# STUDIES ON SEX DETERMINATION AND THE SEX CHROMOSOME MECHANISM IN SCIARA[1]*

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Received February 29, 1930

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## INTRODUCTION

*Sciara coprophila* Lint., like most species of this genus thus far studied (METZ 1928), characteristically gives "unisexual" progenies. That is, the offspring from any pair mating are all or practically all of one sex, either males or females. Earlier papers have shown that the sex of the progeny as a whole is determined by the female (MOSES and METZ 1928) and that the genetic basis responsible for "sex of progeny" is inherited in a simple Mendelian fashion (METZ and MOSES 1928). It was shown also in the latter paper that the female-producing female breeds as if heterozygous, and the male-producing female as if homozygous recessive, for the gene or gene complex responsible for "sex of progeny."

Subsequently it was shown that the sex of the individual fly, as distinguished from that of the progeny as a whole, appears to be dependent on an ordinary XX-XY sex chromosome mechanism, the male being XY and the sperms, therefore, being "sex determining" (METZ and ULLIAN 1929). This conclusion is based on genetic evidence, no cytological distinction between X and Y having been detected thus far. Since a male may give both sons and daughters in large numbers (when mated to two or more

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[1] This investigation has been aided by a grant from the NATIONAL RESEARCH COUNCIL, Committee for Research in Problems of Sex.

* Part of the cost of the accompanying tables is paid by the GALTON AND MENDEL MEMORIAL FUND.

females), it is assumed that he produces X-bearing and Y-bearing sperms in equal numbers.

The latter condition is harmonized with the production of unisexual progenies by experiments which indicate that a selective elimination or inactivation of sperms takes place (METZ 1929). These experiments lead to the conclusion that in the female-producing female the selective action is such that the eggs are fertilized only by X-bearing sperms, while in the male-producing female only the Y-bearing sperms function. Thus the agent responsible for "sex of progeny" apparently finds expression in selective fertilization (see Discussion). Speaking broadly, therefore, we may say that sex is "determined" here by two factors or complexes, the one acting directly and the other indirectly. The sex of the individual fly depends directly on the type of sperm fertilizing the egg; but the type which will so function depends in turn on the zygotic constitution of the female producing the egg.

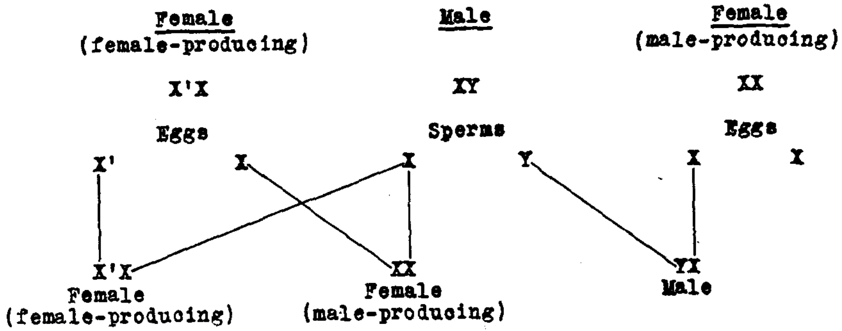


FIGURE 1.—Diagram illustrating mode of sex determination in Sciara.

It is the purpose of the present paper to consider evidence which shows that both of these factors or complexes are transmitted by the sex chromosome pair and that, in this respect at least, we are dealing here with three different kinds of sex chromosomes. The accompanying diagram (figure 1) will serve to illustrate this feature and to summarize the interpretation of sex determination developed below. A brief consideration of this interpretation will facilitate the presentation of data.

The evidence indicates that the male is XY, that the male-producing female is homozygous for the X found in the male, thus being XX, and that the female-producing female has one X of this kind, together with one which differs at least in respect to the agent responsible for sex of progeny. The latter is designated X′. The X′ chromosome, or the portion of it considered here, ordinarily descends directly from mother to daughter, thus being sex-limited in its transmission somewhat like the Y-chromosome, except that it goes to only half the daughters. The X-chromosome, on the other hand, passes back and forth between the males and both kinds of females.

Interest attaches especially to the constitution of the X′ chromosome as compared with that of X and Y, and especial efforts are being made to secure a genetic analysis which will make such a comparison possible. At present the evidence is limited to the following points: (1) X′ and X have similar effects on the morphological characteristics of the wild-type fly, as indicated by the fact that the two types of females look alike, and that when X′ is substituted for X in an "exceptional" male no striking difference results. (2) X′ carries the normal allelomorphs of the two known sex linked genes. (3) No crossing over has been detected thus far between X′ and X, whereas crossovers between X and X have been obtained. These features will receive further consideration below.

In this connection it should be noted that the sex chromosomes considered here are not to be confused with the large androsomes or "male-limited" chromosomes of Sciara, found only in males (METZ, MOSES and HOPPE 1926). The latter chromosomes apparently have no sex-determining function.

For aid in connection with the present work the writers are indebted to Mrs. SILKA S. ULLIAN, who found the mutant character "swollen" and carried out the first experiments with it.

## METHODS

The unusual mode of reproduction exhibited by Sciara imposes certain limitations, as well as offering certain advantages, as regards breeding technique.

For instance, in the present species (and many others of the genus) stocks or strains cannot ordinarily be secured from single wild females; each must come from at least two—a female-producer and a male-producer. Likewise, propagation of the stocks cannot be carried on by means of brother-sister matings, nor can such matings be used regularly in the experiments following crosses. $F_2$ progenies, therefore, must ordinarily be secured by mating sisters from one $F_1$ progeny to brothers from another such progeny.

It has been found in practice that even with these limitations on close inbreeding, fertility is rapidly reduced in inbred stocks, with the result that frequent out-crossing is required. Present indications are that fertility is restored by crossing with laboratory stocks as well as with wild ones, which suggests that loss of fertility has a genetic basis. If so, this in turn suggests a possible advantage in the type of reproduction found here, which clearly restricts inbreeding. These features, however, have not been tested critically enough, as yet, to rule out environment as the causal agent. In any case the practical result is an inability to keep any stock very long without out-crossing. The "Eastern" stock referred to below, for example, is not from one source, but is from Eastern United States sources as distinguished from the "California" stocks mentioned.

It is doubtful whether geographic sources have much significance in this species, however, except within broad limits, for the flies are common in greenhouses and the larvae are readily transported long distances in the soil or decaying matter in shipments of plants. Thus far we have detected no genetic differences between flies of this species from Massachusetts, New York, Michigan and California.

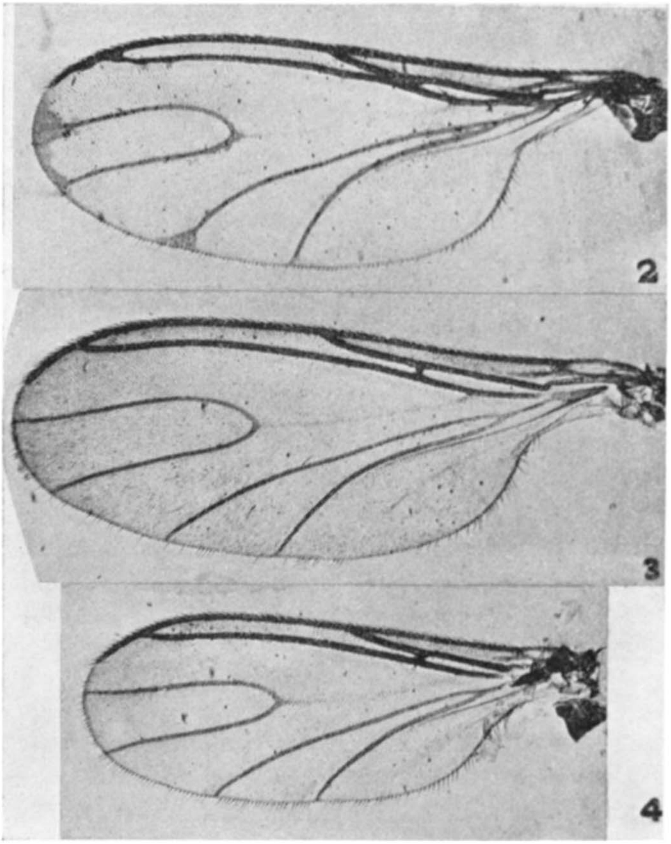
Owing to the fact that the flies in any progeny mature almost simultaneously, and that the adults are very short lived (compare METZ 1929) it often happens that the particular type of mating desired cannot be made because the necessary males and females are not both available at the same time. The effect of this will be noticed in some of the experiments recorded below, particularly where wild-type males were used when narrow or swollen would have been preferable.

The general technique of handling the flies and the culture methods used here are not essentially different from the well known procedures used with Drosophila. The food, however, is very different. That being used at present consists of agar and leaf mold, together with commercial yeast.

## TERMINOLOGY

In addition to the sex chromosome symbols mentioned above (X, X′ and Y) the following symbols are used in this paper: X*s* and X*n* indicate ordinary X-chromosomes (as distinguished from X′) carrying the genes for swollen and narrow, respectively. Thus X′X*s* represents the constitution of a female-producing female in which the X carries swollen. The symbol + is used to represent the wild-type flies as distinguished from those exhibiting mutant characters.

Since the sex of the progeny as a whole is inherited in a definite fashion it is treated as a distinct character, referred to as "sex of progeny." Females giving male progenies are designated *male-producing* or *androgenic*, and those giving female progenies as *female-producing* or *gynogenic*. As noted in earlier papers, the usual type of reproduction in Sciara, in which "unisexual" progenies are produced, is replaced in certain species and races by a type characterized by bisexual progenies (see below, p. 238). These types of reproduction are designated *monogenic* and *digenic*, respectively.[2] The same terms may also be applied to the two corresponding types of females (that is, those giving "unisexual" progenies and those giving bisexual progenies).



FIGURES 2–4.—Photographs of wings of *Sciara coprophila*. Figure 2, swollen. Figure 3, wild-type. Figure 4, narrow. Figures 3 and 4 are from brothers, showing the usual difference in size between the wild-type and narrow wings.

Another term which may be suggested at this time is the term *androsome*, applied to the large chromosomes found only in males.[3] These chromosomes were previously referred to as "sex-limited" or "male-limited."

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[2] We are indebted to Professor E. B. WILSON for these terms.

[3] See Addendum.

Technically the ordinary Y chromosome should also be included under this head, although it is not in the present paper.

As previously noted, the "male progenies" in these flies often contain a few "exceptional" females, and the "female progenies" a few "exceptional" males. In the present paper the term "exceptional" is used in this sense; it refers to the sex of the fly and not to any exceptional genetic characteristics.

## THE SEX LINKED CHARACTERS SWOLLEN AND NARROW

The two mutant characters used in this study are "swollen" and "narrow." A brief description of these, together with an account of their origin, is given below.

### *Swollen*

In swollen flies the wing veins are swollen or thickened in various ways (figure 2). The tips of the M and Ca veins are regularly thickened, delta like, and often the R and R*s* veins are irregularly swollen, lumpy or more or less fused together throughout their entire length.[4] Sometimes the whole wing is distorted by the swellings or by vesicles. Apparently the character is readily influenced by modifiers, since it is much more extreme in some lines than in others. Swollen has no noticeable effect on the viability of males, but it apparently reduces that of females materially and also prolongs their period of development so that they emerge later than their wild-type sisters.

Swollen arose in a laboratory culture of an "eastern" line (compare METZ and ULLIAN 1929).

### *Narrow*

The primary characteristic used in the classification of narrow is the small size of the wings and their somewhat narrow shape (figure 4). The entire fly appears to be affected to some extent, however, as indicated by small body size, shorter antennae, shorter legs and poor viability. Both sexes hatch late, appear in relatively small numbers, are short lived and are much less fertile than their wild-type sibs.

Narrow arose in laboratory stock. It was first observed, by METZ, in two sister cultures in the $F_2$ from a cross between swollen and a bisexual ("digenic") strain (considered elsewhere) derived from Riverside, California stock (2860). The results indicated that the mutation occurred in the X chromosome from the California strain.

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[4] The nomenclature of venation is that used by JOHANNSEN (1912).

## INHERITANCE OF SWOLLEN

The inheritance of swollen has been considered briefly in an earlier paper (METZ and ULLIAN 1929) in which it was shown that the character behaves like a typical sex linked recessive. Narrow has not been discussed previously.

Since the inheritance of these two characters forms the basis upon which the above mentioned interpretation of sex determination rests, it will be considered here in some detail. The account of the early experiments with swollen will be found to differ in certain respects from that given in the paper just mentioned. This is due to several facts, discussed below. It need only be noted here that the difficulties from this source served for a long time to conceal the true association between "sex of progeny" and the other sex linked characters.

Swollen is inherited according to the scheme shown in figure 5. When swollen males are out-crossed to unrelated wild-type females the offspring are all wild-type. When the $F_1$ females are backcrossed to swollen males the resulting progenies include wild-type and swollen in a 1:1 ratio as expected, save for a deficiency of swollen females due to poor viability. When the females of this generation are tested the swollen ones all prove to be male-producers and give exclusively swollen sons, aside from the occasional "exceptional" daughters. Conversely, their wild-type sisters are all female-producers and, if crossed to swollen males, give the same results as their mothers. This process may be repeated over and over. Judging from present evidence it will continue indefinitely, the swollen females regularly being male-producers and their heterozygous sisters female-producers.

1. *Wild-type female×swollen male.*

$F_1$. All wild-type.

2. *Backcross, $F_1$ female×swollen male.*

| *Male progenies* | *Female progenies* |
|---|---|
| Wild-type and swollen | Wild-type and swollen |
| 1:1 ratio | 1:1 ratio |

3. *Tests of swollen and wild-type sisters from 2.*

| *Swollen female* | *Wild-type (heterozygous) female* |
|---|---|
| (by wild-type or swollen male) | (by swollen male) |
| Only male progenies. | Only female progenies. |
| Swollen males. | Wild-type and swollen, 1:1 ratio |

FIGURE 5.—Inheritance of "swollen" in *S. coprophila*.

The initial experiment involving swollen (made by Mrs. ULLIAN) was of the type mentioned above, but in the immediately succeeding experiments the association between swollen and "sex of progeny" was not detected, owing to poor food conditions and the use of mass cultures. The writers' experiments with this character began with a cross of swollen and heterozygous females (singly) to males from Riverside, California stock. The males were the sons of wild females. These matings are summarized in table 1.

The females used here were taken from a mass culture and were selected because they all had the wing veins modified to some extent and were therefore thought to be swollen (the characteristics of swollen not being well known at that time). The second column of table 1 gives the original notes on these females. It will be observed that most of those giving male progenies were definitely recorded as swollen, whereas the others were mostly doubtful. Three of the latter also gave exceptional wild-type sons, in contrast to the sons of the male-producers.

TABLE 1

*Original pair matings of virgin swollen or heterozygous females to wild-type California males.*

| CULTURE NUMBER* | NOTES ON PARENT ♀ ♀ | OFFSPRING | | | |
|---|---|---|---|---|---|
| | | ♀ | | ♂ | |
| | | + | *s* | + | *s* |
| 2843 | Very slight *s* | 56 | 0 | 0 | 0 |
| 2853- 1 | Slight *s*, like spot | 58 | 0 | 0 | 0 |
| 2853- 2 | Slight *s*, like spot | 29 | 0 | 0 | 0 |
| 2854 | *s* fairly extreme | 24 | 0 | 0 | 0 |
| 2855- 1 | Extreme *s* | 0 | 0 | 0 | 59 |
| 2855- 2 | Extreme *s* | 2 | 0 | 0 | 83 |
| 2856- 1 | Slight *s*, like spot | 96 | 0 | 1 | 0 |
| 2856- 2 | Slight *s*, like spot | 67 | 0 | 1 | 0 |
| 2858- 1 | Slight *s*, like spot | 48 | 0 | 0 | 0 |
| 2858- 2 | Slight *s*, like spot | 75 | 0 | 0 | 0 |
| 2859- 1 | Moderate *s* | 12 | 0 | 0 | 0 |
| 2859- 2 | Moderate *s* | 43 | 0 | 0 | 0 |
| 2859- 3 | Moderate *s* | 75 | 0 | 2 | 0 |
| 2859- 4 | Moderate *s* | 10 | 0 | 0 | 0 |
| 2872- 7 | *s* some extreme | 3 | 0 | 0 | 93 |
| 2872- 8 | *s* | 4 | 0 | 0 | 58 |
| 2872- 9 | *s* | 23 | 0 | 0 | 0 |
| 2872-14 | *s* | 30 | 0 | 0 | 0 |
| 2973 | *s* | 0 | 0 | 0 | 25 |
| 2983 | *s* | 0 | 0 | 0 | 23 |
| 2984 | *s* | 0 | 0 | 0 | 27 |

* In this and other tables it will be noted that several similar matings are often recorded under one main number, as, for example 2859-1, 2859-2, etc. This is done purely for convenience. Each represents a separate mating.

TABLE 2

*Tests of virgin females* from progenies shown in table 1.*†

| MATING | CULTURE NUMBER | OFFSPRING | | | | TOTAL PROGENIES |
|---|---|---|---|---|---|---|
| | | ♀ | | ♂ | | |
| | | + | *s* | + | *s* | ♀:♂ |
| ♀ from 2843 by *s* ♂ | 2951- 1 | 100 | 0 | 3 | 1 | 6:7 |
| | 2951- 2 | 0 | 0 | 25 | 26 | |
| | 2965- 1 | 0 | 0 | 10 | 15 | |
| | 2965- 2 | 0 | 0 | 35 | 38 | |
| | 2965- 3 | 42 | 0 | 2 | 1 | |
| | 2965- 4 | 0 | 0 | 1 | 5 | |
| | 2965- 5 | 0 | 0 | 17 | 29 | |
| | 2965- 6 | 52 | 0 | 2 | 1 | |
| | 2965- 7 | 0 | 0 | 9 | 12 | |
| | 2965- 8 | 36 | 0 | 0 | 1 | |
| | 2965- 9 | 0 | 0 | 16 | 27 | |
| | 2965-10 | 15 | 0 | 0 | 0 | |
| | 3019 | 54 | 0 | 3 | 1 | |
| ♀ from 2853-1 by +♂ | 2954 | 43 | 0 | 3 | 0 | |
| ♀ from 2853-2 by +♂ | 2953- 1 | 2 | 0 | 110 | 64 | 0:2 |
| | 2953- 2 | 0 | 0 | 63 | 15 | |
| ♀ from 2854 by +♂ | 2962- 1 | 11 | 0 | 0 | 0 | 3:0 |
| | 2962- 2 | 95 | 0 | 0 | 0 | |
| | 2962- 3 | 95 | 0 | 0 | 0 | |
| "Exceptional" ♀ from 2855-2 by *s* ♂ | 2985 | 0 | 0 | 19 | 20 | 0:1 |
| "Exceptional" ♀ from 2872-7 by *s* ♂ | 2990- 1 | 1 | 0 | 22 | 25 | 0:3 |
| | 2990- 2 | 0 | 0 | 24 | 31 | |
| | 2990- 3 | 0 | 0 | 3 | 4 | |
| "Exceptional" ♀ from 2872-8 by *s* ♂ | 2989- 1 | 0 | 0 | 80 | 80 | 0:3 |
| | 2989- 2 | 0 | 0 | 53 | 48 | |
| | 2989- 4 | 0 | 0 | 51 | 42 | |
| ♀ from 2872-9 by *s* ♂ | 2980- 1 | 0 | 0 | 19 | 33 | 1:4 |
| | 2980- 3 | 0 | 0 | 41 | 44 | |
| | 2980- 4 | 0 | 0 | 16 | 24 | |
| | 2980- 5 | 84 | 1 | 0 | 2 | |
| | 2980- 6 | 0 | 0 | 5 | 14 | |

* Seven of these are "exceptional" females, hence male-producers (series 2985, 2989 and 2990).

† The source of the mother and the genetic constitution of the father are given in column one of the table.

In the light of recent evidence it is clear that the male-producing mothers here were swollen (X*s*X*s*) and the female-producing mothers heterozygous for swollen (X′X*s*). The latter had modified wing veins due to the presence of "spot," an irregular autosomal character which is apparently exaggerated in the presence of the gene for swollen.

On such a basis it would be expected that only half the females from this cross would carry swollen. The complete records are given in table 2. Since the first thirteen of these involve sisters from one culture (2843) mated singly to swollen males they may be considered separately. Seven of the sisters proved to be male-producers, all heterozygous for swollen. The remaining six were female-producers. One of the latter gave only wild-type daughters (2965–10). The other five, however, gave, in addition to wild-type daughters, one or more "exceptional" sons, at least one of which, in each case, was classified as swollen. Some of these sons were extreme swollen and were unquestionably classified correctly. Their presence was largely responsible for the earlier conclusion that the mothers here were all heterozygous for swollen (METZ and ULLIAN 1929).

Tests of females from other progenies noted in table 1 are likewise included in table 2. Of the eighteen involved here, seven were "exceptional" individuals (2985, 2989, 2990) and hence male-producers (compare METZ and MOSES 1928). Six others were also male-producers, and, as in the other cases, all gave both wild-type and swollen, usually in a ratio of approximately 1:1. Of the five female-producers, four were mated to wild-type males and, as expected, gave only wild-type offspring. The other (2980–5) was mated to swollen and gave, in addition to wild-type daughters, one extreme swollen daughter and two swollen sons. These latter present the same difficulty as the swollen "exceptional" males mentioned in the preceding paragraph (see below).

In the next generation, when females from progenies in table 2 were tested, it was found that those from swollen fathers were heterozygous for swollen and that when mated to swollen males the female-producers gave the same type of results as the male-producers. This is shown in table 3. The swollen female class is deficient in numbers due to poor viability.

When the females from this generation were tested (table 4) it was found that the swollen ones were male-producers (X*s*X*s*) while their heterozygous sisters were all female-producers (X′X*s*). The latter were mated to swollen males and gave the same results as their mothers. Owing to difficulties with food the counts were small here in most cases.

In both of the generations just considered the results agree with the interpretation outlined in the Introduction. It remains, therefore, to account for the results obtained in the second generation (table 2) as noted above. On the present interpretation no swollen offspring would be expected from the female-producing females in that generation. The few obtained are presumably due to non-disjunction or to other chromosomal disturbances (which appear to be unusually frequent in this material). Although a few might be due to contamination or errors in recording, this is unlikely and, in any event, such an assumption could not account for all the cases. The one extreme swollen female, for example, was particularly noted and could

TABLE 3

*Tests of females from progenies given in table 2.**

| MATING | CULTURE NUMBER | OFFSPRING | | | | TOTAL PROGENIES |
|---|---|---|---|---|---|---|
| | | ♀ | | ♂ | | |
| | | + | *s* | + | *s* | ♀ : ♂ |
| ♀ from 2965–6 by *s* ♂ | 3030 | 36 | 12 | 0 | 0 | 2:0 |
| | 3031 | 17 | 9 | 0 | 0 | |
| ♀ from 2965–10 by *s* ♂ | 3020– 1 | 0 | 0 | 56 | 73 | 2:5 |
| | 3020– 2 | 0 | 0 | 55 | 40 | |
| | 3020– 3 | 0 | 0 | 74 | 58 | |
| | 3026– 1 | 0 | 0 | 25 | 1 | |
| | 3026– 2 | 7 | 5 | 0 | 0 | |
| | 3026– 3 | 0 | 0 | 43 | 40 | |
| | 3078 | 79 | 39 | 0 | 2 | |
| ♀ from 3019 by *s* ♂ | 3024 | 48 | 27 | 0 | 1 | 11:6 |
| | 3025– 1 | Many | Many | 0 | 0 | |
| | 3025– 2 | 30 | 27 | 0 | 0 | |
| | 3025– 3 | 0 | 0 | 30 | 28 | |
| | 3025– 4 | 55 | 17 | 0 | 0 | |
| | 3025– 5 | 0 | 0 | 59 | 51 | |
| | 3025– 6 | 29 | 14 | 0 | 0 | |
| | 3027 | 0 | 0 | 14 | 21 | |
| | 3037– 1 | 25 | 10 | 0 | 0 | |
| | 3037– 2 | 0 | 0 | 18 | 10 | |
| | 3037– 3 | 0 | 0 | 0 | 18 | |
| | 3037– 4 | 0 | 0 | 15 | 23 | |
| | 3037– 5 | 25 | 8 | 0 | 0 | |
| | 3037– 7 | 31 | 19 | 0 | 0 | |
| | 3037– 8 | 18 | 8 | 0 | 0 | |
| | 3037–10 | 9 | 2 | 0 | 1 | |
| | 3037–11 | 24 | 21 | 0 | 0 | |

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* The source of the mother and the genetic constitution of the father are given in column one of the table.

not have been due to contamination because no other swollen females were in the laboratory at the time. This female gave no offspring, apparently being sterile. It is possible that she was a mosaic in which the wings were male and exhibited swollen, although the fly was genetically female and heterozygous. Individuals of this type have been obtained in subsequent experiments. It should be noted that exceptional swollen males were only obtained from matings in which the father was swollen. Six of the seven matings of this type gave such males, whereas the four in which the father

TABLE 4

*Tests of females from table 3.*
*A. swollen females Xs/Xs. B. heterozygous females X'/Xs.*

| MATING | CULTURE NUMBER | OFFSPRING ♀ + | OFFSPRING ♀ *s* | OFFSPRING ♂ + | OFFSPRING ♂ *s* | TOTAL PROGENIES ♀ : ♂ |
|---|---|---|---|---|---|---|
| A. | | | | | | |
| ♀ from 3025–6 by + or *s* ♂ | 3093 (mass) | 0 | 0 | 0 | 14 | 0:1 |
| ♀ from 3030–1 by + or *s* ♂ | 3090– 1 | 0 | 0 | 0 | 40 | 0:2 |
| | 3090– 2 | 0 | 0 | 0 | 88 | |
| ♀ from 3078 by + or *s*♂ | 3082– 1 | 0 | 0 | 0 | 101 | 0:1 |
| B. | | | | | | |
| ♀ from 3024 by *s* ♂ | 3085– 3 | 12 | 4 | 0 | 2 | 11:0 |
| | 3085– 5 | 8 | 2 | 0 | 1 | |
| | 3085– 6 | 24 | 11 | 0 | 0 | |
| | 3085– 8 | 7 | 5 | 1 | 3 | |
| | 3085–10 | 21 | 14 | 0 | 0 | |
| | 3085–15 | 13 | 8 | 0 | 0 | |
| | 3088– 4 | 9 | 7 | 0 | 0 | |
| | 3088– 5 | 21 | 15 | 2 | 0 | |
| | 3088– 8 | 15 | 13 | 0 | 1 | |
| | 3088–12 | 17 | 3 | 1 | 0 | |
| | 3088–13 | 10 | 3 | 0 | 0 | |
| ♀ from 3078 by *s* ♂ | 3079– 1 | Many | Many | 0 | 0 | 6:0 |
| | 3079– 2 | Many | Many | 0 | 0 | |
| | 3079– 3 | Many | Many | 0 | 0 | |
| | 3079– 4 | 36 | 20 | 0 | 1 | |
| | 3079– 5 | Many | Many | 0 | 0 | |
| | 3143 | 51 | 15 | 0 | 0 | |

TABLE 5

*Test of swollen and heterozygous sisters in successive generations.*

| A. SWOLLEN $\frac{X_s}{X_s}$ | | | | | | | B. HETEROZYGOUS $\frac{X'}{X_s}$ | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Source of ♀ | Parent ♂ | Offspring | | | | Culture Number | Source of ♀ | Parent ♂ | Offspring | | | | Culture Number |
| | | ♀ | | ♂ | | | | | ♀ | | ♂ | | |
| | | + | s | + | s | | | | + | s | + | s | |
| 3085- 5 | + | 1 | 0 | 0 | 30 | 3160- 2 | 3085- 5 | + | 18 | 0 | 0 | 0 | 3156-1 |
| | | | | | | | 3085- 5 | + | 79 | 0 | 0 | 0 | 3156-2 |
| | | | | | | | 3085- 5 | + | 17 | 0 | 0 | 0 | 3156-3 |
| | | | | | | | 3085- 5 | s | 16 | 13 | 0 | 0 | 3162 |
| 3085-10 | + | 0 | 0 | 0 | 12 | 3164- 1 | 3085-10 | s | 39 | 26 | 0 | 0 | 3163-1 |
| 3085-10 | + | 0 | 0 | 0 | 35 | 3223- 1 | 3085-10 | s | 45 | 24 | 0 | 0 | 3163-2 |
| 3085-10 | + | 0 | 0 | 0 | 33 | 3223- 2 | 3085-10 | s | 22 | 5 | 0 | 0 | 3163-3 |
| 3085-10 | + | 0 | 0 | 0 | 74 | 3223- 5 | | | | | | | |
| 3085-10 | + | 0 | 0 | 0 | 14 | 3223- 7 | | | | | | | |
| 3085-10 | + | 0 | 0 | 0 | 30 | 3223-10 | | | | | | | |
| 3085-11 | + | 0 | 0 | 0 | 14 | 3172- 2 | 3085-11 | s | 14 | 5 | 1 | 0 | 3174-2 |
| 3085-11 | + | 0 | 0 | 0 | 26 | 3173- 1 | | | | | | | |
| 3085-11 | + | 3 | 0 | 0 | 23 | 3173- 2 | | | | | | | |
| 3143 | s | 0 | 0 | 0 | 13 | 3144 | 3143 | s | 32 | 54 | 0 | 0 | 3145-1 |
| 3143 | s | 0 | 0 | 0 | 29 | 3148- 1 | 3143 | s | 39 | 17 | 0 | 0 | 3145-6 |
| 3143 | s | 0 | 0 | 2? | 23 | 3148- 2 | 3143 | s | 33 | 8 | 0 | 0 | 3145-7 |
| 3143 | s | 0 | 0 | 0 | 14 | 3148- 4 | 3143 | ? | 16 | 11 | 0 | 0 | 3149 |
| 3143 | s | 0 | 0 | 0 | 86 | 3148- 6 | | | | | | | |
| 3143 | s | 0 | 0 | 0 | 29 | 3148- 7 | | | | | | | |
| 3143 | s | 0 | 0 | 0 | 16 | 3148- 8 | | | | | | | |
| 3143 | s | 0 | 0 | 2? | 19 | 3148- 9 | | | | | | | |
| 3143 | s | 0 | 0 | 0 | 41 | 3148-10 | | | | | | | |
| 3143 | s | 0 | 0 | 0 | 52 | 3148-11 | | | | | | | |
| 3143 | s | 0 | 0 | 0 | 44 | 3148-12 | | | | | | | |
| 3186- 2 | + | 11 | 0 | 0 | 41 | 3260- 1 | 3186- 2 | s | 19 | 22 | 0 | 0 | 3259-2 |
| 3186- 2 | + | 0 | 0 | 0 | 76 | 3260- 4 | 3186- 2 | s | 16 | 0 | 0 | 0 | 3259-5 |
| 3186- 2 | + | 0 | 0 | 1 | 71 | 3260- 5 | | | | | | | |
| 3186- 2 | + | 9 | 0 | 0 | 70 | 3260- 7 | | | | | | | |
| 3197-10 | + | 1 | 0 | 0 | 102 | 3274- 1 | 3197-10 | s | 53 | 40 | 0 | 0 | 3275-1 |
| 3197-10 | + | 0 | 0 | 0 | 102 | 3274- 2 | 3197-10 | s | 27 | 10 | 0 | 0 | 3275-2 |
| 3197-10 | + | 0 | 0 | 0 | 12 | 3274- 3 | 3197-10 | s | 18 | 19 | 0 | 0 | 3275-3 |
| 3197-10 | + | 1 | 0 | 0 | 75 | 3274- 4 | 3197-10 | s | 28 | 29 | 0 | 0 | 3275-4 |
| 3197-10 | + | 0 | 0 | 0 | 59 | 3274- 5 | | | | | | | |
| 3197-10 | + | 0 | 0 | 0 | 20 | 3274- 7 | | | | | | | |
| 3197-10 | + | 0 | 0 | 0 | 97 | 3274- 8 | | | | | | | |
| 3197-10 | + | 0 | 0 | 0 | 97 | 3274- 9 | | | | | | | |

TABLE 5 (*continued*)

| A. SWOLLEN $\frac{X_s}{X_s}$ | | | | | | | B. HETEROZYGOUS $\frac{X'}{X_s}$ | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Source of ♀ | Parent ♂ | Offspring | | | | Culture Number | Source of ♀ | Parent ♂ | Offspring | | | | Culture Number |
| | | ♀ | | ♂ | | | | | ♀ | | ♂ | | |
| | | + | *s* | + | *s* | | | | + | *s* | + | *s* | |
| 3388- 1 | + | 0 | 0 | 0 | 57 | 3467- 4 | 3388- 1 | *s* | 30 | 6 | 0 | 0 | 3468-1 |
| 3388- 1 | + | 0 | 0 | 0 | 131 | 3467- 5 | 3388- 1 | *s* | 38 | 29 | 1 | 0 | 3468-2 |
| 3388- 1 | + | 0 | 0 | 0 | 17 | 3467- 6 | 3388- 1 | *s* | 77 | 65 | 0 | 1 | 3468-3 |
| | | | | | | | 3388- 1 | *s* | 47 | 48 | 0 | 1 | 3468-4 |
| | | | | | | | 3388- 1 | *s* | 26 | 28 | 0 | 0 | 3468-5 |
| 3847- 5 | + | 2 | 0 | 0 | 70 | 4063- 1 | 3847- 5 | *s* | 20 | 10 | 0 | 0 | 4066-2 |
| 3847- 5 | + | 0 | 0 | 0 | 7 | 4063- 2 | 3847- 5 | *s* | 22 | 19 | 0 | 0 | 4066-3 |
| 3847- 5 | + | 9 | 0 | 0 | 19 | 4063- 3 | 3847- 5 | *s* | 50 | 34 | 0 | 0 | 4066-4 |
| 3847- 5 | + | 11* | 0 | 0 | 20 | 4063- 4 | | | | | | | |
| 3847- 5 | + | 0 | 0 | 0 | 43 | 4063- 5 | | | | | | | |
| 3847- 5 | + | 0 | 0 | 0 | 29 | 4063- 7 | | | | | | | |
| 3847- 5 | + | 49* | 0 | 0 | 25 | 4063- 8 | | | | | | | |

* The females in these two progenies, although unusually numerous, are apparently all true "exceptional" individuals. Three of the eleven and fourteen of the forty-nine were tested and proved to be male-producers.

was wild-type gave none. Similar cases in other experiments make it probable that such males get their X-chromosome from the father.

Soon after the above results were obtained another cross was made between swollen and the California strain, to serve as a check on the earlier experiments. In this cross a "digenic" strain (giving bisexual progenies) was used, and the cross was the reciprocal of that made first. This digenic strain had arisen from the California stock used in the other case. Females from this were mated to swollen males and the daughters backcrossed to swollen. These daughters all should have been heterozygous for swollen, and since they gave bisexual progenies it was thought that the results would serve as a critical check on those previously secured. The counts from the backcross showed an almost complete absence of swollen females. Such a result seemed to confirm the earlier, erroneous, conclusion that the absence of swollen females following the supposed backcross was due to some genetic peculiarity of the California race (see METZ 1929, pp. 491–492). It was only after numerous experiments with both strains that the two sets of results were found to be due to different causes.

TABLE 6

*Descendants from a heterozygous female-producing female X'/Xs by wild male (see text for explanation).*

| MATING | CULTURE NUMBER | OFFSPRING | | | | TOTAL PROGENIES |
|---|---|---|---|---|---|---|
| | | ♀ | | ♂ | | ♀:♂ |
| | | + | s | + | s | |
| ♀ from 3340–1 by + ♂ | 3429– 1 | 0 | 0 | 58* | | 6:5 |
| | 3429– 2 | 0 | 0 | 101 | | |
| | 3429– 3 | 69 | 0 | 0 | 0 | |
| | 3429– 4 | 0 | 0 | 61 | | |
| | 3429– 5 | 0 | 0 | 31 | 34 | |
| | 3429– 6 | 139 | 0 | 0 | 0 | |
| | 3429– 7 | 0 | 0 | 28 | 54 | |
| | 3429– 8 | 66 | 0 | 1? | 0 | |
| | 3429– 9 | 122 | 0 | 2 | 0 | |
| | 3429–10 | 162 | 0 | 0 | 0 | |
| | 3429–11 | 146 | 0 | 0 | 0 | |
| ♀ from 3340–1 by *s* ♂ | 3434– 1 | 144 | 0 | 1 | 0 | 2:2 |
| | 3434– 2 | 116 | 0 | 3 | 0 | |
| | 3434– 3 | 0 | 0 | 85 | 78 | |
| | 3434– 4 | 1 | 0 | 70 | 73 | |
| ♀ from 3429–3 by *s* ♂ | 3565– 1 | 0 | 0 | 12 | 0 | 2:4 |
| | 3565– 3 | 0 | 0 | 93 | 0 | |
| | 3565– 4 | 134 | 0 | 1 | 0 | |
| | 3565– 5 | 188 | 0 | 0 | 0 | |
| | 3565– 6 | 1 | 0 | 132 | 0 | |
| | 3565– 7 | 4 | 0 | 23 | 0 | |
| ♀ from 3429–6 by + ♂ | 3543– 1 | 154 | 0 | 0 | 0 | 2:2 |
| | 3543– 2 | 0 | 0 | 110 | 0 | |
| | 3543– 3 | 0 | 0 | 14 | 0 | |
| | 3543– 4 | 147 | 0 | 0 | 0 | |
| ♀ from 3429–8 by *s* ♂ | 3566– 1 | 161 | 0 | 0 | 0 | 5:1 |
| | 3566– 2 | 174 | 0 | 1 | 0 | |
| | 3566– 4 | 68 | 0 | 0 | 0 | |
| | 3566– 5 | 0 | 0 | 69 | 0 | |
| | 3566– 6 | 139 | 0 | 0 | 0 | |
| | 3566– 7 | 91 | 0 | 3 | 0 | |
| ♀ from 3429–9 by *s* ♂ | 3576– 2 | 48 | 0 | 0 | 0 | 3:1 |
| | 3576– 3 | 0 | 0 | 123 | 0 | |
| | 3576– 4 | 170 | 0 | 2 | 0 | |
| | 3576– 5 | 159 | 0 | 0 | 0 | |
| ♀ from 3429–11 by *s* ♂ | 3567– 2 | 181 | 0 | 0 | 0 | 3:2 |
| | 3567– 4 | 0 | 0 | 141 | 0 | |
| | 3567– 5 | 0 | 0 | 183 | 0 | |
| | 3567– 6 | 96 | 0 | 0 | 1 | |
| | 3567– 7 | 22 | 0 | 0 | 0 | |

* Records in the central column are from progenies in which the two classes of flies were present but were not counted separately.

The behavior of the "digenic" strain will be considered in another paper. It is distinctly different from that of the "monogenic" strains,[5] due apparently to some chromosome disturbance.

In the monogenic strains the inheritance of swollen has been followed for more than ten generations, with regular conformity to the scheme outlined above. The experiments have involved various out-crosses as well as a continuation of tests of swollen and heterozygous sisters in successive generations following that shown in table 4. The latter data are too extensive to be given fully in the tables. For this reason only a few have been included from any one generation. These are given in table 5.

One of the out-crosses just mentioned was a repetition of the original cross considered in this paper (table 1), that is, a cross between a female-producing female heterozygous for swollen ($X'Xs$) and a wild-type male ($XY$) from Riverside, California stock (Line 2860). The $F_1$ consisted of 92 wild-type females and no males (No. 3340). Half of these females should be homozygous wild-type and half heterozygous for swollen, and on our hypothesis the former should all be female-producers ($X'X$) and the latter all male-producers ($XXs$).

Eleven of the females were mated singly to wild-type males, also from the Riverside stock, with the results shown in the first part of table 6 (3429 1–11). Six gave female progenies and five male progenies. The former progenies consisted entirely of wild-type flies, the latter all included both wild-type and swollen in large numbers, showing that the male-producing mothers were all heterozygous for swollen. At the same time four $F_1$ females were backcrossed to swollen males, with the same type of results, as shown in table 6 (3434 1–4). The two male progenies included both wild-type and swollen.

These results agree fully with expectation, the $F_1$ male-producers all being heterozygous for swollen, and the female-producers pure wild-type so far as tested. In the 3429 series the latter feature is uncertain since the fathers were wild-type. On our hypothesis none of the daughters in this series (3429 1–11) should carry swollen. To test this 29 were mated to swollen males. Twenty-five gave offspring, as shown in the latter part of table 6 (series 3543, 3565, 3566, 3567, 3576). Both the male and the female progenies were wild-type, as expected. The one exceptional swollen male in 3567–6 is evidently like those considered above—due presumably to non-disjunction.

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[5] This difference, however, is not such as to cast doubt on any essential features in the present paper.

Additional data on the inheritance of swollen are given in the experiments dealing with narrow.

## INHERITANCE OF NARROW

The mode of inheritance of narrow is the same as that of swollen, although the percentage of narrow flies is usually considerably reduced by poor viability, which in this case affects males as well as females. Owing to the fact that narrow first appeared in a digenic strain, as noted above, the earlier experiments with this character will be considered in another paper. Those treated here are from matings of narrow males to monogenic females, either pure wild-type or heterozygous for swollen.

In one experiment (3930) a female-producing female from wild stock 3059 (pure Anaheim, California stock) was mated to narrow males.[6] The $F_1$ consisted of approximately 125 wild-type females, no males. Four of these females were backcrossed to narrow males (mass culture 4116). Presumably only one gave offspring, for the progeny consisted of 12 wild-type and 15 narrow flies, all females. The former should all be female-producers ($X'Xn$) and the latter all male-producers ($XnXn$). Nine of the former were tested by mating to wild-type males (all but two from Anaheim stock 3059)

TABLE 7

*Tests of narrow and heterozygous sisters (see text).*

| A. NARROW ♀ $\frac{Xn}{Xn}$ —BY + ♂ | | | | | | B. HETEROZYGOUS ♀ $\frac{X'}{Xn}$ —BY + ♂ | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Source of ♀ | Culture Number | Offspring | | | | Source of ♀ | Culture Number | Offspring | | | |
| | | ♀ | | ♂ | | | | ♀ | | ♂ | |
| | | + | *n* | + | *n* | | | + | *n* | + | *n* |
| 4116 | 4256–1 | 0 | 0 | 0 | 52 | 4116 | 4255–1 | 198 | 0 | 1 | 1 |
| 4116 | 4256–2 | 0 | 0 | 0 | 65 | 4116 | 4255–2 | 183 | 0 | 0 | 2 |
| 4116 | 4256–3 | 0 | 0 | 0 | 69 | 4116 | 4265–1 | 200± | 0 | 0 | 0 |
| 4116 | 4280–2 | 0 | 0 | 0 | 34 | 4116 | 4265–3 | 60± | 0 | 0 | 0 |
| 4116 | 4280–4 | 0 | 0 | 0 | 8 | 4116 | 4265–5 | 50± | 0 | 0 | 0 |
| 4116 | 4293–1 | 0 | 0 | 0 | 46 | 4116 | 4265–6 | 150± | 0 | 2 | 0 |
| | | | | | | 4116 | 4265–7 | 100± | 0 | 0 | 0 |
| | | | | | | 4116 | 4265–8 | 125± | 0 | 0 | 0 |
| | | | | | | 4116 | 4279 | 150± | 0 | 0 | 0 |

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[6] Owing to the poor viability of narrow males it has been customary to use several in each mating rather than try to mate them singly. Presumably the female is in each case fertilized by only one male. (Compare MOSES and METZ 1928.)

and six of the latter by mating to wild-type males, also partly from Anaheim stock. The results conform to expectation as shown in table 7.

The next experiment was of a similar nature but more extensive. It is summarized in tables 8 to 10. Here narrow males were mated to a wild-type female from pure San Juan Capistrano, California stock, number 3086. This mating (3932) gave approximately 100 wild-type females, no males. Fourteen of these females were tested singly by mating to swollen males as shown in table 8A (4108 series). At the same time three mass matings were made of three females each to narrow males, with the result shown in table 8B (4136 series).

TABLE 8

*Tests of $F_1$ female from pure wild-type ♀ by narrow ♂. A. $F_1$ ♀ by s ♂. B. $F_1$ ♀ ♀ by n ♂♂ (mass matings).*

| SOURCE OF ♀ | CULTURE NUMBER | OFFSPRING | | | |
|---|---|---|---|---|---|
| | | ♀ | | ♂ | |
| | | + | *n* | + | *n* |
| A. | | | | | |
| 3932 | 4108- 1 | 120 | 0 | 0 | 0 |
| 3932 | 4108- 2 | 0 | 0 | 60 | 63 |
| 3932 | 4108- 3 | 0 | 0 | 80 | 52 |
| 3932 | 4108- 4 | 147 | 0 | 0 | 0 |
| 3932 | 4108- 5 | 0 | 0 | 88 | 69 |
| 3932 | 4108- 6 | 147 | 0 | 0 | 0 |
| 3932 | 4108- 7 | 0 | 0 | 86 | 47 |
| 3932 | 4108- 8 | 167 | 0 | 0 | 0 |
| 3932 | 4108- 9 | 0 | 0 | 39 | 31 |
| 3932 | 4108-10 | 0 | 0 | 47 | 62 |
| 3932 | 4108-11 | 0 | 0 | 55 | 64 |
| 3932 | 4108-12 | 0 | 0 | 85 | 64 |
| 3932 | 4108-14 | 97 | 0 | 0 | 0 |
| 3932 | 4108-15 | 0 | 0 | 52 | 61 |
| | | | | 592 | 513 |
| B. | | | | | |
| 3932 | 4136- 1 | 70 | 51 | 0 | 0 |
| 3932 | 4136- 2 | 0 | 0 | 64 | 33 |
| 3932 | 4136- 3 | 36 | 10 | 39 | 17 |

From the former series the daughters were, as expected, all wild-type. Thirty-three of them were tested singly by mating to narrow males, as shown in table 9A. These should be of two kinds, half female-producers

TABLE 9

*Tests of virgin females from progenies shown in table 8.*

A. $\frac{X'}{Xs}$ ♀ *and* $\frac{Xn}{Xs}$ ♀ *from table 8A.* B. $\frac{X'}{Xn}$ ♀ *and* $\frac{Xn}{Xn}$ ♀ *from table 8B.**

| MATING | CULTURE NUMBER | OFFSPRING | | | | | | TOTAL PROGENIES |
|---|---|---|---|---|---|---|---|---|
| | | ♀ | | ♂ | | | | ♀:♂ |
| | | + | *n* | + | *n* | *s* | *ns* | |
| A. | | | | | | | | |
| | 4267- 1 | 0 | 0 | 0 | 4 | 17 | 2? | |
| | 4267- 2 | 67 | 0 | 0 | 0 | 0 | 1? | |
| ♀ from 4108-4 by *n*♂ | 4267- 4 | 112 | 0 | 0 | 0 | 0 | 0 | 4:1 |
| | 4267- 5 | 69 | 0 | 0 | 0 | 2 | 0 | |
| | 4267- 8 | 13 | 0 | 0 | 0 | 0 | 0 | |
| | 4245- 2 | 0 | 0 | 1 | 43 | 90 | 0 | |
| | 4246- 1 | 128 | 0 | 0 | 0 | 1 | 0 | |
| | 4246- 2 | 0 | 0 | 0 | 56 | 80 | 0 | |
| | 4246- 3 | 192 | 0 | 0 | 0 | 0 | 0 | |
| | 4247- 1 | 108 | 0 | 0 | 0 | 0 | 0 | |
| | 4247- 2 | 2 | 0 | 0 | 30 | 51 | 0 | |
| | 4247- 3 | 0 | 0 | 0 | 12 | 27 | 0 | |
| | 4247- 4 | 38 | 0 | 0 | 0 | 0 | 0 | |
| | 4247- 5 | 76 | 0 | 0 | 0 | 1 | 0 | |
| | 4247- 6 | 0 | 0 | 0 | 20 | 49 | 2? | |
| | 4247- 7 | 53 | 0 | 0 | 0 | 0 | 0 | |
| | 4247- 8 | 111 | 0 | 0 | 0 | 0 | 0 | |
| | 4247- 9 | 0 | 0 | 0 | 29 | 50 | 0 | |
| ♀ from 4108-6 by *n*♂ | 4247-10 | 0 | 0 | 1 | 67 | 78 | 0 | 15:13 |
| | 4247-11 | 138 | 0 | 0 | 0 | 0 | 0 | |
| | 4285- 5 | 101 | 0 | 0 | 0 | 0 | 0 | |
| | 4285- 6 | 0 | 0 | 0 | 7 | 25 | 2? | |
| | 4285- 7 | 83 | 0 | 0 | 0 | 0 | 0 | |
| | 4285- 8 | 0 | 0 | 0 | 8 | 26 | 0 | |
| | 4285-10 | 0 | 0 | 0 | 16 | 24 | 10? | |
| | 4285-11 | 0 | 0 | 0 | 14 | 26 | 2? | |
| | 4285-12 | 70 | 0 | 0 | 0 | 0 | 0 | |
| | 4285-13 | 0 | 0 | 0 | 17 | 33 | 0 | |
| | 4285-14 | 78 | 0 | 0 | 0 | 0 | 0 | |
| | 4285-16 | 84 | 0 | 0 | 0 | 1 | 0 | |
| | 4289- 2 | 0 | 0 | 0 | 39 | 63 | 3? | |
| | 4289- 4 | 35 | 0 | 0 | 0 | 0 | 0 | |
| | 4292 | 50± | 0 | 0 | 0 | 0 | 0 | |
| B. | | | | | | | | |
| | 4264 | 80 | 38 | 0 | 0 | 0 | 0 | |
| + ♀ from 4136-1 by *n*♂ | 4281 | 6 | 2 | 0 | 1 | 0 | 0 | 3:0 |
| | 4291 | 18 | 13 | 0 | 0 | 0 | 0 | |

TABLE 9 (*continued*)

| MATING | CULTURE NUMBER | OFFSPRING | | | | | | TOTAL PROGENIES |
|---|---|---|---|---|---|---|---|---|
| | | ♀ | | ♂ | | | | ♀:♂ |
| | | + | *n* | + | *n* | *s* | *ns* | |
| + ♀ from 4136-1 by +♂ | 4295-1 | 125± | 0 | 0 | 0 | 0 | 0 | 7:0 |
| | 4295-2 | 100± | 0 | 0 | 0 | 0 | 0 | |
| | 4295-3 | 28 | 0 | 0 | 0 | 0 | 0 | |
| | 4295-4 | 50± | 0 | 0 | 0 | 0 | 0 | |
| | 4295-5 | 100± | 0 | 0 | 0 | 0 | 0 | |
| | 4295-6 | 50± | 0 | 0 | 0 | 0 | 0 | |
| | 4295-7 | 150± | 0 | 0 | 0 | 0 | 0 | |
| + ♀ from 4136-1 by *s*♂ | 4352 | 50± | 0 | 0 | 0 | 0 | 0 | |
| *n* ♀ from 4136-1 by ?♂ | 4317-1 | 0 | 0 | 0 | 10 | 0 | 0 | 0:3 |
| | 4317-2 | 0 | 0 | 0 | 10 | 0 | 0 | |
| | 4317-3 | 0 | 0 | 0 | 13 | 0 | 0 | |
| *n* ♀ from 4136-1 by +♂ | 4294-1 | 0 | 0 | 0 | 40 | 0 | 0 | 0:2 |
| | 4294-2 | 0 | 0 | 0 | 54 | 0 | 0 | |
| + ♀ from 4136-3 by *n* and +♂♂ | 4269 | 100± | 0 | 0 | 0 | 0 | 0 | 15:0 |
| | 4299-1 | 30 | 0 | 0 | 0 | 0 | 0 | |
| | 4299-2 | 200± | 0 | 0 | 0 | 0 | 0 | |
| | 4299-3 | 200± | 0 | 0 | 0 | 0 | 0 | |
| | 4299-4 | 200± | 0 | 0 | 0 | 0 | 0 | |
| | 4299-5 | 100± | 0 | 0 | 0 | 0 | 0 | |
| | 4315-1 | 43 | 0 | 0 | 0 | 0 | 0 | |
| | 4315-2 | 89 | 0 | 0 | 0 | 0 | 0 | |
| | 4315-3 | 18 | 0 | 4 | 0 | 0 | 0 | |
| | 4315-4 | 105 | 0 | 0 | 0 | 0 | 0 | |
| | 4315-5 | 92 | 0 | 0 | 0 | 0 | 0 | |
| | 4315-6 | 128 | 0 | 0 | 0 | 0 | 0 | |
| | 4315-7 | 30 | 0 | 0 | 0 | 0 | 0 | |
| | 4315-8 | 100 | 0 | 0 | 0 | 0 | 0 | |
| | 4315-9 | 125± | 0 | 0 | 0 | 0 | 0 | |
| + ♀ from 4136-3 by +♂ | 4282-1 | 75 | 0 | 0 | 0 | 0 | 0 | 2:0 |
| | 4282-2 | 86 | 0 | 0 | 0 | 0 | 0 | |
| *n* ♀ from 4136-3 by *n* and +♂♂ | 4313-3 | 19 | 0 | 0 | 30 | 0 | 0 | 0:4 |
| | 4313-4 | 0 | 0 | 0 | 12 | 0 | 0 | |
| | 4313-5 | 0 | 0 | 0 | 24 | 0 | 0 | |
| | 4313-6 | 0 | 0 | 0 | 55 | 0 | 0 | |

* The source of the mother and the genetic constitution of the father are given in column one of the table.

heterozygous for swollen but not for narrow (X′X*s*) and half male-producers heterozygous for both swollen and narrow (X*s*X*n*). If any of the former carried narrow they should give some narrow daughters, and if any of the latter failed to carry either narrow or swollen the corresponding class of sons should be absent. The results are: 19 female progenies, all wild-type aside from the few expected "exceptional" swollen sons; and 14 male progenies, all of which consist of narrow and swollen males together with a few "crossover" individuals. Those classified as "*n s* ?" are probably all merely swollen, not narrow (see below under linkage).

From the second series of matings of $F_1$ females (4136 series in table 8B) both wild-type and narrow daughters were obtained, as expected. The former should be female-producers and the latter male-producers. Thirty-seven were tested, with the expected results, as shown in table 9B. Most of the matings were to wild-type males. In the three cases where female progenies were sired by narrow males both wild-type and narrow daughters were obtained, as expected. In the case of culture 4313–3 where 19 females and 30 males were secured it is possible that two mothers were accidentally put together, although the females probably were true "exceptional" individuals. Seven were mated to test this feature, but only one gave offspring. She gave wild-type and narrow males as would be expected if she were "exceptional."

From two of the progenies just considered, in which both wild-type and narrow females were secured (4264 and 4281) a few additional matings were made. The narrow females gave no offspring. The wild-type matings are summarized in table 10. Five of these are pair matings and one (4476) a mass mating, in which, judging by the large count, at least two females

TABLE 10

*Tests of heterozygous sisters of narrow females (see text).*

| MATING | CULTURE NUMBER | OFFSPRING ♀ + | OFFSPRING ♀ *n* | OFFSPRING ♂ + | OFFSPRING ♂ *n* | TOTAL PROGENIES ♀:♂ |
|---|---|---|---|---|---|---|
| ♀ from 4264 by *s* ♂ | 4459–1 | 50± | 0 | 0 | 0 | 3:0 |
| | 4459–2 | 50± | 0 | 0 | 0 | |
| | 4468–2 | 50± | 0 | 0 | 0 | |
| ♀ (mass) from 4264 by *n*♂ | 4476 | 135 | 93 | 0 | 1 | 1:0 |
| ♀ from 4281 by *n*♂ | 4473–1 | 82 | 38 | 0 | 0 | 2:0 |
| | 4473–2 | 76 | 39 | 0 | 0 | |

gave offspring. All of the females were female-producers as expected, and in the three cases where matings were made to narrow males the offspring included both wild-type and narrow as expected.

Another series of experiments (4061 line) involved both narrow and swollen. Here a female-producing female heterozygous for swollen, from swollen "stock," was mated to a narrow male (or males?). The $F_1$ consisted of 16 wild-type females. These were mated singly to narrow or swollen males, with the results shown in table 11, which is divided into two parts to separate female from male progenies. The type of parent male used in each mating is shown in the second column. As expected, the females proved to be of two types, half female-producers heterozygous for narrow,[7] and half male-producers heterozygous for both narrow and swollen.

TABLE 11

*Tests of daughters from heterozygous female* $\frac{X'}{Xs}$ *by narrow male* $\frac{Xn}{Y}$ *(4061 line).*

| A. ♀—PROGENIES | | | | | | | B. ♂—PROGENIES | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Source of ♀ | Parent ♂ | Offspring | | | | Culture Number | Source of ♀ | Parent ♂ | Offspring | | | | | | | Culture Number |
| | | ♀ | | ♂ | | | | | ♀ | | | ♂ | | | | |
| | | + | *n* | + | *n* | | | | + | *n* | *s* | + | *n* | *s* | *ns* | |
| 4061 | *n* | 64 | 14 | 0 | 0 | 4231- 2 | 4061 | *n* | 1 | 1 | 0 | 0 | 21 | 53 | 0 | 4231-1 |
| 4061 | *n* | 55 | 39 | 1 | 1 | 4231- 4 | 4061 | *n* | 1 | 0 | 0 | 2 | 3 | 24 | 0 | 4231-3 |
| 4061 | *n* | 46 | 16 | 0 | 0 | 4237- 2 | 4061 | *n* | 2 | 0 | 0 | 0 | 26 | 55 | 0 | 4237-3 |
| 4061 | *n* | 38 | 10 | 0 | 0 | 4237- 5 | 4061 | *n* | 0 | 0 | 0 | 0 | 8 | 14 | 0 | 4237-4 |
| 4061 | *n* | 60 | 19 | 0 | 0 | 4237- 6 | | | | | | | | | | |
| 4061 | *s* | 64 | 0 | 0 | 0 | 4239- 7 | 4061 | *s* | 0 | 1 | 0 | 1 | 32 | 45 | 0 | 4239-1 |
| 4061 | *s* | 96 | 0 | 0 | 0 | 4239- 9 | 4061 | *s* | 1 | 0 | 0 | 1 | 5 | 47 | 0 | 4239-2 |
| 4061 | *s* | 66 | 0 | 0 | 0 | 4239-10 | 4061 | *s* | 0 | 0 | 0 | 0 | 18 | 27 | 0 | 4239-3 |
| | | | | | | | 4061 | *s* | 2 | 0 | 3 | 0 | 37 | 65 | 2 | 4239-8 |

From the female progenies wild-type and narrow sisters were tested. The former should be female-producers and be heterozygous for narrow ($X'Xn$). They were, therefore, mated to narrow males, with one exception. As shown in table 12 they proved to be of the expected constitution. Only two of the narrow females gave offspring. One gave four and the other thirteen sons, all narrow as expected.

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[7] Three of these were mated to swollen males and consequently did not reveal their heterozygous constitution.

TABLE 12

*Tests of* $\frac{X'}{Xn}$ *females (4061 line).*

| SOURCE OF ♀ | PARENT ♂ | OFFSPRING ♀ + | OFFSPRING ♀ *n* | OFFSPRING ♂ + | OFFSPRING ♂ *n* | CULTURE NUMBER |
|---|---|---|---|---|---|---|
| 4231-2 | + | 36 | 0 | 0 | 0 | 4451 |
| 4237-5 | *n* | 37 | 18 | 0 | 0 | 4407 |
| 4237-5 | *n* | 30 | 13 | 0 | 0 | 4421-1 |
| 4237-5 | *n* | 84 | 33 | 0 | 0 | 4421-2 |
| 4237-5 | *n* | 22 | 6 | 0 | 0 | 4421-3 |
| 4237-5 | *n* | 68 | 28 | 0 | 0 | 4421-5 |
| 4237-5 | *n* | 63 | 40 | 0 | 1 | 4421-6 |
| 4237-5 | *n* | 19 | 7 | 0 | 0 | 4421-7 |
| 4237-6 | *n* | 47 | 26 | 0 | 1 | 4423-2 |
| 4237-6 | *n* | 99 | 63 | 0 | 0 | 4423-3 |
| 4237-6 | *n* | 94 | 58 | 0 | 1 | 4423-4 |

## LINKAGE OF SWOLLEN AND NARROW

It will be seen from the data presented above (tables 9A and 11B) that narrow and swollen are closely linked. To supplement these records a few additional counts are given in table 13. For present purposes the exact amount of crossing over between the two is not especially important. The significant fact is that crossing over does occur, and with sufficient frequency to make it readily detected. The evidence for this conclusion will be considered in detail because of its bearing on the features considered in the following section. Since the crossover classes are both small, and since irregularities in chromosome behavior are evidently frequent in this material, it is particularly necessary to make sure that the flies in these classes

TABLE 13

*Tests of* $\frac{Xn}{Xs}$ *females by narrow and swollen males.*

| CULTURE NUMBER | OFFSPRING ♀ + | OFFSPRING ♀ *n* | OFFSPRING ♂ + | OFFSPRING ♂ *n* | OFFSPRING ♂ *s* | OFFSPRING ♂ *ns* |
|---|---|---|---|---|---|---|
| 4437 | 0 | 0 | 4 | 20 | 42 | 1 |
| 4444-1 | 0 | 0 | 1 | 14 | 35 | 7? |
| 4472-3 | 0 | 0 | 0 | 32 | 42 | 0 |

are not due to such irregularities. As noted in considering the inheritance of swollen alone, a male appears occasionally which evidently received his X-chromosome from his father. This casts some doubt on the origin of wild-type males wherever the father is wild-type. Consequently in the matings under consideration only narrow or swollen males have been used. It seems certain, therefore, that the flies recorded in the wild-type crossover class are actually due to crossing over. The only other obvious possibilities are contamination, reverse mutation or mistakes in classification. Since the characters swollen and narrow are both readily distinguished from wild-type in males, and since particular attention was given to the classification here, the latter possibility may be ruled out. That contamination is not responsible seems certain for three reasons (1) because of the methods used, (2) because similar results are not found in other experiments and (3) particularly because of the presence of the reciprocal crossover class, which cannot be due to contamination. The last two reasons apply with equal force to the possibility of reverse mutation and, in our opinion, effectively eliminate this as a causal factor here.

In considering the narrow swollen crossover class it is to be observed first that the double recessive males here (females of this sort are, of course, not obtained) have very poor viability and have all failed to breed. As a consequence it has not been possible to make the reciprocal type of matings involving narrow and swollen in the same chromosome. Likewise in considering the narrow swollen crossover class, it will be observed that most of the records in this class are followed by a query (?). Flies thus designated were swollen, but had their wings incompletely expanded or otherwise affected in such a way as to resemble narrow or to prevent the detection of narrow. A few of them may have been narrow, but most of them must have been merely swollen. On the other hand a few unquestionable narrow swollen flies were secured and most, if not all, cases so recorded are of this type.

Taking the tables as they stand, and omitting the few questionable individuals just considered, we find a total of 1486 non-crossover to 8 crossover individuals, or a crossover frequency of approximately 0.5 percent. This value is probably too small, due to the extreme inviability of narrow swollen flies. A better calculation may be that based on only the wild-type and swollen classes, which gives 0.62 percent.

## SEX LINKED INHERITANCE OF "SEX OF PROGENY"

It is evident throughout the experiments considered in this paper that "sex of progeny" is inherited as a distinct character, that it is sex linked, and that it is determined by the sex chromosome constitution of the mother, irrespective of the male parent. It is also seen that the difference between the two types of mothers in this respect is a definite and constant one. The two sex chromosomes of the male-producing female are essentially alike in constitution and origin and are interchangeable. One is derived directly from the father and the other indirectly from the maternal grandfather. Those of the female-producing female, on the other hand, are unlike in both make-up and derivation and are not interchangeable. One comes from the father and is like those in the male-producer; the other comes from the mother, grandmother, etc., in a direct female line of descent, without having passed through either a male-producing female or a male (ordinarily).[8] The difference between this latter chromosome (X′) and the ordinary X, represents at least the differential responsible for determining sex of progeny, in accordance with the scheme shown in figure 1.

## POSSIBLE ABSENCE OF CROSSING OVER BETWEEN X′ AND X

At the present time it is too early to attempt a detailed comparison between X′ and X. We know that these two chromosomes differ in respect to the differential responsible for sex of progeny. But in the absence of crossing over between the two (see below) we do not know whether this differential is a single gene or a complex of genes; nor do we know whether the difference in this respect constitutes the sole difference between the two chromosomes. On the other hand, several significant lines of evidence have been obtained which bear on the relation between these chromosomes and serve at least to limit the possibilities. These are summarized below in two categories—those indicating resemblances and those indicating differences. Particular consideration is given to the crossing over relationships.

### *Indications of similarity*

It has been possible, thus far, to identify five combinations of sex chromosomes in this material, namely, XX, X′X, X′X′, XY and X′Y.[9] The first three of these produce females and the last two males. The three kinds of females appear to be indistinguishable somatically. Similarly the two kinds of males look alike, at least in general morphological features. All five types are viable and fertile. It appears, therefore, that X′ can be substituted for X in any combination without noticeable effect on the external characteristics or viability of the fly. From this we infer that X and X′ are

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[8] See discussion of exceptional X′ males in next section.

[9] The combinations X′Y and X′X′ are derived rarely, as considered elsewhere (METZ and SCHMUCK 1929).

fundamentally alike and that their genic constitutions are much more nearly the same than, for example, those of X and Y.

Further support for this view is given by the evidence presented above showing that X′ carries the normal allelomorphs of the two mutant genes thus far found in X.

### *Indications of dissimilarity*

Contrasted with the above, and possibly equally significant, is the fact that in using the two mutant genes just mentioned we have been unable to detect any crossing over between X and X′, and have, in consequence, been unable to get either gene transferred from X to X′. The weight of this evidence is, of course, influenced by the fact that the two genes (swollen and narrow) are closely linked and show only a small amount of crossing over in XX females.

If we assume that sex of progeny is "determined" by a single gene (pair) we may consider the linkage relations between this gene and the genes for swollen and narrow. Should the locus of the former not lie between the loci of swollen and narrow on the chromosome then it should cross over more freely with one of the latter than these two do with one another—providing the rate of crossing over between X and X′ were the same as between X and X. On the other hand, if the gene for sex of progeny lay between the loci of swollen and narrow the reverse should be true. In this case, however, the frequency of crossing over with one of the latter two genes should be at least half that between the two (swollen and narrow) alone. Such a frequency (probably not over 0.5 percent) would obviously be difficult to detect in the present case.

However, it is to be observed that in addition to using swollen and narrow in pair matings as noted above, both characters have been used in mass matings on a large scale. These latter have served both as experiments and for the purpose of keeping stock. Where swollen is involved, for example, each culture received swollen males, swollen male-producing females and heterozygous female-producing females. Thus all the X chromosomes carry swollen, and as long as swollen does not cross over into the X′ chromosome the stock is self perpetuating. If such crossing over should occur, however, it would be manifest by the presence of wild-type males or swollen female-producing females in large numbers. In the case of narrow any such crossing over would be shown in the same way.

It is difficult to estimate how many flies have been tested in this manner, but the numbers must be large, particularly in the case of swollen, which has thus been under observation for fifteen generations or more. If the (hypothetical) gene for sex of progeny were "located" very close to that for swollen it is possible that crossing over between X′ and X might occur as frequently as between X and X without having been detected in our experiments. In any other position, however, such a frequency should have been detected.

As the evidence stands it suggests that either X and X′ differ in respect to more than one gene, or else this gene influences not only sex of progeny but also the synaptic behavior of the sex chromosomes—reducing or eliminating crossovers between X and X′. However, a study of additional mutant characters will probably be required to clear up this point, for it is possible that the general rate of crossing over in this material is low, as compared, for example, with that in Drosophila, and that genes actually far apart on the chromosome show close linkage.

At present only one other feature calls for comment. This is the widespread distribution throughout the genus Sciara of the characteristics found in the present species,[10] that is, production of unisexual progenies and presence of two types of females presumably differentiated by X and X′ chromosomes. Such evidence tends to emphasize the relative stability of the distinction between X and X′, whatever its magnitude.

## DISCUSSION

The numerous genetic and cytological peculiarities in Sciara obviously invite speculation and comparison—particularly speculation as to the mode of origin and phylogenetic significance of the principal features. In our papers, however, we have endeavored to avoid considerations of this kind, so far as possible, in the belief that they would be of little value until more evidence is available. We still hold to this belief and consequently limit the present discussion to a few topics. Most of the special aspects have been discussed above under the separate headings or in the Introduction.

So far as we are aware no parallel to the processes of sex determination in Sciara has been recorded among other organisms. Unisexual progenies are well known in various groups of animals, such as Nematodes, Rotifers, Daphnids, Aphids, Phylloxerans, Coccids, etc.,[11] but in these groups the unisexual type of progeny is connected with such phenomena as parthenogenesis, gynogenesis[12] and alternation of generations, none of which is found in Sciara. A more nearly comparable case may be that recently recorded

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[10] Compare METZ 1928.

[11] Conditions in these groups have been reviewed frequently and exhaustively. See especially SCHRADER 1928, WILSON 1925, SHULL 1929, GOLDSCHMIDT 1923 and BELAR 1928.

[12] See WILSON 1925 and BELAR 1928.

by BARNES (1929) in the gall midge *Rhabdophaga heterobia* H. Lw. Here unisexual families are found and a case is recorded in which sister females gave progenies of opposite sexes. It is not yet known, however, which parent is responsible for the sex of the progeny or how the unisexuality is brought about. Should it be found that the phenomena here are fundamentally like those in Sciara it would suggest that the condition is widespread among the lower Diptera.

As regards selective fertilization, any discussion or conclusions must be tentative, for it has not been possible to prove directly that such a process occurs here, and one alternative possibility has been specifically outlined (METZ 1930). If we consider the present indirect evidence conclusive, however, it is of interest to compare conditions here with those in other organisms, and also to consider their mode of origin.

Numerous cases have been described in which one type of sperm appears to be more effective than the other,[13] but in none of these, so far as we are aware, are there regularly two types of sister females exhibiting selective fertilization of opposite types and almost one hundred percent efficiency.

These two types of females, and of selective fertilization, in Sciara present a particularly interesting problem. If only one type of selective fertilization were present it would be simple to postulate the occurrence of a mutation in the X chromosome which produced the effect; but the origin of two opposite types in the same material is not so readily accounted for. It is difficult to conceive of the two arising simultaneously. It would seem more probable that they arose through a succession of steps. If so, the difference between the two types of females might well involve more than one pair of genes.

In respect to the sex chromosomes themselves, it seems probable that we are dealing with a modification of the ordinary XX–XY mechanism, although the extent of the modification cannot be determined at present. The widespread distribution of the X′ chromosome throughout the genus, as noted above, indicates that the condition has been in existence a long time. Any consideration of its origin, however, is complicated by other features, especially the presence of the large "androsomes" or "male-limited" chromosomes, whose behavior suggests that they have at some time been directly concerned with sex determination (see Addendum).

## SUMMARY

See last six paragraphs of the Introduction and concluding paragraph of the Discussion.

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[13] See reviews by KING 1929 and by JONES 1928.

## ADDENDUM

After the manuscript of this paper was sent to press additional cytological evidence was obtained which may throw a new light on the problems discussed above. This evidence indicates that the so-called "androsomes" or "male-limited" chromosomes may be present in the *germ line* of both sexes, but not in the soma of either sex. It also indicates that in the *male* one sex chromosome is eliminated from the soma at an early stage, and that this process of elimination may be concerned with sex determination. A preliminary note on this subject is in press in the *Biologische Zentralblatt.*

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