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Studies on the Scutellar Bristles of *Drosophila melanogaster*. IV.* Selection for Low Bristle Number in Oregon-RC Wild-type Lines

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Abstract

Results are presented of 130–145 generations of selection for low scutellar bristle number in four lines of *D. melanogaster* derived directly from an Oregon-RC wild-type stock and in one derived from an Oregon-RC line selected for low sternital bristle number. The most rapid initial response and the lowest mean scutellar bristle number ultimately reached, just below 2 bristles, occurred in a line in which the response was due to a new recessive gene located at approximately 17·4 on the X chromosome. Three of the other four lines reached a plateau just above a mean of 2 bristles after different patterns of response. These plateaux reflected a new canalization or threshold phenomenon at 2 bristles in these lines. The remaining line reached a mean of about 2·5 bristles after some 50 generations and remained at that level or slightly higher thereafter, but had no indication of canalization at 2 bristles. Two relaxed lines were derived from each selection line at different times and showed variable patterns of regression towards the base population level.

In the early generations of selection, as the mean bristle number slowly dropped below the canalized wild-type level of 4 bristles, flies with more than 4 bristles continued to appear, i.e. the probit width of the 4-bristle class tended to drop from its unselected level of 5·4–5·8σ to quite low levels in the selection lines and to recover in the relaxed lines as their mean bristle number moved back towards the unselected level. This could not be interpreted in the same way as similar phenomena in high-selection lines, i.e. selection of poor regulators of the scute locus. Other possible explanations for these results and for the new canalization observed at 2 bristles were considered without being able to accommodate them fully within a modified model of regulation of the scute locus. The most likely possibility seems to be that the low selection response is due to selection of less-efficient alleles of a gene which is the inducer of the scute locus. A large reduction in the degree of dominance of sc^+ over scute (sc^l) was also observed in these selection lines, which may be compatible with the above explanation.

Correlated responses in sternital bristle number in the selection and relaxed lines, while generally positive, were not closely related to the pattern of change in scutellar bristles. The dominance of sc^+ over sc^l in respect of sternital bristles showed little change except in one line where it increased, while dominance in respect of scutellar bristle score decreased.

Introduction

The character scutellar bristles has been widely used in selection studies in *Drosophila melanogaster*, especially in relation to the mechanism of canalization of the wild-type phenotype at 4 scutellar bristles. A series of selection and related experiments by Rendel and colleagues led to the development and subsequent modification of a model attributing this canalization to regulatory gene control over the scute locus (Rendel *et al.* 1965; Rendel 1967, 1976; Sheldon and Milton 1972). The model seems to have accommodated

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satisfactorily the results of a range of experiments, most of which involved lines selected for high number of scutellar bristles (Sheldon and Evans 1981). Many experiments have been reported in which no difficulty was experienced in selecting for *high* number of scutellar bristles starting from a canalized wild-type base population (see Sheldon 1968; Sheldon and Milton 1972; Sheldon and Evans 1981 for reports of their own work and references to other work referred to in the discussion and in Appendix 2). Gibson (1968) concluded from the previous literature that successful selection for low number of scutellar bristles usually involved the presence of a major mutant which reduced the number below four. He referred to Payne (1918) whose single attempt to establish a low line from wild type was unsuccessful, though a low line was developed successfully from his mutant strain 'reduced'. This strain was derived from a single scute male which turned up in the sixth generation of his high wild-type selection line (Payne 1918, 1920). Gibson also referred to one of Fraser's (1963) *D. simulans* low lines in which apparently a single major mutant 'Bare' was present. However, Fraser's paper also gave pooled results of other *melanogaster* and *simulans* low lines, not containing such a mutant, in which bristle number was reduced by selection over five generations. The number of such lines and the number of unsuccessful attempts were not given. In the light of Fraser's results, Gibson's generalization from these two references was probably not justified. Nevertheless, other results from the present authors did tend to support the Gibson (1968) generalization.

Sheldon (1968) reported two attempts to establish low-selection lines from an Oregon-RC wild-type stock. In one line virtually no change occurred in frequency of flies with less than 4 bristles over four generations of selection in which a total of 14 533 females and 14 588 males were scored, so it was discontinued. In the other attempt the very large random Oregon-RC base population had 10 females with 3 bristles out of 10 031 scored (0·10%) and 50 males with 2 or 3 bristles out of 9861 scored (0·51%). These were selected to start the low line, but the low bristle number of over a quarter of these 50 males was subsequently shown to be due to the presence of a major sex-linked recessive mutant not located at the scute locus, so the attempt to establish a selection line was abandoned. Sheldon and Evans (1981) began a low-selection line from a further large random sample of Oregon-RC wild-type stock which had five females with 3 bristles out of 7237 (0·07%) and 12 males out of 7302 (0·16%). After four generations, starting from these selected 3-bristle flies, had yielded only two females and two males with 3 bristles out of about 10 000, this attempt too was abandoned.

The results of several later attempts which were successful are presented in this paper. Their analysis, as with our high-selection lines referred to above, is particularly directed to the mechanisms of genetic regulation responsible for dominance of wild-type (sc^+) over scute (sc^1) and for canalization of development at 4 scutellar bristles.

Materials and Methods

Samples of larvae from the Oregon-RC wild-type strain exposed to heat shock at 37°C form the basis of four of the five low-scutellar bristle selection lines reported in this paper. The scutellar bristles of wild-type *D. melanogaster* are highly canalized at 4 bristles, the appearance of a 5-bristle fly at 25°C being rare (approximately 1% in females and 0·5% in males) and that of a 3-bristle fly even rarer (0·2% in males, 0·1% in females). To establish wild-type low-scutellar lines, therefore, it was considered necessary to expose some of the underlying variation by heat shock and try to select upon this variation.

A sample of 60 just-hatched (0 h) larvae were placed in bottles at 25°C, exposed to 37°C for specific periods of the third larval instar, and then allowed to complete development at 25°C. The bristle scores of flies arising from the heat treatments are given in Table 1. Flies arising from heat treatment at 78–89 h, which were used to establish high-selection line A5 of Sheldon and Evans (1981), are included for comparison.

Selection lines A1, A2, A3 and A4 were established from resulting single males with 3 scutellar bristles, i.e. A1 from the 3-bristle fly with posterior bristle missing, and A2 from the 3-bristle fly with anterior bristle missing, of the 61–71 h treatment; A3 from the 3-bristle fly with anterior bristle

missing, of the 71–77 h treatment; and A4 from the 3-bristle fly with anterior bristle missing, of the 72–82 h treatment. In each case the single male with 3 bristles was mated to one female with 4 scutellar bristles.

Table 1. Distribution of scutellar bristle scores following heat treatment at 37°C of larvae at different stages of development

a, anterior bristle missing; p, posterior bristle missing

Larval development stage at time of heat treatment (h)	Number of females in scutellar bristle class					Number of males in scutellar bristle class			
	3	4	5	6	7	3	4	5	6
61–71	—	251	12	2	—	1a, 1p	260	2	—
68–74	—	455	28	1	—	2p	445	7	—
71–77		323	20	2	—	1a, 2p	325	8	—
72–82	1a	75	1	1	—	1a	78	—	—
78–89		154	52	16	1	—	162	71	1
Control (from Sheldon 1968)	5 (2a, 3p)	7151	81	—		12 (3a, 9p)	7278	21	—

For the first 40 generations, the matings among the flies selected for low-scutellar bristle number were usually assortative, i.e. lowest by lowest, etc. This resulted in some single-pair matings especially in the early generations. Table 2 gives the bottle numbers, selection intensities, numbers scored and numbers selected for females in generations 1–8 and 9–40. Generations 1–8 showed variable incidence of low-bristle flies, so parent and bottle numbers were quite variable. After this time, five bottles were set up each generation in each line, and parent numbers were more stable.

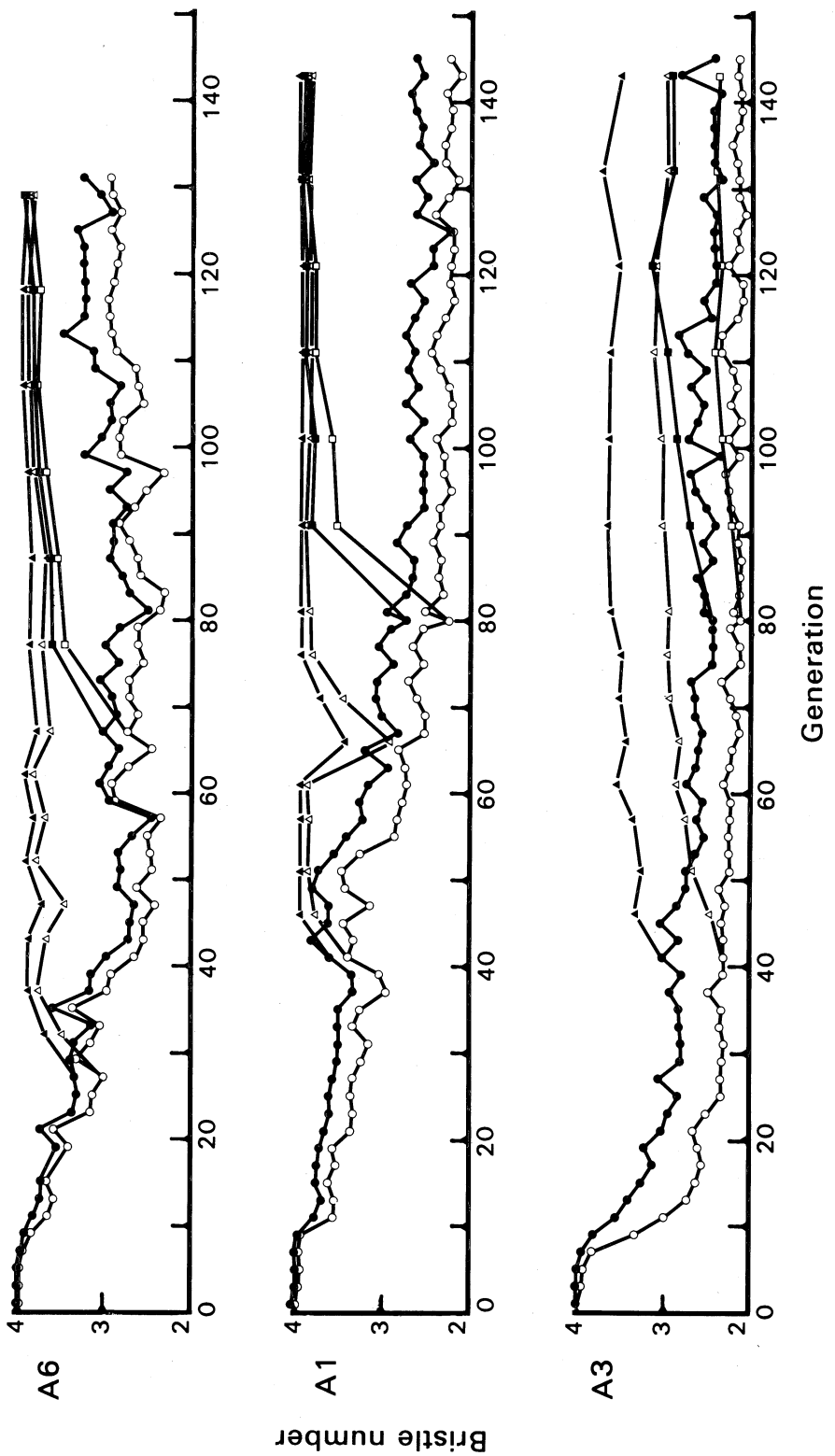
Table 2. Management details of lines A1–A4

Line	Generations 1–8							
	Bottle numbers		No. scored[A]		No. selected[A]		Selection intensity (%)[A]	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
A1	1	6	76	862	3	60	39·5	0·5
A2	3	15	91	1006	16	71	33·0	3·3
A3	2	6	70	565	9	45	42·86	1·54
A4	1	6	67	900	1	30	44·78	0·79

Line	Generations 9–40								
	Number scored[A]			Number selected[A]			Selection intensity (%)[A]		
	Min.	Max.	Av.	Min.	Max.	Av.	Min.	Max.	Av.
A1	112	703	337·2	20	35	29·3	28·6	6·6	15·0
A2	62	662	266·1	14	46	31·7	46·8	5·5	19·6
A3	95	696	417·4	25	34	30·5	31·6	7·7	13·8
A4	95	809	423·7	25	50	34·0	31·6	8·2	16·3
A6[B]	161	1328	—	10	124	—	38·9	1·01	—

[A] Values given are for females (male values similar). [B] Generations 1–32.

In each line a sample of flies was scored for number of abdominal bristles on the fifth sternite, in both sexes in the eighth, tenth and eleventh generations and every alternate generation to generation 35, then generation 38. In the first three generations of abdominal scoring 10–15 flies per scutellar bristle class were scored in each of the five bottles, but in all subsequent scorings this number was five per scutellar class. Generations scored for abdominal bristles were scored to the ninth day rather than the usual third or fourth day of emergences. Selected flies, however, were taken from the first 3–4 days of emergence in all generations.


A6
A1
A3
Bristle number
Generation
0
20
40
60
80
100
120
140
2
3
4

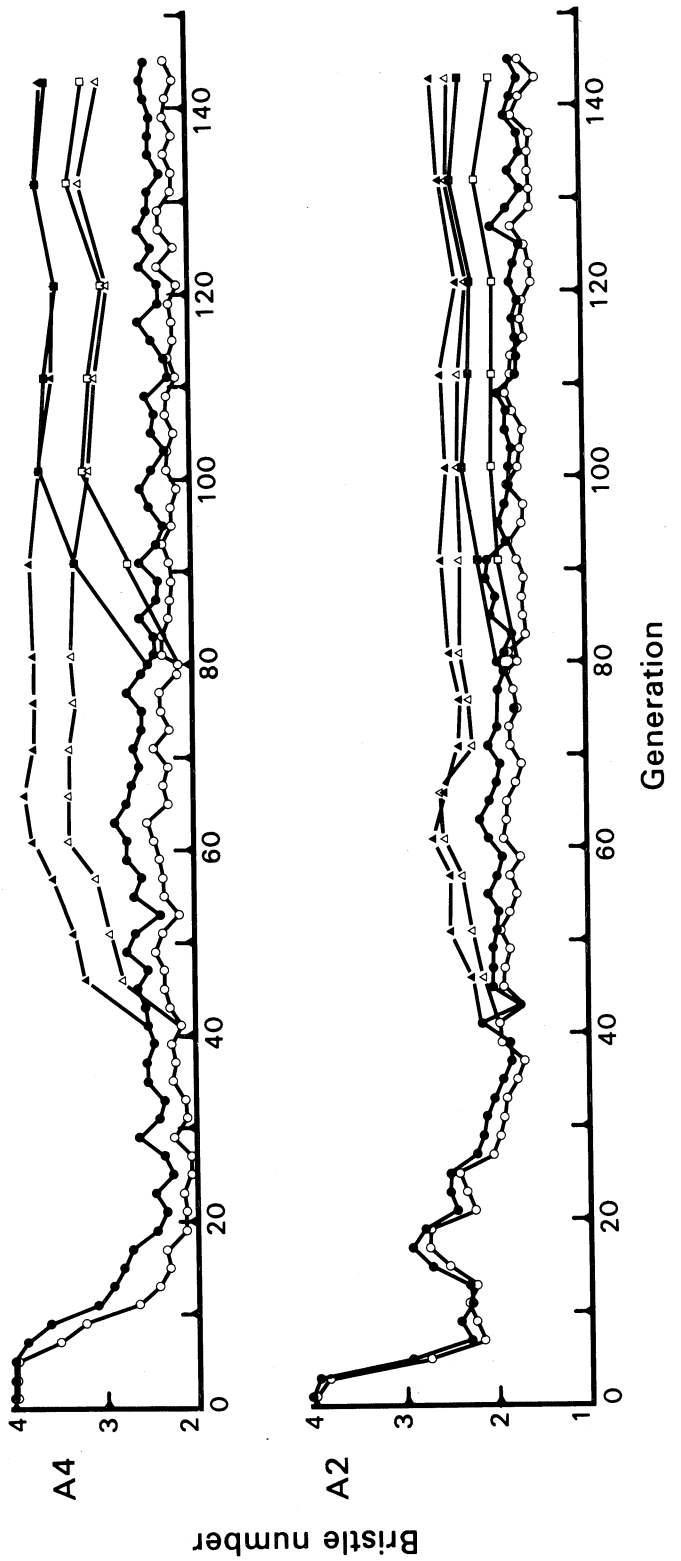


Fig. 1. Scutellar bristle selection response lines A1, A2, A3, A4, A6 and in the relaxed lines, Random 1 and Random 2, derived from each of them. Selection line females (●), males (○). Random 1 females (▲), males (△). Random 2 females (■), males (□).

The A6 line arose as a separate attempt to establish a low line. Two males with 3 scutellar bristles were scored in the first backcross generation of a random scute (sc^1) population backcrossed to a low abdominal bristle line (Young and Sheldon 1965) and were set up with females with 4 scutellar bristles from that line. The F_2 of this cross (generation 1 of A6 selection) yielded one female and six males with 3 bristles and one type A female and three type A males with 4 bristles out of 1328 females and 1293 males scored. Type A flies had 1 anterior and 1 posterior scutellar bristle on one side, i.e. normal, but 2 anterior and no posterior bristles on the other side. They usually also had a nick or indentation on the posterior margin of the scutellum where the posterior bristle was missing. They subsequently occurred in all the low lines at frequencies up to 20% of 4-bristle flies, but in all except A6 they were not selected. In A6 type A flies were selected as well as flies with less than 4 bristles.

As in other low lines reported here, A6 was assortatively mated for the first 26 generations. Up to generation 10, matings were made of type A × type A and type A × normal 4-bristle flies as well as between flies with less than 4 bristles. After generation 10, enough of the latter were available as parents and no further type A matings were made. Minimum and maximum values for number scored, number selected and selection intensity for either sex are given in Table 2. Abdominal bristles were not scored in A6 before generation 32 (see below for details).

From generation 40 in lines A1–A4 and generation 26 in A6, the selection procedure was standardized. In the following description of the later selection procedures, the first generation numbers refer to lines A1–A4 and the following numbers in brackets to line A6.

In generations 41–93 (27–80) 120 pairs were scored and the lowest 40 pairs selected. These flies were then set up in five bottles, eight pairs per bottle. In generations 94–145 (81–131) 60 pairs were scored, the lowest 30 selected and set up in five bottles. From generation 146 (132) the lines were maintained by pooling all emerged flies and selecting the first 30 pairs with 2 scutellar bristles or less and setting these up in two bottles, each with 15 pairs.

All flies emerging to the 19th day after cultures were set up were scored for scutellar bristles, and a sample of five flies per bristle class per bottle scored for abdominals at generations 46, 51, 57, 61, 71, 110, 145 (32, 37, 43, 47, 57, 96, 131).

At generation 41 (26) a relaxed line (Random 1) of five bottles, eight pairs per bottle, was taken off each selection line. Full scorings (see previous paragraph) of these lines were made at the following generations of the selection line: 46, 51, 57, 61, 66, 71, 76, 81, 91, 101, 111, 121, 132, 143 (32, 37, 43, 47, 52, 57, 62, 67, 71, 87, 97, 107, 118, 129).

At generation 80 (66) a second relaxed line (Random 2) was taken off each selection line and maintained in the same way. Full scorings occurred at generations 91, 101, 111, 121, 132, 143 (77, 87, 97, 107, 118, 129) of the selection line.

The random lines were scored in the same manner as the selection lines. After generation 145 these lines were maintained in one bottle with 40 pairs of parents.

The scute (sc^1) mutant was backcrossed into each selection line for five generations starting from generation 41 (27). From the fifth backcross generation single pair matings were set up to produce +/+, +/*sc*, *sc*/*sc*, +/*Y* and *sc*/*Y* genotypes which were scored for scutellar bristles and for abdominal bristles (five scored per scutellar bristle class per bottle).

Results

Scutellar Bristles

Selection response

Fig. 1 shows the selection response in each selection line and the regression of the relaxed lines towards base population level. The selection lines are shown in order of increasing rate and absolute level of response. All lines except A2 have an initial period of 5–10 generations of little response in bristle number before steady downward response begins. Then each line exhibits a different pattern of response, though three out of five (A1, A3 and A4) plateau at the same level, just above 2 bristles, at different times. Only in A2 does the mean bristle number decline to below 2 bristles. The sex difference varies both between and within lines. The pattern of regression of response on relaxation of selection also varies between lines. In A1 and A6 the relaxed lines regress almost back to unselected level; in A3 and A4 they stabilize at an intermediate level, and in A2 only slight regression occurs.

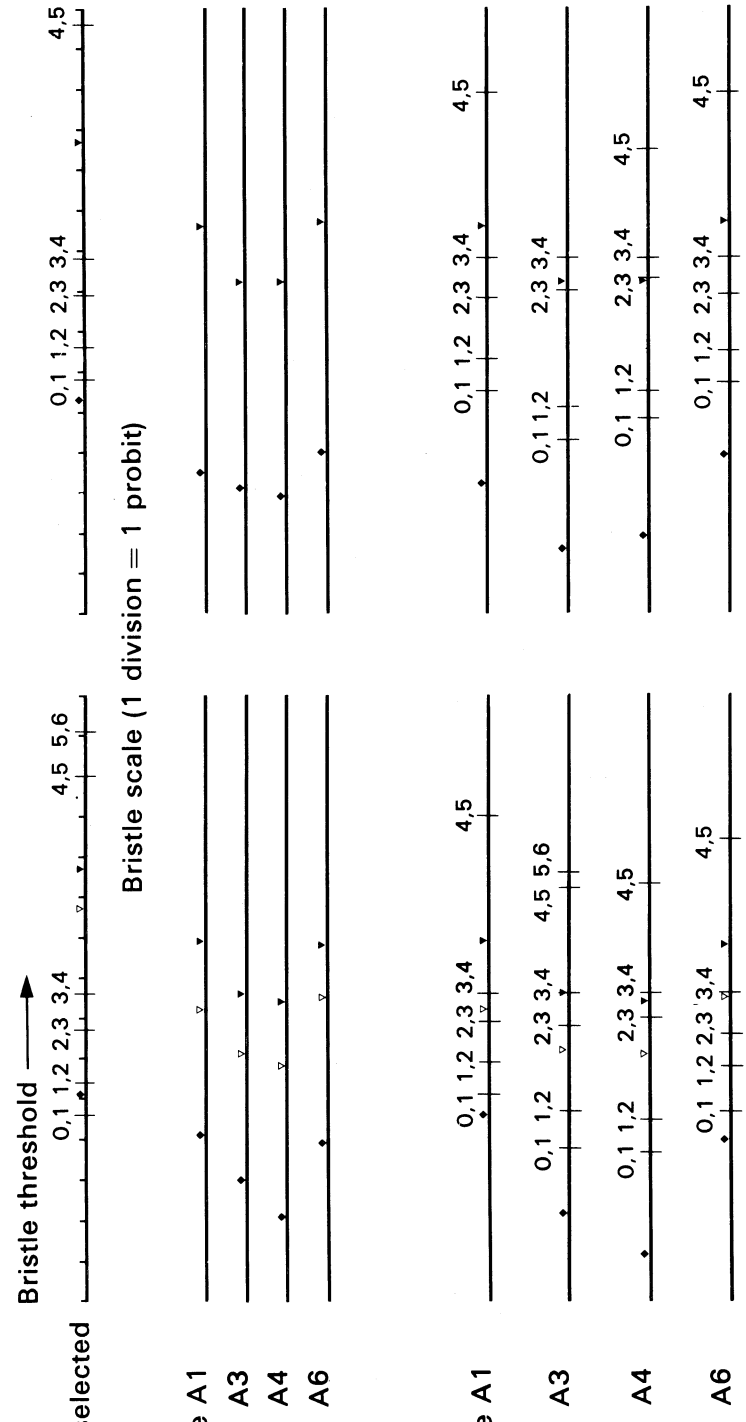


Fig. 2. Positions of genotypes *sc/sc*, +/*sc*, +/+, *sc/Y* and +/*Y* in unselected flies and in the scute backcross populations of lines A1, A3, A4, A6, plotted (*a*) on a common probit scale as in the unselected population, and (*b*) having a common 3,4 bristle threshold, but individual line values for the other bristle thresholds where the actual value or a minimum estimate below the 3,4 or above the 4,5 thresholds could be calculated. Otherwise the value for the common scale was used. In females the values used are for +/+ and not +/*sc*. Females: ◆ = *sc/sc*, ▽ = +/*sc*, ▼ = +/+. Males: ◆ = *sc/Y*, ▼ = +/*Y*.

Probit transformation

Probit transformation of the data represented in Fig. 1 provides distributions of probit widths (standard deviations) of each scutellar bristle class and therefore information on

Table 3. Probit widths (standard deviations) of different scutellar bristle classes in lines A1 and A3

Generations	Line A1 females			Line A1 males			Line A3 females			Line A3 males		
	3-	4-	5-class	2-	3-	4-class	2-	3-	4-class	2-	3-	4-class
2		4·77	0·98		0·96	4·71			5·53	0·76	0·59	4·23
3		4·96			0·15							
5									5·31		0·75	4·53
7		4·84						0·76	4·63		1·15	
8		4·98			1·02	4·91		1·27		1·62	1·16	
9	0·53				0·98	4·55		1·28		1·67	1·20	
10	0·80	3·79			1·09							
11–15	1·07	3·12			0·96	3·26	1·46	1·04	2·94	2·34	1·08	
16–20	0·89	3·02			0·95	2·74		1·00		2·70	1·10	
21–25	0·91	2·86	0·88		0·89	2·88		0·93		2·77	1·01	
26–30	0·93	3·05			0·86	2·83	2·33	0·99		2·95	1·07	
31–35	0·90	2·85			1·01	2·69		0·96		3·24	1·03	
36–40	1·01	2·39		2·07	0·96		2·30	1·05		3·17	1·09	
46	0·90	3·40			0·97							
51	1·01	3·54			0·94			1·13		3·37	1·32	
57	0·91				0·99		2·99	1·13		3·77	1·06	
61	1·03	2·71		2·92	0·86			1·08		3·38	1·22	
66	0·99	2·21			0·88			1·13			0·91	
71	0·95			3·00	0·87			1·21		3·66	1·32	
110	0·79[A]			2·76[B]	0·84		2·93	1·19		3·51	1·61	
145	0·87			3·49	0·91		3·38	1·21			1·60	

[A] 2-class width: 2·69. [B] 1-class width: 0·76.

Table 4. Probit widths (standard deviations) of different scutellar bristle classes in lines A2 and A4

Generations	Line A2 females			Line A2 males			Line A4 females			Line A4 males		
	1-	2-	3-class	1-	2-	3-class	2-	3-	4-class	2-	3-	4-class
2						0·66[C]			5·68			5·46
3			0·89[A]			0·66						
4		1·51	0·53[B]		2·32	1·04						
6–10		2·21	0·95	1·01	2·33	1·14						
11–15	0·74	2·23	1·16	1·03	2·11	1·24	2·39	0·93		3·00	0·79	
16–20	1·00	2·06	1·02	0·77	2·03	1·06	2·07	0·97	2·13	3·61	0·80	
21–25	1·04	1·93	1·20	1·39	1·84	1·60	3·53	1·05		4·35	0·93	
26–30	1·15	2·14	0·95	1·39	2·19	1·13		0·91		3·87	0·77	
31–35	1·40	1·97	1·07	1·34	2·13	1·06	3·22	0·86		3·84	0·66	
36–40	1·13	2·28	1·33	1·30	2·12	1·16		0·83	1·48	3·56	0·72	
46	1·01	1·93	1·50	1·34	2·28	0·88						
51	1·14	2·01	1·11	1·58	1·76	1·29		0·63		3·41	0·78	
57	1·19	2·13	1·10	1·25	2·15	0·99		0·50			0·73	
61	1·06	1·57	1·24	1·24	1·92	1·54		0·60		3·31	0·76	
66		1·81	1·26	1·13	2·15	1·25		0·55		3·21	0·52	
71		1·40	1·23	1·10	2·83		3·17	0·48		3·03	0·79	
110	1·72	2·28	1·10	1·26	2·33		3·60	0·81		4·10	0·97	
145	1·13	2·12		1·79	2·04			0·84		3·38	0·98	

[A] 4-class width: 4·48. [B] 4-class width: 3·03. [C] 4-class width: 3·72.

changes in degree of canalization at 4 scutellar bristles, on general changes in variance and on any tendency to canalization at other bristle classes (Rendel 1967). Because of the large volume of data to be summarized, and because relevant changes occur mainly in the 4- or 2-bristle classes, presentation of data is restricted to those early generations where measures of the 2- or 4-class probit widths were possible, then to five generation averages up to generation 40, and finally to the generations when large numbers of flies were scored for scutellars. These data are presented for lines A1 and A3 in Table 3, for A2 and A4 in Table 4, for A6 in Table 5 and for the relaxed lines in Table 6. As the mean bristle number declines in the selection lines, the probit width of the canalized 4-bristle class decreases from the base population level of $5 \cdot 4\sigma$ in females and $5 \cdot 8\sigma$ in males, and continues to decrease until it is no longer measurable. In the relaxed lines where the mean bristle number regresses most towards 4 bristles the probit width of the 4-bristle class increases again towards base population level. This pattern of change in probit width of the 4-class, with selection and relaxation of selection, is similar to what happens in high-selection lines (Sheldon and Milton 1972; Sheldon and Evans 1981) and will be discussed later.

Table 5. Probit widths (standard deviations) of scutellar bristle classes in line A6

Gener-	Line A6 females					Line A6 males				
ations	1-	2-	3-	4-	5-class	1-	2-	3-	4-	5-class
1				5·65					5·77	
2				5·04					4·98	
3				4·67	0·67				4·88	
5			0·62	4·42	0·99				4·72	
6–10			0·99	4·07				0·88	4·27	0·47
11–15			1·08	3·32				1·09	3·25	
16–20			0·94	3·66				1·06		
21–25		1·60	0·87	3·23			1·53	0·86	3·39	
26–30	0·23	1·16	0·93			0·52	1·44	0·84		
32		1·92	0·96			0·24	2·01	0·88		
37	0·76	1·56	0·79			0·90	1·72	0·74		
42	0·71	1·74	0·81				1·77	0·88		
47	0·80	1·64	0·82			0·64	1·93	0·94		
52		1·46	1·05			0·57	1·64	1·00		
57		2·85	0·93			0·47	2·16	0·82		
96		1·87	0·82			0·73	1·86	0·91		
131		2·10	0·92			0·41	1·92	1·07		

The second main feature of the data is the large increase in probit width of the 2-bristle class in lines A1, A3 and A4, the three lines that reached a plateau of response just above 2 bristles. The probit data show that this plateau is a real barrier to further response in those lines, the increase in width of the 2-class to 3 or 4σ representing the presence or development of a canalization phenomenon at 2 bristles. In the relaxed lines the 2-class widths decrease towards unselected level of about $1 \cdot 5\sigma$ as the mean bristle number increases again.

Scute backcross populations

The scores of the scute backcross population are given in Table 7. Five generations of backcrossing were not sufficient to bring the mean bristle scores of the +/+ and +/*Y* segregants in the backcross populations to the level of the selection lines at generation 46 (32 for A6) though 97% of the backcross autosomal genotype should have been the same as the selection line by then. The +/+ genotype scores for backcross lines A1, A3, A4 and A6 in Table 7 are 0·24, 0·43, 0·56, and 0·68 bristles respectively above their contemporary selection line scores. The corresponding +/*Y* differences are 0·38, 0·57, 0·40 and 0·76 bristles. A possible reason for this lack of effectiveness of the backcrossing procedure could

Table 6. Probit widths (standard deviations) of scutellar bristle classes in relaxed lines

Generations	Line A1 females	Line A1 males	Line A2 females			Line A2 males			Line A3 females			Line A3 males		Line A4 males		Line A6 females[A]		Line A6 males[A]		
	4-	4-	1-	2-	3-	1-	2-	3-	2-	3-	4-	2-	3-	2-	3-	3-	4-	2-	3-	4-class
Random 1																				
46	3·78	3·59	0·88	1·96	1·18		2·02	1·08		1·18		2·91	1·29	2·51	1·01					
51	4·44			1·59	1·13	1·45	1·65	1·11		1·22		2·88	1·25			1·17	4·11		1·16	
57	3·98	4·09		1·72	1·23	1·39	1·87	1·40	1·85	1·18	2·99	2·58	1·18			1·12	3·69		1·35	
61	4·32	4·29	0·94	1·55	1·15	1·18	1·66	1·12		1·20		2·45	1·13							
66				1·46	1·13		1·81	1·20[B]		1·27		2·27	1·27			1·29	3·53		1·25	3·05
71		3·27	1·49	1·56	1·28	1·29	1·85	1·25		1·37		2·36	1·18							
76	3·85		1·33	1·72	1·09	1·15	1·79	1·21		1·23		2·30	1·25	1·95	1·19					
81	4·25	4·02	1·11	1·81	1·06		1·95	1·04		1·26	3·30	2·45	1·20			0·69	4·10		0·68	3·68
91	4·37			1·88	1·00	1·26	2·09	1·12		1·34	3·51	2·40	1·26	2·06	1·27	0·77	4·06	1·80	0·65	3·87
101	4·80		1·44	1·75	1·18	1·26	1·78	1·17		1·18	3·64	2·28	1·21	2·36	1·23					
111			1·12	1·80	1·15	1·59	1·90	1·25		1·32		2·37	1·31							
121	3·37		1·15	2·00	1·22	1·58	1·98	1·19								1·12	4·58	0·95	0·85	
132	4·62		1·29	1·45	1·09	0·83	1·75	1·14						2·04	1·33		4·90		0·85	
143	4·89			1·87	1·12	1·42	1·82	1·00		1·17	3·37	2·54	1·23	2·39	1·28	0·91	4·61		0·86	
Random 2																				
91	3·68		1·15	1·86	1·19	1·06	2·11	1·11		1·30		3·29	1·29	2·90	1·17	0·90[D]		1·89	0·93	
101			1·50	1·72	1·40	1·34	1·86	1·39		1·30		3·27	1·28		1·11[C]					
111	4·30		1·43	1·99	1·04	1·14	2·03	1·45	2·52	1·32		3·26	1·36							
121	4·69		1·07	2·15	1·04	1·23	2·25	1·19		1·36		3·09	1·36							
132	5·07			1·95	0·91	1·16	2·09	1·28		1·44		2·99	1·30							
143	4·97		1·48	2·14	1·06	1·16	2·25	1·40	2·13	1·22			1·41							

[A] Line A6 generations are 14 behind those given in column 1. [B] 4-class width: 1·74. [C] 4-class width: 2·7. [D] 2-class width: 1·68.

be the absence of crossing over in two of the five generations of backcrossing, because *sc w*^{bl} males had to be crossed back to the selection line for the second and fourth backcrosses. In the other three generations ++/*sc w*^{bl} females were used. However, this

Table 7. Means and frequency distributions of scutellar bristle number for all genotypes in the scute backcross populations of lines A1, A3, A4, A6

Line	Geno-type	Scutellar bristle class 0	1	2	3	4	5	6	Arithmetic mean	Probit mean
A1	+/+			18	58	769	1		3·89	1·34 above 3,4
	+/*sc*		2	304	419	390	1		3·08	0·38 below 3,4
	sc/sc	185	53	24					0·39	0·54 below 0,1
	+/*Y*			76	366	1562	1		3·74	0·77 above 3,4
	sc/Y	478	5						0·01	2·31 below 0,1
A3	+/+			111	147	263	2	1	3·30	0·02 above 3,4
	+/*sc*			759	183	109			2·38	0·59 below 2,3
	sc/sc	405	23	3					0·07	1·55 below 0,1
	+/*Y*		2	864	635	616			2·88	0·55 below 3,4
	sc/Y	914	3						0·00	2·72 below 0,1
A4	+/+			190	134	219	1		3·06	0·24 below 3,4
	+/*sc*		3	796	136	48			2·23	0·89 below 2,3
	sc/sc	298	2						0·00	2·47 below 0,1
	+/*Y*	1	7	1014	343	478	1		2·70	0·64 below 3,4
	sc/Y	575							0·00	at least 2·93 below 0,1
A6	+/+			9	60	540	3		3·88	1·21 above 3,4
	+/*sc*	1	3	244	324	454			3·20	0·14 below 3,4
	sc/sc	169	49	8					0·29	0·67 below 0,1
	+/*Y*	2	—	80	284	1488	1		3·76	0·85 above 3,4
	sc/Y	461	15	2					0·04	1·80 below 0,1

explanation would require a sizable *X*-chromosome effect in all the selection lines located towards the distal (scute locus) end of the chromosome. This can be ruled out because of the absence of differences between the reciprocal crosses, in the score of male progeny,

Table 8. Summary of genotype comparisons shown in Fig. 2

Line	Scale[A]	Distance in probits (σ) from unselected base *sc/Y*	*sc/sc*	+/*sc*	+/*Y*	+/+	Distance in probits (σ) within lines +/*Y*− *sc/Y*	+/*sc*− *sc/sc*	+/+− +/*sc*	Dominance ratio $\frac{(+/+-+/sc)}{(+/sc-sc/sc)}$
A1	C	1·8	1·0	2·5	2·1	1·8	6·1	3·1	1·7	0·55
	I	2·1	0·6	2·5	2·1	1·8	6·2	2·6	1·7	0·65
A3	C	2·2	2·1	3·6	3·5	3·1	5·1	3·1	1·5	0·48
	I	3·7	2·8	3·4	3·5	3·1	6·6	4·0	1·4	0·35
A4	C	2·4	3·0	3·9	3·5	3·3	5·3	3·7	1·6	0·43
	I	3·4	4·0	3·7	3·5	3·3	6·3	4·9	1·3	0·27
A6	C	1·3	1·2	2·2	2·0	1·9	5·7	3·6	1·3	0·36
	I	1·4	1·0	2·2	2·0	1·9	5·8	3·5	1·3	0·37
Unselected base	C						6·4	4·6	1·0	0·22

[A] C, on common (standard) probit scale as in Fig. 2*a*; I, on individual probit scales as in Fig. 2*b*.

when the selection lines were crossed to the base population Oregon-RC at about generation 200 (M. Evans and B. L. Sheldon, unpublished data). Therefore, the reason remains unknown, though such lack of full effectiveness of backcrossing has been fairly common

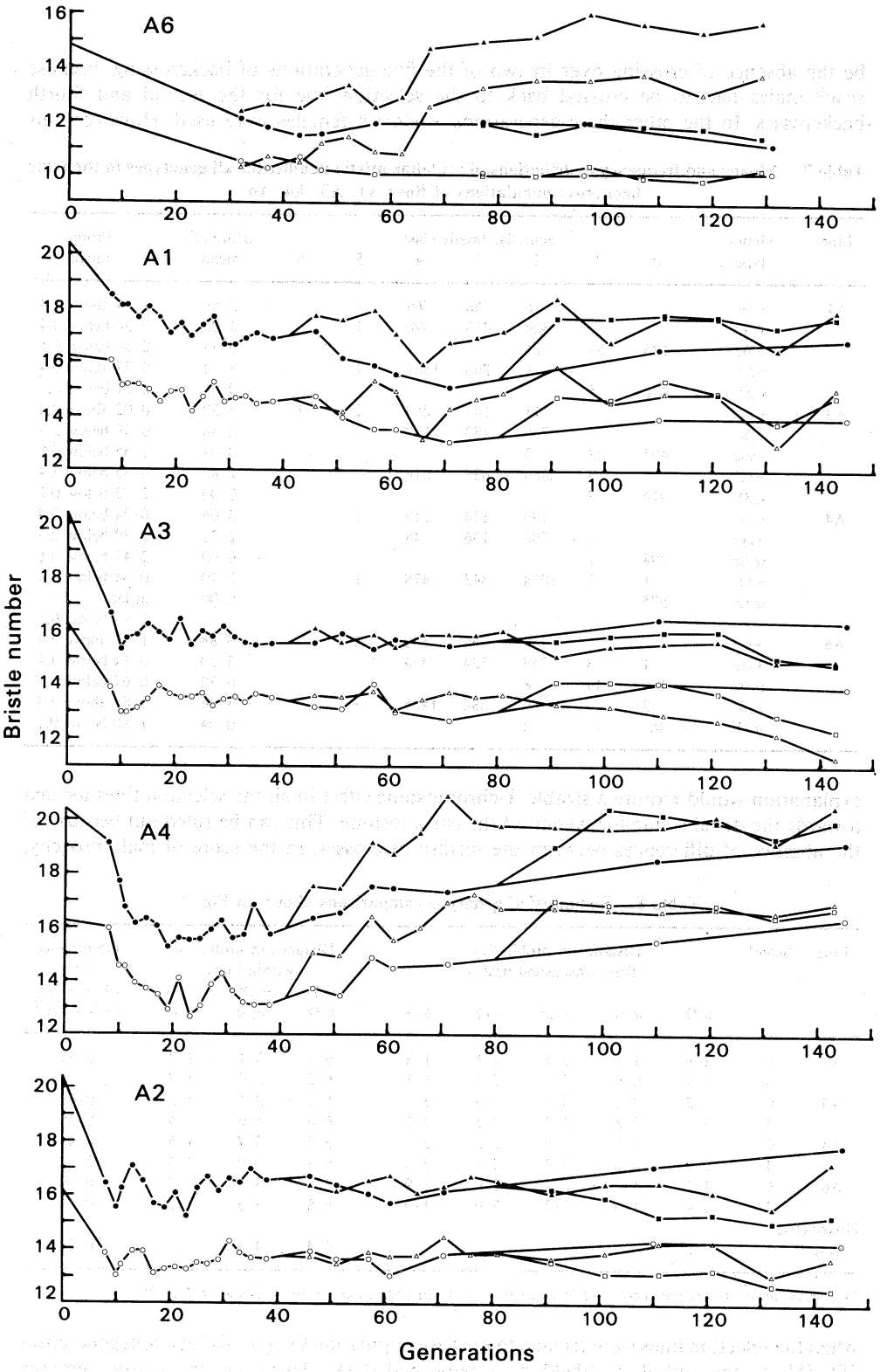


Fig. 3. Abdominal bristle correlated response in lines A1, A2, A3, A4, A6 and in the relaxed lines, Random 1 and Random 2, derived from each of them. Selection line females (●), males (○). Random 1 females (▲), males (△). Random 2 females (■), males (□).

in our experience (see Sheldon and Milton 1972; Sheldon and Evans 1981). Because of the proximity of +/+ and +/*Y* mean scores to the 3, 4 bristle threshold it is better to compare the effect of the selection responses in *sc* flies with the responses in + flies on the probit scale. Fig. 2 shows the genotypes in these four backcross lines plotted firstly on a standard probit scale, as used by Sheldon and Milton (1972) and Sheldon and Evans (1981), and secondly on the individual line probit scales, which reflect the variation between lines in probit widths of the different bristle classes.

Table 8 summarizes the movement of the different genotypes from unselected base on the two different probit scales, as well as the effects of the first and second substitutions of + for *sc*. Within lines the +/*Y* males have in general moved down further than the +/+ females, and the +/*sc* females further than both except in line A3. The *sc*/*Y* and *sc*/*sc* have moved less than the +/*Y* and +/+ except in line A4, but the ranking of the lines is similar for both *sc* and + segregants. As in the + segregants, the *sc*/*Y* males have moved further than the *sc*/*sc* females except in line A4. The ratios of the effects of second and first substitutions of + for *sc* are all increased, reflecting a reduction in degree of dominance of + over *sc* in all four lines, especially A1. This is also shown on the arithmetic (bristle) scale, where the ratios are 0·30, 0·40, 0·37 and 0·23 in A1, A3, A4, A6 compared with 0·02 approximately in the base population.

When the single-pair matings of the line A2 backcross population were scored, a sex-linked recessive gene for low bristle number, not located at the scute locus, was found to be segregating at a high frequency, indicating that this gene was virtually fixed in selection line A2. The details of this phenomenon are presented in Appendix 1.

Abdominal Bristles

The correlated responses in mean abdominal bristle number are shown in Fig. 3. The lines are presented in the same order as in Fig. 1, i.e. in order of increasing rate of scutellar bristle response. The maximum reduction in number of abdominal bristles was similar in all five selection lines 3·6 to 5·4 bristles (24–26%) in females and 2·4 to 3·6 bristles (19–22%) in males. However, the patterns of abdominal response were not highly correlated with the patterns of scutellar response. In all lines except A4, the maximum abdominal response occurred significantly earlier than the maximum scutellar response—some 10 generations earlier in A6 and A1, 20 generations in A3 and 30 generations in A2. Only in A4 did they coincide, at about generation 20. A second unusual feature was the subsequent increase of 1–2 bristles in abdominal mean in lines A1, A3 and A2, while the scutellar bristle mean remained at its minimum level, and in the case of A2, while the scutellar level was still decreasing. The opposite occurred in A6, where the abdominal bristle mean remained at the minimum level attained while the scutellar mean increased by about half a bristle.

Similarly, changes in abdominal bristles in the relaxed lines did not correlate well with the variable increase in scutellar bristles in all those lines. In several relaxed lines [A6 R(andom)2, A1R1, A2R1] the abdominal bristle means did not increase but merely fluctuated around their starting levels. In three lines (A1R2, A4R1, A4R2) the abdominals increased on roughly the same time scale as the scutellars. However, in A1R2, the abdominal increase was rather less than the increase in scutellars, while in the A4R lines it was considerably greater, since their abdominal means regressed back to the base population level, or slightly above it. In relaxed line A6R1, the abdominals regressed similarly to about 1 bristle above the base population mean but over a much longer time than the relatively smaller regression of the scutellar mean. In the remaining three lines, A3R1, A3R2, A2R2, the abdominal bristle mean actually decreased further (1–2 bristles) while the scutellar mean increased as a result of relaxing selection.

The abdominal bristle scores of all genotypes in the scute backcross populations of each selection line except A2 are given in Table 9. As with the scutellar bristles the backcrossing was not sufficient to bring the abdominal bristle means of +/+ and +/*Y* down to selection line levels. Line A6 was the best of the four lines in this respect for abdominals, reaching over 80% of the selection line level in the backcross, whereas it was the worst for scutellars. The percentage of the selection line response achieved in the other backcrosses was about 70% in both sexes for A1, 60% in females and 45% in males for A3, 60% in females and 30% in males for A4, the relativity between these three lines being broadly in line with that for scutellar bristles.

Table 9. Mean abdominal bristle scores within scutellar bristle classes in the scute backcross populations

Genotype	Scutellar bristle class								Weighted mean	Decrease from base population (%)
	0	1	2	3	4[A]	4	5	6		
Line A6										
+/+			12·2	12·2	12·3	12·5	13·0		12·4	16
+/*sc*			11·0	11·3	11·4	11·5			11·3	15
sc/*sc*	4·8	4·7	4·3						4·7	19
+/*Y*	12·0		10·8	10·7	11·0	11·0	13·0		10·9	13
sc/*Y*	4·1	3·9	4·0						4·1	10
Line A1										
+/+			17·1	17·1	18·3	18·0	20·0		17·9	12
+/*sc*		15·5	15·9	16·2	15·7	16·4	17·0		16·1	12
sc/*sc*	8·3	8·6	8·5						8·4	2
+/*Y*			15·0	14·9	15·1	15·2	13·0		15·1	7
sc/*Y*	6·5	7·0							6·5	0
Line A3										
+/+			16·9	16·8	16·7	18·2	16·5	17·0	17·5	14
+/*sc*			15·1	16·3	16·3	17·4			15·5	15
sc/*sc*	7·7	9·7	11·5						7·8	9
+/*Y*		14·0	14·2	15·0	15·4	15·7			14·9	8
sc/*Y*	5·6								5·6	14
Line A4										
+/+			15·6	17·6	17·4	18·5	22·0		17·2	16
+/*sc*		15·0	16·1	18·1	17·0	18·5			16·5	10
sc/*sc*	7·5	9·0							7·6	12
+/*Y*	13·0	14·5	14·3	15·7	16·6	16·8	16·0		15·2	6
sc/*Y*	6·2								6·2	5

[A] Type A.

The base population abdominal bristle means relevant to lines A1, A3 and A4 are 6·5, 8·6, 16·2, 18·3 and 20·4 for *sc*/*Y*, *sc*/*sc*, +/*Y*, +/*sc* and +/+ flies respectively, and 4·5, 5·8, 12·5, 13·3 and 14·8 respectively for line A6 (Young and Sheldon 1965). In general, the male scores in Table 9 have not decreased as much as the female scores, within either *sc* or + genotypes, but the *sc* genotypes (*sc*/*sc* and *sc*/*Y*) have decreased less than the + genotypes (+/+ and +/*Y* respectively) in some cases and more in others. That is, the response in *sc* genotypes is not well correlated with the response in the corresponding + genotypes. The dominance ratios calculated from the data of Table 9, i.e. (+/+−+/*sc*)/(+/*sc*−*sc*/*sc*) are 0·23, 0·26, 0·08 for lines A1, A3, A4 respectively, compared with 0·22 in their base population and 0·17 in A6 compared with 0·20 in its base population. In contrast to the scutellar bristle data line A4 is the only one showing a large difference from the base population, but here it is an increased dominance of + over *sc* rather than a reduction as in the scutellar data.

Discussion

Reduction in Canalization at 4 Scutellar Bristles

An unexpected feature of the selection response in these low lines was the decrease in probit width of the 4-bristle class as the mean bristle number declined under selection and its increase in the relaxed lines as the mean bristle number increased again towards the base population level. Similar decreases in the 4-class probit width in their high-selection lines and increases in the relaxed lines derived from them led Sheldon and Milton (1972) and Sheldon and Evans (1981) to postulate that the initial response in the high lines was due to selection for poor regulators of the scute locus. This hypothesis is shown graphically in Fig. 4, reproduced from Sheldon and Milton (1972). The first question to ask is whether

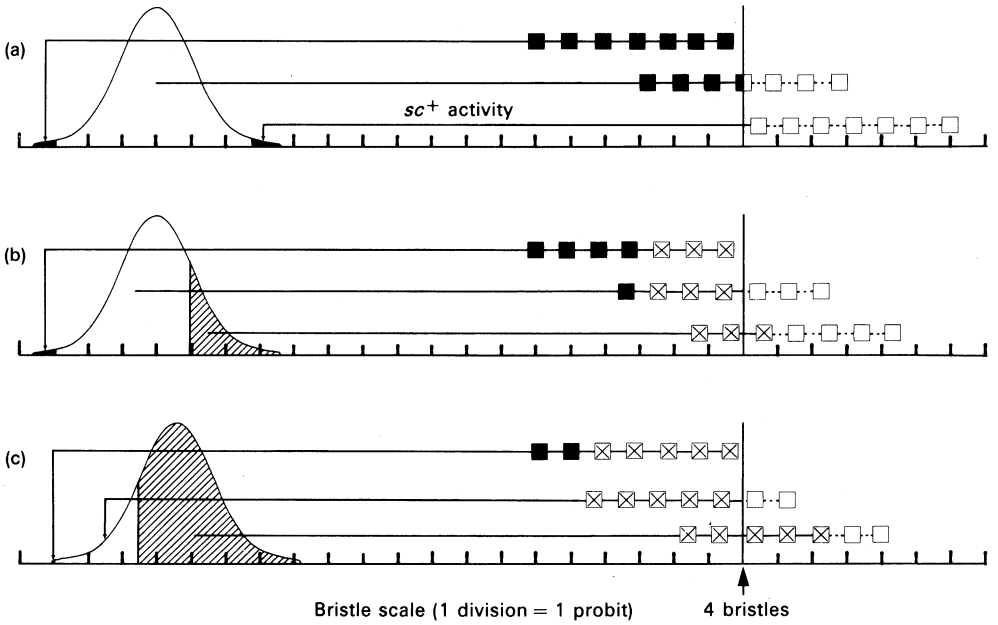


Fig. 4. Postulated relationship between the distribution of minor gene activity and the activity of the sc^+ allele in relation to the 4-bristle phenotype (*a*) in the unselected base population; (*b*) in a high-selection line as a result of initial selection for poor regulator(s) of sc^+ activity; (*c*) in the same high line following further selection for poor regulators of sc^+ as well as some upwards movement of the minor gene background. Activity of sc^+ which is not repressible is represented by a straight line, repressible activity by filled squares and repressed activity by unfilled squares. The crossed squares represent formerly repressible sc^+ activity which is no longer repressible. Note that in (*c*) occasional 3-bristle flies still occur even when over half the population has 5 or more bristles, i.e. the probit width of the 4-bristle class is very much reduced. [Reproduced from Sheldon and Milton 1972.]

the present results can be accommodated in this model or an extension of it. Since the postulated poor regulators allow an increase in realized total activity of the scute locus, such genes are unlikely to be selected under selection for low bristle number. A first alternative might be that selection for low bristle number led to selection of only low activity genes in the minor gene background, in which case flies with 5 bristles would cease to occur as soon as the mean bristle number began to decrease (Fig. 5*b*). Hence, the probit width of the 4-class would not be measurable. This cannot be the explanation for the reduction in probit width of the 4-class in the lines reported here. If better or more efficient regulators of the scute locus had been selected, it would have led to an increase in the probit width of the 4-class (Fig. 5*c*), which did not occur.

Another explanation for a decrease in the probit width of the 4-class in the low-selection lines is that alleles of the scute locus have been selected which have less total activity and less repressible activity (Fig. 5*d*) than the wild-type allele (sc^+). This would allow an increase in flies with 2 or 3 bristles while retaining a small frequency of flies with 5 bristles. The latter would continue to appear until selection of the minor gene background also occurred

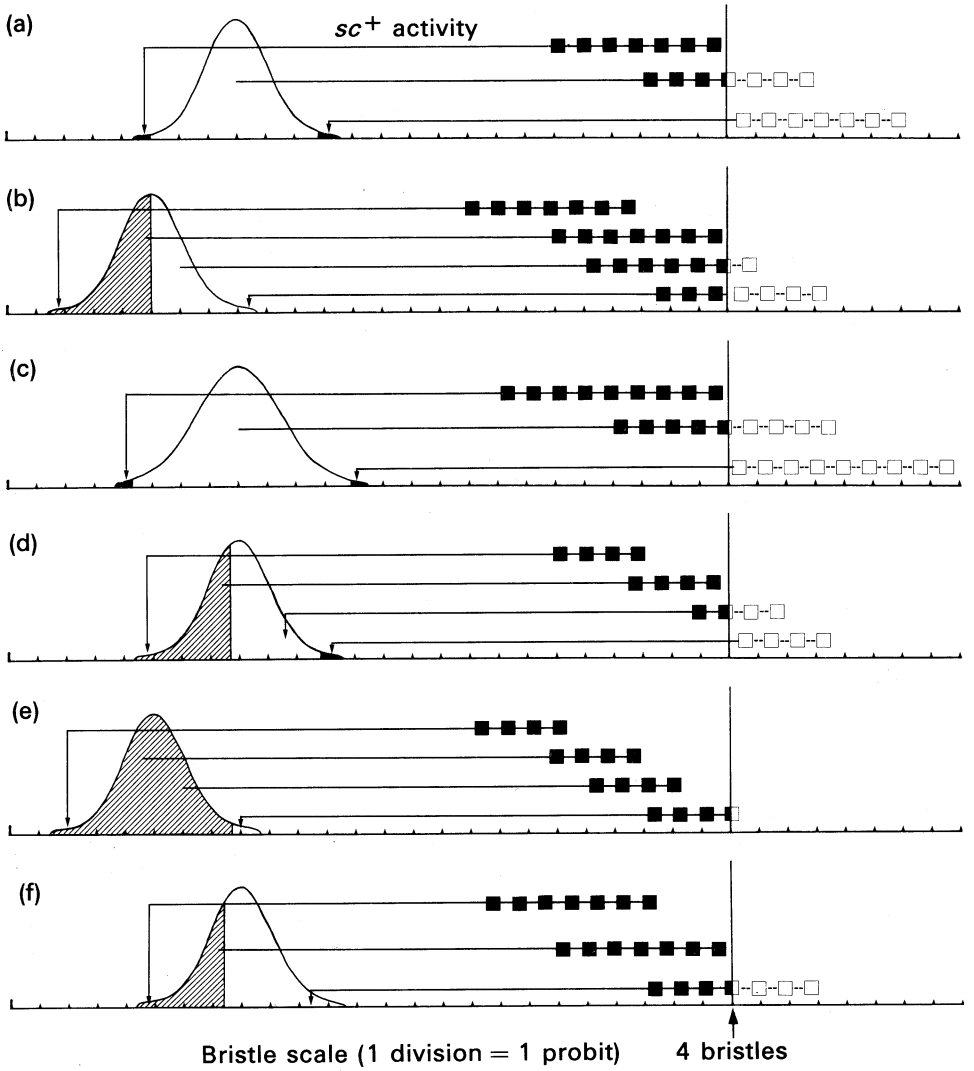


Fig. 5. Graphical representation of consequences of alternative explanations considered for reduction in probit width of the 4-bristle class in the low-selection lines. (*a*) Unselected base population; (*b*) selection of low minor gene background only; (*c*) selection of better regulators of sc^+ activity; (*d*) selection of scute locus alleles with less total activity and less repressible activity than sc^+; (*e*) selection of low minor gene background following (*d*); (*f*) selection of inefficient alleles at inducer locus of the scute locus (see text). Symbols the same as in Fig. 4.

to a sufficient extent to disallow the occurrence of any 5-bristle flies (Fig. 5*e*). However, this explanation has been ruled out by backcrossing the scute locus alleles from each of the selection lines into an Oregon-RC unselected background stock, marked with y^2sc^1 at the distal end of the X chromosome. In each such backcross population (A1, A3, A4, A6) the distribution of scutellar bristle number was the same as in unselected Oregon-RC, that

is, the scute locus alleles in each selected line were indistinguishable from the original wild-type alleles.

It seems, therefore, that the present results cannot be accommodated within the framework proposed by Sheldon and Milton (1972), as exemplified in Figs 4 and 5, unless the model is expanded substantially. Up to this point the mechanism envisaged for the occurrence of, or changes in, canalization at 4 scutellar bristles has involved only genetic regulation of the scute locus by repression of its activity at the 4,5 bristle threshold. This view was developed largely from considering the results of high- selection lines. We were able to represent changes in 4-class probit width etc. in the high lines in terms of poor regulators affecting the amount of repressible and non-repressible sc^+ activity. The increased realized total sc^+ activity due to poor repression was represented graphically as an excess beyond the 4-bristle class, represented as a single point on the scale (Fig. 4). As there were no other obvious constraints at the time the data were represented as simply as possible. It was not necessary in formal terms to consider any mechanism involved at the 3,4 threshold.

However, results of the low-selection lines require, in addition, consideration of aspects of the regulation mechanism affecting more specifically the 3,4 bristle threshold. If the scute locus is regulated in a similar way to the model proposed for the bithorax locus by Capdevila and Garcia-Bellido (1981), it is possible that, in the low lines, alleles of an inducer gene (analogous to their *Rg-bx*) have been selected which cause a depletion of the inducer of the scute locus, hence a reduction in total scute locus activity, and therefore an increase in the frequency of flies with less than 4 bristles. This is depicted in Fig. 5*f*, which shows that in this situation no flies with 5 bristles should occur. Thus, the effect of such alleles in a population in which the minor gene background had not changed would be operationally similar to the effect of reducing the minor gene background, as was shown in Fig. 5*b*.

Therefore, the persistence of 5-bristle flies in the 2-61 generations (Tables 3, 4, 5), depending on the line, remains unexplained. These flies are unlikely to be due to the continuing segregation of wild-type alleles at the inducer locus (loci) in the period before fixation of the alleles responsible for reduced level of inducer, since in line A1 the frequency of 5-bristle flies remains at base population level for about 25 generations. Neither are they likely to be due to poor repression of the scute locus at the 4,5 threshold being associated by chance or through selection, with the selected inducer-locus allele(s). If regulation of the scute locus is the mechanism responsible for canalization at 4 scutellar bristles, some additional factor(s) would seem to be required to explain the low line results other than the main components of the model invoked so far, i.e. minor gene background, allele at the scute locus, allele at the repressor locus or loci, and allele at a postulated inducer locus. The nature of such additional factor(s) remains unknown at this stage. However, further genetic and developmental analysis of genotypes such as these low-selection lines should help to modify and complete the models of the role of the achaete–scute complex in bristle differentiation which have been developed in recent years by Garcia-Bellido and his colleagues (Garcia-Bellido 1981; Botas *et al.* 1982; Carromolino *et al.* 1982).

A further question arises as to whether the pattern of early selection response (Fig. 1) is compatible with the hypothesis of selection for a single autosomal recessive gene. At first sight the answer would appear to be negative. Because the matings giving rise to the first selected generation in lines A1, A3, A4 involved a single selected male and a single female with the normal 4 bristles, the gene frequency of such a gene in the second generation would be 0·5. With full penetrance and expressivity one-quarter of the second generation would be expected to have less than 4 bristles. The actual frequencies were 1/862 and 16/882 in A1, 1/972 and 41/1035 in A3, 1/900 and 4/898 in A4 for female and males respectively. Even if the gene were not completely recessive but additive in action, i.e. detectable in the heterozygote, the gene frequency in the first generation would be 0·25

and, with full penetrance and expressivity, one-half of that generation would be expected to have less than 4 bristles. In fact only one such fly was observed (in A4 males) among about 70 of each sex scored in each line. Again, with full penetrance and expressivity, by the third generation a recessive gene could have been fixed or an additive gene be up to a frequency of 0·5, even allowing for no effective selection in the first generation, with rapid increase in frequency after that. Therefore, the very slow response in the first 6–10 generations in all lines except A2 seems incompatible with these expectations. A single-gene explanation remains a possibility only if the initial penetrance and expressivity of the gene were very low. This is likely because detection of the initial selected variants occurred after heat shock in A1, A3 and A4 and in a low bristle selection background in A6.

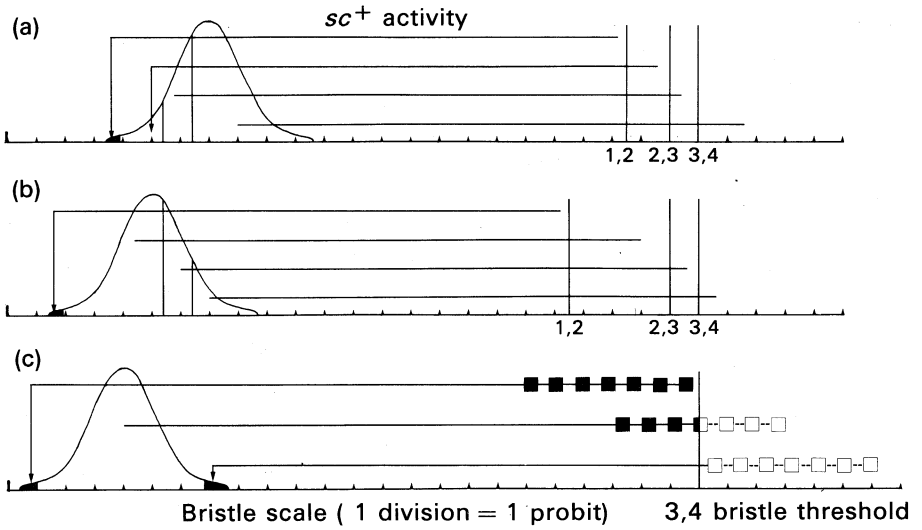


Fig. 6. (*a*) Repeat of Fig. 5*f* showing detail of bristle-class thresholds; (*b*) representation of detail of bristle threholds in line shown in Fig. 6*a* after downward movement of minor gene background by 2σ and increase in width of 2-bristle class to $3{\cdot}5\sigma$; (*c*) representation of enhanced sc^+ activity in presence of normal inducer of sc^+ following selection of low minor gene background (see text).

Occurrence of Canalization at 2 Scutellar Bristles

The long-sustained plateau in selection response just above a mean of 2 bristles observed in three of the five selection lines (A1, A3 and A4) was associated with the development of a real threshold at 2 bristles. The probit width of the 2-bristle class was $3{\cdot}0$–$3{\cdot}5\sigma$ in those lines compared with about $1{\cdot}5\sigma$ in unselected scute (sc^1) flies and about $2{\cdot}0\sigma$ in lines A2 and A6, while the probit widths of the 1- and 3-bristle classes in all lines were about the same as in unselected scute flies. Thus the canalization at 2 bristles in these lines is comparable to that arising from direct selection for it in a scute (sc^1) population (Rendel and Sheldon 1960; Rendel *et al.* 1966).

In a similar way to the above problem of interpretation with the reduced canalization at 4 bristles, it is also difficult to fit this increase in developmental buffering (canalization) at 2 bristles into the framework of the general model depicted in Figs 4 and 5. Fig 6*a* repeats the information in Fig. 5*f* with greater attention to the detail of correspondence between distribution of bristle classes superimposed on the normal distribution of minor gene background (left-hand side) and location of bristle thresholds on the probit scale (right-hand side). As before, the initial selection response is shown as being due to reduced sc^+ activity, due to alleles at an inducer locus causing a depletion of the inducer of the scute

locus. The 2-class width is shown still at the normal unselected level. Fig. 6*b* shows the situation when the minor gene background has been moved down the scale by selection (say by about 2σ) and the probit width of the 2-class increased to $3 \cdot 5\sigma$.

However, the mechanism for the observed canalization at 2 bristles is not apparent. A simple repression of *sc* locus activity at the 2,3 threshold, similar to that at the 4,5 threshold, does not seem a likely response to selection for low bristle number. It appears almost as though the activity of the sc^+ allele increases as the minor gene background is decreased in order to allow most individuals to reach 2 bristles.

Because of the difficulty of suggesting an explanation within this framework, consideration was given to the relevance of bristle position on the scutellum, because Robertson (1965), Scowcroft *et al.* (1968), Latter and Scowcroft (1970), and Scowcroft (1973) have questioned the validity of using total scutellar bristle number to analyse changes in canalization of the character (see Appendix 2).

However, 2-bristle canalization could not be explained satisfactorily in terms of bristle position, so the possibility that the activity of the sc^+ allele is somehow adjusted (increased) in low-selected background so as to allow most individuals to reach 2 bristles was explored further. There is some evidence that something like this happens with the sc^+ allele in low-selected background in relation to the 3,4 threshold, so as to allow most individuals to reach 4 scutellar bristles. For example the low line in Rendel *et al.* (1965) was about 2σ below the unselected line, as measured by the difference between sc^1 males in the two lines, but the sc^+ male mean in both lines was about the same, about 3σ above the 3,4 threshold. Similar lack of movement of the mean phenotype of the sc^+ segregants has been observed in at least two other low lines, selected down primarily on the bristle number of the sc^1 segregants, the scores of which had moved down $1\text{–}2\sigma$ at the same time (M. Evans, J. M. Rendell and B. L. Sheldon, unpublished data). Such a capacity to enhance the output of the normal sc^+ allele in low-selected background but presumably in the presence of the normal wild-type inducer of scute, is represented graphically in Fig. 6*c*, in contrast to the interpretation shown in Fig. 5*b*. No extra factor needs to be invoked except that the normal sc^+ allele stays 'switched on' longer when the minor gene background is lower, so that the sc^+ allele can perform its function of ensuring the production of the wild-type phenotype, i.e. 4 bristles in the case of the scutellum. Thus all, or nearly all, flies with the sc^+ allele will reach the 3,4 threshold beyond which level the usual repression of further activity will occur, preventing most individuals from reaching beyond the 4,5 threshold. Further modification of the Sheldon and Milton (1972) model of this regulation mechanism of canalization at 4 bristles (Fig. 4) is not required in order to accommodate the notion that activity of the normal sc^+ allele will always, or nearly always, be adjusted (increased) in low minor gene background so as to reach the 3,4 threshold. This notion is also in harmony with the recognized difficulty of selecting low lines from wild-type populations (see Introduction) and with our, admittedly insufficient, interpretation that initial response in the present lines is due to selection of alleles at an inducer locus (loci) which cause depletion of the inducer of the scute locus.

In an analogous way to the above proposal that normal sc^+ activity is always adjusted in the presence of the normal inducer genes so as to reach the 3,4 threshold, the activity of sc^+ alleles in three of the four present low lines might always reach the 1,2 bristle threshold due to minimum activity of the selected inducer alleles. The fact that the canalization at 2 bristles occurs in lines A1, A3 and A4 but not A6 might indicate it was a function of the particular inducer allele being considered. A further control mechanism at the 2,3 threshold would not be required since the main effect in lines A1, A3 and A4 is an inability to go below the 1,2 threshold rather than an inability to go above the 2,3 threshold.

Some information on these questions is provided by the results of crosses among the four low lines at about generation 200 (Evans and Sheldon, unpublished data). Reciprocal crosses among A1, A3 and A4 all have canalization at 2 bristles in both sexes similar to

the pure lines, but in reciprocal crosses between A6 and the other three lines canalization at 2 bristles is lost in both sexes, while the mean bristle number of the crosses is generally about mid-parent level. Therefore, canalization at 2 bristles seems to be due to a recessive, autosomal gene(s) in the three lines A1, A3 and A4, presumably the postulated, selected poor-inducer alleles. As these arose in three lines at the same time, it is likely that they are the same gene which was present at a significant frequency in the base population from which the three lines were derived. Possibly their detection and initial selection were mediated by the initial heat-shock treatment. Line A6 was derived from a different base population, and without heat shock.

Correlated Responses and Changes in Dominance

The low correlation of abdominal bristles (sternital chaetae) with response curves of scutellar bristles in selection and relaxed lines is difficult to explain unless one resorts to chance as the major factor involved. A possible reason for the maximum abdominal response occurring significantly earlier than the maximum scutellar response in four out of the five selection lines could be that the abdominal response was due almost entirely to the postulated single (depleted-inducer) gene in each line responsible for the initial scutellar response. The sex-linked recessive gene identified in line A2 is seen as similar to the postulated main-effect genes in the other lines for the present purpose. The remainder of the scutellar response could be due to minor modifier genes affecting scutellars but not abdominals. However, this simple view is not well supported by the inconsistent results of the relaxed lines. For example, in six out of the 10 relaxed lines (A1R1, A2R1, A2R2, A3R1, A3R2, A6R2) the abdominal mean was either unaffected or actually decreased further while the scutellar mean increased by variable amounts. In addition, in line A4 where the maximum abdominal and maximum scutellar responses occurred together (as early as generation 20) the abdominal response was lost completely in both relaxed lines, though only about half of their scutellar response was lost. Similarly, within each of A1 and A6, where both relaxed lines had a similar large increase in scutellars, only one of the two relaxed lines had any increase in abdominals.

When the results for scutellars and abdominals in the various genotypes of the scute backcross populations are compared, a similar inconsistency becomes obvious. The scutellar results (Tables 7 and 8; Fig. 2) show a general trend within lines to greatest response in the $+/sc$ genotype, followed in order by $+/Y$, $+/+$, sc/Y and sc/sc. For abdominal bristles (Table 9) the response in $+/sc$ is not generally different from that in $+/+$, in which it is generally greater than in $+/Y$, the opposite of the above. Similarly, the response in abdominals tends to be greater in sc/sc than in sc/Y, also the opposite if the scutellar pattern, while the abdominal responses in $+/+$ and $+/Y$ are generally greater than in sc/sc and sc/Y respectively, as for scutellars.

These trends are reflected in the changes observed in the dominance of + over *sc*. For scutellars, all four lines (Table 8) show a relatively large increase in the dominance ratio, i.e. a large reduction in the degree of dominance of + to *sc*, on both the genotype (probit) and phenotypic (arithmetic) scales, except for line A6 on the arithmetic scale. This reflects the greater reduction in the $+/sc$ genotypes relative to $+/+$ and sc/sc, except in A4 where it is rather more complicated. This generally smaller effect of the first dose of the + gene and larger effect of the second dose, compared with the unselected base population, is probably consistent with the possibility, discussed earlier, that the scutellar selection responses are mainly due to selected variants of an inducer-of-scute locus, which have the effect of less efficient induction of the wild-type allele of *sc*. No such consistency can be seen in the dominance ratios calculated from the abdominal bristle results (see Results, p. 290) which showed little change in three out of the four lines in Table 9 and a decrease, rather than an increase, in the fourth line, A4. If we can put to one side the problem of interpretation of the abdominal results for the present, the general trend to reduction in

degree of dominance of + over *sc* may be of considerable general importance. This general trend contrasts with the lack of a general trend in dominance changes among five high-scutellar selection lines reported earlier (Sheldon and Evans 1981). Initial selection responses in these high lines were postulated to be due to selection of genes for poor regulation (repression) of the scute locus. If the low-line responses reported here are mainly due to inefficient inducer-of-scute locus alleles, as postulated, the dominance results may indicate that dominance control is mainly due to the regulation imposed by the inducer, rather than the repressor, of the structural gene.

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Appendix 1

Single Gene Effect in Line A2

In the *sc* w^{bl} backcross for line A2 single-pair matings revealed the probability that line A2 contained a single, sex-linked gene causing the decrease in scutellar bristle number. The five generations of backcrossing had been carried out in this line in the same manner as for each of the other lines. At the end of this period single female matings of the following type were made, identified by segregation in the progeny, and the progeny scored:

$++/++ \times ++/Y$, $++/++ \times sc\ w^{bl}/Y$, $++/sc\ w^{bl} \times ++/Y$ and $++/sc\ w^{bl} \times sc\ w^{bl}/Y$.

The $++/++ \times ++/Y$ matings were expected to be at least identifiable as A2. Although none of the backcrosses had been completely successful in attaining the selection line mean level of bristles, the matings were all expected to yield progeny with mean bristle number well below 4 bristles. The 10 matings identified as $++/++ \times ++/Y$ on the basis of absence of the w^{bl} in the progeny could be divided into at least three groups based on progeny bristle scores:

Group 1. A2 males and females as expected, female mean slightly above 2, male mean slightly below 2.

Group 2. Biomodal distributions in both males and females. Range 1–4 bristles with modes at 2 and 4.

Group 3. Wild-type females (not A2, i.e. 4 bristles) and A2 males (mean below 2).

The explanation proposed for these different groups was that a single recessive gene present on the X chromosome was responsible for the A2 phenotype and that it was some distance removed from the scute locus allowing crossing over to occur during the scute backcross procedure. The group 1 matings would then have been $A2/A2 \times A2/Y$; group 2 $+/A2 \times A2/Y$; and group 3 $A2/A2 \times +/Y$.

The A2 line was then crossed to a *ycvvf* stock in order to confirm the presence of a sex-linked recessive and to ascertain its approximate position. The cross was carried out in five bottles and separate samples of F_1 females were backcrossed to either *ycvvf* males or line A2 males. The combined results on 1386 male progeny showed that the recessive gene is approximately 3·7 map units proximal to crossveinless (*cv*), i.e. at a map location of approximately 17·4. The effect of the gene is to reduce the number of scutellar bristles very specifically, there being little or no effect on macrochaetae at other positions. There is, however, a reduction in number of sternital microchaetae. There appears to be no previous indication of a gene of this kind in that region of the X chromosome (Lindsley and Grell 1968). We propose that it be called *rss* (reduced scutellars and sternitals).

Appendix 2

Relevance of Bristle Position to Strength of Canalization

Scowcroft *et al.* (1968) concluded from a study of the effects of dosage at the scute locus that posterior scutellars are more strongly canalized than anterior scutellars, and that the 3,4 bristle threshold on the probit scale for total scutellar bristle number is mainly a function of the 1,2 threshold for posteriors, while the 4,5 threshold is mainly a function of the 2,3

threshold for anteriors. The results of Latter and Scowcroft (1970) on degree of regulation of the one-bristle-per-site phenotype, in inbred lines, F_2's and lines selected for extra anteriors, tended to support the above conclusions, at least for scute alleles of relatively high activity (sc^+, $sc^{59}k$, $sc^{60}e$). However, Scowcroft and Latter's (1971) results with a scute allele of lower activity ($sc^{60}d$) showed little evidence that posteriors are more strongly canalized than anteriors. Scowcroft's (1973) study of high and low selection for anteriors, posteriors or total score tended to confirm the conclusion that change in a population straddling the 3,4 threshold for total score is mainly a function of change at the posterior sites, while change in a population straddling the 4,5 threshold is mainly a function of change at the anterior sites. However, the conclusions from their study were not supported by an analysis of changes in the probit widths (degree of canalization) of the 4-bristle class (for the total score) or 2-bristle class (for anteriors or posteriors separately).

The above approach of Scowcroft and Latter was followed in further analysis of the present low-selection lines and their base population. Analysis of large base population scores for Oregon-RC in which bristle position was scored (Sheldon 1968), confirms that posterior scutellars are to some extent more strongly canalized than anterior scutellars. The relevant results are as follows:

	Females	Males
Probit width of 4-class (total score)	$5 \cdot 65\sigma$	$5 \cdot 77\sigma$
Probit width of 2-class (anteriors)	6·17	6·21
Probit width of 2-class (posteriors)	7·35	6·90[A]
Ratio (anteriors/posteriors)	0·84	0·90
Probit width of 'one-bristle-per-site' class (anteriors)	6·50	6·60
Probit width of 'one-bristle-per-site' class (posteriors)	7·70	7·27[A]
Ratio (anteriors/posteriors)	0·84	0·91

[A] Minimum estimate.

The comparable results in Latter and Scowcroft's (1970) Canberra base population were $5 \cdot 98\sigma$ and $7 \cdot 73\sigma$ for the one-bristle-per-site class in females for anteriors and posteriors respectively. The results seem quite similar for the two base populations though the difference between anteriors and posteriors is less in Oregon-RC.

Bristle position was scored in the low lines at about generation 200, i.e. considerably later than the response period represented in the present paper. However, the mean bristle numbers were still very similar to the earlier scores reported in this paper, indicating stability of the lines, so the data can be regarded as reliable for the present purpose. In all four selection lines, including A6, the low-bristle number was due primarily to bristles being lost from the posterior sites, over 95% of the bristles in 2- or 1-bristle flies being at the anterior sites. The probit widths of the 2-bristle class and the one-bristle-per-site class for anteriors are given below, the comparable values for posteriors being unavailable due to absence of flies with 3 posterior bristles or with 2 bristles at one posterior site.

Line	Probit width of 2-bristle class (anteriors)	Probit width of one-bristle-per-site class (anteriors)
A6 (F)[A]	$2 \cdot 72\sigma$	$3 \cdot 18\sigma$
(M)	2·57	3·13
A1 (F)	3·09	3·73
(M)	3·20	3·86
A3 (F)	4·03	4·61
(M)	3·86	4·44
A4 (F)	3·98	4·56
(M)	4·30	4·62[B]
Oregon-RC (F)	6·17	6·50
(M)	6·21	6·60

[A] F, females; M, males. [B] Minimum estimate.

It is clear that the apparent degree of canalization of anterior bristles is much reduced compared with the base population. It is not possible to say whether the degree of canalization of posterior bristles is also reduced. Therefore, it cannot be concluded that reduction in probit width of the 4-bristle class (total score) is due primarily or solely to reduction in probit width of the 2-anterior bristles class. However, it is fairly certain that the reduced 4-class (total score) probit width in the low lines is due to generalized loss of posterior bristles with some increase in incidence of missing anteriors accompanied by retention of the capacity to produce an extra anterior bristle occasionally. The probit analyses of anteriors and posteriors or of number of bristles per site do not provide a more basic explanation or mechanism.

In high-selection lines a reduced 4-class probit width (total score) might be expected to be due to a generalized increase in anterior bristles, accompanied by retention of the capacity to produce an occasional fly with a posterior missing. The high-selection lines of Sheldon and Milton (1972) and Sheldon and Evans (1981) do not support this simple expectation, because flies with an anterior bristle missing continued to occur in the early generations of those lines as the mean bristle number increased. In addition, in some lines at least, the early response in extra scutellar bristles included a large component (up to 25%) of extra interstitial (intermediate) and posterior (other than apical or posterior–central) bristles as well as the main effect on extra anteriors. The existence of an anterior–posterior gradient of some kind cannot be denied, but it seems doubtful that changes in bristle number and in degree of canalization around 4 scutellar bristles are simply a composite function of essentially independent anterior and posterior components, as concluded by Scowcroft (1973). Extra bristles in the interstitial position are inexplicable even in the *unselected* base population in Oregon-RC, where they are nearly half as frequent as extra anteriors in females and almost as frequent as extra anteriors in males (Sheldon 1968). Latter and Scowcroft (1970) did not report any appreciable incidence of interstitial bristles in unselected Canberra populations or in two generation selection lines for high anteriors taken from the Canberra population. In the pattern of missing bristles though, unselected Canberra and Oregon-RC were quite similar. While it is not possible to reconstitute the frequency distributions of bristle number, and therefore probit widths of bristle classes, from the results of the derivatives of the Canberra population presented by Latter and Scowcroft (1970), the following distributions were obtained for a sample of the Canberra stock raised in the present authors' laboratory at about generation 120 of the low-selection lines reported here (a, anterior missing; p, posterior missing; a′, extra anterior; p′, extra posterior; the probit width estimates given in brackets are minimum estimates):

	Frequency distribution scutellar bristle No.			Probit width 4-class	Probit width 2-class	
	3	4	5	Total score	Anterior	Posterior
Females	—	2462	32 (31a′, 1p′)	(5·58)	(5·60)	(6·71)
Males	7 (3a, 4p)	2341	7 (7a′)	5·50	5·76	(6·28)

The probit widths of the one-bristle-per-site class in males are $6 \cdot 21\sigma$ for anteriors and $6 \cdot 69\sigma$ (minimum estimate) for posteriors. In females they are $6 \cdot 04\sigma$ and $7 \cdot 08\sigma$ respectively (both minimum estimates). The ratio of degree of canalization of anterior bristles to degree of canalization of posterior bristles varies from 0·83 to 0·93, i.e. closer to the Oregon-RC values given above than to the value of 0·72–0·77 given by Latter and Scowcroft (1970) for lines derived from the Canberra base population. Therefore, the emphasis of Scowcroft *et al.* (1968), Latter and Scowcroft (1970), Scowcroft (1973) on posterior bristles being much more strongly canalized than anterior bristles is not well supported by data from the Oregon and Canberra wild-type stocks. Support for their proposal comes mainly from analysis of effects of scute alleles other than sc^+, either from extra doses or in different

selection backgrounds. The relevance of those results to the mechanism of canalization at 4 scutellar bristles needs further assessment.

The question remains whether the information on bristle position in the low lines has any bearing on the mechanism for the observed canalization at 2 bristles in lines A1, A3 and A4. It is conceivable that, if the selected genotype's primary action were the removal of posterior bristles, then the buffered capacity to produce 1 bristle per anterior site might not be affected and canalization at 2 scutellar bristles (nearly all anteriors) would be observed. However, the degree of canalization at one-bristle-per-anterior-site *is* affected (reduced) by the selected genotype, measuring 3–4·5σ in A1, A3 and A4 instead of 6·5σ in the unselected population. So the residual degree of canalization at 2 bristles in A1, A3 and A4 is not due simply to a specificity of the selected genotypes for removing posterior bristles. A further persuasive argument against this idea is the absence of canalization at 2 bristles in A6 even though it is similar to A1, A3 and A4 in regard to bristle position, i.e. over 95% of bristles in 2-bristle flies being anteriors. Actually line A6 is even more extreme in this respect than the other 3 lines, over 99% of the bristles in 1- or 2-bristle flies being anteriors.