NEW MUTANTS IN SCIARA AND THEIR GENETIC BEHAVIOR

H. V. CROUSE AND HELEN SMITH-STOCKING
Department of Embryology, Carnegie Institution of Washington, Baltimore, Maryland

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THE present paper deals with six new mutant characters in Sciara found in this laboratory. In addition, two mutants are recorded which appear to be identical with or allelic to two of these characters. Of the six, one is an autosomal dominant in *Sciara coprophila* Lintner, and one a sex-linked recessive in *Sciara ocellaris* Comstock. The remaining four, including one autosomal dominant, two sex-linked dominants, and one sex-linked recessive, are in *Sciara reynoldsi* Metz (METZ, in press). Selective segregation of chromosomes has previously been established in three species of Sciara (METZ 1926, 1928, 1929). The present paper establishes selective segregation in two other species; namely, *S. ocellaris* and *S. reynoldsi.*

The dominant characters were found by the second author among the descendants of flies which had been exposed to radium. The radiation was done at the Howard A. Kelly Hospital in Baltimore through the kindness of Dr. FRED WEST, to whom we are greatly indebted. Whether the mutations were produced as a result of the radiation cannot be stated definitely,

TABLE 1

Linkage data for the character "Stop" in S. coprophila.

TEST	CASES	TOTAL FLIES	CLASSIFICATION OF FLIES				PERCENTAGE OF CROSSING OVER
			D	*F*	*DF*	+	
D×*F*	16	1177	297	279	301	300	Not linked
			S	*C*	*SC*	+	
S×*C*	9	405	109	73	80	143	Not linked
			S	*F*	*SF*	+	
S×*F*	18	688	338	349	1	0	0.15
			S	*Dl*	*SDl*	+	
S×*Dl*	32	1160	587	570	1	2	0.26
			S	*B*	*SB*	+	
S×*B*	22	852	445	404	0	3	0.35
			S	*D*	*SD*	+	
S×*D*	12	393	152	190	21	30	12.98
			S	*tr*	*Str*	+	
S×*tr*	24	1357	563	414	183	197	28.00

since Sciara has proved to be very resistant to radiation. Since the characters are dominants, it seems probable that some of them, at least, were produced at the time of radiation. Otherwise, they should have appeared previously in the stock cultures.

The sex-linked recessive in *S. reynoldsi* was found by the first author, and the genetical tests, analyses, and descriptions presented here (with the exception of the sex-linked recessive in *S. ocellaris*, which was found and analyzed by Mrs. E. GAY LAWRENCE) are by the first author.

I. *The mutant character Stop in S. coprophila*

a) *Origin.* Stop is an autosomal dominant which was found on February 20, 1936, in a female, the mother of which had been treated with 8 gm. hrs. of radium.

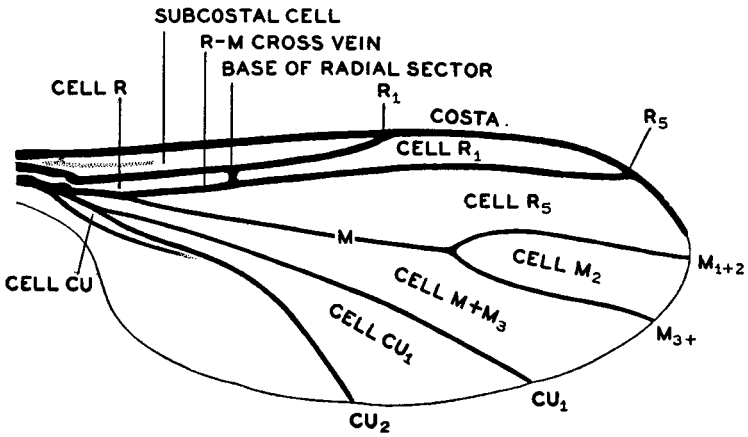

FIGURE 1. Diagram of normal Sciara wing. Terminology after Johannsen. R1, first branch of radius; Rs, posterior branch of radius; M, media; M1+2, anterior branch of media; M3+, posterior branch of media; Cu1, anterior branch of cubitus; Cu2, posterior branch of cubitus.

b) *Description.* In the Stop wing (see fig. 1 for diagram of normal Sciara wing) the posterior branch of the radius vein and the anterior and posterior branches of the media vein end before they reach the wing margin. Stop is a clear-cut and constant character, which can be recognized easily in crosses that involve other wing characters. Stop flies exhibit excellent viability as shown by the fact that heterozygous Stop females crossed to wild type males give progenies which closely approximate a 1:1 ratio. Seven pair matings of this type selected at random gave 132 wild type to 118 Stop flies.

c) *Genetic behavior of males.* The transmission of Stop through males follows the typical Sciara pattern, that is, males transmit only the genes derived from their mothers. From crosses of wild type virgin females to

Stop males which received Stop from their mothers, the offspring are all Stop. On the other hand, the offspring from crosses of wild type virgin females to Stop males which received Stop from their fathers, are all wild type.

d) *Linkage.* Genetic tests, corroborated by cytological observations, as shown below, indicate that Stop involves a translocation between chromosomes II and IV.

Crosses of virgin wild type females to Stop males (which received Stop from their mother) revealed that Stop was not sex-linked. If it were sex-linked, the F_1 males from such a cross would all be wild type, since the paternal X is eliminated from the soma cells in the male at about the eighth cleavage division (DUBOIS 1933). The F_1 males from such a cross, however, are all Stop, indicating that the Stop character is an autosomal dominant. Three autosomal linkage groups have been identified in *S. coprophila* (SMITH-STOCKING 1936): chromosome II, with the characters *truncate* and *Dash;* chromosome III, with the *Curly* character; and chromosome IV, with *Blister*, *Delta*, and *Fused.*

(1) *Tests with Chromosome III:* Stop×Curly (*S*×*C*). Tests summarized in table 1 show that Stop is not in Chromosome III.

(2) *Tests with Chromosome IV:* Stop×Fused (*S*×*F*). The data, given in table 1, indicate that Stop is "in" chromosome IV and closely linked to Fused.

Stop×Delta (*S*×*Dl*), and Stop×Blister (*S*×*B*). Similarly, Stop was found to be linked to Delta and Blister. From table 1 we find the crossover value between Stop and Delta to be 0.26 percent, while that between Stop and Blister is 0.35 percent. Delta and Blister are probably alleles. SMITH-STOCKING (1936) reports 6.9 percent crossing over between Delta and Fused and 7.0 percent crossing over between Blister and Fused.

(3) *Tests with Chromosome II:* Stop×Dash (*S*×*D*). Crosses between Stop and Dash revealed that Stop is linked also to a character in chromosome II. Tests between Stop and Dash gave a crossover value of 12.98 percent between Stop and Dash. The question arose as to whether Dash was really in a linkage group distinct from Blister, Delta, and Fused. SMITH-STOCKING'S report (1936) gives clear-cut evidence that neither Blister nor Delta is linked to Dash; however, no direct tests between Fused and Dash are recorded. In order to clarify this point, tests were made between Dash and Fused. Classifying the offspring from these crosses was somewhat complicated since Fused obliterates one of the characteristic effects of the Dash gene, that is, the "Dash" vein situated between the anterior and posterior branches of the cubitus vein. However, Fused does not obliterate the brownish marking along the posterior branch of the radius which is also a characteristic effect of Dash. The tests be-

tween Dash and Fused indicate definitely that Dash and Fused are located in different chromosomes.

Stop×truncate (*S*×*tr*). Tests between Stop and truncate gave further proof that Stop is linked to characters in chromosome II as well as to those in chromosome IV. Such tests gave a crossover value of 28 percent between Stop and truncate.

e) *Conclusion.* In view of the genetic evidence presented above, Stop is believed to be due to (or accompanied by) a translocation between chromosomes II and IV. Cytological examination of the salivary gland chromosomes of heterozygous Stop flies shows that there is a translocation between two of the four pairs of synapsed somatic chromosomes. This translocation makes it possible to identify cytologically the four linkage groups in *S. coprophila;* the translocation distinguishes chromosomes II and IV, and the X chromosome is distinguishable from chromosome III by its unpaired condition in the male soma (that is, in salivary gland cells).

The Stop translocation apparently affects crossing over in both chromosomes, II and IV. In chromosome IV SMITH-STOCKING (1936) found 6.9 percent crossing over between Delta and Fused and 7.0 percent crossing over between Blister and Fused. From table 1 we find the crossover value between Stop and Fused to be 0.15 percent, between Stop and Delta 0.26 percent, and between Stop and Blister 0.35 percent. It appears, therefore, that the Stop translocation cuts down crossing over in chromosome IV. On the other hand, Stop apparently increases crossing over in chromosome II, since the crossover value between Stop and Dash is 12.98 percent and that between Stop and truncate 28 percent; while the crossover value between truncate and Dash reported by SMITH-STOCKING (1936) is only 2.8 percent.

II. The mutant character "yellow" in S. ocellaris

a) *Origin.* A yellow male was found in a normal wild type culture of *Sciara ocellaris* on February 11, 1935 by Mrs. E. GAY LAWRENCE.

b) *Description.* Yellow is a body color which extends to most parts of the fly except the eyes and bristles. It is clear-cut and constant and can be readily distinguished from wild type.

c) *Genetic behavior.* Yellow behaves as a sex-linked recessive (first analyzed by Mrs. E. G. LAWRENCE). Yellow females from the monogenic strain give either male or female families (a few "exceptional" males and females are found). Thus, if a yellow female-producing female is mated to wild type males, all of her daughters should be phenotypically wild type. On the other hand, if a yellow male-producing female is mated to wild type males, all of her sons should be yellow, since the paternal sex chromosome is normally eliminated from the male soma at an early cleav-

age stage (DuBois 1933). However, it may be mentioned here that there are many cases of irregular sex-chromosome elimination in this yellow strain (unpublished data of Mrs. E. Gay Lawrence and of Crouse). For instance, a number of males have been found which retained the paternal sex chromosome in their soma instead of the maternal sex chromosome.[1] Normally Sciara males transmit only those characters which are maternal in origin. An attempt has been made to determine whether these irregular males which retain the paternal sex chromosome in the soma line transmit this chromosome, but all such males tested have proved to be sterile.

III. Mutant characters in S. reynoldsi

1. Puff

a) *Origin.* Puff is an autosomal dominant which appeared in a digenic strain of *S. reynoldsi.* It was found on January 4, 1936 in a male, the mother of which had been treated with 5 grm. hrs. of radium.

b) *Description and genetic behavior.* Puff is very similar to the character "Blister" in *S. coprophila.* It appears as a blister or vesicle at the juncture of the posterior and anterior branches of the media vein. The Puff character is variable; it ranges all the way from a large blister to a slight swelling, and in some cases overlaps normal. Fifteen pair matings of Puff females × wild type males, selected at random, gave the following offspring: 294 wild type females, 204 Puff females, 283 wild type males, 165 Puff males, that is, approximately 63 offspring per female. On the other hand, fifteen pair matings selected at random of wild type females by wild type males gave 515 females and 903 males in the F_1, that is, approximately 95 offspring per female.

Homozygous Puff females have never been found. Puff females derived from the cross, Puff female × Puff male (Puff from mother), have all proved to be heterozygous. Apparently, therefore, Puff is lethal in homozygous condition. The transmission of Puff through the male line agrees with that of other characters in Sciara. Puff males which receive the character from their mother transmit it to all their offspring, whereas Puff males which receive Puff from their father do not transmit it at all.

2. Vesiculated

a) *Origin.* A Vesiculated female was found on January 6, 1936 in a digenic culture of *S. reynoldsi.* The parents of this Vesiculated fly had been exposed to 3 grm. hrs. of radium.

[1] Such irregular elimination does not appear to be associated with the yellow locus itself, since the paternal sex chromosome retained in some cases has carried yellow and in other cases its normal allele.

b) *Description and genetic behavior.* In appearance, Vesiculated is identical with Puff; it is likewise variable, ranging all the way from a large blister to a normal juncture of the posterior and anterior branches of the media vein. Like Puff, Vesiculated is lethal in homozygous condition. However, it is much less viable when heterozygous. From ten pair matings selected at random of Vesiculated females × wild type males, there were 123 wild type females, 72 Vesiculated females, 64 wild type males, and 35 Vesiculated males in the F_1, that is, approximately 29 offspring per female. To determine whether Puff and Vesiculated are alleles is practically impossible, since the two characters are so similar. However, Puff females were mated to Vesiculated males (the reciprocal cross was made also) and all of the F_1 females backcrossed to wild type. Without exception, each mating gave two types of offspring: wild type and Puff (or Vesiculated?). That is, in no case were Puff and Vesiculated obtained in the same fly. This fact, together with the fact that neither Puff nor Vesiculated has been found in homozygous condition, suggests that the two characters are allelic or perhaps identical. The considerable difference in viability makes it probable that they are not identical.

3. Jagged and Jagged-2

a) *Origin.* A Jagged female appeared in a digenic culture of *S. reynoldsi* on January 6, 1936. Its parents had been treated with 5 grm. hrs. of radium.

b) *Description.* The Jagged character appears as nicks or incisions along the wing margin between the posterior branch of the cubitus vein and the anterior branch of the media vein. The position and number (usually one or two) of these marginal nicks are somewhat variable, and in some instances the Jagged character is detectable only by missing marginal hairs. Jagged showed poor viability from the time of its origin, and the stock was finally lost.

c) *Genetic behavior.* The first Jagged female found was mated to wild type males. The offspring from this cross fell into three groups: wild type females, Jagged females, and wild type males. During the eighteen months that Jagged was kept in the laboratory, the offspring from Jagged females mated to wild type males always fell into these three groups. No Jagged males ever appeared. This fact indicates that Jagged is a sex-linked dominant which is lethal in homozygous condition, and also lethal in the male where one sex chromosome is present in the soma.

d) *Jagged-2.* On the same day that Jagged appeared, Jagged-2 was found in an F_1 female of the same digenic stock of *S. reynoldsi.* The parents of this J-2 fly had been treated with 5.4 grm. hrs. of radium. The J-2

character proved to be identical with Jagged in appearance, viability, and genetic behavior.

4. Ruffled

a) *Origin.* A Ruffled male was found in January, 1936, in a digenic strain of *S. reynoldsi.* The parents of this male had been treated with 2.9 grm. hrs. of radium.

b) *Description.* In the female heterozygote the wings appear stiff and are characterized by a wave approximately midway of their length. The degree of waviness varies, and in many cases the female heterozygotes are not distinguishable from wild type. On the other hand, the female homozygotes never overlap normal. The wings of these flies are wavy, extremely wrinkled, and have something of the appearance of the wings of newly-hatched imagos. In other words, the wing size, shape, and venation are altered in the female homozygotes. The wing of the Ruffled male seems to occupy a position intermediate between these heterozygotic and homozygotic extremes. The wings are only slightly wrinkled, and the venation can be seen. However, the wave in the wing is distinct, and Ruffled males can always be distinguished from wild type.

c) *Genetic behavior.* Ruffled shows the same type of inheritance as other sex-linked dominants in Sciara.

5. Yellow

a) *Origin.* A yellow Ruffled male was found in a mass culture of Ruffled stock on October 23, 1936 by the first author.

b) *Description.* Yellow in *reynoldsi*, like yellow in *ocellaris*, is a body color which extends to most parts of the fly except the eyes and bristles.

c) *Genetic behavior.* The original yellow Ruffled male was mated to wild type females. The F_1 generation consisted of 60 Ruffled females and 33 wild type males, showing that yellow is a recessive. These Ruffled F_1 females backcrossed to wild type males gave, without exception, four classes of offspring: wild type males, yellow Ruffled males, wild type females, and Ruffled females. Yellow thus behaved as a sex-linked recessive. When these F_2 Ruffled females (carrying yellow) were mated to yellow Ruffled males, yellow Ruffled females, Ruffled females, yellow Ruffled males, and wild type males were obtained. During the twelve months that yellow has been kept in the laboratory, it has always appeared with Ruffled. Evidently little, if any, crossing over occurs between the two loci. Due to the decreased viability of homozygous Ruffled, the stock carrying yellow has to be kept outcrossed. Apparently the yellow gene does not decrease viability, since yellow Ruffled flies are as viable as Ruffled flies.

The fact that *S. ocellaris* and *S. reynoldsi* can be hybridized (METZ and LAWRENCE in press) has made it possible to cross *ocellaris* yellow and *reynoldsi* yellow and to demonstrate that the two genes are alleles.

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SUMMARY

Six new mutants have been found in Sciara, among descendants of radium-treated flies. Stop, an autosomal dominant in *S. coprophila*, involves a translocation between chromosomes II and IV. Yellow is a sex-linked recessive in *S. ocellaris*. Four mutations have been found in *S. reynoldsi:* Puff and Vesiculated, autosomal dominants which are lethal when homozygous and may be allelic or perhaps identical; Jagged, a sex-linked dominant, lethal when homozygous; Ruffled, a sex-linked dominant; and yellow, a sex-linked recessive closely linked to Ruffled.

The yellow mutations of *S. reynoldsi* and *S. ocellaris* are alleles.

The genetic behavior of these characters establishes selective segregation in *S. ocellaris* and *S. reynoldsi.*

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