# GENETIC STUDIES ON *DROSOPHILA SIMULANS*. III. AUTOSOMAL GENES. GENERAL DISCUSSION[1]

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## INTRODUCTION

There is given in this paper a description of the autosomal mutations that have been studied in *Drosophila simulans*, together with the data concerning their genetic behavior and interrelations. One of these autosomal genes is responsible for the appearance of intersexes; and a discussion of intersexes and gynandromorphs in other Diptera is appended to the description of this character.

The general discussion includes a summary of all the genetic data obtained with *D. simulans* and reported in this and the two preceding Parts of these studies, and conclusions based on those data.

[1] Contribution from the CARNEGIE INSTITUTION OF WASHINGTON.

### THIRD-CHROMOSOME GENES

*Scarlet.*  This mutation was first observed, August 6, 1919, in two indi-
viduals from a mass culture of the pure Florida stock that formed a part
of the non-disjunction experiments described in Part II of these studies.

Scarlet was soon found to be an autosomal recessive,—the first non-
sex-linked mutant gene in *simulans.*  It closely resembles vermilion and
scarlet in *melanogaster* (see LANCEFIELD 1918 and RICHARDS 1918), and
its allelomorphism to scarlet *melanogaster* was accordingly tested.  Six
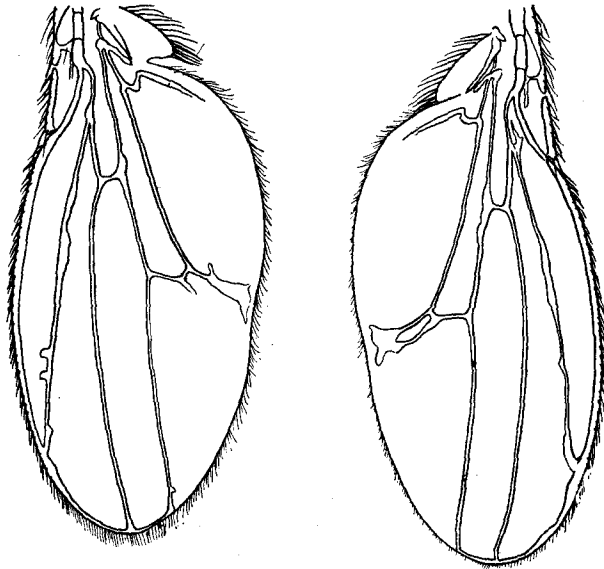*melanogaster* females from a stock pure for scarlet were mated to six scarlet



FIGURE 1.—Wings of a delta specimen of *Drosophila simulans.*

*simulans* males.  The offspring were 102 in number (101 ♀ + 1 ♂),[2]
and were all clearly scarlet.  In two later cultures females from a *melano-
gaster* stock pure for yellow and for scarlet were mated to *simulans* males
heterozygous for scarlet.  The offspring were all not-yellow females, 26
of them wild-type and 16 scarlet.  Since both scarlets are known, from
other matings, to be recessive in hybrids, there can be no question that
scarlet *simulans* is allelomorphic to scarlet *melanogaster.*  Since the two
characters look the same, we may conclude that they represent identical
mutations.

[2] This male was clearly a hybrid, and not due to non-virginity of his mother.  He was evi-
dently caused by non-disjunction, but whether by primary or by secondary non-disjunction it
is not possible to state.

Scarlet in *melanogaster* is located about 35 units to the right of roughoid, the leftmost known gene of the third chromosome. It follows that the *simulans* chromosome that contains scarlet may be identified as corresponding to the third chromosome of *melanogaster*. Though it was the second to be studied in *simulans*, we shall hereafter refer to it as the *third chromosome*.

*Delta.* This mutation appeared, December 25, 1919, as a single male from a pair-mating of pure Florida ancestry. Both parents were heterozygous for scarlet, but the mutant male did not show the scarlet character. He had 29 wild-type and 10 scarlet brothers and sisters. The original delta male was mated to rubyoid females, and produced 5 wild-type females, 7 delta females, 10 rubyoid males, and 4 rubyoid delta males. This result showed the gene to be autosomal and dominant, so its relation to scarlet was then tested. Delta males from the mating of scarlet by delta were mated to scarlet females, and produced only scarlet and delta offspring; thus showing that delta is in the third chromosome. Matings of this nature (mostly from males that were themselves the offspring of such back-crosses) have given a total of 560 scarlet: 616 delta, with no other classes present. The delta females have been found to be sterile, so that it has not been possible to determine the amount of crossing over between delta and any other third-chromosome locus, or to see if the delta gene has a recessive lethal effect as do many of the dominants known in *melanogaster*.



FIGURE 2.—Head and thorax of a delta *simulans*.

Delta flies differ from the wild-type in several respects, as appears from figures 1 and 2. The name is derived from the thickening of the second vein at its apex, which is often Δ-shaped. The whole second vein and the apex of the fifth are thickened, and other veins are often slightly so. There is usually a branch on the posterior side of the posterior cross-vein,—this being the character that was first noticed. The acrostichal hairs (on the dorsal surface of the thorax) are more numerous than in the wild-type, and are not arranged in eight definite rows as they are in the wild-type. A few small extra bristles are usually present on the margin of the scutellum. To these peculiarities must be added the sterility of the females mentioned above. Owing partly to this sterility, the mutant has now been lost.
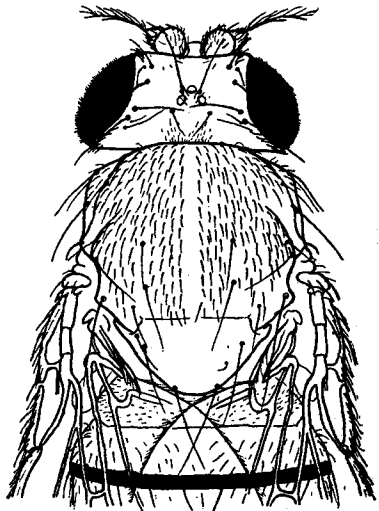
*Roughish.* In February, 1920, a few flies with slightly roughened eyes were found in a stock from Rochester, Minnesota, and also in descendants of this stock in which the intersex character was being studied. The roughish eyes are only slightly different from the wild-type, and in a mixed culture a few of them are probably often classified as wild-type. When roughish and scarlet were crossed, the $F_1$ was wild-type, and the following $F_2$ was obtained:

| WILD-TYPE | ROUGHISH | SCARLET | SCARLET ROUGHISH |
|-----------|----------|---------|------------------|
| 201 | 91 | 83 | 0 |

This result shows that roughish is a third-chromosome recessive. In later generations scarlet roughish flies were obtained, and were used for a few back-cross tests, as follows:[3]

TABLE 1

| LOCI | TYPE OF CROSS | | NON-CROSSOVERS | | CROSSOVERS | | TOTAL |
|------|---------------|---|----------------|---|------------|---|-------|
| $s_t\, r_h$ | ♀ tests $\begin{cases} s_t\, r_h \times + \\ s_t \times r_h \end{cases}$ | | 182 <br> 176 | 161 <br> 142 | 159 <br> 109 | 114 <br> 134 | 616 <br> 561 |
| | ♂ test $s_t \times r_h$ | | 6 | 18 | 0 | 0 | 24 |

These data give a total of 516 crossovers among 1177 flies, or 43.8 percent, from the tests of females. Allowing for double crossovers, which would certainly occur in a distance as great as this, we may conclude that the third chromosome of *simulans* is at least 45 units long. The number of flies from the back-cross tests of a male is very small, but, taken in connection with the large amount of crossing over in the female and the absence of double recessives in the $F_2$, it is sufficient to indicate that this chromosome agrees with the third chromosome of *melanogaster* in showing no crossing over in the male.

Roughish has been crossed to rough and to roughoid, two similar but more extreme mutant characters whose genes are located in the third chromosome of *melanogaster:* in both cases the hybrids were wild-type.

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[3] In this and the other tables in this paper that give the results of back-cross tests, the same convention that was used in Part II of these studies has been followed. The first column shows the loci concerned and their sequence. The second column indicates the nature of the tested individuals (whether the test is one of "coupling" or of "repulsion"). The next two columns show the numbers of the two non-crossover classes produced, and the class that bears the dominant allelomorph in the locus lying to the left is set down first. Similarly for the crossover classes; the class bearing the dominant allelomorph in the left-hand locus precedes the class bearing the recessive allelomorph in that locus.

*Peach.* On August 6, 1920, several flies (males and females) with eyes resembling the peach of *melanogaster* (but distinctly lighter in color) were found in a wild stock collected at Kushla, Alabama, in May, 1920. The character was found to be recessive, both in pure *simulans* and in *melanogaster-simulans* hybrids. Its allelomorphism to peach *melanogaster* (also known, from other crosses, to be recessive in hybrids) was tested by mating peach spineless kidney sooty rough *melanogaster* females to peach *simulans* males. Two cultures of this type gave 87 and 126 females, respectively,—all of them peach and rather dark in body-color because of heterozygosis for sooty. Peach *simulans* is accordingly an allelomorph of peach (and therefore also of pink) *melanogaster*. It may be noted that mutations in this locus have been discovered about five times in *melanogaster*.

Peach × scarlet (*simulans*) gave the following $F_2$:

| WILD-TYPE | PEACH | SCARLET | SCARLET PEACH |
|---|---|---|---|
| 237 | 137 | 133 | 0 |

It follows that the two loci concerned are in the same chromosome; which was to be expected, since in *melanogaster* they are both in the third chromosome. $F_2$ peach and $F_2$ scarlet flies were mated together. Two such cultures produced the double recessive, scarlet peach, in $F_3$. This type is easily distinguishable from both single recessives, having a clear yellowish-colored eye. Back-crosses made with these flies have resulted as follows:

TABLE 2

| TYPE OF CROSS | NON-CROSSOVERS | | CROSSOVERS | | TOTAL |
|---|---|---|---|---|---|
| $s_t$ × $p_e$ (♀ test) . . . . . . . | 369 | 337 | 269 | 298 | 1273 |
| + × $s_t$ $p_e$ (♀ test) . . . . . | 43 | 27 | 25 | 26 | 121 |
| $s_t$ × $p$ (♂ test) . . . . . . . | 218 | 215 | 0 | 0 | 433 |

The tests of doubly heterozygous females thus show that 44.3 percent of crossing over occurs, without any allowance being made for double crossing over. This result is very surprising, as the two loci are only about 3 units apart in *melanogaster*. We have seen in Part II of these studies that the sex-linked genes of *melanogaster* and *simulans* do not always show the same crossover values; but no such great difference as the present one was observed. It is hoped that more third-chromosome parallels can be found, in order that the maps may be compared in more detail.

## SECOND CHROMOSOME.

We have seen in Part II of these studies (STURTEVANT 1921) that the first or X chromosome of *simulans* corresponds to that of *melanogaster* in that it carries the sex-determining gene (or genes) and also the genes for yellow, prune, rubyoid, carmine, and forked. The third chromosome has just been identified by means of the scarlet and peach genes. Since METZ'S results indicate that the two species have identical chromosome groups, two more linkage groups should be expected in *simulans*. Of these, one (the second chromosome) should include a large number of loci and should show much crossing over; the other, the fourth chromosome, should include very few loci and should show very little if any crossing over. In fact, as might have been expected, only one other group ha's so far been found. This group contains six mutant genes (one less than is known for the third chromosome), and at least 45 percent of crossing over occurs in it. We may safely conclude, then, that it represents the second chromosome, even though none of the mutant genes in it have been shown to be allelomorphic to genes of *melanogaster*.

This is the linkage group to which the intersex gene belongs. A preliminary statement of its existence has already been published (STURTEVANT 1920 a).

*Plum.* On December 20, 1919, a single male was found in a wild stock from Staten Island, New York, that had purplish eyes. This eye-color is much like the purple of *melanogaster*, but is somewhat paler. Like purple, it darkens considerably with age. The original plum male was mated to yellow females: $F_1$ was normal in eye-color, and $F_2$ included plums of both sexes, showing the gene to be an autosomal recessive. Since the original mutant was found in a large mass culture no analysis of his origin can be made.

Plum was crossed to scarlet, and in $F_2$ the following count was obtained:

| WILD-TYPE | PLUM | SCARLET | PLUM SCARLET[4] |
|-----------|------|---------|-----------------|
| 502 | 160 | 162 | 44 |

Plum by roughish has given in $F_2$:

| WILD-TYPE | PLUM | ROUGHISH | PLUM ROUGHISH |
|-----------|------|----------|---------------|
| 198 | 52 | 58 | 15 |

[4] Plum scarlet is a yellowish-colored eye, much like vermilion pink in *melanogaster*.

All three mutants show somewhat reduced viability, but evidently the above are both 9:3:3:1 ratios, indicating that plum is not in the third chromosome.

There are several second-chromosome mutants of *melanogaster* that resemble plum more or less closely, and its possible allelomorphism to them has been tested, as follows:

TABLE 3

| *Simulans* PARENT | *Melanogaster* PARENT | HYBRID OFFSPRING | | |
| --- | --- | --- | --- | --- |
| | | Eyes wild-type | | Eyes purplish |
| | | ♀ | ♂ | |
| Plum ♂ | Purple ♀ | 112 | 0 | 0 |
| Plum ♂ | Purple brown ♀ | 157 | 0 | 0 |
| Plum ♂ | Purploid ♀ | 235 | 0 | 0 |
| Plum ♀ | Safranin ♂ | 2 | 16 | 0 |

These results show that none of the four mutant types, purple, brown, purploid or safranin, is allelomorphic to plum. It is to be noted that brown and plum look almost exactly alike, thus furnishing a case similar to that of the tiny-bristles reported in Part II of these studies.

*Frayed.* On November 30, 1919, a few flies, of both sexes, that were taken to be tiny-bristle, appeared in a culture (prune carmine linkage test, of pure Florida stock) where they were unexpected. A few matings were made to determine the cause of this unexpected appearance, and in later generations it was found that the character was not tiny-bristle, but a new autosomal recessive. The original culture was a brother-sister mating, so the actual mutation can safely be referred to some preceding generation.

The character, called frayed, is a complex one. The name is derived from the fact that the marginal hairs of the wings are very irregular, as though they had been rubbed the wrong way. Many of the thoracic hairs, especially the acrostichals, are missing, and one or more of the dorsocentral bristles is usually absent. The bristles are a little shorter than usual. The eyes are often slightly roughened or pitted. The flies always emerge several days later than their normal brothers and sisters, and are usually dwarfed and somewhat pale. They are often sterile— especially the females. Owing to these latter peculiarities the mutant has been lost.

Crossed to plum, the following F$_2$ was obtained:

| WILD-TYPE | FRAYED | PLUM | PLUM FRAYED |
| --- | --- | --- | --- |
| 761 | 221 | 358 | 0 |

Since no double recessives were obtained, the two genes are in the same chromosome. Double recessives were obtained in later generations, and were used for a few back-cross tests to doubly heterozygous females:

TABLE 4

| LOCI | TYPE OF CROSS | NON-CROSSOVERS | | CROSSOVERS | | TOTAL |
|------|---------------|----------------|---|------------|---|-------|
| $pm\ fr$ | $pm\ fr \times +$ | 34 | 9 | 4 | 18 | 65 |
| | $pm \times fr$ | 49 | 126 | 133 | 29 | 337 |

These data give a total of 184 crossovers among 402 flies, or a percentage of 45.8. It may be supposed that a distance as great as this would include much double crossing over, so that in spite of the small numbers obtained and the serious viability complications, we may conclude that the chromosome is at least 45 units long. Since there is almost free assortment in the female, yet no double recessives were obtained in the $F_2$ count, it follows that there is no crossing over in the male.

*Spread.* On February 22, 1920, it was found that there were a number of flies in the yellow prune stock (of mixed Florida and Cold Spring Harbor ancestry) that had their wings spread out almost at right angles to their bodies. Females of the new type mated to males of other stocks produced only offspring with wild-type wings, and spreads mated together were found to breed true, thus showing the character to be an autosomal recessive. Spread mated to scarlet (third-chromosome) gave the following $F_2$:

| WILD-TYPE | SPREAD | SCARLET | SPREAD SCARLET | TOTAL |
|-----------|--------|---------|----------------|-------|
| 261 | 76 | 79 | 19 | 435 |

This result indicated that the two genes were in different chromosome pairs, and a spread by plum (second chromosome) $F_2$ was accordingly obtained, as follows:

| WILD-TYPE | PLUM | SPREAD | SPREAD PLUM | TOTAL |
|-----------|------|--------|-------------|-------|
| 224 | 95 | 101 | 0 | 420 |

Evidently spread and plum are in the same chromosome pair. In later generations the double recessive, spread plum, was easily obtained, and was used for the following back-cross tests of doubly heterozygous females:

TABLE 5

| LOCI | TYPE OF CROSS | NON-CROSSOVERS | | CROSSOVERS | | TOTAL |
|---|---|---|---|---|---|---|
| $s_d$ $p_m$ | $s_d$ $p_m$ × + | 670 | 633 | 156 | 157 | 1616 |
| | $s_d$ × $p_m$ | 468 | 507 | 168 | 151 | 1294 |

These data give a total of 632 crossovers among 2910 flies, or 21.7 percent. Taken in connection with the absence of double recessives in the F$_2$ from plum × spread, they also indicate that there is no crossing over in the male. This conclusion is verified by the single back-cross test of a doubly heterozygous male, that has been made:

TABLE 6

| LOCI | TYPE OF CROSS | NON-CROSSOVERS | | CROSSOVERS | | TOTAL |
|---|---|---|---|---|---|---|
| $s_d$ $p_m$ | $s_d$ $p_m$ × + (♂ test) | 121 | 107 | 0 | 0 | 228 |

*Intersex.* A preliminary account of this mutation has already been published (STURTEVANT 1920 a). On January 1, 1920, a stock from Rochester, Minnesota, was found to contain individuals that appeared to be partly male and partly female. Examination of numerous specimens showed that all belong to the same type. Their peculiarities, compared with normal males and females, are shown in figures 3, 4, and 5 and in table 7.

TABLE 7

| | MALES | FEMALES | INTERSEXES |
|---|---|---|---|
| Sex-combs........................... | Present | Absent | Absent |
| Number of dorsal abdominal tergites........ | Five | Seven | Seven |
| Ovipositor........................... | Absent | Present | Present but abnormal |
| Spermathecae........................ | Absent | Two | Two |
| Penis.............................. | Present | Absent | Absent |
| First genital tergite.................... | Present | Absent | Present but abnormal |
| Anal plates.......................... | Lateral | Dorsal and ventral | Lateral |
| Claspers............................ | Present | Absent | Present |
| Tip of abdomen...................... | Black | Banded | Black |
| Gonads............................. | Testes | Ovaries | Rudimentary |

The gonads being extremely rudimentary,—so small as to be very difficult to find,—it is not surprising that the intersexes are sterile. Their sexual behavior is indifferent, but they are courted by males. In addition,

the intersexes often have one character not normally present in either sex,—their wings are spread out, almost at right angles to the thorax. This character resembles the spread mutant character so closely that it has not seemed advisable to use the two mutations in the same experiment.

The genital ducts and even the spermathecae of the intersexes often lie in or just outside the genital opening, the ovipositor plates being forced
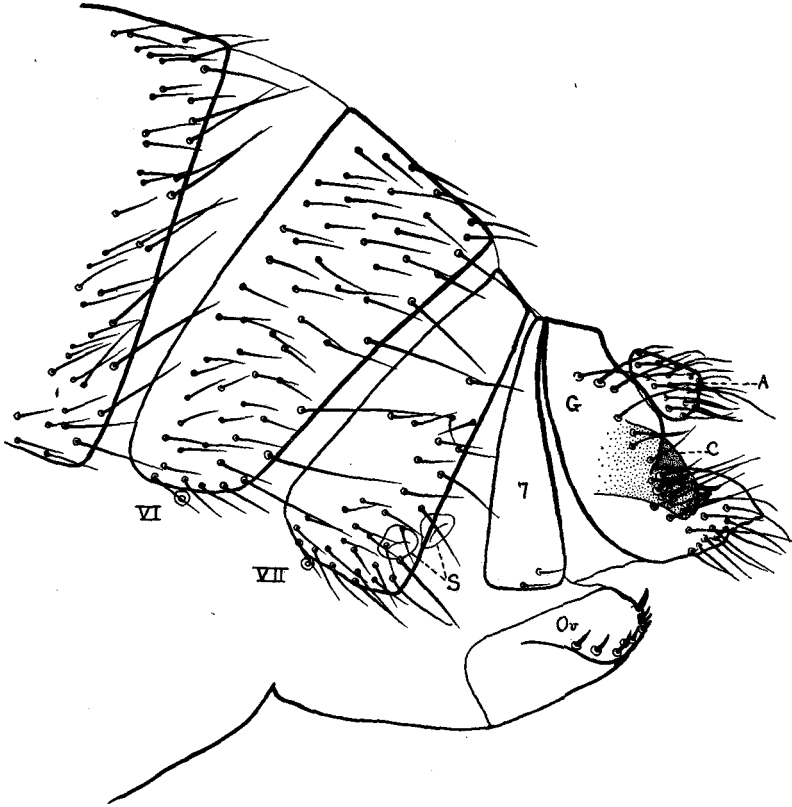


FIGURE 3.—Posterior portion of the abdomen of an intersexual *D. simulans*. A, anal plate. C, clasper. G, first genital tergite. Ov, ovipositor plate. S, spermathecae. 7, seventh dorsal tergite. VI, VII, spiracles.

far apart. Similar malformations have been observed in a number of intersexes in other animals and also in gynandromorphs (cf. KEILIN and NUTTALL 1919).

A comparison of figures 3, 4, and 5 indicates that the first genital tergite of the normal male does not correspond to the seventh dorsal tergite of the female, as might have been supposed, since both are present in the

intersexes.   There is a small weakly chitinized piece sometimes to be seen between the 5–6 tergite and the first genital tergite of cleared males; this probably represents tergite seven.   The female apparently has no structure corresponding to the first genital tergite of the male.
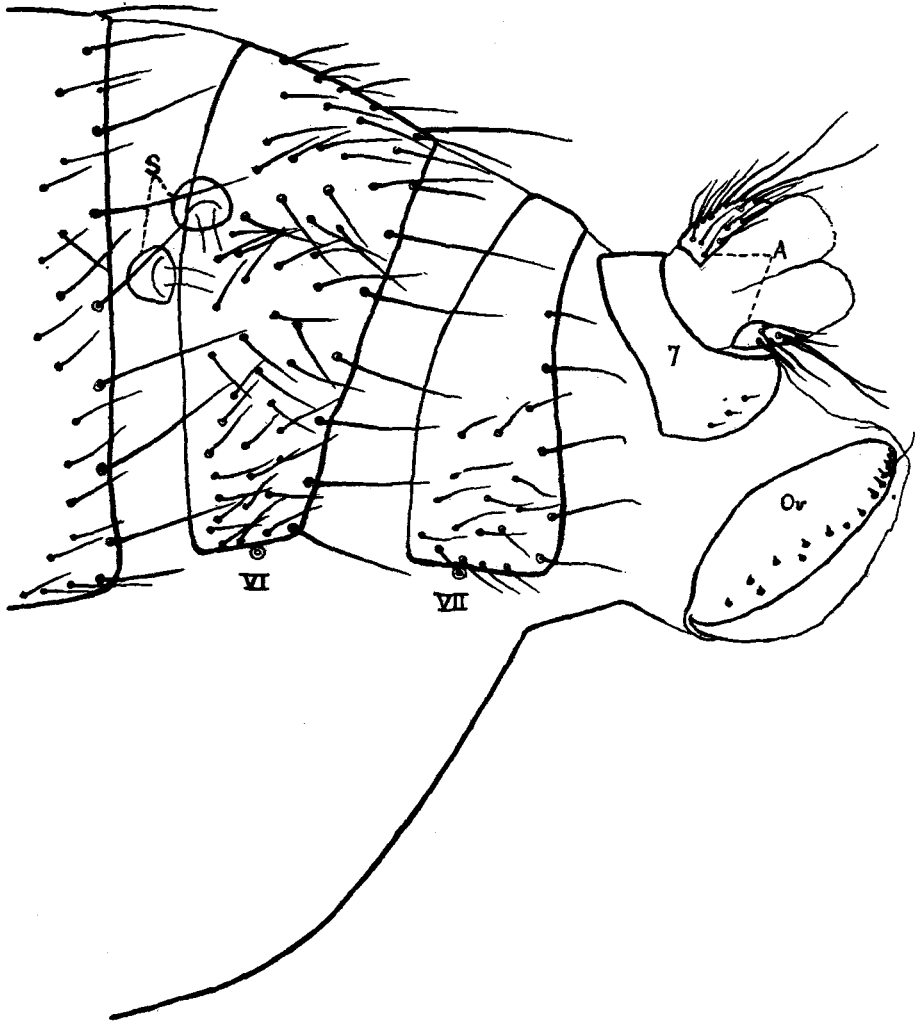


FIGURE 4.—Posterior portion of the abdomen of a normal female of *D. simulans.*   A, anal plate.   Ov, ovipositor plate.   S, spermathecae.   7, seventh dorsal tergite.   VI, VII, spiracles.

Crosses of normal brothers and sisters of intersexes to unrelated stocks have never produced intersexes in $F_1$, but have often produced them in $F_2$, showing that the gene is recessive.   Such $F_2$ counts, from pairs in which

other mutant genes that might affect viability were not present, have given the following totals: 758 ♀, 224 intersex, 1104 ♂. This is an approximation to a 3:1:4 ratio, suggesting that the intersexes are females modified by a recessive autosomal gene.

That they are modified females has been shown by cultures in which sex-linked recessive characters were present in half or in all the males,
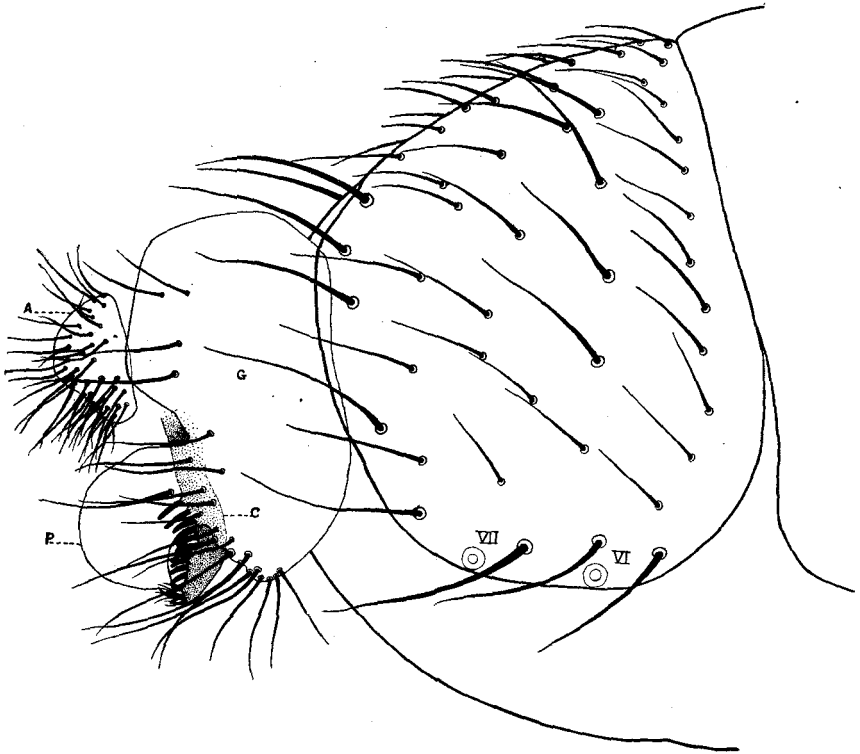


FIGURE 5.—Posterior portion of the abdomen of a normal male of *D. simulans*. A, anal plate. C, clasper. G, first genital tergite. VI, VII, spiracles.

but in none of the females. In such cultures these sex-linked characters are never present in the intersexes, which must therefore carry two X chromosomes.

The intersex stock was crossed to plum, and the $F_1$ pairs that produced intersexes gave the following $F_2$ totals:

TABLE 8

| FEMALE | | INTERSEX | | MALE | |
|---|---|---|---|---|---|
| Wild-type | Plum | Wild-type | Plum | Wild-type | Plum |
| 264 | 120 | 110 | 0 | 371 | 96 |

The absence of the intersex plum class shows that the gene is in the second chromosome. In later generations a number of intersex plums were obtained, showing that the loci are not very close together; but the exact amount of crossing over has not been determined.

It will be seen from the two counts given that cultures producing intersexes give a total of females and intersexes that is about equal to the number of males (1476:1571). It follows that many of these males are homozygous for the intersex gene. It has been observed that there are in such cultures about as many males with spread wings as intersexes with the same character, and that these spread males are, so far as tested, all sterile. Some of the males without spread wings are also known to be sterile; and no cultures have been obtained that seemed to come from males homozygous for intersex (i.e., the ratio of females to intersexes has never been 1:1). The males homozygous for the intersex gene are therefore sterile, and have spread wings as frequently as do the intersexes themselves. They appear normal in other respects, and two sterile males that were probably of this type proved, on dissection, to have a complete set of normal-appearing internal genital organs. Though the testes were perhaps slightly smaller than usual, they contained motile sperm.

As previously stated (STURTEVANT 1920 a), 104 intersexes have been produced by mothers heterozygous for yellow, and the male parts were not yellow in any of them. This result shows that these male parts contain in all cases a paternal X chromosome. Six intersexes have since been obtained from a yellow father and a not-yellow mother, and these also failed to show any yellow male parts. Therefore the male parts also carry a maternal X chromosome, and are XX in constitution. Intersexes are thus not gynandromorphs, but represent females in which an autosomal gene has modified the development so as to cause male characters to appear in parts that are still XX in constitution. The normal sex-determining mechanism is functioning as usual; but the end result is modified by a gene that is not even in the sex chromosomes.

The present case serves to emphasize the distinction between sex-determination (the mechanism determining whether an individual is to develop into a male or into a female) and the physiology of the development of the sexual characters. The direction in which the reaction is to proceed is commonly determined by a single factor (or at most by genes in a single chromosome pair); the details of the reaction after its direction has been determined must be supposed to be dependent upon many genes, presumably located in different chromosome pairs. In the case of intersexual *simulans*, apparently, a mutation has occurred in one of these latter genes.

The mutated gene is active in determining visible sexual characters only in the females, so it may be taken as probable that the same is true of its normal allelomorph.

Four *simulans* males with a plum gene in one second chromosome and an intersex gene in the other were mated to four yellow scarlet *melanogaster* females. The offspring were 82 in number, all wild-type females and sterile so far as tested. This result shows that the intersex gene is recessive in hybrid females, just as it is in *simulans* females, and also indicates that heterozygosis for it does not cause such hybrids to be fertile. Such a result was, of course, to be expected. It serves, however, to emphasize the fact that there is no relation between the intersexes and the peculiar sex-ratios of the hybrids—a point that is of interest in connection with the hybrid intersexes obtained by GOLDSCHMIDT (1916, 1917, 1919), by HARRISON (1919), and perhaps by KEILIN and NUTTALL (1919).

### Intersexual Diptera from the systematic literature

In many groups of Diptera the males have large eyes that are very close together in front, while in the females the eyes are distinctly further apart, being separated by a relatively broad "front." This relation holds in the majority of the Syrphidae and also of the Anthomyiinae and Dexiinae. In these three groups, especially the first two, numerous specimens have been described in which the distance between the eyes (or some other secondary sexual character) is intermediate between the characteristic male and female types. These specimens must evidently be considered as intersexual, and it therefore becomes of interest to see how they compare with the intersexes of *Drosophila simulans*.

The Syrphid examples belong to the genera Syrphus, Platychirus, and Melanostoma, which are closely allied forms with similar habits. The most common type of intersex here is one with a "front" of intermediate width, and external genitalia entirely of one or the other sex. In Platychirus the sexes differ markedly in the color and shape of the first pair of legs; and in the intersexual specimens described by VILLENEUVE (1910) and by LUNDBECK (1916) these were also intermediate. BECKER (1888) described three specimens of *Syrphus lunulatus* with male external genitalia; two had broad female-like fronts, but the front of the third was intermediate between the characteristic male and female types. In general, it appears that in the Syrphidae the intersexes are of several types, even within the same species. No explanation of their occurrence seems to have been proposed.

VILLENEUVE (1910) has described the Dexiine, *Anacamptomyia* (*Roubaudia*) *rufescens*, from Africa. The males from the Congo agreed with most Dexiine males in having narrow fronts that did not bear external orbital bristles; but three males from Dahomey agreed with the females in having broad fronts and two external orbitals. Some of this material was known to have been parasitized by small Hymenoptera; and VILLENEUVE suggests that we may be dealing with an instance of "parasitic castration." In view of the influence of parasitization on secondary sexual characters that has been demonstrated for Andrena (Hymenoptera) by PÉREZ (1886) and for Thelia (Hemiptera) by KORNHAUSER (1919), this suggestion must be considered not only for Anacamptomyia but also for the intersexual Syrphidae and Anthomyiinae.

STEIN (1895) thought that the unusual specimens of Fannia (Homalomyia), one of the Anthomyiinae, that he found, were the result of hybridization between *F. scalaris* and *F. incisurata*. VILLENEUVE (1910) has seen a number of similar specimens, and states that a new species (*Gymnochoristomma bosnica*) was described by STROBL on the basis of still others. The range of this type is at least from Poland to Spain, and fully a dozen specimens have been seen. VILLENEUVE is quite certain that they are not hybrids, but are *F. scalaris* with female-like heads and male external genitalia. He suspects that they may be due to parasitic castration, as in the case just discussed. The width of the front and the character of the legs are not constant in these specimens, but several stages occur that are intermediate between normal males and females.

Cases somewhat similar to the one just described have been recorded for a few other Anthomyiinae by STEIN (1889), VILLENEUVE (1912), and SCHNABL (1890). The case recorded by SCHNABL is that of *Mydaea* (*Spilogaster*) *duplicata*. He saw two specimens, collected at different times and places, that agreed in most respects. They showed a mixture of male and female secondary sexual characters in the head, legs, etc. A long ovipositor tube was present, but at its tip were somewhat abnormal male external genital plates. In addition, both specimens had a cross-vein missing. This case shows points of resemblance with the one here described for *Drosophila simulans*, especially in the structure of the external genitalia and in the presence of another character, not normal for either sex (spread wings in Drosophila, missing cross-vein in Mydaea). This similarity suggests that here also we are dealing with a mutation, though parasitic castration remains as a possible interpretation.

There are a number of other records of Diptera (other than Drosophila) that show mixtures of male and female parts. These, however, are most

likely gynandromorphs rather than intersexes, since the descriptions indicate that they are mosaics. Each part is either male or female, not intermediate as are some of the parts of all the specimens so far discussed. These forms are distributed as follows:

Culicidae: *Aedes (Culex) abserratus*, 1 (FELT 1904).

           *Aedes (Culicada) pullatus*, 1 (FELT 1904).

           *Culex theileri*, 1 (BEDFORD 1914).

Empididae: *Hilara wheeleri*, 1 (MELANDER 1901).

Dolichopodidae: *Synarthrus cinereiventris*, 1 (LOEW 1874).

Stratiomyidae: *Beris nitens*, 1 (LOEW 1846).

Anthomyiinae: *Hydrotaea meteorica*, 1 (STEIN 1890).

Some of the Syrphidae described by VILLENEUVE (1912), and the one recorded by WAHLBERG (1847), may also be gynandromorphs, rather than intersexes. For *Drosophila melanogaster*, MORGAN and BRIDGES (1919) have described about 80 gynandromorphs; and seven gynandromorphic *D. simulans* were recorded in Part II of these studies.[5]

### CHARACTERS DEPENDENT ON GENES IN TWO CHROMOSOMES

*Kidney-like.* On December 31, 1919, it was noticed that a number of males and females with eyes resembling the "kidney" mutant character of *melanogaster* were present in a culture of pure Florida ancestry that formed part of the yellow prune linkage experiments. The character was used in a number of experiments, but was found difficult to classify, and to be often associated with sterility (in the males) or with low productivity (in the females), and has accordingly been discarded.

The character was found to be recessive and not sex-linked, but appeared in much less than one-fourth of the $F_2$ flies when out-crossed. Crossed to other mutant stocks it produced the following $F_2$ results:

Kidney-like × plum (second chromosome):

| WILD-TYPE | KIDNEY-LIKE | PLUM | PLUM KIDNEY-LIKE |
|:---:|:---:|:---:|:---:|
| 367 | 57 | 116 | 0 |

Kidney-like × scarlet (third chromosome):

| WILD-TYPE | KIDNEY-LIKE | SCARLET | SCARLET KIDNEY-LIKE |
|:---:|:---:|:---:|:---:|
| 231 | 48 | 81 | 5 |

[5] The wingless Phorid fly, Termitoxenia, that occurs in Termite nests, was described by WASMANN (1901) as being normally a protandrous hermaphrodite; but the studies of BUGNION (1913) make it seem certain that all the specimens examined have been females. What WASMANN took to be testes are probably seminal receptacles full of sperm received at copulation. The males are unknown, but are probably winged as in other Phoridae with degenerate females.

The results with plum indicate that the kidney-like eye does not appear except in flies homozygous for a second-chromosome gene; and the results with scarlet indicate that it usually fails to appear unless a third-chromosome gene is also present in homozygous form.

*Branched.* This mutation was discovered March 7, 1920, in a culture of mixed Florida, Minnesota, and Staten Island ancestry. The culture was a brother-sister pair-mating and formed a part of the intersex plum experiments. Both parents were heterozygous for plum. The following count was obtained:
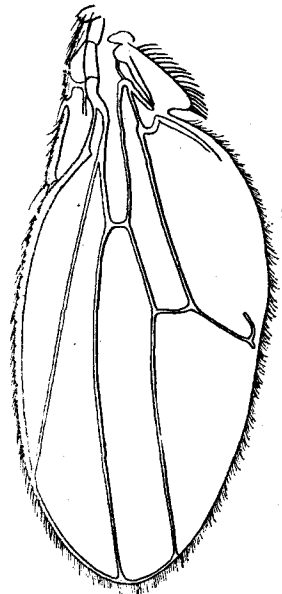
TABLE 9

| FEMALES | | | | MALES | | | |
|---|---|---|---|---|---|---|---|
| Wild-type | Branched | Plum | Branched plum | Wild-type | Branched | Plum | Branched plum |
| 82 | 7 | 35 | 1 | 82 | 5 | 28 | 0 |

A number of closely related pairs were tested, for other purposes, but did not produce branched offspring, so that the mutation was probably of recent origin, and at least one of the necessary genes was not widely scattered through the plum or intersex stocks.

The character is named from its most striking peculiarity,—the branching of the fifth vein, illustrated in figure 6. This characteristic is somewhat variable, and probably sometimes overlaps the normal. The wings of branched flies are usually not held quite flat, but are tipped slightly upward on the inner side. The mutant is also characterized by a tendency to sterility, especially among the males.

When branched was crossed to scarlet (third chromosome) the following $F_2$ was obtained:



FIGURE 6.—Wing of a branched *D. simulans.*

| WILD-TYPE | BRANCHED | SCARLET | SCARLET BRANCHED |
|---|---|---|---|
| 149 | 26 | 27[6] | 0 |

[6] There is reason to believe that there was a third-chromosome lethal present in this experiment, and that this is the reason more scarlets were not produced. Since this view was not definitely established, such a lethal has not been included among the known mutant genes of *simulans.*

Branched by plum spread (both second-chromosomal) gave this $F_2$:

| WILD-TYPE | SPREAD | PLUM | SPREAD PLUM | BRANCHED | BRANCHED SPREAD | BRANCHED PLUM | BRANCHED SPREAD PLUM |
|---|---|---|---|---|---|---|---|
| 100 | 6 | 12 | 32 | 10 | 1 | 0 | 0 |

These two crosses indicate that branched does not appear except in flies homozygous for a third-chromosome gene, and also that it usually does not appear except in flies homozygous for a second-chromosome gene. Both of these relations were verified by the following $F_2$, from branched by plum spread scarlet:

| WILD-TYPE | SPREAD | PLUM | SPREAD PLUM | SCARLET | SCARLET SPREAD | SCARLET PLUM | SCARLET SPREAD PLUM | BRANCHED | BRANCHED PLUM |
|---|---|---|---|---|---|---|---|---|---|
| 211 | 22 | 26 | 79 | 107 | 6 | 5 | 48 | 27 | 1 |

No other classes were present,—i.e., there were no branched flies among the scarlet or spread $F_2$'s.

Kidney-like and branched thus both differ from the ordinary wild-type flies in two genes, one second-chromosomal, the other third-chromosomal. The cases are thus analogous to that of vortex in *melanogaster* (BRIDGES and MOHR 1919). In åll three cases one of the two genes must be present in homozygous form, while the other need not always be so. In the case of kidney-like the necessary gene is in the second chromosome; in that of branched it is the third-chromosome gene that is necessary. That the genes concerned are different in the two cases, as might have been supposed, is indicated by the following $F_2$ from branched × kidney-like:

| WILD-TYPE | KIDNEY-LIKE | BRANCHED | BRANCHED KIDNEY-LIKE |
|---|---|---|---|
| 489 | 77 | 82 | 3 |

### BRISTLES OF THE HYBRIDS

The hybrids have been briefly described in Part I of these studies. It was there stated that they frequently lack some of the bristles that are normally present in both pure species. More recently some counts have been made of the bristles of hybrid females from the mating of melanogaster female by *simulans* male. The following values were obtained for the dorsocentrals:

TABLE 10

|  | MEAN | STANDARD DEVIATION | COEFFICIENT OF VARIABILITY |
|---|---|---|---|
| Pure *melanogaster*............. | 4.016 ± 0.003 | 0.146 ± 0.002 | 3.63 ± 0.04 |
| Pure *simulans*................ | 4.002 ± 0.00004 | 0.002 ± 0.00003 | 0.05 ± 0.001 |
| Hybrids.................... | 3.003 ± 0.061 | 1.589 ± 0.047 | 52.60 ± 1.80 |

The normal number of scutellars and also of notopleurals, in both parent species, is 4. No exact data are available, but observation of many specimens indicates that these bristles are at most not appreciably more variable than are the dorsocentrals. In the hybrids they show the following relations:

TABLE 11

|  | MEAN | STANDARD DEVIATION |
|---|---|---|
| Scutellars.............. | 3.450 ± 0.040 | 0.865 ± 0.029 |
| Notopleurals........... | 3.235 ± 0.044 | 0.927 ± 0.031 |

A preliminary study of the correlation of these bristles in the hybrids indicates that in general there is little or no correlation between bristles lying on opposite sides of the middle line of the body; but there is a definite positive correlation between bristles that lie on the same side and close together. This matter is now being investigated further; and the original data, together with a more detailed analysis, will be published later.

COMPARISON OF *simulans* AND *melanogaster*—GENERAL SUMMARY

The chief object in studying the genetics of *Drosophila simulans* has been the accumulation of data bearing on the nature and extent of the differences and similarities between that species and the closely related *D. melanogaster*. The summary below includes not only the data presented in the present paper, but also the points taken up in the two preceding parts of these studies. In some cases more data than were presented in the earlier papers are now available, and these have been included in the summary. The details concerning such points will be published in full later.

1. The two species can be crossed. The following numbers of offspring have been obtained:

TABLE 12

|  | FEMALES | | | | MALES | | | | GRAND TOTAL |
|---|---|---|---|---|---|---|---|---|---|
|  | Regular | Non-disjunctional exceptions | Not classifiable | Total | Regular | Non-disjunctional exceptions | Not classifiable | Total | |
| *Melanogaster* ♀ × *simulans* ♂.... | 901 | 0 | 2779 | 3680 | 0 | 59 | 2 | 61 | 3741 |
| *Simulans* ♀ × *melanogaster* ♂.... | 153 | 6 | 12 | 171 | 563 | 0 | 25 | 588 | 759 |

2. The sex of the hybrid offspring is not changed over: XX hybrids are always female, X hybrids are always male.

3. Analysis of these results shows that hybrids do not live unless they carry a *simulans* X.   If they do carry a *simulans* X survival is usual unless a *melanogaster* X is also present and the combination is made in a *simulans* egg.   Under these latter circumstances the result is variable, some cultures showing that none of the flies under consideration live, while in other cultures they apparently all live.   These differences are, to judge from certain unpublished data, due in part at least to the nature of the *simulans* egg in which the combination is made.

4. The hybrids are all completely sterile, with rudimentary gonads. They are intermediate between the parent species in the respects in which the latter differ, but they often show a few characters not normally present in either parent species.

5. *D. simulans* apparently has the same chromosome group as *melanogaster*, viz., (haploid group) a rod-shaped X, two large V-shaped autosomes, and a small spherical autosome.   The mutant genes of *simulans* form three linkage groups: 8 sex-linked and therefore in the X, 7 in a group that corresponds to the third chromosome of *melanogaster*,[7] and 6 in another group that evidently corresponds to the second chromosome of *melanogaster*.   No mutation has yet appeared in the fourth chromosome.   These proportions agree well with those observed among the mutant genes of *melanogaster*.

6. The mutant genes of each species show the same relations of dominance and recessiveness in hybrids that they do in the pure species themselves.   The tests of this point that have been made may be summarized as follows:

A. Recessive mutant genes of *melanogaster* that are known to be recessive in hybrids:

Group I.   Yellow, scute, white, eosin, coral, echinus, ruby, cut, vermilion, tiny-bristle, garnet, small, forked.

Group II.   Telegraph, aristaless, dumpy, dachs, pink-wing, black, purple, safranin, vestigial, curved, arc, plexus, brown, purploid, speck.

Group III.   Roughoid, sepia, scarlet, peach, color, spineless, kidney, sooty, ebony 2, white-ocelli, rough, claret.

Group IV.   Eyeless.

[7] This includes one mutant gene not recorded in this paper, but definitely known to be linked to peach and to scarlet.   It is now being studied.

B. Recessive mutant genes of *simulans* that are known to be recessive in hybrids:

Group I.   Yellow, prune, rubyoid, carmine, forked, tiny-bristle.

Group II.  Plum, intersex, spread.

Group III. Scarlet, peach, roughish.

C. Sex-linked recessive mutant genes of *simulans* that are known to produce their usual effects in hybrid males:

Yellow,[8] prune, rubyoid, carmine,[8] forked.[8]

D. Dominant mutant genes of *melanogaster* that are known to be dominant in the hybrids:

Group I.   Notch 8,[9] bar.

Group II.  Star.[9]

Group III. Dichaet.[9]

7. The following mutant genes of the two species have been shown to be allelomorphic to each other:

Group I.   Yellow *simulans* with yellow *melanogaster*

Prune *simulans* with prune *melanogaster*

Rubyoid *simulans* with ruby *melanogaster*

Carmine *simulans* with garnet *melanogaster*

Forked *simulans* with forked *melanogaster*

Group III. Scarlet *simulans* with scarlet *melanogaster*

Peach *simulans* with peach *melanogaster*

8. The five sex-linked parallels occupy loci that are in the same sequence in the two species, but the corresponding percentages of crossing over are not the same in all the intervals concerned, being greater near the left-hand end of the *simulans* map than in the same part of the *melanogaster* map.

9. The two third-chromosome parallels show about fifteen times as much crossing over in *simulans* as in *melanogaster*, no correction for double crossing over having been made.

10. Coincidence of crossing over in the X chromosome is about the same in the two species.

11. Non-disjunction of the sex-chromosomes occurs in *simulans*, and so far as investigated is closely similar to the same phenomenon in *melanogaster*.

12. Seven gynandromorphs found in *simulans* lead to the same conclusions as the much larger series known in *melanogaster*.

[8] Hybrid *females* homozygous for *simulans* yellow, carmine, or forked, are also known to show the characters concerned.

[9] The recessive lethal effects of these genes are also recessive in hybrids.

13. In *simulans*, as in *melanogaster*, there is no crossing over of auto-somal genes in the male.

<div align="center">COMPLEMENTAL GENES</div>

The extraordinary variability that has been observed in the $F_2$ generation of many species crosses (cf. BAUR 1911, EAST 1916, 1920, CORRENS 1909, NAUDIN 1865, etc.) indicates that such species differ in many factors that are of the nature of specific modifiers, which can produce their maximum effects only in the presence of genes supplied by the other species that is used in the cross. In the case of *melanogaster* and *simulans* a similar state of affairs is indicated by the fact that the $F_1$ hybrids show characters not present in either parent.

Such genes are perhaps to be thought of as having arisen by mutation and having been perpetuated through chance. Since they do not produce any significant effect in the genetic complex in which they arose, they are not eliminated by natural selection, and some of them will sooner or later happen to be incorporated into the race.

This process is presumably going on within the species, and it seemed possible that it might there be feasible to get evidence of its existence. Wild races from widely separated localities might be expected to carry such complementary genes, and occasionally to give rise to unusual types in $F_2$. Numerous such crosses have been carried out with *Drosophila melanogaster*. DUNCAN (1915), for example, crossed three mutant races to wild races from Arkansas, California, Illinois, Massachusetts, Minnesota, Ohio, Wyoming, Porto Rico, Cuba, Australia, and France. A total of 16,637 $F_2$ flies was examined, and no evidence of any unusual results due to the crosses was obtained. Similar negative results have been obtained by others with wild races from Alabama, Florida, Indiana, New Jersey, New York, Oregon, South Carolina, South Dakota, Washington, Nova Scotia, and elsewhere. I have crossed races of *D. busckii* from Norway and Massachusetts; of *D. funebris* from Norway, New Hampshire, Massachusetts, New York, Michigan, Minnesota, South Dakota, and California; of *D. immigrans* from Norway, New York, Maryland, and Florida; and of *D. simulans* from New Hampshire, New York, Minnesota, Alabama and Florida. In all these cases, also, $F_2$ showed no indication of unusual types resulting from the crosses. The only conclusion to be drawn from these extensive negative results is that, within these widely distributed species, local races do not usually differ by complementary genes conditioning the appearance of conspicuous new characters. It should, however, be remembered that all five species mentioned are forms that

occur around houses, grocery stores, garbage piles, and similar places. They are undoubtedly frequently transported from one locality to another, and this may act to prevent the differentiation of local races. It remains possible that different results might be obtained with some of the native species that are seldom found except in woods (such as *D. melanica, robusta, affinis,* or *quinaria,* all of which can be bred in the laboratory).

## THE GENETIC CONSTITUTION OF RELATED SPECIES

It cannot be doubted that closely related species have many genes in common, since the characters that they have in common must have, in large part, an identical genetic basis. This being the case, it is probable that identical mutations will sometimes occur in different species, since such recurrences within one species are relatively frequent. But to prove either of these points in any given case is exceedingly difficult.

Even within a given species the identity of two mutations can never be assumed merely because the two characters look alike. There is reason to believe that there are at least 2000,—probably many times that number —different loci in *Drosophila melanogaster*.[10] It is known that genes in many of these loci are capable of producing similar or almost identical results. There are, in *D. melanogaster,* mutations in more than 25 loci that affect eye color, and in more than 15 loci that affect bristle number. About 10 genetically different roughened eyes are known. The eye-colors vermilion (first chromosome) and scarlet (third chromosome) are practically identical in appearance. Sable (first chromosome), black (second chromosome), and sooty (third chromosome) are closely similar body-colors. This list might be extended indefinitely; but it will already be clear that similar appearance is never sufficient proof of identity. Two genes can be shown to be identical or to occupy the same locus only when they are shown to be allelomorphic to each other or to the same other gene. Proof that they occupy the same locus can be approximated by other methods, and under certain conditions may be made almost as convincing as the test of allelomorphism, but is never entirely conclusive.

When an attempt is made to show the identity of mutations in different species the danger of error becomes even greater. Within a given species it is clear that certain loci are more mutable than others, and this fact obviously increases the likelihood of two similar mutations being identical; but in another species the more mutable loci might be different ones, so that

[10] This minimum number is deduced, by a method devised by Dr. H. J. MULLER, from the relation between the total number of mutations discovered and the number of loci in which those mutations occurred.

this factor would now decrease the probability of identity. Furthermore, identical mutations in different species, having a somewhat different genetic complex to react with, might produce characters that looked different. The case of tiny-bristle, reported in Part II of these studies (STURTEVANT 1921), is an example of the danger of interspecific comparisons that are unchecked by tests of allelomorphism. Not only are the two mutations (in *D. melanogaster* and *D. simulans*) closely similar in many respects (small bristles, irregular eyes, small size, late emerging, female sterility), but both genes are sex-linked and occupy loci at considerable distances from the left-hand end of the X. Yet the data previously presented show conclusively that they are not allelomorphs and that their respective loci are on opposite sides of the garnet-carmine locus.

Certain students of mimicry have suggested that model and mimic resemble each other because they have identical genes, i.e., because identical mutations have occurred in them. This view is open to serious objection because it places mimicry in an entirely separate category from such examples of protective coloration as are furnished by Kallima or by leaf-insects and stick-insects. Nor can it apply to cases of mimicry such as occur in certain Syrphid flies (Spilomyia, Temnostoma, etc.), where the antennae of wasps are mimicked by the front legs of flies. Even in the cases to which the view was intended to apply, it is rendered very questionable by the considerations elaborated above.

Among mammals, more especially among the rodents, the normal ticked or agouti pattern shows similar variations (black, yellow, brown, dilute, white, piebald, etc.) in a number of different species. It has often been stated or implied that these are due to identical mutations. In certain cases there is specific evidence against such a view. In mice, for example, yellow is dominant to agouti, and is allelomorphic to the gene that differentiates black from agouti. In other rodents yellow is recessive, and is not allelomorphic to black. Clearly then the yellow of mice is different from the yellow of other rodents. In most of the other cases there is no evidence of this nature indicating that the genes are different; but except in the cases now to be discussed I am not aware of any evidence, other than similarity, indicating identity.

In mice (MORGAN 1914, etc.) and in guinea-pigs (DETLEFSEN 1914) there are three similar types,—light-bellied agouti, ticked-bellied agouti, and black,—that are due to allelomorphic genes. In mice yellow is in this same locus, and in rabbits agouti, black-and-tan and black are allelomorphic. In rats two allelomorphic genes (agouti and black) are known. Here then we have three related forms in which the locus bearing the differ-

entiator between agouti and black has produced two or more different mutant allelomorphs, and in the case of mice and guinea-pigs three *similar* color patterns occur.

A somewhat similar parallelism occurs in the case of the locus that bears the differentiator between intense pigmentation and albinism. In mice two allelomorphs are known,—intense and albino. In rats there are three allelomorphs,—intense, dilute, and albino (WHITING and KING 1918). In rabbits we have intense, Himalayan, and albino (STURTEVANT 1913). In guinea-pigs four allelomorphs are present,—intense, dilute, red eye, and sooty albino (WRIGHT 1916). Dr. WRIGHT informs me that in all the intermediates between intense and albino "black is diluted toward sepia (instead of maltese) and red to cream or white, and [red] is affected to a greater extent than black." In the case of rats and mice there is still further evidence bearing on this locus. HALDANE, SPRUNT and HALDANE (1915), CASTLE (1919) and DUNN (1920) have shown that in mice the albino locus is linked to the pink-eye locus, giving about 14.5 percent of crossing over with it. CASTLE (1919) finds that in rats closely similar mutations (albino and pink eye) give about 21 percent of crossing over. Here then we have two loci that have given similar mutations in the two species, and that are also known to be in the same chromosome in each species. If further parallels could be found in this chromosome (it contains a third mutated gene in rats), or if further parallel variations could be found in the albino locus in mice (which are the only thoroughly studied rodents in which there is no known third allelomorph of albinism), this case might become quite convincing. As it stands at present, however, parallelism seems to me to be not demonstrated, in view of the difficulties enumerated above.

DETLEFSEN (1914) has, however, obtained clear evidence of identical loci in the guinea-pig (*Cavia porcellus*) and the related *C. rufescens*. These two species are sufficiently close so that they can be crossed; though that they are "good species" is indicated by their different appearance and by the fact that the F₁ males were all sterile. DETLEFSEN has studied the descendants of the hybrid females when mated to *porcellus* males, and has used known *porcellus* mutant races in the crosses. He has shown that at least seven loci are present in both species and behave in the hybrids in the same way as in *porcellus*. Six of these loci are occupied by wild-type allelomorphs that seem to be identical in the two species: the seventh locus is the agouti-black locus mentioned above, and the light-bellied agouti there listed is the "wild-type" allelomorph, present in *porcellus*, while ticked-bellied agouti is the only type known in *rufescens* and is not known

at all in *porcellus*. This case makes it certain that the two species carry some identical loci, and identical genes in some of these loci; but it does not show that identical mutations, or mutations in identical loci, have occurred in separate species; for no mutant races of *rufescens* have been studied.[11]

It is clear that the likelihood of two mutations being identical is increased if the characters concerned are complex or are unique in any respects. METZ (1916) has found a mutation (confluent) in *Drosophila virilis* that resembles one of the same name in *D. melanogaster*, in which this condition is fulfilled. It is also fulfilled in the cases of hairless and notch in *D. funebris* and *D. melanogaster*. In the latter instance (notch) the case is somewhat strengthened by the facts that both genes are sex-linked and that in *D. melanogaster* notch is a frequently recurring mutation, so that it might be expected to be likely to occur in another species.

This last point,—high mutability,—is applicable to two other loci that have apparently given identical mutations in Drosophila species. Yellow is a relatively frequent mutation in *melanogaster*, and we have seen that it has occurred (probably twice) in *simulans*. METZ (1916) has described what appears to be the same thing in *virilis*. Forked has certainly appeared both in *melanogaster* and in *simulans*, and mutations closely similar to these have appeared both in *virilis* and in *funebris*.

As has been pointed out in Part II of these studies (STURTEVANT 1921) yellow and forked in *virilis* give nearly the same amount of crossing over as in *melanogaster* and *simulans;* and notch and forked in *funebris* give about three-fourths as much crossing over as in *melanogaster*. This constitutes still another line of evidence indicating that these genes in *virilis* and *funebris* are identical, or at least allelomorphic, with those in *melanogaster*. But in the absence of direct evidence of allelomorphism, the case is not established. If still more parallels could be found, and could be shown to have the same sequence in the maps, the case would be still stronger, and might become practically conclusive. But until such evidence is available, only direct tests of allelomorphism can be accepted as convincing evidence that identical loci are concerned. Such evidence can be obtained only through crosses, and has actually been obtained in only a very few cases.

EAST (1916) has crossed *Nicotiana Langsdorffii* and *N. alata*. As frequently happens in species crosses, $F_2$ presented a bewildering array of

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[11] I am indebted to Dr. SEWALL WRIGHT for much of the information included in the above discussion of parallelism in rodents and for several suggestions concerning the treatment. Dr. WRIGHT is not, however, responsible for any of the opinions expressed.

types; but EAST was able to show that in respect to corolla color and to pollen color the results are due to simple Mendelian differences between the parent species. This constitutes evidence that 'the wild-type genes present in the two species behaved as allelomorphs, and that these species therefore had at least two loci in common.

CORRENS (1909) crossed *Mirabilis Jalapa* (Four-o'clock) with *M. longiflora*. Here again F₂ was extremely variable. If, however, the recessive "*chlorina*" mutant of *Jalapa* was used as a parent, about one-fourth of the F₂ plants showed the *chlorina* character. It follows that the normal allelomorph of the *chlorina* gene was present in *longiflora*, and that this locus behaved in the maturation of the hybrid germ-cells as it does in pure *Jalapa*.

BAUR (1911) has crossed *Antirrhinum majus* (Snapdragon) and *A. molle*, again with the production of an extremely variable F₂. BAUR believes that most of the specific differences here are Mendelian. He has also used at least five mutant races of *A. majus* in such crosses, and has obtained results similar to those of CORRENS with Mirabilis. The two species evidently have at least five wild-type genes in common.

The data obtained by DETLEFSEN in crosses between *Cavia porcellus* and *C. rufescens*, that have already been discussed, should be compared with those just described, since the conclusions are based on similar evidence.

The evidence presented in these studies has shown that 44 recessive mutant genes (in 41 loci) of *Drosophila melanogaster* and 12 recessive mutant genes of *D. simulans* (in 12 loci) are also recessive in the *melanogaster-simulans* hybrids. Allowing for loci that are included in both totals (see below), this constitutes evidence[12] that 46 wild-type allelomorphs are common to the two species, or (since the evidence does not actually prove these allelomorphs to be identical), at least that each species has a wild-type allelomorph in every one of these 46 loci. And these 46 are the only loci so investigated.[13]

In the case of seven of the loci of *melanogaster* and *simulans* each species has produced a mutation, and crosses of these mutated races have shown that the mutant genes are allelomorphic, thus furnishing conclusive evidence that the two species are alike to this extent. These are, I think, the

[12] Not conclusive evidence, however; for it is possible that in some cases recessiveness is not due to the counteracting influence of the dominant allelomorph, but rather to an insufficient amount of the recessive allelomorph in heterozygotes.

[13] It would appear that the mule affords an opportunity for similar studies. Color inheritance in the horse is well understood, and most of the colors that occur in the horse may also be seen in mules. The relations of the various colors of the ass do not seem to have been worked out.

first cases in which parallel mutations in distinct species have been demonstrated.

Five of the parallel mutations are in the X chromosomes, so that it has been possible for the first time to construct parallel maps based on loci known to be identical but occurring in distinct species. As we have seen, these maps show that the five loci have the same sequence in the two species, but that the amount of crossing over in different regions is not identical.

These examples furnish definite proof that related species do have many genes in common, and that identical mutations may occur in different species. The data from *D. simulans* show, what was suggested by the other results and by much cytological data, that the constitution of a chromosome may be essentially the same in two different species. That the crossing-over percentages are different is not surprising, since these are known to be variable even within one species.

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