

VARIATION OF SCUTELLAR BRISTLES IN *DROSOPHILA*

XIII.* EFFECTS OF *SCUTE* ALLELES†

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Summary

The *sc*¹ and *sc*⁵ alleles have been substituted for *sc*⁺ in a number of lines selected for extra (supernumerary) scutellar bristles. The gene *extra-vert*, which causes a marked increase in the number of scutellar bristles, is either present or absent in these lines. The substitution of *sc* for *sc*⁺ results in the suppression of *extra-vert* and its modifiers (termed the β -system), but does not markedly affect the modifiers of *sc*⁺ (termed the α -system).

I. INTRODUCTION

Fisher (1929) noted that genetic variation in a metric character may be present even though it is not phenotypically detectable. He suggested that the observable distribution be regarded as a natural example of a normally distributed variation grouped in equal intervals. If the units of grouping are much larger than the standard deviation then very few individuals would be expected to deviate from the common type. Such a character is the number of scutellar bristles in *Drosophila* with the added complication that the grouping is not based on equal intervals. The common number of 4 bristles is expressed in 95% or more of wild-type flies (Fraser 1963). Payne (1918), Sismanidis (1942), Rendel (1959), Fraser (1963), and Latter (1964) have shown, by the effectiveness of selection for change of number of scutellar bristles, that the normal constancy of number of these bristles involves a variable underlying genotype.

The concept of a single, homogenous, underlying genotype determining the number of scutellar bristles has been questioned by Fraser and Green (1964) who concluded that one set of genes was responsible for variation of the number of bristles below the norm of 4 bristles, another set of genes being responsible for variation of number of bristles above the norm, with a third set of genes acting to determine variation around the norm. They based this conclusion on the effects of substituting *sc*¹ and *sc*⁺ in a number of selection lines that had been selected for increased number of scutellar bristles above the norm. Fraser (1965) considered a set of crosses between *sc*⁺ lines and concluded that two sets of genes were operative in determining the number of bristles above the norm.

The concept of a number of separate systems of genes controlling the number of scutellar bristles raises the problem of their interaction and regulation. Waddington

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(1940), considering the interactions of the *aristapaedia* locus with arista-modifying and leg-modifying genes, concluded that some genes act to switch development into one or another of a restricted set of alternatives, with other genes acting to modify a particular path of development. He used the terms "switch" and "buffer" genes.

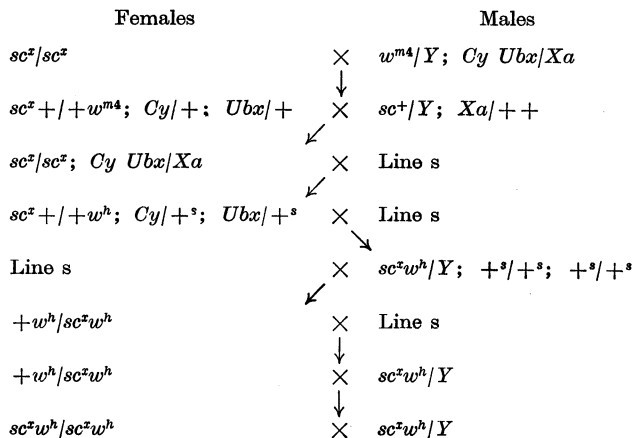
Erway (personal communication) has shown that three of the extra (super-numerary) scutellar lines described by Fraser *et al.* (1965) are homozygous for an autosomal recessive factor that causes a marked increase of the numbers of scutellar, dorsocentral, and vertical bristles. Segregation of this factor could not be diagnosed from its effect on scutellar bristles, but its effects on vertical bristles allows its detection. The factor has been tentatively termed "extra-verticals" (*x-vert*). In this paper the hypothesis that the *sc* and *x-vert* loci act as switch genes, determining the effectiveness of the different systems of genes postulated by Fraser and Green (1964) and Fraser (1966), is considered in terms of the substitution of *sc*¹ and *sc*⁵ for *sc*⁺ in lines selected for extra scutellar bristles. In some of these lines the selection response involved homozygosity for *x-vert*, in others the *x-vert* gene was not involved.

II. MATERIALS AND METHODS

Fraser *et al.* (1965) found three levels of response to selection for increased number of scutellar bristles, which they termed first level (no response, with a mean in the range 4.0–4.2), second level (moderate response, with a mean in the range 4.5–5.5) and third level (marked response, with a mean in the range 6.5–8.0). It is now known from Erway's analysis that the third-level lines are *x-vert/x-vert*, and that all but one of the second-level lines are *x-vert*⁺/*x-vert*⁺. (An anomalous second-level line A4, not included in the present study, is probably polymorphic for *x-vert* and *x-vert*⁺.) Five of the lines described by Fraser *et al.* (1965) have been used in the present study: lines A1, A9, and A18 are *x-vert/x-vert*, and lines A6 and A21 are *x-vert*⁺/*x-vert*⁺. The early selection history of these lines is shown in Figure 1.

An additional set of selection lines has also been used in the present study. These were derived from a mass cross of lines A1, A9, and A18. Selection was practised for increased number of scutellar bristles in two of these lines—AH1 and AH2. Selection was practised for a fixed number of scutellar bristles in lines derived from the AH1 line, e.g. AS4 was derived by selecting flies with 4 scutellar bristles. The mean number of scutellar bristles of males in these lines is shown in Table 5.

The *sc*¹ and *sc*⁵ genes were substituted for *sc*⁺ in the A set of lines, using the *w*^{m4}, *Cy*, and *Ubx* inversion chromosomes and the *Xa* translocation, by the procedure outlined below:



Line *s* is a selection line derived by Fraser *et al.* (1965), and is marked by white-honey (w^h); $+$ ^s designates a chromosome from line *s*. sc^z is either sc^1 or sc^5 . After substitution, further backcrosses were made of the sc -substituted stocks to their parent lines with the result that only a small section of the first chromosome (from 0.0 to the w^h locus, about 1.5 map units as a maximum) bearing the *scute* allele was introduced into the selection lines.

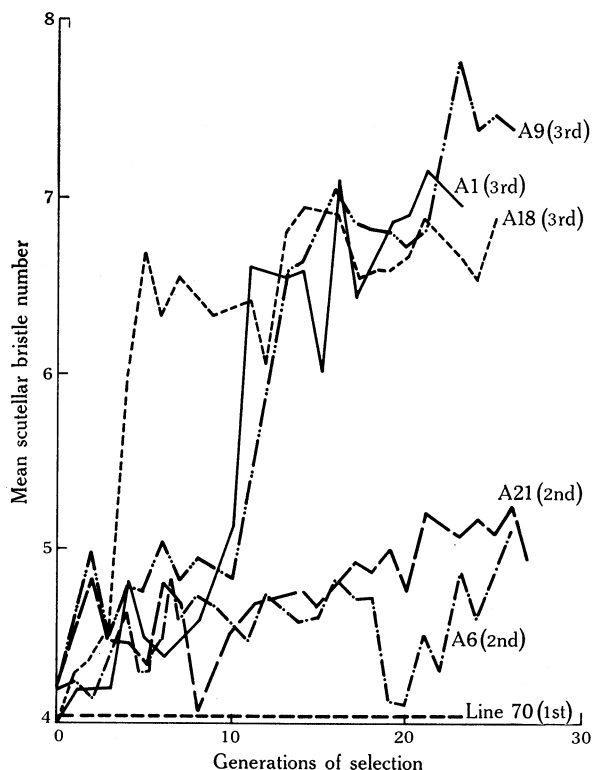


Fig. 1.—Initial selection history of the A set of selection lines expressed as the mean number of scutellar bristles in females plotted against generation of selection.

The substitution of sc alleles into some of the AS and AH lines was accomplished by nine generations of backcrossing. The sc^1 and sc^5 alleles were derived from sc -substituted x -vert/ x -vert lines: A1, A9, and A18, and from an unselected stock. The original unselected line is termed line 70 after Fraser (1963); the selection lines are described as sc^z A*i* (*j*), e.g. sc^5 A6 (2nd) would be the second-level line A6 with sc^5 substituted into it.

Two sets of crosses were made. In the first set, in a series of diallel crosses of the *scute* and *scute*⁺ A lines, all possible crosses were made between the sc^1 and sc^+ , and between the sc^5 and sc^+ genotypes (Table 1). Each cross was made of four females with four males in quarter-pint bottles with a standard agar-cornmeal media. Two replicates were made and progeny were scored after 14 days. Fifty females and 50 males randomly selected from 300 to 400 progeny were scored for number of bristles. The main data and analyses are available in a thesis by Miller (1967) and, therefore, only reduced versions of the data will be presented here. Tests of consistency between replicates, between reciprocal crosses, and between the same genotype produced in different alleles showed no significant differences except for the reciprocal crosses producing progeny of the sc^1/Y genotype, involving the A9 and A18 lines. Consequently, the data have been reduced by averaging over replicate, reciprocal, and diallel crosses for all but the sc^1/Y genotypes. In the second set of crosses, the AH1, AH2, AS4, AS5, and AS9 lines were crossed with the sc^1 A1 (3rd), sc^1 A9 (3rd), sc^5 A1 (3rd), and sc^5 A9 (3rd) lines. The data from these crosses involved two replicate cultures, and all crosses were made reciprocally.

III. RESULTS

(a) *Location of x-vert Gene*

A series of tests were made to determine the location of the *x-vert* locus. The results, which are accurate to ± 6 map units, are given in Table 2, and show that *x-vert* is located in the vicinity of *thread* and *scarlet* on chromosome III. A gene, *polychaetoid* (*pyd*), that is located in this region has similar effects to those of *x-vert*.

TABLE 1
PROGENY GENOTYPES OF THE DIALLEL SETS OF CROSSES, WITH THE PARENTAL CROSSES THAT PRODUCE THEM

Progeny Genotype	Parental Cross	Progeny Genotype	Parental Cross
sc^+/Y	$sc^+/Y \times sc^+/sc^+$ $sc^1/Y \times sc^+/sc^+$ $sc^5/Y \times sc^+/sc^+$	sc^+/sc^1	$sc^+/Y \times sc^1/sc^1$ $sc^1/Y \times sc^+/sc^+$
sc^1/Y	$sc^+/Y \times sc^1/sc^1$ $sc^1/Y \times sc^1/sc^1$	sc^+/sc^5	$sc^+/Y \times sc^5/sc^5$ $sc^5/Y \times sc^+/sc^+$
sc^5/Y	$sc^+/Y \times sc^5/sc^5$ $sc^5/Y \times sc^5/sc^5$	sc^+/sc^+ sc^1/sc^1 sc^5/sc^5	$sc^+/Y \times sc^+/sc^+$ $sc^1/Y \times sc^1/sc^1$ $sc^5/Y \times sc^5/sc^5$

Crosses between *x-vert* and *pyd* produced progeny whose frequency of extra bristles was midway between those of the parent stocks. It is probable that *x-vert* is an allele of *pyd* but further work is needed to establish this.

TABLE 2
LOCATION OF *x-vert*

Marker	<i>roughoid</i>	<i>sepia</i>	<i>Hairy wing</i>	<i>thread</i>	<i>scarlet</i>	<i>clipped</i>	<i>ebony</i>
Location of marker	0.0	26.0	26.5	43.2	44.0	45.3	70.7
Percentage crossover with <i>x-vert</i>	48.0	15.8	18.1	2.1	4.3	3.1	35.6
Location of <i>x-vert</i>	48.0	41.8	44.6	41.1-45.3	39.7-48.3	42.2-48.4	35.1

(b) *Sex-linked Component*

Mean number of scutellar bristles in sc^1/Y and sc^1/sc^1 progeny of diallel and replicate diallel crosses between the A lines are given in Table 3. There are no significant differences between row and column means for the A1, A6, and A21 lines, but there are consistent differences for the A9 and A18 lines: the sc^1/Y progeny where the sc^1 chromosome comes from lines A9 and A18 have a lower mean number

of scutellar bristles than equivalent crosses in which the sc^1 chromosome comes from lines A1, A6, or A21. No such differences were found for female progeny of the same crosses, which shows that the lack of agreement between reciprocal crosses involves a sex-linked component. It is possible that such a sex-linked component was present in the original unselected sc^1 stock and that it was lost in the process of forming the sc^1 A1 (3rd), sc^1 A6 (2nd), and sc^1 A21 (2nd) lines, but retained in the sc^1 A9 (3rd) and sc^1 A18 (3rd) lines.

TABLE 3
MEAN SCUTELLAR BRISTLE NUMBER IN sc^1/Y AND sc^1/sc^1 PROGENY OF DIALLEL
AND REPLICATE CROSSES BETWEEN THE A LINES

Male Parent	Female Parent					Mean
	A1	A6	A9	A18	A21	
Male Progeny (<i>sc/Y</i>)						
A1	1.93	2.12	0.84	0.89	1.82	1.52
A6	2.09	2.25	0.97	1.05	2.07	1.68
A9	1.96	2.05	0.92	0.99	1.74	1.53
A18	1.98	2.04	0.96	0.75	1.69	1.48
A21	2.25	2.26	1.34	1.25	2.19	1.85
Mean	2.04	2.14	1.01	0.99	1.90	
Female Progeny (<i>sc</i> ¹ / <i>sc</i> ¹)						
A1	2.12	2.28	2.03	2.10	2.28	2.16
A6	2.33	2.36	2.10	2.07	2.37	2.24
A9	1.81	1.96	1.66	1.56	2.15	1.82
A18	1.91	1.96	1.70	1.56	1.92	1.81
A21	2.42	2.44	2.16	2.05	2.51	2.31
Mean	2.11	2.19	1.93	1.86	2.24	

Further backcrosses of the sc^1 alleles from the sc^1 A1, sc^1 A9, and sc^1 A18 (3rd) stocks to the analogous sc^+ stocks for several generations did not result in any change of mean bristle number, indicating that the sex-linked component is either located extremely close to sc^1 , or that it is an intrinsic feature of the original selection lines.

(c) *The Base Stocks*

The A1, A9, and A18 lines are $x\text{-vert}/x\text{-vert}$ whereas the A6 and A21 lines are $x\text{-vert}^+/x\text{-vert}^+$ as is the base stock, line 70. The mean number of scutellar bristles for these lines is given in Table 4. Values are averages over lines of the same level, except for the sc^1/Y genotypes in which a distinct difference occurs between the A1 line, and the A9 and A18 lines. Values for line 70 are included in Table 4 as representative of unselected first-level lines.

Consider first the effect of substitution of sc^5 for sc^+ in females. In lines A6 and A21, $x\text{-vert}^+/x\text{-vert}^+$, the mean number of scutellar bristles is 4.60 for sc^+/sc^+ , 4.04 for sc^+/sc^5 , and 3.23 for sc^5/sc^5 . These can be contrasted with the values for line 70 which are 4.05, 4.00, and 2.66 for the three genotypes respectively. It would appear, as Rendel (1959) has previously shown, that *scute* alleles cannot be considered as recessive in a background of selection for extra scutellar bristles since the heterozygous expression is 4.04 compared with 4.60 in sc^+/sc^+ . Another feature of this comparison is that the selection response of 0.55 in sc^+/sc^+ does not differ from that of 0.57 found in sc^5/sc^5 . It would appear that the genes selected for increased number of scutellar bristles in sc^+ have the same effect in sc^5 and sc^+ . There is, apparently, a fairly marked sex dimorphism of expression of the selection difference, since the selection response is 0.96 in sc^5/Y compared to 0.57 in sc^5/sc^5 .

TABLE 4

MEAN NUMBER OF SCUTELLAR BRISTLES FOR LINE 70 (UNSELECTED), LINES A6 AND A21 ($x\text{-vert}^+$ SELECTED), AND FOR LINES A1, A9, AND A18 ($x\text{-vert}$ SELECTED)

Results given are averages for base lines and for base lines and crosses within genetic types

Line	sc^+/sc^+	sc^1/sc^1	sc^5/sc^5	sc^+/sc^1	sc^+/sc^5	sc^+/Y	sc^1/Y	sc^5/Y
Base lines								
70	4.05	1.48	2.66	4.00	4.00	4.01	0.66	2.07
A6 and A21	4.60	2.43	3.22	4.04	4.04	4.12	2.22	3.03
A1, A9, and A18	6.96	1.77	2.90	4.96	4.74	5.78	1.93*	2.58
							0.83†	
Base lines and crosses								
A6, A21, and A6 × A21	4.60	2.42	3.23	4.05	4.04	4.12	2.19	3.04
A1, A9, A18, A1 × A9, A1 × A18, A9 × A18	6.89	1.81	2.97	4.90	4.75	5.79	1.96*	2.63
							0.90†	

* Mean value for A1 line only.

† Mean value for A9 and A18 lines.

The lack of expression of differences between selected and control lines in sc^+/sc^5 can be explained by proximity to the canalization zone of 4 which can also explain the selection difference being so much less in sc^+/Y than in sc^+/sc^+ .

The analogous comparisons of the effects of substitution of sc^5 for sc^+ in lines A1, A9, and A18, $x\text{-vert}/x\text{-vert}$, give values for females of 6.96 (sc^+/sc^+), 4.74 (sc^+/sc^5), and 2.90 (sc^5/sc^5). Clearly, sc^5 cannot be considered as recessive in the presence of $x\text{-vert}/x\text{-vert}$. The selection response in the $x\text{-vert}$ lines is 2.91 in sc^+/sc^+ , which is in marked contrast to the value of 0.24 in sc^5/sc^5 . This can be explained by sc^5 being epistatic to $x\text{-vert}$, suppressing its expression either completely or to a major degree. The comparison of sc^+/Y and sc^5/Y in $x\text{-vert}$ lines leads to the same conclusion. The selection response of 1.77 in sc^+/Y is reduced to 0.51 in sc^5/Y .

It is possibly not fortuitous that the comparison of the $x\text{-vert}^+$ selection difference was 0.57 in sc^5/sc^5 and 0.96 in sc^5/Y compared with the $x\text{-vert}$ selection difference of 0.24 in sc^5/sc^5 and 0.51 in sc^5/Y , i.e. the selection difference that is expressed in sc^5/sc^5 is half that expressed in sc^5/Y .

The effects of substitution of sc^1 for sc^+ are also shown in Table 4. In the $x\text{-vert}^+$ stocks, lines A6 and A21, the mean number of scutellar bristles for females is 4.60 (sc^+/sc^+), 4.04 (sc^+/sc^1), and 2.43 (sc^1/sc^1) contrasting with the values of 4.05, 4.00, and 1.48 for the unselected stock. The selection difference of 0.55 in sc^+/sc^+ is reduced to effectively zero in sc^+/sc^1 . In males the values for sc^+/Y and sc^1/Y are 4.12 and 2.22. The selection difference of 0.11 in sc^+/Y is increased to 1.56 in sc^1/Y . It would appear that the substitution of sc^1 for sc^+ enhances the expression of the genes selected for increased number of scutellar bristles in sc^+ , $x\text{-vert}^+$ stocks. This effect could be a consequence of sc^1 reducing the number of scutellar bristles more than sc^5 , i.e. the genes concerned with increasing the number of bristles in these stocks have a greater effect when the mean level of bristle production is of the order of 2 bristles (sc^1 level), than when it is of the order of 3 bristles (sc^5 level).

The analogous comparisons of the effects of substitution of sc^1 for sc^+ in $x\text{-vert}$ lines give values for females of 6.96 (sc^+/sc^+), 4.96 (sc^+/sc^1), and 1.77 (sc^1/sc^1). The selection response in $x\text{-vert}$ lines is 2.91 in sc^+/sc^+ , 0.96 in sc^+/sc^1 , and 0.29 in sc^1/sc^1 . It appears, as for the sc^5 gene, that substitution of sc^1 for sc^+ is epistatic to $x\text{-vert}$, suppressing its expression either completely or to near zero. The comparison of sc^+/Y and sc^1/Y in $x\text{-vert}$ lines is complicated by the heterogeneity of the three lines, with A9 and A18 having a markedly lower number of scutellar bristles in sc^1/Y than A1. If we consider first the A1 lines, then the sc^1/Y expression of 1.93 is only slightly less than that of sc^1/sc^1 (2.12) and it does not differ markedly from that found in sc^+ , $x\text{-vert}^+$ (2.22). The selection response of 1.77 in sc^+/Y is reduced to 1.27 in sc^1/Y . It could be considered that sc^1 is not epistatic to $x\text{-vert}$ in the A1 line. However, in the A9 and A18 lines the sc^1/Y expression is 0.83. The selection response of 1.77 in sc^+/Y is reduced to 0.17 in sc^1/Y . In lines A9 and A18 the effects of substitution of sc^1 for sc^+ in males lead to the same conclusion of suppression of the $x\text{-vert}$ gene as have been reached for females.

The above data are based on two $x\text{-vert}^+$ and three $x\text{-vert}$ genotypes. A wider basis for comparison can be gained by including the crosses between these lines, i.e. A6 \times A21, A1 \times A9, A1 \times A18, and A9 \times A18. The results, extended by these additions, are given in Table 4, and show very little change from the results for the base lines alone.

These data can be interpreted in terms of the selection response of lines A6 and A21, $x\text{-vert}^+$, being determined by a multigenic system, which we will term the α -system. The substitution of sc^1 or sc^5 for sc^+ in these lines either does not affect the expression of the α -genotype or enhances its expression. The selection response in lines A1, A9, and A18 is postulated to be primarily based on the substitution of $x\text{-vert}$ for $x\text{-vert}^+$ with little if any involvement of the α -genetic system, i.e. the selection for increased number of scutellar bristles in these lines resulted in homozygosity for $x\text{-vert}$, having little effect on the α -genetic system. On this hypothesis we would expect $x\text{-vert}$ stocks in which sc had been substituted for sc^+ not to differ from unselected *scute* stocks, unless they include in their genotype some of the α -genotype. This would be expressed, even enhanced, in *scute* genotypes even though it was not expressed in sc^+ , $x\text{-vert}$ genotypes. The sex-linked genes responsible for the differences between the A9 and A18 group and the A1, A6, and A21 group appear to belong to the α -set. The situation is complicated by the sex dimorphism of

TABLE 5
MEAN SCUTELLAR BRISTLE NUMBER OF F₁ PROGENY OF CROSSES OF THE AH AND AS LINES (*sc*⁺, *x-verl*) WITH THE THIRD-LEVEL LINES *sc*¹Al, *sc*¹A9, *sc*⁵Al, AND *sc*⁵A9. THE PARENTAL VALUES FOR *sc*⁺/Y IN THE AH AND AS LINES ARE GIVEN FOR COMPARISON
The data averaged over replicates and crosses producing the same genotype are plotted in Figure 2

Genotype	<i>sc</i> ⁺ / <i>sc</i> ¹				<i>sc</i> ⁺ / <i>sc</i> ⁵				<i>sc</i> ⁺ /Y				<i>sc</i> ¹ /Y				<i>sc</i> ⁵ /Y			
Parents	Al ♂	Al ♀	A9 ♂	A9 ♀	Al ♂	Al ♀	A9 ♂	A9 ♀	<i>sc</i> ¹ Al ♂	<i>sc</i> ¹ Al ♀	<i>sc</i> ¹ A9 ♂	<i>sc</i> ¹ A9 ♀	Parental Value	Al ♀	A9 ♀	♀	Al ♀	A9 ♀	♀	♀
AS4	4.84 4.88	4.68 4.76	4.72 4.76	5.08 5.06	4.26 4.44	4.74 4.64	4.92 5.06	4.80 5.08	5.54 5.52	4.80 5.00	6.02 5.94	5.60 6.14	5.60	2.00 1.92	1.00 1.04	♀	2.46 2.50	3.08 2.54	♀	♀
AS5	5.00 5.20	5.08 4.76	4.64 4.96	4.72 4.88	4.46 5.06	4.70 4.60	4.84 4.90	4.68 4.86	5.60 5.52	4.90 5.64	5.66 5.66	5.82 5.62	5.00	1.90 2.14	1.20 1.02	♀	2.66 2.58	2.94 2.76	♀	♀
AS9	6.10 5.52	6.44 5.78	5.80 5.80	5.98 5.60	5.96 4.94	5.64 5.18	5.76 5.96	5.52 5.66	6.58 6.28	6.72 5.50	6.68 7.00	6.86 6.76	7.64	2.22 2.10	1.10 1.20	♀	2.64 2.60	2.50 2.46	♀	♀
AH2	5.64 5.64	6.18 5.90	5.69 —	5.88 5.72	4.84 5.58	5.60 5.64	6.10 5.00	5.68 5.54	6.52 6.42	5.28 6.72	6.66 —	6.02 6.66	7.60	2.36 2.28	1.28 1.57	♀	2.96 3.10	2.90 2.62	♀	♀
AH1	6.00 5.98	5.86 —	6.64 5.74	5.89 5.80	5.80 5.78	5.32 —	5.86 6.08	5.52 5.76	6.70 6.50	6.46 6.48	6.80 6.68	7.04 6.70	7.95	2.10 —	1.26 1.25	♀	2.62 2.90	2.80 2.40	♀	♀

expression of the α -genotype and by the degree of its expression being dependent on the *scute* allele involved. Payne (1918) and Fraser (1963) have both identified a factor for extra scutellar bristles located close to the *white* locus. It is possible that an allele of this locus is involved in the present situation.

A number of *x-vert* lines have been produced with a considerable range of scutellar bristle number from AH2 in which females have a mean number in excess of 9, to AS4 in which females have a mean number of 6 or less. It is pertinent to consider whether this variation is due to the α -genetic system or to a second multi-genic system effective only in *x-vert/x-vert*. A first approach to this problem was

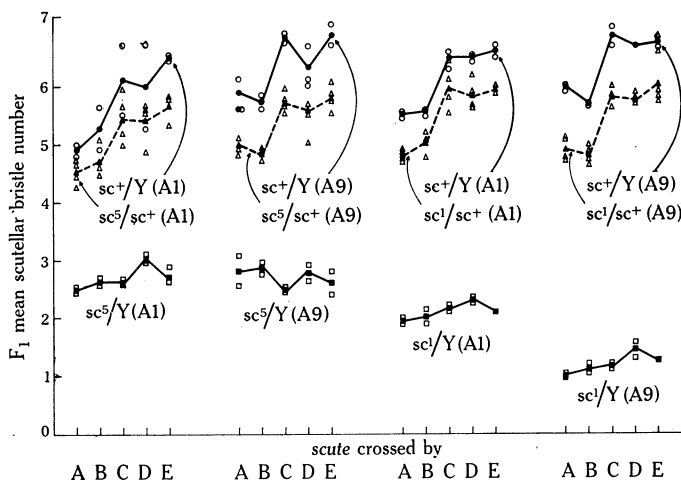


Fig. 2.—Mean scutellar bristle number of F_1 progeny in the reciprocal crosses of sc^1 A1 (3rd), sc^5 A1 (3rd), sc^1 A9 (3rd), and sc^5 A9 (3rd) with the AS and AH set of lines, sc^+ AS4, sc^+ AS5, sc^+ AS9, sc^+ AH2, and sc^+ AH1. The AS and AH lines are represented respectively by the code A, B, C, D, E. The crosses produce five genotypes: sc^+/sc^1 , sc^+/Y , sc^1/Y , sc^+/sc^5 , and sc^5/Y which are shown separately. All progeny of these crosses are *x-vert/x-vert*.

made by crossing sc^1 A1 (3rd), sc^1 A9 (3rd), sc^5 A1 (3rd), and sc^5 A9 (3rd) with the AH and AS lines. Fraser (unpublished data) in a diallelic set of crosses of the AH and AS lines found that the mean scutellar bristle numbers of the lines ranged in females from 9.2 (AH1) to 6.1 (AS4), and in males from 8.10 (AH1) to 5.6 (AS4). It was also found that the variation of scutellar bristle number between these lines is essentially additive. The crosses of the AH and AS lines with another *x-vert* line should result in F_1 progenies having approximately half of the parental range of mean scutellar bristle number, i.e. since the parental range in males is from 7.95 to 5.00, then the cross of these lines to another *x-vert* line, say A9 which has a mean scutellar bristle number of 7.20, should produce a set of F_1 progeny with mean numbers ranging from 7.57 to 6.10, i.e. a range of 1.47 bristles. This provides a range of *x-vert* expression which can be examined in the various *scute* genotypes produced in the cross of the *scute*-substituted A1 and A9 lines with the AH and AS lines. The results from these crosses are shown in Figure 2 and Table 5. The agreement with expectation from an additive mode of inheritance can be seen from the

sc^+/Y progeny in which the ranges of scutellar bristle number were 1.09 and 1.57 for the crosses with sc A1 (3rd), and 0.76 and 1.0 for the crosses with sc A9 (3rd) averaging to 1.1 compared with the expected value of 1.5. The effects of the sc^1 and sc^5 genes in heterozygotes are not marked. The ranges for scutellar bristle number were 1.08 (sc^1/sc^+) and 1.05 (sc^5/sc^+) for the crosses with sc A1 (3rd), and 1.25 (sc^1/sc^+) and 1.17 (sc^1/sc^5) in the crosses with sc A9 (3rd) averaging to 1.1. It

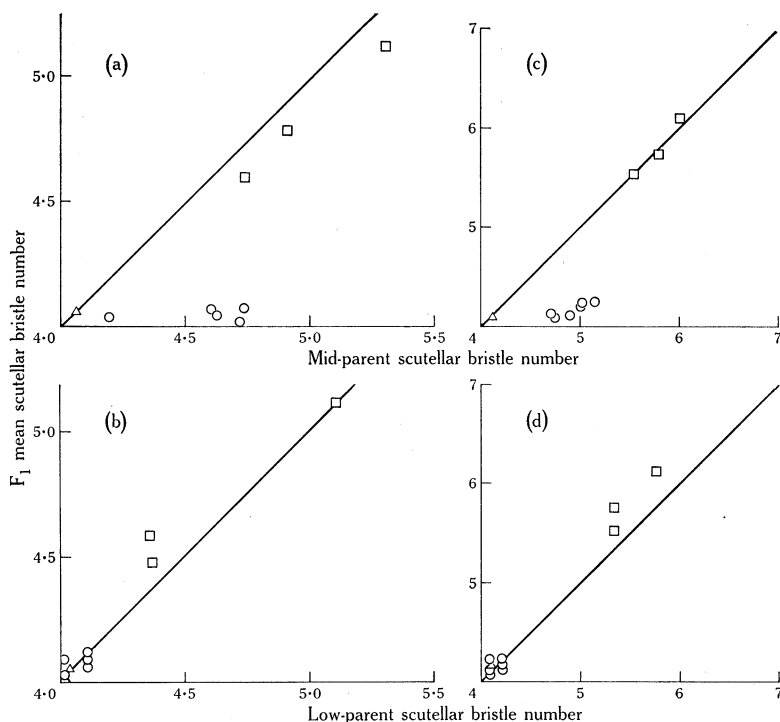


Fig. 3.—Mean scutellar bristle number, averaged over reciprocal crosses (□, 3rd x 3rd; ○, 3rd x 2nd; △, 2nd x 2nd levels), of sc^+/sc^1 F_1 progeny plotted against mid-parent (a) and low-parent (b) scutellar bristle number, and of sc^+/Y F_1 progeny plotted against mid-parent (c) and low-parent (d) scutellar bristle number.

appears that sc^1 and sc^5 in heterozygotes do not affect the expression of the genes modifying $x\text{-vert}/x\text{-vert}$. The effect of sc^1 and sc^5 in males is marked; the ranges of scutellar bristle number were reduced to 0.1–0.2. There is a slight increase of sc^1/Y and sc^5/Y from AS4 to AH1, but it is obvious that most of the variation between the AH and AS lines is not expressed in sc^1/Y and sc^5/Y . The substitution of *scute* alleles for sc^+ in males is epistatic to both $x\text{-vert}$ and the modifiers of the expression of this gene. Since the α -system of genes is not suppressed by the substitution of *scute* alleles for sc^+ , it appears that the variation of the expression of $x\text{-vert}$ lines is not due to the α -system, but rather, is due to another multigenic system, termed the β -system. The β -system is completely or almost completely suppressed by substitution of *scute* alleles for sc^+ .

(d) Crosses between Lines

Fraser (1965) compared means of scutellar bristle number in F_1 progeny with mid-parent expectation for a series of crosses between a set of extra scutellar lines. He found that the bristle number in the F_1 progeny from crosses of third-level lines agreed with their mid-parent expectation, that the bristle number in the F_1 progeny from crosses of second-level lines showed a slight regression towards the norm of 4 bristles, and that the number of bristles in F_1 progeny from crosses of second- with third-level lines showed a marked regression towards the norm of 4.

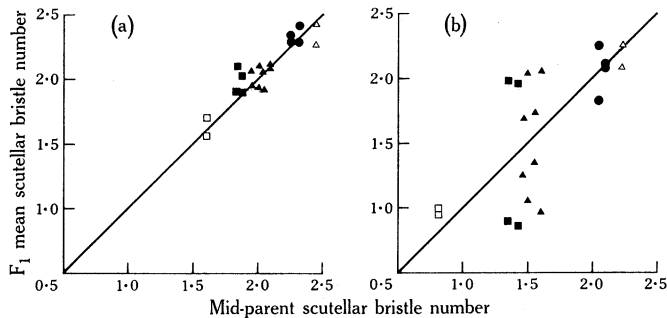


Fig. 4.—Mean scutellar bristle number, with values shown separately for reciprocal crosses between A lines (\triangle , 6×21 ; \blacktriangle , 1×6 , 21; \bullet , $9, 18 \times 6$, 21; \blacksquare , $9, 18 \times 1$; \square , 9×18) of sc^1/sc^1 (a) and sc^1/Y (b) F_1 progeny plotted against mid-parent bristle number.

In the present study there is a general agreement with Fraser's (1965) results of mid-parent expectation for sc^+/sc^+ , sc^+/Y , sc^+/sc^1 , and sc^+/sc^5 . This is illustrated for the sc^+/sc^1 genotype in Figure 3(a), and in Figure 3(c) for the sc^+/Y genotype. Erway's (personal communication) discovery that the third-level lines are homozygous for $x\text{-vert}$ provides an explanation for the regression of the F_1 means from second- \times third-level crosses below the mid-parent means. Such F_1 progeny will be $x\text{-vert}/x\text{-vert}^+$ and since $x\text{-vert}$ is recessive the mid-parent expectation will be an overestimate. Figures 3(b) and 3(d) show the data plotted against low-parent expectation for the sc^+/sc^1 and sc^+/Y genotypes respectively. There is a reasonable agreement showing that the major cause of the deviation of second- \times third-level F_1 means from mid-parent expectation is the recessivity of the $x\text{-vert}$ gene.

The *scute* genotypes sc^1/sc^1 , sc^1/Y , sc^5/sc^5 , and sc^5/Y do not show the heterogeneity of relationship of F_1 to mid-parent values. This is illustrated for sc^1/sc^1 and sc^1/Y in Figures 4(a) and 4(b) in which bristle numbers for the reciprocal crosses are shown separately. The heterogeneity between reciprocal crosses involving sc^1 A9 (3rd) and sc^1 A9 (3rd) lines which has been discussed above is apparent. Bristle number for sc^1/Y F_1 progenies of reciprocal crosses have been averaged in Figure 5. There is a clear agreement of F_1 values with those of mid-parent, indicating that the genetic system controlling variation of scutellar bristle number in *scute* genotypes is essentially additive. Fraser (1965) has shown that the same conclusion is valid for the third-level (sc^+ , $x\text{-vert}$) lines, but he concluded from the marked regression of second- \times third-level crosses towards the low-parent number, that variation of bristle number in second-level lines had a marked epistatic component. The results

above show that this phenomenon can be explained by the recessivity of the *x-vert* gene. A further study is in progress to determine the characteristics of the genetic control of second-level variation.

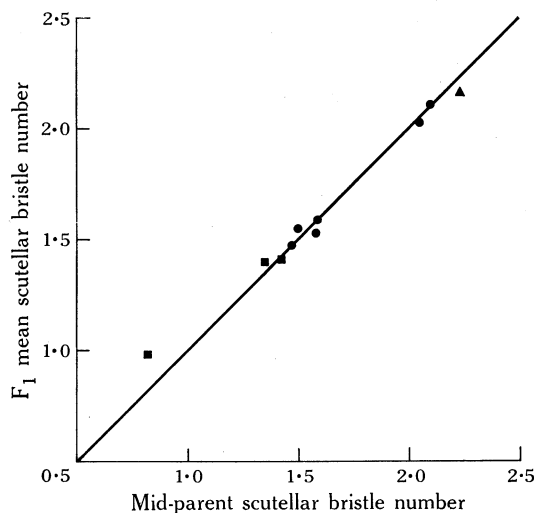


Fig. 5.—Mean scutellar bristle number, averaged over reciprocal crosses (■, 3rd × 3rd; ●, 3rd × 2nd; ▲, 2nd × 2nd levels), plotted against mid-parent values for *sc*¹/*Y* F₁ progeny.

IV. DISCUSSION

Our study involves *scute* lines selected for increased number of scutellar bristles. Two types of response to selection can be distinguished. In one type the *x-vert* gene was not involved; these lines are *x-vert*⁺/*x-vert*⁺. In the other type the *x-vert* gene was involved; these lines are *x-vert*/*x-vert*. The *scute* genes *sc*¹ and *sc*⁵ were substituted for *sc*⁺ in a set of these lines, showing that the genes responsible for the selection advance in the *x-vert*⁺ lines are similarly expressed in *sc*⁺ and *sc* genotypes, which contrasts with the effect on the genes responsible for the selection advance in the *x-vert* lines. In the *x-vert* lines the substitution of *sc* for *sc*⁺ suppresses the genes responsible for the selection advance. There are data (Fraser, personal communication) indicating that the genes responsible for the selection advance in *x-vert*⁺ lines are suppressed by the substitution of *x-vert* for *x-vert*⁺.

These results lead to the conclusion that two multigenic systems, the α - and β -systems, act to determine the variation of scutellar bristle number, with the *scute* and *x-vert* loci acting as a switch system determining which of the multigenic systems is expressed.

Switch Loci	α -System	β -System
<i>sc</i> ⁺ / <i>sc</i> ⁺ , <i>x-vert</i> / <i>x-vert</i>	—*	Expressed
<i>sc</i> ⁺ / <i>sc</i> , <i>x-vert</i> / <i>x-vert</i>	—*	Expressed
<i>sc</i> ⁺ / <i>sc</i> ⁺ , <i>x-vert</i> / <i>x-vert</i> ⁺	Expressed	Suppressed
<i>sc</i> / <i>sc</i> , <i>x-vert</i> / <i>x-vert</i> ⁺		
<i>sc</i> / <i>sc</i> , <i>x-vert</i> ⁺ / <i>x-vert</i> ⁺	Expressed	Suppressed

*There are indications that the α -system is suppressed in the *sc*⁺, *x-vert* genotypes.

A feature of the *x-vert* gene is its effect on a range of bristles, causing increases in the numbers of scutellar, dorsocentral, and vertical bristles (see Fraser, Erway, and Brenton 1968). The expression of this wide range of effects increases from the low to the high *x-vert* lines, i.e. the β -system acts on the wide range of expression. There are data (Fraser, personal communication) showing that the β -system can be expressed in *sc*⁺, *x-vert*⁺ but to a limited degree and only on scutellar bristles. Erway (personal communication) has further observed that the suppression of *x-vert* by *scute* for scutellar bristle number does not extend to the effects of *x-vert* on dorsocentral and vertical bristle number. Clearly, a full understanding of the genetic control of development of scutellar bristles will need to include consideration of other bristles. Fraser, Nay, and Kindred (1959) have shown the utility of such an extension in their analysis of the genetic control of vibrissae and coat development in the mouse.

A speculative working model that we have adopted is the following:

Switch Loci	α -System	β -System
<i>sc</i> ⁺ , <i>x-vert</i>	Suppressed	Enhanced*
<i>sc</i> ⁺ , <i>x-vert</i> ⁺	Expressed†	Expressed†
<i>sc</i> , <i>x-vert</i>		
<i>sc</i> , <i>x-vert</i> ⁺	Enhanced	Suppressed

* Manifold effects.

† Under restrictions of 4-zone canalization.

This model is suggestive of the type of genetic system that could be considered as operative in determining a fixed norm. The two multigenic systems are oppositely enhanced and suppressed as the status of the *sc* and *x-vert* loci determines the deviation from the norm of 4 bristles. Waddington (1955) considering the genetic control of crossvein in *Drosophila* has devised models involving "a number of threshold phenomena or feed-back mechanisms attributing these not to the individual gene loci but to sub-systems of the developmental system." Rendel, Sheldon, and Finlay (1965) consider that the *scute* locus determines the number of scutellar bristles with a suppressor system regulating its action. The analogy with our model is obvious.

The existence of two genetic systems reconciles the results and conclusions derived from selection experiments in *scute* stocks (see Rendel 1959; Fraser 1966) with results derived from selection in non-*scute* stocks (see Fraser and Green 1964). Selection in *scute* stocks acts on the α -system, producing correlated responses in non-*scute* genotypes, whereas selection in non-*scute* stocks may act on the α -system if *x-vert* is absent, or on the β -system if *x-vert* is present. Responses of the latter type will not produce correlated responses in *scute* genotypes. This raises the possibility of accumulating selection responses in both the α - and β -systems. A test can be made by maintaining homozygous *x-vert* lines in segregation for *scute*, selecting for increased number of scutellar bristles in both *scute* and non-*scute* segregants.

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