

VARIATION OF SCUTELLAR BRISTLES IN DROSOPHILA.

III. SEX-DIMORPHISM¹

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THE number of scutellar bristles in unselected wild-type stocks is normally four in both males and females, which contrasts with the marked sex-dimorphism of the number of scutellars in scute stocks. The reduction of scutellar bristle number effected by the scute mutations is greater in males than in females. FRASER (1963) has shown that the frequency of extra scutellar bristles is greater in females than in males, in wild type. He also showed that the frequency of missing scutellar bristles is greater in males than in females, in wild type. These results show that there is a sex-dimorphism of scutellar number in wild type as well as in scute. RENDEL (1959) showed that selection for extra scutellars is more effective in females than in males (see also PAYNE 1918; SISMANIDIS 1942; FRASER (1963); FRASER, SCOWCROFT, NASSAR, ANGELES and BRAVO, in manuscript). There would appear to be a general sex-modification of the expression of scutellar genes which is only obvious when the development of scutellar bristles has been shifted above or below the canalized path leading to four bristles.

The scute locus is located in the left end of the X chromosome, and it is possible that the sex-dimorphism of scutellar number is primarily determined by this locus being present twice in females, and only once in males. The sex-dimorphism may be due to the sex difference of dosage of the scute locus. This can be assayed by adding short sections of the left end of the X chromosome to the Y chromosome. If these short sections of the X chromosome contain sc^+ and sc then comparisons can be made of normal females, with males carrying two sc^+ or sc alleles. Three such duplication Y chromosomes have been studied, and the results are presented and discussed below.

MATERIALS AND METHODS

Since only one scute allele, $scute^1$, was used in our studies, the symbol sc is used in place of sc^1 .

Y chromosomes carrying sc^+ or sc and but few other X chromosome genes were constructed using an attached-XY chromosome recovered by PARKER (1954) and, in principle, methods described by BROSEAU, NICOLETTI, GRELL and LINDSLEY (1961). Synthesis of a Y chromosome marked with γ^2 and sc^+ will serve to illustrate the breeding scheme employed. Males of the genotype $XY^L.Y^S, \gamma^2 su-w^a w^a / Y$ were crossed to attached-X females without a free Y chromosome to produce male progeny also without a free Y chromosome. These males were irradiated with 5000r X rays and crossed to homozygous γ^{59b} females. According to the rules of sex-linked inheritance, all male progeny of this cross should lack a Y chromosome and therefore be sterile. Exceptional fertile males carrying a Y chromosome can occur in at least one of two ways. Non-disjunction in the γ^{59b} females can lead to infrequent $XY^L.Y^S, \gamma^2 su-w^a w^a$ males. Or, deletion

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of most of the X of the XY chromosome should produce male progeny of the genotype $\gamma^{59b}/\gamma^{2sc^+}\cdot Y$. The regular and exceptional males can be readily distinguished from each other phenotypically. In practice the progeny of a moderate number (20 to 40) of crosses of irradiated males by γ^{59b} females were transferred without etherization to fresh media and after an appropriate time-interval, fertile cultures were sought. By this procedure, one $\gamma^{2sc^+}\cdot Y$, three $\gamma^{59b}sc^+\cdot Y$ and one $sc\cdot Y$ chromosomes were found. Genetic tests established that in addition to the marker genes, the $\gamma^{2sc^+}\cdot Y$ and $\gamma^{59b}sc^+\cdot Y$ marked Y chromosomes carry sc^+ and su^+s loci at the left end of the X chromosome while the $sc\cdot Y$ chromosome carries γ^+ and su^+s . Few loci of the right end of the X chromosome are included in these Y chromosomes since genetic tests show none to carry su^+f localized in the X heterochromatin.

Three of the derived Y chromosomes were studied in detail: $\gamma^{2sc^+}\cdot Y$, $\gamma^{59b}sc^+\cdot Y$ and $\gamma^+sc\cdot Y$. These were introduced into a number of wild-type lines which had been selected for extra scutellars, and into one line which had been selected for missing scutellars. These lines are continuations of the selection lines described by FRASER (1963). The introductions were made by the following crosses, where X^S , 2^S , 3^S = selection-line chromosomes, $DpX\cdot Y$ = derived Y chromosome, and $Xa = T(2,3) Xa$.

	Females		Males
(1)	Selection line	×	$DpX\cdot Y$; heterozygous Xa
(2)	Selection line	×	$F_1 X^S/DpX\cdot Y$; 2^S ; $3^S/Xa$
(3)	Selection line	×	$F_2 X^S/DpX\cdot Y$; $2^S/2^S$; $3^S/3^S$

F_3 's were then backcrossed to the selection line for two to three generations, and then maintained by mass mating.

The sc allele was also substituted for the sc^+ allele in a number of the same selection lines. A $\gamma^{2sc} w^a lz^{50ef}$ chromosome was introduced into the selection lines, with a crossover between sc and w^a to minimize the amount of foreign chromosome substituted into the selection lines. The introductions were made by the following crosses. The selection lines contained either w^+ or w^h .

	Females		Males
(1)	Selection line	×	$\gamma^{2sc} w^a lz^{50ef}/Y$; heterozygous Xa
(2)	$F_1 \cdot \gamma^{2sc} w^a lz^{50ef}/\gamma^+sc^+w^h lz^+f^+$; 2^S ; $3^S/Xa$	×	Selection line
(3)	Selection line	×	$F_2 \gamma^{2sc} w^h lz^+f^+/Y$; 2^S ; $3^S/Xa$
(4)	$F_3 \gamma^{2sc} w^h lz^+f^+/\gamma^+sc^+w^h lz^+f^+$; $2^S/2^S$; $3^S/3^S$		

F_3 's were backcrossed to the selection line for five generations, and then maintained by mass mating.

RESULTS

Two counts of scutellar number were made; one within a short time of formation of the stocks, and the other after five to seven generations of mass mating. The frequency distributions of scutellar number are given in Tables 1 and 2 for both the first and second counts. There has been a regression in many lines toward the norm of four scutellars, presumably owing to natural selection acting against the effects of the selection which had been practiced for increased scutellar number (see FRASER *et al.*, in manuscript). The means of scutellar number for the genotypes on the extra-scutellar backgrounds are plotted for various pairs of genotypes in Figure 1. Each point represents the values for a pair of genotypes scored in the same culture. Regression lines have been fitted over all the counts, since the relationship between genotypes was not affected by the decrease of the number of scutellars between the first and second counts.

An obvious feature of these data is that whereas some of the comparisons between genotypes show a positive correlation of the scutellar expression, other comparisons show no such correlation. The positive correlations occur between

TABLE 1

Frequency distributions of scutellar number for cultures containing the named scute genotypes. The number of the selection line into which these genotypes have been substituted is given to the left. Counts made at the time of formation of the stock are listed as (I), and those made after 5-7 generations of mass-matings are listed as (II)

Line	<i>sc⁺/sc⁺</i> females Scutellar number											\bar{x}	<i>sc⁺/y²sc⁺-Y</i> males Scutellar number											\bar{x}
	2	3	4	5	6	7	8	9	10	11	4		5	6	7	8	9	10	11					
1	29	31	27	9	8	1	5.41	..	3	18	14	17	9	8	3	7.75				
II	39	20	6	4	1	2	4.80	2	20	20	19	16	1	3	1	6.57				
4	38	70	26	4.91	14	13	65	28	3	5.94				
I	47	18	6	..	1	4.47	6	14	50	11	3	5.89				
II	53	42	10	4.59	4	8	35	38	13	1	6.51				
6	53	19	2	4.31	12	28	31	1	2	5.36				
I	22	23	30	24	6	2	5.76	..	3	12	21	25	14	7	..	7.68				
II	30	18	16	6	2	1	5.10	2	5	33	17	11	3	3	..	6.68				
15	33	61	42	4	5.12	3	18	35	44	20	5	6.60				
I	12	31	25	5	5.31	2	15	18	24	5	9	6.57				
II	34	43	42	16	4	5.27	..	7	39	42	33	5	3	1	7.02				
18	39	19	10	2	1	4.69	8	13	32	17	3	5.91				
I	103	48	9	4.13	2	33	91	38	9	6.10				
II	46	24	2	4.38	24	28	14	6	5.02				
27	138	45	12	1	1	4.39	36	44	23	10	2	5.11				
I	39	21	10	4.58	18	19	23	11	3	5.48				
II	113	54	7	1	4.35	13	50	83	29	8	5.83				
39	60	13	4.17	20	23	19	8	5.21				
I	123	4	4.03	54	44	20	4.71				

TABLE 1—Continued

Line	sc^+/sc^+ females Scutellar number											$sc^+/y^{298}sc^+Y$ males Scutellar number											\bar{x}					
	2	3	4	5	6	7	8	9	10	11	4	5	6	7	8	9	10	11										
1	I	56	25	14	6	4	5	2	7	40	41	14	11	3	1	..	5.10	5.95
4	II	59	9	4	3	3	21	24	28	2	1	1	1	1	4.47	5.31
	I	39	41	26	1	6	31	60	15	3	4.89	5.80
	II	20	2	32	27	14	2	1	4.33	4.85
6	I	60	45	14	1	10	21	45	31	5	1	4.63	6.02
	II	45	19	11	1	20	26	19	4	4.58	5.06
9	I	21	36	33	17	8	4	1	8	42	38	16	1	2	..	5.75	6.73
	II	33	25	7	5	1	2	4	13	32	4	2	1	1	..	4.93	5.85
15	I	49	40	20	1	14	50	58	26	2	4.75	5.68
	II	17	24	31	2	1	9	16	38	18	2	5.28	5.85
18	I	34	37	20	17	2	1	4	21	59	24	8	1	5.27	6.11
	II	40	27	4	2	17	19	26	3	2	4.56	5.31
21	I	90	11	2	35	36	27	4	1	4.15	5.02
	II	75	3	38	23	13	4	1	4.03	4.82
27	I	89	16	4	1	42	37	21	1	4.25	4.81
	II	45	19	9	39	23	6	3	1	4.39	4.66
39	I	145	18	1	53	43	17	1	1	4.12	4.73
	II	65	8	2	48	18	11	2	4.16	4.58
42	I	110	96	27	3	4.00	4.26
	II	76	75	4.00	4.00

TABLE 1—Continued

Line	I	sc^+/sc^+ females Scutellar number											\bar{x}	sc^+/y^+sc^+ Y males Scutellar number											\bar{x}
		2	3	4	5	6	7	8	9	10	11	4		5	6	7	8	9	10	11					
1	I			10	21	48	23	16	5					18	27	41	18	3				5.56			
	II			37	29	11	2	2						37	16	14						4.75			
4	I			35	51	19	3	1						54	43	13						4.62			
	II			47	16	8								59	14	2						4.24			
6	I			61	47	13	1							66	34	7						4.44			
	II			49	19	7								54	13	1						4.22			
9	I			30	35	25	19	8	1					51	34	24	8	2	1			4.77			
	II			53	13	4	1							52	13	4						4.30			
15	I			52	33	16	4							59	32	12	1					4.56			
	II			28	31	9	3							40	17	4						4.43			
18	I			58	17	16	14	2	1					64	20	22	6	2				4.78			
	II			67	4	1								58	3							4.04			
21	I			50	41	12	1							51	35	15						4.64			
	II			46	19	4								57	12	4						4.27			
27	I			83	26	16								83	20	3						4.24			
	II			47	16	7								59	10	2						4.19			
39	I			67	27	6								65	25	8						4.41			
	II			56	16									55	15							4.21			
42	I			172	1									148								4.00			
	II			73	3									74	1							4.01			

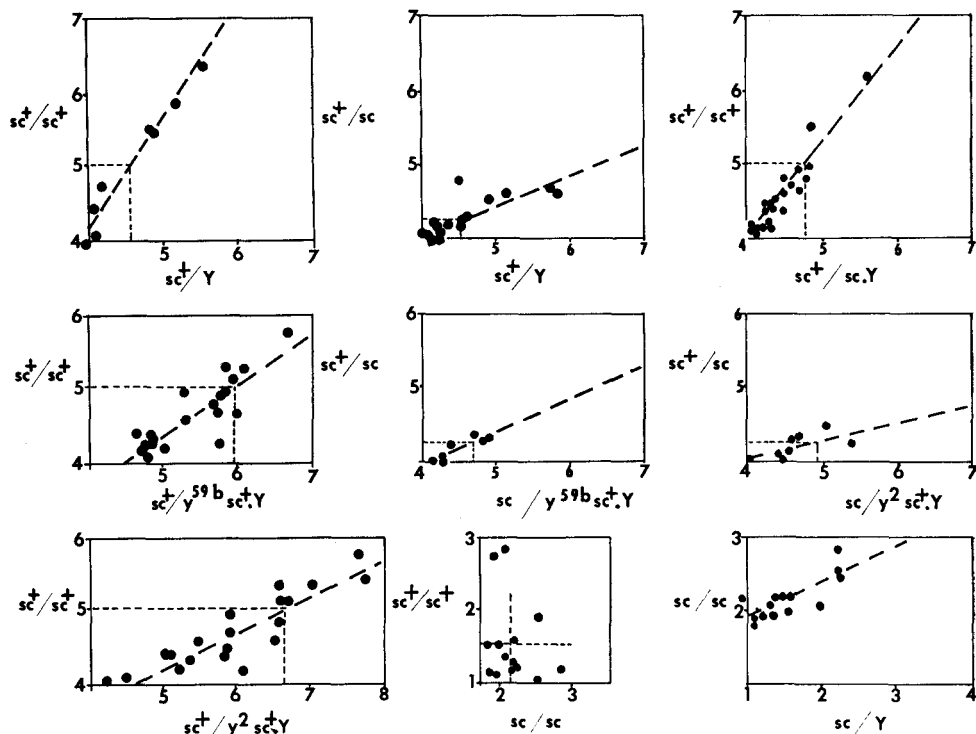


FIGURE 1.—Relations of mean scutellar number for the indicated pairs of genotypes. Regressions have been fitted to all but the sc^+/sc^+ and sc/sc genotypes; these genotypes showed no correlation of expression.

genotypes which have scutellar expressions on the same side of the norm. e.g., the scutellar numbers of sc^+/sc^+ and $sc^+/\gamma^2 sc^+.Y$ which are both above the norm are positively correlated, and there is also a positive correlation of the scutellar number of sc/sc and sc/Y , which are both below the norm.

The sc gene, and the modified Y chromosomes were also substituted into a line in which selection for missing scutellars had been practiced. (Line 42 in Tables 1 and 2.) Selection for missing scutellars was practiced in many separate instances, but it was successful in only one line, without a major degree of success. Although Line 42 has a greater frequency of individuals with missing scutellars, the majority still have the normal number. The selection did not have a very marked effect on the wild-type expression, but it had a marked effect on the scute expression: sc/Y (Line 42) males rarely have any scutellars, and sc/sc (Line 42) females have a mean of 0.32 scutellars. Selection in wild-type for extra scutellars contrasts markedly with selection for missing scutellars in the correlated response on scute expression. The selections for extra scutellars show no such correlated response, where selections for missing scutellars shows a marked correlated response. Clearly there are genes for extra scutellar bristles in wild type which have none, or very little effect on scute, and there are also genes for reduced scutellar bristle number which affect scute expression markedly

but have only a slight effect on wild type. The effects of the modified Y chromosomes are similar in Line 42, to their effects in the extra-scutellar lines.

The regressions shown in Figure 1 allow calculation of the scutellar number for the various scute genotypes adjusted to some standard background. This has been done for a background which would result in the sc^+/sc^+ females having 5.0 scutellars. The scutellar numbers of the various genotypes on this basis are given in Figure 2. Comparison of sc^+/sc^+ , sc^+/sc and sc/sc shows that the sc gene is not completely recessive: sc^+/sc has less scutellars than sc^+/sc^+ . RENDEL (1959) has also found an incomplete dominance of sc^+ over sc in backgrounds selected for extra scutellars. The comparison of sc^+/sc^+ and sc^+/Y , and sc/sc with sc/Y shows that the sex-dimorphism at the scute level also occurs at the wild-type level; females have approximately 0.5 bristles more than males.

Addition of an extra sc^+ gene to the Y chromosome results in an increased number of extra scutellar bristles in genotypes above the norm. This increase of bristle number is shown in the comparison of sc^+/Y with $sc^+/y^2sc^+ \cdot Y$ and $sc^+/y^{59b}sc^+ \cdot Y$. An important feature of this comparison is that the $y^2sc^+ \cdot Y$ chromosome has a greater effect than the $y^{59b}sc^+ \cdot Y$ chromosome. The difference between the $y^2sc^+ \cdot Y$ and $y^{59b}sc^+ \cdot Y$ chromosomes could be due either to their carrying different iso-alleles at the scute locus, to other bristle-determining loci located in this region of the X chromosome, or to differences in the Y chromosome.

Comparison of sc^+/sc^+ with $sc^+/y^2sc^+ \cdot Y$ and with $sc^+/y^{59b}sc^+ \cdot Y$ shows that effect of adding a sc^+ gene to sc^+/Y is greater than would be expected on a simple dosage hypothesis. $sc^+/y^2sc^+ \cdot Y$ and $sc^+/y^{59b}sc^+ \cdot Y$ males have greater numbers

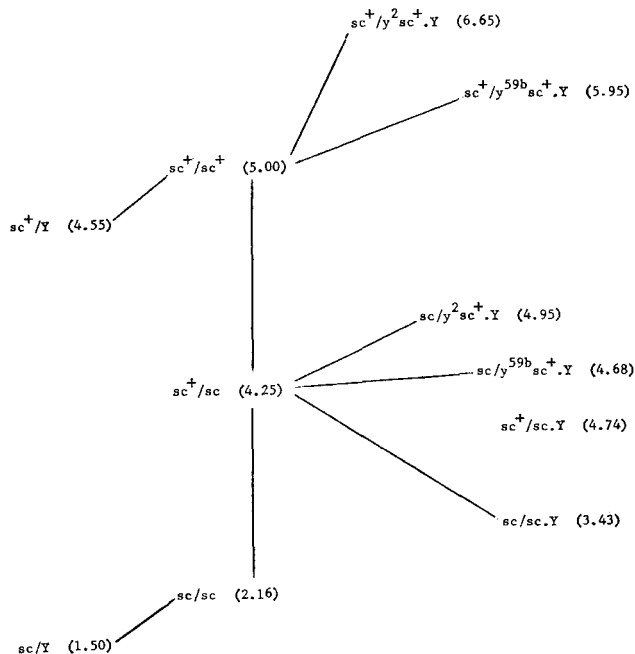


FIGURE 2.—Scutellar numbers for the various scute genotypes, computed by interpolation in the regressions of Figure 1, at a standard value of 5.00 for sc^+/sc^+ females.

Frequency distributions of scutellar numbers in stocks segregating for sc⁺ and sc

Line	Genotype	Scutellar number										\bar{x}	Genotype	Scutellar number	\bar{x}										
		0	1	2	3	4	5	6	7	8	9					10									
1	sc ⁺ /sc ⁺ (I)	22	15	14	10	5	1	..	5.46	+	(I)	4.90
	sc ⁺ /sc (I)	36	10	8	1	4.52	sc	(I)	4.72
	sc/sc (I)	2	22	17	4	2.51	+	(II)	21	7	5	3
4	sc ⁺ /sc ⁺ (I)	49	21	5	4.41	+	(II)	4.01
	sc ⁺ /sc (I)	35	3	4.07	sc	(I)	2	15	4	1.39
	sc/sc (I)	2	2	25	12	1	2.19	+	(II)	6	10	10	1	1.22
9	sc ⁺ /sc ⁺ (I)	8	8	13	14	10	2	1	6.35	+	(I)	5.86
	sc ⁺ /sc (I)	127	102	37	2	sc	(II)	34	10	10	2	4.64
	sc/sc (I)	1	30	140	24	+	(I)	2	12	59	5	1.85
15	sc ⁺ /sc ⁺ (I)	14	37	43	10	1	5.50	+	(II)	2.00
	sc ⁺ /sc (I)	52	26	5	4.74	sc	(I)	4	18	4	4.82
	sc/sc (I)	3	8	5	2.12	+	(I)	47	57	25	4.83
18	sc ⁺ /sc ⁺ (I)	19	16	23	23	6	2	..	5.85	+	(II)
	sc ⁺ /sc (I)	219	68	28	1	4.40	sc	(I)	17	27	35	5	1	1.36
	sc/sc (I)	2	14	127	44	14	1.95	+	(I)	5.16
21	sc ⁺ /sc ⁺ (I)	39	34	13	1	4.72	+	(II)	4.60
	sc ⁺ /sc (I)	107	3	sc	(I)	4	13	1.76
	sc/sc (I)	2	33	6	2	2.19	+	(II)	8	30	4	1	1.95
30	sc ⁺ /sc ⁺ (I)	+	(I)	4.17
	sc ⁺ /sc (I)	103	22	2	4.20	sc	(I)	4.16
	sc/sc (I)	15	21	8	2.84	+	(I)
42	sc ⁺ /sc ⁺ (I)	5	83	3.94	+	(II)
	sc ⁺ /sc (I)	4	45	382	3.87	sc	(I)	50	0.00
	sc/sc (I)	176	25	24	0.32	+	(II)	16	0.00

Counts made at the time of formation of the stock are listed as (I), and those made after five to seven generations of mass-mating are listed as (II).

of scutellars than sc^+sc^+ females. The sex-dimorphism has been reversed. The sc/γ^2sc^+Y , $sc/\gamma^{59b}sc^+Y$ and sc^+/sc genotypes are all heterozygous at the scute locus, but the males have a greater number of scutellars than the females. Further, the sc/γ^2sc^+Y males have more bristles than $sc/\gamma^{59b}sc^+Y$ males; showing that the difference between the γ^2sc^+Y and $\gamma^{59b}sc^+Y$ chromosomes occur to a lesser degree in the presence of a scute gene on the X chromosome.

Comparison of sc/Y and sc/scY shows that the effect of the additional sc gene in males is greater than would be expected on a simple dosage hypothesis. The sex-dimorphism has been reversed.

A comparison which is in strong support of a concept of dosage determining the sex-dimorphism is that of sc/γ^2sc^+Y , $sc/\gamma^{59b}sc^+Y$ and sc^+/scY . These three "synthetic" heterozygotes have scutellar numbers of 4.95, 4.68 and 4.74, respectively. The differences between the three heterozygotes are small, and it is reasonable to suggest that the differences are due to variation at loci linked to the scute locus.

A further comparison of the effect of the addition of the sc gene to the Y chromosome was made in an attached-X stock. The attached-X was $\gamma^2sc w^i$, and the comparison was, therefore, of $sc/sc/scY$ with sc/scY . The counts of scutellar number are given in Table 3 for this culture, with those from a culture containing $\gamma^2sc w^i/\gamma^2sc w^i$ and $\gamma^2sc w^i/scY$. The mean scutellar numbers were 3.08 and 3.21 for $sc/sc/scY$ and sc/scY , and 1.75 and 3.12 for sc/sc and sc/scY . The values for $sc/sc/scY$ and sc/scY are not significantly different, and it can be concluded that the effect of the scY chromosome is independent of the number of sc genes located on the X chromosome.

Conclusions: There are several points demonstrated by the above data. (1) Selection for extra scutellars in wild type does not affect the scutellar number of scute flies when scute is substituted into the selection lines. This is in agreement with HASKELL (1943) but contrary to RENDEL (1959), who found a positive correlation between wild-type and scute expression in lines selected on scute expression. (2) There is a sex dimorphism of scutellar number which is reduced in genotypes with scutellar numbers approximating to the norm of four bristles. ($sc/Y < sc/sc$; $sc^+/Y < sc^+/sc^+$). (3) There is an increase of scutellar number consequent on the introduction of a derived Y chromosome, which reverses the sex-dimorphism ($sc/scY > sc/sc$; $sc^+/sc^+Y > sc^+/sc^+$). (4) The increase of scutellar number caused by the introduction of a derived Y chromosome is independent of the scute allele carried in the derived Y, but dependent on the scute genotype ($sc^+/scY \approx sc/sc^+Y$, but $sc/scY \neq sc^+/scY \neq sc^+/sc^+Y$). (5) The increase of scutellar number caused by the introduction of a scY chromosome is

TABLE 3

Frequency distributions of scutellar number in two stock containing the named scute genotypes

	Scutellar number					\bar{x}		Scutellar number			
	0	1	2	3	4			2	3	4	\bar{x}
$\gamma^2sc w^i/scY$ females	..	1	21	22	29	3.08	$\gamma^2sc w^i/scY$ males	16	16	29	3.21
$\gamma^2sc w^i/\gamma^2sc w^i$ females	5	7	32	5	..	1.75	$\gamma^2sc w^i/scY$ males	11	13	16	3.12

independent of the number of scute alleles. ($sc/sc \cdot Y = \text{attached-X } sc/sc \cdot Y$). (6) Different derived $sc^+ \cdot Y$ chromosomes vary in their effect on scutellar number. ($\gamma^2 sc^+ \cdot Y \neq \gamma^{59b} sc^+ \cdot Y$).

It appears that the modification of the attached-XY chromosome to produce the derived Y chromosomes causes a variable increase of the scutellar potency which is independent of the scute allele located in the derived Y chromosome. This is evident from the lack of difference between the synthetic heterozygotes (point 4 above), and from the difference between the two $sc^+ \cdot Y$ chromosomes.

An obvious explanation of the general effect of the derived Y chromosomes is that their presence maintains a dosage compensation mechanism in the presence of two scute alleles, with the result that males with derived Y chromosomes have greater scutellar numbers than females with the same scutellar genotype. The expectation from this hypothesis is that derived-Y males should have twice the scutellar number of normal males with the same scutellar genotype. The values given in Figure 2 show that derived-Y males have more than twice the scutellar number of normal males in scute, and less than twice the scutellar number in wild type.

No correlation was found between variability above and below the norm of four scutellars (point 1 above), and it is possible that the effects of dosage and dosage compensation for genotype with scutellar numbers above 4 should be measured from 4 as a base point. On this basis there is little if any dosage compensation, and a markedly greater effect of $sc^+ \cdot Y$ than can be explained by either dosage or dosage compensation. The change of base of reference between scute and wild type results in a rationalization of the effect of derived-Y chromosomes, which then have an effect of increasing scutellar number above any effect explicable by dosage or dosage compensation. This will need considerable further explanation but there seems little doubt that the derived Y chromosomes have a scutellar enhancement which is independent of dosage and dosage compensation (see point 5 above).

DISCUSSION

RAFFEL and MULLER (1940) have suggested that the scute locus is complex, consisting of several parts whose effectiveness is conditioned by their genetic location. FRASER (1963) has shown that a locus affecting scutellar number is located close to the scute locus, and the presence of achaete and Hairy wing in close proximity to scute supports MULLER's contention that bristle development is focussed on a tightly linked group of genes located on the left end of the X. It should be noted that SPENCER (1949) has located a mutant, extra-scutellar, in *D. hydei* which is tightly linked to scute. Many of the mutations to scute have been found to be associated with inversions, translocations and transpositions with one breakage point in the immediate vicinity of salivary bands 1B3,4. The modified-Y chromosomes all have a breakage point to the right of the scute locus, and as a working hypothesis, it can be suggested that there is an enhancing locus located to the left of scute, and an inhibiting locus located to the right. On this hypothesis, it is suggested that the constancy of scutellar development is to a large degree determined by a balance between the potencies of these various elements. It is then plausible to suggest that one set of modifiers act on one element,

another set act on another element, and a third set act on a central controlling element. (This hypothesis provides a basis for reconciling the differences between RENDEL'S (1959), HASKELL'S (1943) and our own data.) One set of modifiers can be considered as working on the inhibitors, another set on the enhancers, and yet another set working across the whole complex locus. The work of SUTTON (1943) argues against this model. Her analysis of a series of rearrangements, all of which have clear-cut scute phenotypes, showed that scute is localized to a doublet 1B3-4 in the salivary gland chromosomes. This doublet is in itself of interest because it suggests that scute is a complex locus. Her analysis of nine rearrangements with scute effects showed five to have a breakpoint to the left, and four to have a breakpoint to the right of the scute locus. These results show that a simple concept of a right-to-left sequence consisting of inhibitor, central, and enhancing loci cannot be given too much weight.

It is clear that no decision can be reached on the determination of the sex-dimorphism of scutellar number until more detail is known of the fine structure of the scute locus.

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SUMMARY

The effects on scutellar number of the addition of the left end of the X chromosome to the Y chromosome, have been determined for two additions carrying sc^+ , and one carrying sc . These three modified Y chromosomes were substituted into a number of stocks selected for extra scutellar bristles. There is a general enhancement of scutellar number by the modified Y chromosomes, and a strong indication that the sex-dimorphism of scutellar number is due both to the difference in number of scute loci between males and females, and to a dosage compensation of the effect of scute alleles in males.

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