. region 1–2 (ha m 1; f 0)	1
Total	166

Per cent cross-overs, ha–m 3.6; m–f 1.8.

EXP. 30.—*Magenta forked triangle.*

Mating: magenta forked × triangle.
2 cultures (P 911–12).

Non-cross-overs (m f 109; T 129)	238
Co. region 1 (m T 1; f 1)	2
Co. region 2 (m f T 5; + 24)	29
Total	269

Per cent cross-overs, m–f 0.7; f–T 10.7; counting only T flies, f–T 3.7.

EXP. 31.—*Magenta forked droop.*

Mating: magenta forked × droop.
4 cultures (E 1270–1, 1310–11).

Non-cross-overs (m f 50; d 47)	97
Co. region 1 (m d 1; f 1)	2
Co. region 2 (m f d 15; + 45)	60
Co. region 1–2 (m 1; f d 1)	2
Total	161

Per cent cross-overs m–f 2.5; f–d 38.5; counting only d flies, f–d 25.0.

EXP. 32.—*Triangle short droop.*

Mating: Triangle short × droop.
4 cultures (M 184, 205, 210, 225).

Non-cross-overs (T s 120; d 117)	237
Co. region 1 (T d 7; s 6)	13
Co. region 2 (T s d 31; + 32)	63
Co. region 1–2 (T 0; s d 2)	2
Total	315

Per cent cross-overs: T–s 4.8, s–d 20.6.

EXP. 33.—*Short rugose droop.*

Mating: short droop × rugose.
6 cultures (M 280, 283, 304–7).

Non-cross-overs (s d 138; r 149)	287
Co. region 1 (s r 20; d 15)	35
Co. region 2 (s 57; r d 11)	68
Co. region 1–2 (s r d 0; + 19)	19
Total	409

Per cent cross-overs, s–r 13.2; r–d 21.3, counting all flies; counting only d flies, r–d, 6.7.

EXP. 34.—*Sepia crossveinless singed short.*

Mating: sepia crossveinless × singed short.

Culture No.	Non-cross-overs.		Cross-overs in region.																Total.
			1		2		3		1–2		1–3		2–3		1–2–3				
	se c	si s	se si s	c	+	se c si s	se c s	si	se c	si s	se si	s c	se c si	s	se s	c si			
M 302	14	10	3	4	4	0	7	12	2	0	2	2	1	3	0	1			65
M 308	12	15	7	4	5	4	6	14	1	1	1	3	2	1	0	0			76
Total..	26	25	10	8	9	4	13	26	3	1	3	5	3	4	0	1			141

Per cent cross-overs: se–c, 21.9; c–si, 17.7; si–s, 39.0.

EXP. 35.—*Sepia crossveinless short rugose.*

Mating: sepia crossveinless short × rugose.

Culture No.	Non-cross-overs.		Cross-overs in region.														Total.
			1		2		3		1-2		1-3		2-3		1-2-3		
	r	se c s	se r	c s	se c r	s	+	se c s r	se s	c r	se	c s r	se c	s r	c	se s r	
M 348	18	12	3	4	8	13	2	1	2	2	1	1	5	2	0	1	75
M 349	14	15	2	9	10	12	4	0	4	3	1	1	5	4	3	0	87
M 350	18	12	4	6	12	14	2	0	2	2	0	0	2	0	0	0	74
M 351	20	14	7	1	8	17	4	2	0	5	1	0	3	0	1	1	84
M 352	21	23	2	6	9	23	2	3	5	0	1	0	4	2	2	2	105
Total..	91	76	18	26	47	79	14	6	13	12	4	2	19	8	6	4	425

Per cent cross-overs: se–c, 20.0; c–s, 44.2; s–r, 14.8.

EXP. 36.—*Yellow crossveinless vermilion vesiculated.*

Mating: yellow crossveinless × vermilion vesiculated.

Culture No.	Non-cross-overs.		Cross-overs in region.						Total.
			1		2		3		1-2		
	y c	v vs	y v vs	c	y c v vs	+	y c vs	v	y	c v vs	
P 900	22	28	5	4	0	0	0	0	0	1	60
P 901....	35	33	5	6	0	0	1	1	0	0	81
P 902	24	16	3	16	0	0	0	0	0	0	59
P 903	47	25	6	17	0	0	0	0	0	0	95
P 904	39	39	13	6	0	1	1	1	0	0	100
Total..	167	141	32	49	0	1	2	2	0	1	395

Per cent cross-overs: y–c, 20.7; c–v, 0.5; v–vs 1.0; counting only v–vs, 1.1.

EXP. 37.—*Yellow hairy magenta forked.*

Mating: yellow hairy × magenta forked.

Culture No.	Non-cross-overs.		Cross-overs in region.								Total.
			1		2		3		1-2		1-3		
	y ha	m f	y m f	ha	y h m f	+	y ha f	m	y	ha m f	y m	ha f	
V 1101	14	7	6	11	0	2	0	0	0	1	2	0	43
V 1101a	14	7	9	14	3	3	0	0	0	0	0	1	51
V 1102a	19	20	11	21	1	0	1	0	0	1	2	2	78
V 1103	11	10	9	17	0	1	0	1	0	0	1	1	51
Total.....	58	44	35	63	4	6	1	1	0	2	5	4	223

Per cent cross-overs: y–ha, 48.8; ha–m, 5.4; m–f, 4.9.

EXP. 38.—*Yellow vesiculated forked rugose.*
Mating: yellow rugose × vesiculated forked.

Culture No.	Non-cross-overs.		Cross-overs in region.														Total.
			1		2		3		1–2		1–3		2–3		1–2–3		
	y r	vs f	y vs f	r	y f	vs r	y	vs f r	y vs r	f	+	y vs f r	vs	y f r	y vs	f r	
V 945	15	13	1	9	10	13	7	8	0	5	4	0	5	2	1	1	94
V 948	6	8	2	2	4	10	3	5	1	2	2	0	3	0	0	0	48
Total..	21	21	3	11	14	23	10	13	1	7	6	0	8	2	1	1	142

Per cent cross-overs: y–vs, 21.1; vs–f, 40.1; f–r, 28.8; counting only vs flies, y–vs, 7.1; vs–f, 47.1.

EXP. 39.—*Yellow vesiculated forked glazed.*
Mating: yellow × vesiculated forked glazed.

Culture No.	Non-cross-overs.		Cross-overs in region.														Total.
			1		2		3		1–2		1–3		2–3		1–2–3		
	y	vs f r^g	y vs f r^g	+	y f r^g	vs	y r^g	vs f	y vs	f r^g	y vs f	r^g	y f	vs r^g	y vs r^g		
V 947	40	22	1	8	8	15	10	11	5	0	0	3	5	6	0	1	135
V 948	3	5	0	2	0	3	6	8	0	0	2	2	4	10	1	2	48
V 950	34	11	10	9	12	23	20	16	7	1	4	4	10	4	4	2	171
V 989	6	1	0	2	1	4	1	2	0	0	1	0	0	0	0	0	18
V 996	11	3	0	4	1	2	3	2	0	0	0	1	0	0	0	1	28
V 996*a*	16	2	0	2	1	5	3	4	0	0	0	1	3	2	0	1	40
V 997	16	3	1	0	3	2	4	2	1	2	1	0	2	1	0	0	38
Total..	126	47	12	27	26	54	47	45	13	3	8	11	24	23	5	7	478

Per cent crossovers: y–vs, 17.9; vs–f, 32.4; f–r^g, 35.5; counting only vs flies, y–vs, 18.3; vs–f, 45.9.

EXP. 40.—*Crossveinless vermilion magenta forked.*
Mating: vermilion × crossveinless magenta forked.

Culture No.	Non-cross-overs.		Cross-overs in region.										Total.
			1		2		3		1–2		2–3		
	v	c m f	c v	m f	c	v m f	c m	v f	c v m f	+	c f	v m	
E 986	29	12	0	0	18	10	0	0	0	0	0	1	70
E 987	36	28	0	0	17	15	2	0	0	0	2	0	100
E 988	59	21	0	0	36	20	1	1	0	0	0	0	138
E 990	17	17	0	0	14	2	0	1	1	0	0	0	52
E 991	56	29	0	0	35	23	1	0	0	0	1	0	145
E 992	58	43	1	0	28	11	1	0	0	0	1	0	143
E 993	46	29	0	0	23	23	0	0	0	0	0	1	122
E 1024	32	14	1	0	18	13	1	0	0	0	0	0	79
E 1025	33	18	0	0	24	16	2	0	0	0	0	0	93
E 1026	33	14	1	0	15	17	1	2	0	0	1	0	84
E 1027	44	15	1	0	17	8	1	1	0	0	0	0	87
E 1046	53	22	0	0	29	14	1	1	0	0	0	0	120
E 1047	26	19	0	1	19	15	0	2	0	0	0	0	82
E 1048	32	28	0	0	21	13	0	2	0	0	0	0	96
Total....	554	309	4	1	314	200	11	10	1	0	5	2	1411

Per cent cross-overs: c–v, 0.4; v–m, 36.9 m–f, 1.9.

EXP. 41.—*Vermilion singed magenta forked.*

Mating: vermilion singed × magenta forked.

Culture No.	Non-cross-overs.		Cross-overs in region.												Total.
			1		2		3		1-2		1-3		2-3		
	v si	m f	si	v m f	v si m f	+	v si f	m	v	m si f	v m	si f	f	v m si	
P 645	28	28	3	5	2	11	0	2	0	0	0	1	0	2	82
P 646	27	20	9	7	2	11	0	0	0	1	1	0	0	2	80
P 648	26	22	6	2	2	10	0	1	3	0	0	0	0	3	75
P 678	9	5	3	0	0	3	0	1	0	0	1	0	0	0	22
P 679	25	10	3	5	2	5	1	1	0	1	0	0	0	0	53
Total..	115	85	24	19	8	40	1	5	3	2	2	1	0	7	312

Per cent cross-overs: v–si, 16.3; si–m, 19.2; m–f, 5.1.

EXP. 42.—*Vesiculated hairy magenta forked.*

Mating: vesiculated hairy × magenta forked.

Culture No.	Non-cross-overs.		Cross-overs in region.								Total.
			1		2		3		1-2		
	vs ha	m f	vs m f	ha	vs ha m f	+	vs ha f	m	vs	ha m f	
V 1143	35	30	5	14	1	5	0	1	1	0	92
V 1143*a*	19	9	5	15	0	1	0	0	0	0	49
V 1144	10	11	4	8	0	3	0	0	0	2	38
V 1147	9	10	4	9	0	2	3	1	0	0	38
Total....	73	60	18	46	1	11	3	2	1	2	217

Per cent cross-overs: vs–ha, 30.9; ha–m, 6.9, m–f, 2.3; counting only vs flies, vs–ha, 19.8.

EXPS. 43 AND 44.—*Vesiculated magenta forked rugose.*

Mating: vesiculated forked × magenta rugose.

Culture No.	Non-cross-overs.		Cross-overs in region.																Total.
			1		2		3		1-2		1-3		2-3		1-2-3				
	vs f	m r	vs m r	f	vs r	m f	vs f r	m	vs m f	r	vs m	f r	vs	m f r	vs m f r	+			
V 923	20	29	14	14	2	0	13	7	1	1	5	3	0	0	0	0			109
V 924	39	40	6	15	0	1	11	8	1	0	3	6	0	1	1	0			132
V 926	15	17	5	3	0	0	3	4	0	0	1	2	1	0	1	0			52
V 927	44	36	11	7	1	0	12	14	0	0	6	1	0	0	2	0			134
V 928	3	5	0	1	1	0	1	1	0	0	1	0	0	0	0	1			14
V 929	21	31	7	4	0	2	5	10	1	1	4	2	1	0	0	0			89
V 930	20	15	1	5	0	0	1	8	0	1	3	0	0	1	0	0			55
V 931	12	4	1	3	0	1	0	3	0	1	2	0	0	0	0	0			27
V 933	17	19	2	4	0	2	1	7	0	0	3	0	0	0	1	0			56
V 934	9	22	4	3	0	0	3	7	0	0	1	2	0	0	1	0			52
Total..	200	218	51	59	4	6	50	69	3	4	29	16	2	2	6	1			720

EXPS. 43 AND 44.—*Vesiculated magenta forked rugose*—Continued.
Mating: vesiculated magenta × forked rugose.

Culture No.	Non-cross-overs.		Cross-overs in region.																Total.
			1		2			3		1–2		1–3		2–3		1–2–3			
	vs m	f r	vs f r	m	vs m f r	+	vs m r	f	vs	m f r	vs f	m r	vs m f	r	vs r	m f			
V 917	8	3	3	6	0	1	1	2	1	0	0	0	0	1	0	0			26
V 918	7	3	1	4	0	1	4	3	0	0	0	3	0	0	1	0			27
V 921	38	29	11	27	2	0	7	10	1	1	6	5	0	0	3	0			140
V 935	5	5	7	5	1	1	1	5	0	2	1	1	0	0	0	0			34
V 936	17	12	14	19	0	0	6	11	0	0	6	4	0	0	0	0			89
V 937	24	16	17	21	1	3	5	11	1	0	5	6	0	0	1	1			112
V 938	10	12	8	8	0	0	6	3	0	1	2	1	0	0	0	3			54
V 939	11	9	6	3	1	2	3	5	1	0	3	3	0	0	0	0			47
V 940	17	12	4	7	1	2	9	5	1	0	3	4	0	0	0	0			65
V 941	11	6	5	3	0	2	2	6	0	0	2	1	0	0	0	0			38
V 942	12	10	8	12	0	1	2	8	2	0	6	6	0	0	0	0			67
V 943	29	12	14	15	0	0	6	8	1	1	3	7	0	1	0	0			97
V 944	20	15	13	14	0	4	6	10	0	1	4	4	0	0	1	0			92
V 949	23	11	13	18	1	3	4	13	2	2	3	3	0	3	0	1			100
Total..	232	155	124	162	7	20	62	100	10	8	44	48	0	5	6	5			988
Grand Total..	432	373	175	221	11	26	112	169	13	12	73	64	2	7	12	6			1708

Per cent cross-overs: vs–m, 33.7; m-f, 5.2; f–r, 26.0; counting all flies; vs–m, 32.8, counting only vs flies.

EXP. 45.—*Singed magenta forked short.*
Mating: singed short × magenta forked.

Culture No.	Non-cross-overs.		Cross-overs in region.																		Total.
			1			2			3			1–2			1–3				2–3			
	si s	m f	si m f	s		si f	m s		si	m f s	si m s		f	si m f s		+	si f s		m		
M 385	29	19	5	18		1	1		9	1	1	0		0	5		0	0			89
P 916*a*	20	28	3	11		0	0		9	2	0	1		0	5		0	3			82
Total....	49	47	8	29		1	1		18	3	1	1		0	10		0	3			171

Per cent cross-overs: si–m, 28.6; m–f, 4.1; f–s, 19.8.

EXP. 46.—*Yellow crossveinless vermilion magenta forked.*
Mating: yellow crossveinless × vermilion magenta forked.

Culture No.	Non-cross-overs.		Cross-overs in region.																										Total.
			1					2					3				4				1–3									
	y e		v m f		y v m f		e		y e v m f			+	y e m f			v	y e f			v m	y v				m e f				
L 721	17	15	7	8	0	0	5	15	1	1	2	0																	
L 722	32	13	2	10	0	0	15	17	1	0	4	1																	
L 724	58	58	13	15	0	1	28	42	2	6	9	3																	
L 725	29	17	6	11	0	0	8	20	0	0	2	3																	
L 726	27	15	4	3	0	0	15	9	0	0	3	2																	
E 916	17	12	0	4	1	0	2	12	0	0	1	0																	
E 918	3	4	1	1	0	0	0	2	0	0	0	0																	
Total.	183	134	33	52	1	1	73	117	4	7	21	9																	

EXP. 46.—*Yellow crossveinless vermilion magenta forked.*—Continued.

Mating: yellow crossveinless × vermilion magenta forked.

Culture No.	Cross-overs in region.								Total.
	2–3		3–4		1–2–3		1–3–4		
	y c v	m f	y c m	v f	y m f	c v	y v f	c m	
L 721	0	0	0	0	0	0	0	0	71
L 722	0	0	0	1	0	0	0	0	96
L 724	0	0	0	0	0	1	1	0	237
L 725	0	0	0	0	0	0	0	0	96
L 726	0	0	0	0	0	0	0	0	78
E 916	0	1	0	0	0	0	0	0	50
E 918	0	0	0	0	0	0	0	0	11
Total.	0	1	0	1	0	1	1	0	639

Per cent cross-overs: y–c, 18.3; c–v, 0.6; v–m, 35.0, m–f, 2.0.

EXP. 47.—*Yellow vesiculated magenta forked rugose.*

Mating: yellow magenta × vesiculated forked rugose.

Culture No.	Non-cross-overs.		Cross-overs in region.											
			1		2		3		4		1–2		1–3	
	y m	vs f r	y vs f r	m	y f r	vs m	y m f r	v s	y m r	vs f	y vs m	f r	y vs	m f r
V 958	29	5	3	4	3	10	0	2	12	0	4	0	1	0
V 959	30	7	3	8	6	15	0	1	7	3	0	0	0	0
V 960	14	7	5	11	5	10	0	0	6	5	3	0	0	0
V 962	25	12	2	5	11	7	0	4	9	12	1	2	1	0
Total..	98	31	13	28	25	42	0	7	34	20	8	2	2	0

Culture No.	Cross-overs in region.										Total.
	1–4		2–3		2–4		1–2–4		3–4		1–3–4		
	y vs f	m r	vs m f r y		vs m r	y f	y vs m r	f	y m f	vs r	y vs r	m f	
V 958	0	2	0	2	2	1	1	2	0	0	0	0	83
V 959	1	1	0	1	1	2	0	1	0	1	1	0	89
V 960	1	2	0	0	2	3	0	5	0	0	0	0	79
V 962	3	1	0	3	5	5	0	1	0	0	0	0	109
Total..	5	6	0	6	10	11	1	9	0	1	1	0	360

Per cent cross-overs: y–vs, 20.8; vs–m, 31.6; m–f, 4.7; f–r, 27.2; counting only vs flies, y–vs, 21.2; vs–m, 43.2.

EXP. 48.—*Sepia crossveinless singed magenta forked short.*

Mating: sepia crossveinless singed short × magenta forked.

Culture No.	Non-cross-overs.		Cross-overs in region.									
			1		2		3		4		5	
	se c si s	m f	se m f	c si s	se c m f	si s	se c si m f	s	se c si f	m s	se c si	m f s
P 908	12	15	6	4	2	3	3	9	2	0	3	1
P 909	9	14	3	1	2	2	5	7	0	1	6	0
P 910	25	36	4	4	3	4	5	11	0	0	5	0
P 917	1	25	6	0	4	0	1	7	0	0	2	0
P 918	10	22	3	3	7	2	1	11	0	0	11	1
Total	57	112	22	12	18	11	15	45	2	1	27	2

Culture No.	Cross-overs in region.											
	1–2		1–3		1–4		1–5		2–3		2–4	
	se si s	cm f	se s	c si m f	se m s	c si f	se m f s	c si	se c s	si m f	se c m s	si f
P 908	0	0	2	2	0	0	0	1	0	0	0	0
P 909	0	1	1	0	1	0	0	4	0	0	0	0
P 910	0	3	3	4	0	0	0	2	3	0	0	0
P 917	0	0	1	1	0	0	0	0	1	1	0	0
P 918	0	2	0	3	0	0	1	0	1	2	1	0
Total	0	6	7	10	1	0	1	7	5	3	1	0

Culture No.	Cross-overs in region.											
	2–5		3–4		3–5		4–5		1–2–3		1–2–5	
	se c m f s	si	se c si m s	f	se c si m f s	+	se c si f s	m	se si m f	c s	se si	c m s f
P 908	0	3	0	0	1	3	0	0	0	0	0	0
P 909	0	2	0	0	0	3	0	1	0	1	0	1
P 910	0	0	0	0	1	1	0	2	1	0	0	0
P 917	0	2	0	0	0	5	0	0	0	0	0	0
P 918	0	1	1	0	0	3	0	0	0	1	0	0
Total	0	8	1	0	2	15	0	3	1	2	0	1

EXP. 48—*Sepia crossveinless singed magenta forked short*—Continued.

Mating: sepia crossveinless singed short × magenta forked.

Culture No.	Cross-overs in region.								Total.
	1-3-5		3-4-5		1-2-3-4		1-3-4-5		
	se c si m f s		se c si m f s		se si m s c f		se f s c m si		
P 908	0	0	0	0	0	0	0	0	72
P 909	2	1	0	0	1	0	0	0	69
P 910	0	0	1	0	0	0	0	0	118
P 917	1	0	0	0	0	0	0	0	58
P 918	0	0	1	0	0	0	0	1	89
Total	3	1	2	0	1	0	0	1	406

Per cent cross-overs: se–c, 18.7; c–si, 14 0; si–m, 28 0; m–f, 3 2; f–s, 17 9.

EXP. 49.—*Oblique magenta forked short.*

Mating: oblique short × magenta forked.

Culture No.	Non-cross-overs.		Cross-overs in region.												Total.
			1		2		3		1-2		1-3		2-3		
	o s	m f	o m f	s	o f	m s	o	m f s	o m s	f	o m f s	+	o f s	m	
M 344	19	23	0	12	0	2	3	2	0	1	0	2	0	1	65

Per cent cross-overs: o–m, 35; m–f, 9; f–s, 12; counting only not–o flies.

EXP. 50.—*Sepia crossveinless oblique short.*

Mating: sepia crossveinless × oblique short.

Culture No.	Non-oblique flies.									Total.	Oblique flies.	
	Non-cross-overs.	Cross-overs in region.										
		1	2	3	1-2	1-3	2-3	1-2-3				
	se c	c	+	se c s	se	c s	s	se s			o s	not-s
M 244	10	3	1	3	0	3	1	0		21	9	5
M 246	7	2	2	7	0	3	1	1		23	0	0
Total..	17	5	3	10	0	6	2	1		44	9	5

Per cent cross-overs: se–c, 27; c–o, 14; o–s, 43.2; counting only not–o flies.

EXP. 51.—*Oblique singed.*

Mating: oblique × singed.

Culture No.	Non-cross-overs.		Cross-overs.		Total.
	o	si	o si	+	
M 394	23	23	0	2	48

Per cent cross-overs: o–si, 4.2.

EXP. 52.—*Sepia oblique singed short.*

Mating: sepia oblique short × singed.

Culture No.	Non-cross-overs		Cross-overs in region.										Total
			1		2		3		1–3		2–3		
	se? o s	si	se si	o s	se? o si	s	se? o	si s	se si s	o	se? o si s	+	
M 392	12	19	5	..	1	1	7	11	1	..	0	0	57
M 399	7	14	6	..	1	0	7	4	1	..	0	2	42
M 400	3	5	1	..	0	0	1	0	0	..	0	1	11
Total..	22	38	12	(?)	2	1	15	15	2	(?)	0	3	110
Correction[a]	15	..	..	7	..	..	..	..	..	..	..	..	...
Corrected total....	15	38	12	7	2	1	15	15	2	0	0	3	110

Per cent cross-overs: se–o, 19.1; o–si, 5.4; si–s, 31.8; counting all flies. se–o, 19.7; o–si, 5.6; si–s, 28.1, counting only not-o flies.

[a] After apportioning se, o, and o.

EXP. 53.—*Sepia oblique singed.*

Mating: sepia oblique × singed.

Culture No.	Non-cross-overs		Cross-overs in region.						Total
			1		2		1–2		
	se? o	si	se si	o	se? o si	+	se	o si	
M 393	14	22	3	..	1	2	0	..	42
M 395	21	28	9	..	1	2	1	..	62
Total....	35	50	12	(?)	2	4	1	(?)	104
Correction[a]	30	..	..	5	..	..	..	..	...
Corrected total....	30	50	12	5	2	4	1	0	104

Per cent cross-overs: se–o, 17.3; o–si, 6.7; counting all flies. se–o, 19.4; o–si, 7.4, counting only not-o flies.

[a] After apportioning se o, and o.

LINKAGE EXPERIMENTS ON GENES GROUP II.

(Experiments 54 and 55.)

EXP. 54.—*Confluent concave.*

Mating: confluent × concave.
2 cultures (V 674, 729).

Non-cross-overs (C 59; cc 64)	123
Cross-overs (C cc 36; + 54)	90
Total	213

Per cent cross-overs, C–cc 42.2.

EXP. 55.—*Confluent broken.*

Mating: confluent × broken.
2 cultures (M 299, 318).

Non-cross-overs (C 74; b 65)	139
Cross-overs (C b 38; + 55)	93
Total	232

Per cent cross-overs, C–b 40.0.

LINKAGE EXPERIMENTS ON GENES IN GROUP III.

(Experiments 56 to 61.)

EXP. 56.—*Scaly spread.*

Mating: scaly × spread.
5 cultures (M 363–5, 368–9).

Non-cross-overs (S 86; sp 87)	173
Cross-overs (S sp 23; + 31)	54
Total	227

Per cent cross-overs, S–sp 23.8; counting only S flies, S–sp 21.1.

EXP. 57.—*Scaly hunch.*

Mating: scaly × hunch.
2 cultures (L 421, 426).

Non-cross-overs (S 55; h 44)	99
Cross-overs (S h 9; + 26)	35
Total	134

Per cent cross-overs, S–h 26.1; counting only S flies, S–h 14.0.

EXP. 58.—*Scaly telescoped.*

Mating: scaly × telescoped.
2 cultures (V 1256, 1258).

Non-cross-overs (S 145; t 168)	313
Cross-overs (S t 95; + 142)	237
Total	550

Per cent cross-overs, S–t 43.0; counting only S flies, S–t 39.6.

EXP. 59.—*Spread garnet.*

Mating: spread × garnet.
2 cultures (M 379, 386).

Non-cross-overs (sp 39; G 43)	82
Cross-overs (sp G 24; + 35)	59
Total	141

Per cent cross-overs, sp–G 41.8.

EXP. 60.—*Scaly hunch telescoped.*

Mating: scaly × hunch telescoped.
8 cultures (E 519–20, 522–24, 530, M 252, 295).

Non-cross-overs (S 261; h t 279)	540
Co. region 1 (S h t 123; + 260)	383
Co. region 2 (S t 68; h 64)	132
Co. region 1–2 (S h 27; t 55)	82
Total	1,137

Per cent cross-overs, S–h 40.8, h–t 18.8; counting only S flies, S–h 31.3.

EXP. 61.—*Scaly hunch telescoped garnet.*

Mating: scaly hunch telescoped × garnet.
2 cultures (M 375–6).

Non-cross-overs (S h t 32; G 50)	82
Co. region 1 (S G 19; h t 15)	34
Co. region 2 (S h G 1; t 2)	3
Co. region 3 (S h t G 23; + 33)	56
Co. region 1–2 (S t 2; h G 4)	6
Co. region 1–3 (S 5; h t G 22)	27
Co. region 2–3 (S h 2; t G 4)	6
Co. region 1–2–3 (S t G 0; h 5)	5
Total	219

Per cent cross-overs, S–h 32.8, h–t 9.1, t–G 42.9; counting only S flies, S–h 30.9.

LINKAGE EXPERIMENTS ON GENES IN GROUP IV.

(Experiments 62 and 63.)

EXP. 62.—*Pinched hump.*

Mating: pinched hump × wild-type.
(*a*) (P hp − +) ♀ × P hp ♂, 1 culture (L 339)

Non-cross-overs P hp 25; (P) 32	57
Cross-overs P 0; (P) hp 0	0
Total	57

(*b*) (P hp − +) ♀ × hp ♂, 2 cultures (L 350, (393).

Non-cross-overs (P) hp 38; + 56	94
Cross-overs (P) 1?; hp 0	1?
Total	95

Per cent cross-overs, P–hp 0.0.

EXP. 63.—*Pinched acute.*

Mating: pinched × acute.
9 cultures (L 565, 579; E 971–2, 1089, 1096–99).

Non-cross-overs (P) 515; ac 463	978
Cross-overs (P) ac 0; + 0	0
Total	978

Per cent cross-overs, P–ac 0.0.

LINKAGE EXPERIMENTS ON GENES IN GROUP V.

(Experiments 64 to 70.)

EXP. 64.—*Fused interrupted.*

Mating: fused × interrupted.
6 cultures (E 788, 826, 953, 974, 1116–7).
Non-cross-overs (fu 343; i 279)..... 622
Cross-overs (fu i 64; + 233)..... 297

Total..... 919
Per cent cross-overs, fu–i, counting only i, 18.6.

EXP. 65.—*Fused branched.*

Mating: fused × branched.
2 cultures (E 606, 614).
Non-cross-overs (fu 111; B 111)..... 222
Cross-overs (fu B 28; + 21)..... 49

Total..... 271
Per cent cross-overs, fu–B 18.0.

EXP. 66.—*Fused approximated.*

Mating: fused approximated × wild-type.
4 cultures (M 8–11).
Non-cross-overs (fu and fu a 225; + 183) 408
Cross-overs (fu not a 13; a 97)..... 110

Total..... 518
Per cent cross-overs, fu-a counting only not fu flies, 35.0.

EXP. 67.—*Interrupted branched.*

Mating: interrupted × branched.
6 cultures (E 902, 924, 953, 974, 1116–7).
Non-cross-overs (i 163; B 149)..... 312
Cross-overs (i B 4; + 199)..... 203

Total..... 515
Per cent cross-overs, i–B, counting only i, 2.4.

EXP. 68.—*Interrupted approximated.*

Mating: interrupted approximated × wild-type.

	Culture No.	Non-cross-overs.		Cross-overs.		Doubtful class.	Total.
		i a	+	i	a	i, a?	
A	E 915	80	106	16	9	.....	211
A	E 974	36	16	2	23	.....	77
A	Total.....	116	122	18	32	.....	288
B	M 5	42	80	4	13	40	179
B	M 6	31	107	5	19	56	218
B	M 7	22	100	10	22	64	218
B	M 12	37	106	11	23	50	227
B	Total.....	132	393	30	77	210	842
	Grand total.....	248	515	48	109	210	1,130
	Total.....	175?	...	35?	...	.....	.....
		423	515	83	109	.....	1,130

Per cent cross-overs, after apportioning doubtful flies, i–a 17.

EXP. 69.—*Branched ruffled.*

Mating: branched × ruffled.

4 cultures (M 314, 353–4, 367).
Non-cross-overs (B 97; ru 103)..... 200
Cross-overs (B ru 88; + 110)..... 198

Total..... 398
Per cent cross-overs, B–ru 49.7.

EXP. 70.—*Fused branched approximated.*

Mating: branched × fused approximated.

Culture No.	Non-cross-overs.		Cross-overs in region.						Doubtful classes.		Total.
			1		2		1-2				
	B	fu a	B fu	a	B a	fu	+	B fu a	fu a?	B fu a?	
M 118	21	8	3	1	5	8	2	0	0	0	48
M 135	45	36	5	9	21	21	12	4	7	0	160
M 141	37	33	4	10	24	19	11	4	2	5	149
M 160	33	35	9	3	22	18	7	6	11	0	144
Total.	136	112	21	23	72	66	32	14	20	5	501
	...	13?	3?	..	..	7?	..	2?	..	..	...
Total.	136	125	24	23	72	73	32	16	..	..	501

Per cent cross-overs, after apportioning doubtful classes, fu–B 19.0; B–a, 38.5; or B–fu, 19.0; fu–a, 38.5.

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