

STUDIES ON THE SCUTELLAR BRISTLES OF *DROSOPHILA MELANOGASTER*

I. BASIC VARIABILITY, SOME TEMPERATURE AND CULTURE EFFECTS, AND RESPONSES TO SHORT-TERM SELECTION IN THE OREGON-RC STRAIN

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Summary

The results of short runs of disruptive and high selection for scutellar bristles in wild-type *Drosophila* are explained in terms of the hypothesis that canalization at four bristles is due to regulation of the major gene in the developmental system (Rendel, Sheldon, and Finlay 1965). Selection response has probably been due to selection for modifier (minor) genes rather than for isoalleles of the major gene or weak regulator alleles. Some environmental effects on the character, short runs of selection for low bristle number or different bristle types, and effects of relaxing selection are also reported.

I. INTRODUCTION

Rendel and co-workers have studied various aspects of canalization of development of scutellar bristles in *Drosophila melanogaster*, mainly in populations homozygous for, or segregating for the scute (*sc'*) mutant (Rendel 1959*a*, 1959*b*; Rendel and Sheldon 1960; Sheldon, Rendel, and Finlay 1964; Rendel, Sheldon, and Finlay 1965, 1966). The results of selection in wild-type populations are also relevant to this subject and have been studied by Payne (1918), Sismanidis (1942), Fraser (1963), Latter (1964, 1966), Fraser *et al.* (1965), and Scowcroft (1966*a*, 1966*b*). This report deals with a similar study in the Oregon-RC wild-type strain. Short runs of high, low, or disruptive selection are reported, and analysed for their bearing on the genetic mechanism of canalization at four scutellar bristles.

II. METHODS AND OBSERVATIONS

(a) *Variability in the Base Population*

(i) *Types of Scutellar Variants*

The main types that occur in the unselected Oregon-RC population are shown in Figure 1. In general they agree with Fraser's (1963) observations and classification. One difference is in the 5*a* type which may have the extra bristle in a variety of positions close to one of the main *anterior* sites. Most frequently it is anterior to the main site as in Fraser's material. However, as indicated in Figure 1, the average reduction in size compared with the main bristle is not nearly as marked as Fraser reported. Another difference concerns the posterior bristles. Since normal extra bristles do occur, though rarely, next to a normal *posterior* site, it seems desirable to refer to this type of extra bristle as *p* in conformity with previous usage (Child 1935*a*,

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1935*b*; Ives 1939; Bridges and Brehme 1944). The small, fine, extra, hair-like bristles which are located on the extreme *posterior central* margin of the scutellum, which Fraser (1963) designated *p*, and Latter (1964) referred to as "apical", are referred to here as *p.c.* Of the extra bristle classes, *a*, *i* (intermediate or interstitial), and *p* were classified separately only in some of the unselected samples in this study. The *p.c.* and 4- classes have been classified separately in most samples. In the classes with missing bristles *a* and *p* have been classed separately in some unselected samples and in certain selection lines.

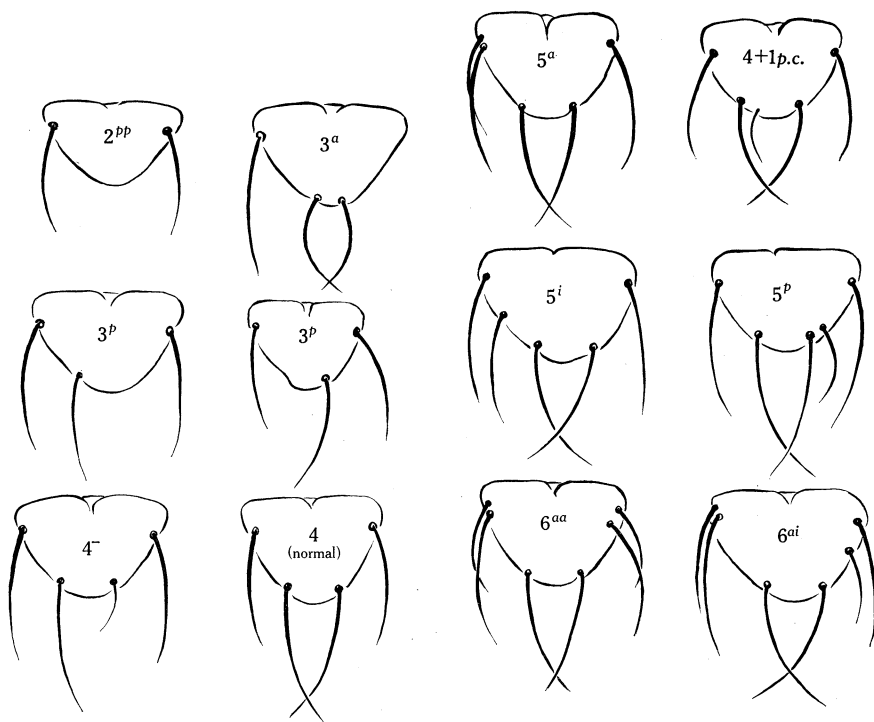


Fig. 1.—Types of scutellar variants in the unselected Oregon-RC population.

The following variations also occur in the Oregon-RC population or lines derived from it:

- (1) It is not unusual to find a small percentage of flies with a bristle or two missing but the complete basal ring(s) present. It has been concluded that in this stock most of these are due to "accidental" removal of fully developed bristles, since this type is extremely rare in freshly emerged flies but increases with the age of the sample, and it is possible to increase the proportion of such flies in the same sample to as high as 30% by a few transfers from the storage bottle to the confined space of an etherizer and back. However, a very small proportion of such flies are undoubtedly of a different origin. These have a more generalized loss of bristles, both macro- and microchaetae, on parts of the thorax and head, but with basal rings usually present. Sometimes a very small bristle fragment projects, rather

more commonly a colourless, fine, spindly "bristle" occurs in one or more of the scutellar basal cells. These flies are fairly typical of *Hairless* (*H*) mutants, including a slight shortening of wing veins L4 and L5 (Bridges and Brehme 1944). That is, a *Hairless*-type allele is present in this stock either at a low frequency or with low penetrance or both. The frequency of this phenotype never exceeded 0.05% in the present material (unselected or selected). It seems to be similar to the *Bare* phenotype in Fraser's (1963) study. None of this set of phenotypes (accidental or *Hairless*) has been recorded separately in the present study. Flies with four normal basal rings have all been classified in the normal or 4-bristle class except for the 4- type referred to above. No further attempt has been made to sort out the reasons for accidental removal of bristles. As the *Hairless*-type condition remained equally rare in all the selection lines, errors of interpretation introduced from this source can be ignored.

- (2) Occasionally, when one of the four normal bristles is missing, the site is marked by a spot of dark pigment under the undifferentiated surface of the cuticle. Such spots are observed less frequently at positions other than the normal site. At least one such "attempt to form a bristle" has been observed in the very centre of the scutellum.
- (3) At various times, in both unselected and selected populations, many flies have been observed with scutellar bristles which are bent at a sharp, well-defined angle ($< 90^\circ$) about half-way along their length, in contrast to the normal slightly curved bristle. Such bristles are quite fragile at this point and the upper half can be broken off easily with pressure from a needle. Many flies in cultures where bent bristles occur do in fact have broken bristles. The frequency of this condition seems to be dependent on the particular culture conditions prevailing. However, neither the environmental nor the genetic aspects of this phenomenon have been studied and no separate classification of this variant is made in the present report.

(ii) *Temperature and Culture Effects*

The frequencies of scutellar variants already reported by Rendel and Sheldon (1960) for this Oregon-RC stock at different temperatures during development are reproduced in Table 1, together with some larger samples scored since then. The culture medium in these samples was the standard wheatmeal-agar-treacle used in this laboratory. Results obtained on two other culture media are also given in Table 1. Fortified Sydney medium is similar to the standard one except for the addition of approximately 20% by weight of compressed baker's yeast. "Caltech" medium is that normally used at the California Institute of Technology (Lewis 1960).

The most obvious temperature effect is the dependence of expression of the *p.c.* class on high temperature. Approximately 10–20% of females and 1.5–7% of males are of this type at 30°C, while the proportion at 25°C is always less than 0.1% in females and 0.05% in males. Of the other bristle types, the number of flies with five bristles increases at lower temperatures and the number in the 4- class increases at higher temperature, but the data on flies with three bristles are conflicting.

The proportions of flies in the *p.c.*, 2, 3, 4—, 5, or 6 classes are not different on enriched culture medium. However, where a bristle is missing, it is rather more likely to be an anterior than a posterior one in enriched cultures whereas the opposite occurs on standard medium. When extra bristles occur in enriched cultures they are

TABLE 1
FREQUENCY DISTRIBUTIONS OF NUMBER OF SCUTELLAR BRISTLES IN DIFFERENT SAMPLES OF OREGON-RC FLIES RAISED AT DIFFERENT TEMPERATURES ON SYDNEY STANDARD, SYDNEY FORTIFIED, AND CALTECH CULTURE MEDIUM

A question mark indicates that this class was not scored separately in this sample

Culture Medium	Sample	Temp. (°C)	Bristle Class									
			2	3	4—	4	4+1 <i>p.c.</i>	4+2 <i>p.c.</i>	5	6	7	
Standard	1960*	30	—	—	?	557	99	28	6	4	—	
	1961	30	—	1	?	1441	?	?	35	3	—	
	1960*	25	—	1	?	788	—	—	7	—	—	
	1961	25	—	1	?	3955	?	?	106	6	—	
	1962	25	—	5 ^a	2	7141	7	1	81 ^b	—	—	
	1960*	20	—	1	?	533	—	—	13	1	—	
	1960*	15	—	1	?	443	—	—	16	2	—	
	1961	15	—	—	?	926	?	?	28	1	—	
Standard	1960*	30	—	1	?	612	19	5	5	—	—	
	1961	30	—	1	?	1483	?	?	9	—	—	
	1960*	25	—	2	?	823	—	—	—	—	—	
	1961	25	—	5	?	3759	?	?	19	1	—	
	1962	25	—	12 ^c	8	7269	1	—	12 ^d	—	—	
	1960*	20	—	3	?	694	—	—	2	—	—	
	1960*	15	—	4	?	515	—	—	2	—	—	
	1961	15	—	3	?	955	?	?	10	—	—	
Fortified	—	25	—	—	6	6905	2	—	70 ^e	—	—	
	1	30	—	2	?	327	75	10	—	—	—	
	2	30	—	10	43	9021	840	80	36	1	—	
	Caltech	—	25	—	—	?	2262	2	—	24	—	—
		1	18	—	3	?	4977	—	—	116	7	—
		2	18	—	—	5	1853	—	—	51	2	—
Fortified	—	25	1 ^f	12 ^g	15	6784	2	—	17 ^h	—	—	
	1	30	—	1	?	375	26	1	—	—	—	
	2	30	5	45	53	9589	142	1	26	—	—	
	Caltech	—	25	—	1	?	2172	1	—	7	—	—
		1	18	—	1	?	4859	—	—	29	3	1
		2	18	1	8	1	1838	—	—	17	1	—

* Rendel and Sheldon (1960).

^a 2a, 3*p.* ^b 44a, 36*i.* 1*p.* ^c 3a, 9*p.* ^d 6a, 6*i.* ^e 58a, 12*i.* ^f *pp.* ^g 8a, 4*p.* ^h 10a, 7*i.*

less often in the intermediate position and more frequently in the anterior position, than is the case in standard cultures. In general, males have fewer extra bristles and more missing bristles than females.

Probit transformation of the data allows interpretation in terms of an underlying variable (Rendel 1962, 1963). The probit widths of the 4-bristle class in the distri-

butions in Table 1 are given in Table 2. Males have a rather wider 4-bristle zone and can be considered to be more strongly canalized than females. The degree of canalization is affected also by temperature. Departure from 25°C in both directions tends to be accompanied by a reduction in width of the 4-bristle class.

TABLE 2
PROBIT DISTANCES SPANNED BY THE 4-BRISTLE CLASS IN THE FREQUENCY
DISTRIBUTIONS GIVEN IN TABLE 1

Values in parentheses are minimum estimates calculated by assuming the presence of one 3-bristle or one 5-bristle fly in the distributions where none actually occurs

Culture Medium	Sample	Temp. (°C)	Females	Males
Standard	1960	30	(5.18)	5.37
	1961	30	5.14	5.70
	1960	25	5.38	5.87
	1961	25	5.45	5.57
	1962	25	5.47	5.78
	1960	20	4.86	5.39
	1960	15	4.61	4.97
	1961	15	(4.97)	5.06
Fortified	—	25	(5.96)	5.70
Caltech	1	30	(4.61)	(5.61)
	2	30	5.77	5.34
	—	25	(5.66)	5.76
	1	18	5.14	6.03
	2	18	(5.21)	4.93

(b) *Disruptive Selection*

Sample 1 at 18°C, recorded in Table 1, was the base population for this selection line. Disassortative matings of extreme phenotypes were made for a period of six generations on Caltech culture medium. Because the extreme phenotypes were scarce and to ensure a large number of parents for each generation, many normal flies (i.e. with 4 bristles) were also used in matings to flies with more or less than 4 bristles, as set out in the following tabulation:

	Bristle Class of Flies Mated				Bristle Class of Flies Mated		
	Males		Females		Males		Females
Base population	6 or 7	×	3 or 4	Generation 3	3	×	5 or 6
matings to yield	3 or 4	×	6		4—	×	4
generation 1	5	×	4		5	×	3
	4	×	5		5	×	4—
					4	×	4
Generation 2	Random matings from generation 1*			Generations 4, 5, and 6	5 or 6	×	3 or 4—
					3 or 4—	×	5, 6, or 7

* Random matings used because of the absence of female and shortage of male flies with 3 or 4— bristles.

The frequency distributions for each generation of this selection line are given in Table 3. As will be seen from this table, temperature during development was varied to try to increase the frequency of extreme phenotypes for selection purposes.

TABLE 3
FREQUENCY DISTRIBUTIONS OF SCUTELLAR BRISTLES IN THE DISRUPTIVE SELECTION LINE

A question mark indicates that this class was not scored separately in this sample

Generation	Temp. (°C)	Bristle Class									
		2	3	4—	4	4+1 <i>p.c.</i>	4+2 <i>p.c.</i>	5	6	7	8
Females											
0	18	—	3	?	4977	—	—	116	7	—	—
1	18	—	—	?	1731	1	—	121	9	—	—
2	18–30	—	3	4	2564	39	2	12	1	—	—
3(a)	18–30	—	1	6	2322	26	1	36	3	—	—
3(b)*	18–30	—	—	1	812	6	—	14	—	—	—
3(c)*	30	—	1	2	476	28	—	2	—	—	—
4(a)	18–30	—	—	4	2546	46	3	95	11	1	—
4(b)†	30	—	—	11	2399	254	43	84	1	1	—
5(a)‡	30	—	3	8	1643	352	55	62	8	—	—
5(b)§	30	—	2	4	880	117	28	13	1	—	—
5(c)‡	18	—	3	—	1583	—	—	361	132	8	1
5(d)§	18	—	—	—	940	1	—	104	20	1	—
6	30	—	2	22	2377	416	91	149	21	3	—
Males											
0		—	1	?	4859	—	—	29	3	1	—
1		1	1	?	1708	—	—	30	5	—	—
2		—	4	15	2532	2	—	12	—	—	—
3(a)		—	6	12	2408	3	—	13	1	—	—
3(b)*		—	2	3	824	2	—	5	—	—	—
3(c)*		—	3	3	439	3	—	1	—	—	—
4(a)		—	3	14	2749	10	1	52	3	—	—
4(b)†		—	1	22	2666	73	11	33	1	—	—
5(a)‡		—	6	20	1956	83	6	26	—	1	—
5(b)§		—	4	8	882	26	2	6	—	—	—
5(c)‡		—	2	—	1684	—	—	250	46	—	—
5(d)§		—	2	—	885	—	—	46	9	—	—
6		—	3	34	2794	121	16	50	4	—	—

* Partial replicate. † Full replicate. ‡ Selected parents. § Random parents.

|| Cultures were held at 18°C from about 5 p.m. to 9 a.m. and at 30°C from 9 a.m. to 5 p.m.

Cultures were usually started off at 25°C and transferred to the stated temperature 3 days after matings were made. Previous experience with scute flies had indicated that they were sensitive to temperature changes of this order only some time after 72 hr from hatching at 25°C.

This selection line had a small but significant increase in mean bristle number, as shown by the increased proportion of flies with more than 4 bristles, ranging up to 8 bristles in females. The proportion of flies in the *p.c.* class showed no consistent change. A small increase occurred in the 4— class. The 3-bristle class did not decrease

as the mean of the population increased. In other words the degree of canalization at 4 bristles, as expressed by the probit span of the 4-bristle class, decreased during the few generations involved (Table 4). At first sight it seemed that disruptive selection had been successful in partly decanalizing the developmental pattern at 4 bristles. However, this interpretation is not the exclusive one, and this will be discussed in Section III.

TABLE 4

PROBIT WIDTHS OF BRISTLE CLASSES IN THE FREQUENCY DISTRIBUTIONS GIVEN IN TABLE 3
Values in parentheses are minimum estimates calculated by assuming the presence of one 3-bristle or one 5-bristle fly in the distributions where none actually occurs

Generation	Temp. (°C)	Bristle Class (females)			Bristle Class (males)	
		4	5	6	4	5
0*	18	5·14, (5·21)	1·09, 1·17		6·03, 4·93	0·69, 0·95
1	18	(4·77)	1·11		5·11	0·71
2	18-30 †	5·64	0·77		5·42	
3(a)	18-30 †	5·49	0·87		5·34	0·82
3(b)	18-30 †	(5·15)			5·42	
3(c)	30	5·54			5·33	
4(a)	18-30 †	(5·11)	0·86	0·73	5·13	0·99
4(b)	30	(5·22)	1·32	0·16	5·60	1·10
5(a)	30	4·83	0·83		4·99	1·06
5(b)	30	5·10	0·88		5·11	
5(c)	18	3·70	0·79	1·13	4·13	0·95
5(d)	18	(3·54)	0·87	1·06	4·43	0·77
6	30	4·83	0·83	0·67	5·19	0·91

* Base population (two values are from Caltech samples 1 and 2 in Table 1).

† See footnote to Table 3.

(c) Selection for High Bristle Number

The flies with more than 4 bristles which had been crossed to flies of lower bristle number to establish the disruptive selection line [Section II(b)] were afterwards mated together to begin a high selection line, which for the most part was carried through at 18°C and on Caltech culture medium (the sexes were separated after 1 day of the original disruptive selection matings, the new high selection matings were set up 1 week later, and the cultures of these matings to be used for scoring were set up 4 days later).

These parents of generation 1 were mated as follows: males with 6 bristles to females with 6 or 5 bristles, and males with 5 bristles to females with 5 bristles. All the following generations were produced by random matings among flies with the highest bristle numbers. The proportion of males selected varied between 1 and 7% of the sample scored, depending on the generation, and selected females between 2 and 10%. The actual number of parents varied between 25 and 60 males and 36 and 100 females. The frequency distributions for this high selection line are given in Table 5. Generations 5(b) and 5(c) were produced from the same parents as 5(a), but allowed to develop at 25 and 30°C respectively. Selection from each of generations 5(a), 5(b), and 5(c) gave rise respectively to generations 6(a), 6(b), and 6(c). The selected flies from each of the latter were then pooled to produce generation 7. Generation 8(a) was the F₂ of two males with 10 and 12 bristles from generation 6(b) mated to random females from the same generation. Selected flies from generations 8 and 8(a) were pooled to produce generation 9, after which selection was relaxed completely [see Section II(f)].

The rapid response to selection is evident from the frequency distribution of Table 5. Selection gains at 18°C are effectively realized at 25 and 30°C, as shown in generation 5, and the variance increases as selection proceeds. The probit widths of

TABLE 5
FREQUENCY DISTRIBUTIONS OF SCUTELLAR BRISTLES IN THE HIGH SELECTION LINE

Gener- ation	Temp. (°C)	Bristle Class															
		2	3	4-	4	4+	4+	5	6	7	8	9	10	11	12	13	14
		1p.c.						2p.c.									
Females																	
0*	18	—	3	—	4977	—	—	116	7	—	—	—	—	—	—	—	—
1	18	—	—	—	1158	—	—	89	19	1	—	—	—	—	—	—	—
2	18	—	—	—	1589	—	—	265	64	8	—	—	—	—	—	—	—
3	18	—	1	—	756	—	—	342	160	7	—	—	—	—	—	—	—
4	18	—	1	—	690	—	—	431	329	36	2	—	—	—	—	—	—
5(a)	18	—	—	—	403	—	—	357	318	57	9	—	—	—	—	—	—
5(b)	25	—	1	—	843	3	1	343	125	29	2	—	1	1	—	—	—
5(c)	30	—	—	—	651	98	14	52	13	1	—	—	—	—	—	—	—
6(a)	18	—	—	—	101	—	—	99	1112	27	7	—	—	—	—	—	—
6(b)	18	—	—	—	109	—	—	92	104	35	11	—	—	—	1	—	—
6(c)	18	—	—	—	120	—	—	91	87	22	4	—	—	—	—	—	—
7	18	—	—	—	223	—	—	246	310	115	39	3	2	—	1	—	1
8	18	—	—	—	65	—	—	71	132	80	55	2	1	1	—	—	2
8(a)	18	—	—	—	132	—	—	88	81	27	2	4	4	6	3	—	—
9	18	—	—	—	73	—	—	82	132	67	34	3	2	4	2	1	—
Males																	
0*	18	—	1	—	4859	—	—	29	3	1	—	—	—	—	—	—	—
1	18	—	3	—	1272	—	—	54	4	—	—	—	—	—	—	—	—
2	18	—	—	—	1768	—	—	160	21	3	—	—	—	—	—	—	—
3	18	—	1	1	770	—	—	235	67	1	—	—	—	—	—	—	—
4	18	—	3	2	865	—	—	411	160	16	—	—	—	—	—	—	—
5(a)	18	2	3	—	621	—	—	311	220	38	2	1	—	1	—	—	—
5(b)	25	—	4	2	1024	1	—	251	45	4	3	3	—	—	—	—	—
5(c)	30	—	2	—	739	24	—	47	6	1	—	—	—	—	—	—	—
6(a)	18	—	—	—	136	—	—	118	87	15	7	—	—	—	—	—	—
6(b)	18	—	1	—	128	—	—	92	80	17	3	—	1	—	1	—	—
6(c)	18	—	—	—	131	—	—	95	97	22	4	—	—	—	1	—	—
7	18	—	1	—	340	—	—	272	256	61	16	2	10	1	1	1	—
8	18	—	—	—	94	—	—	99	105	65	24	—	4	1	3	—	1
8(a)	18	—	—	—	164	—	—	86	52	16	3	4	4	7	—	—	—
9	18	—	—	—	118	—	—	91	107	55	38	5	4	3	1	2	3

* Base population.

the bristle classes in the data of Table 5 are given in Table 6, in which also the means of distributions are expressed as distance in probits from the 4,5 threshold. The means show a progression from about two probits below the 4,5 threshold to about one probit above it, and it appears that a steady increase has been made in total bristle-making resource. However, Table 6 also shows that the probit width of the 4-bristle class decreased under selection for more bristles. If the means on the probit scale are estimated from the 3,4 threshold, rather than the 4,5 threshold, it appears

that barely any increase was obtained in the mean on the underlying scale, and that a disruption of the canalization genotype was the main effect of selection showing up as a narrower 4-bristle zone. This is shown graphically in Figure 2 (in which some

TABLE 6

POSITION OF THE MEAN ON THE PROBIT SCALE AND WIDTH IN PROBITS OF BRISTLE CLASSES IN THE FREQUENCY DISTRIBUTION GIVEN IN TABLE 5

Values in parentheses are minimum estimates calculated by assuming the presence of one 3-bristle fly in the distributions where none actually occurs

Genera- tion	Temp. (°C)	Mean Relative to 4, 5 Threshold	Probit Width of Bristle Class									
			4	5	6	7	8	9	10	11	12	
			Females									
0*	18	-1.90, -1.92	5.14	1.09								
1	18	-1.37	4.53	0.78	1.01							
2	18	-0.94	(4.23)	0.98	0.72							
3	18	-0.25	3.41	0.87	1.42							
4	18	+0.09	3.10	0.78	1.26	1.06						
5(a)	18	+0.37	(2.75)	0.80	1.15	0.83						
5(b)	25	-0.33	3.52	0.86	0.78	0.78	0.22					
5(c)	30	-1.41	(4.45)	0.71	0.92							
6(a)	18	+0.54	(2.22)	0.74	1.09	0.76						
6(b)	18	+0.48	(2.29)	0.67	0.93	0.71	0.94					
6(c)	18	+0.33	(2.41)	0.72	1.02	0.84						
7	18	+0.71	(2.35)	0.71	0.95	0.71	0.78	0.19	0.23			
8	18	+0.99	(1.83)	0.56	0.83	0.64	1.14	0.15	0.11	0.14		
8(a)	18	+0.30	(3.13)	0.65	0.77	0.48	0.06	0.12	0.16	0.44		
9	18	+0.90	(1.91)	0.62	0.86	0.62	0.68	0.13	0.10	0.32	0.38	
			Males									
0*	18	-2.47, -2.34	6.03	0.69	0.38							
1	18	-1.71	4.54	1.04								
2	18	-1.31	(4.59)	0.94	0.72							
3	18	-0.58	3.70	0.95	1.59							
4	18	-0.25	3.11	0.92	1.12							
5(a)	18	-0.06	2.70	0.72	1.03	0.91	0.21	0.23				
5(b)	25	-0.74	3.50	1.00	0.69	0.18	0.24					
5(c)	30	-1.51	4.33	0.87	0.66							
6(a)	18	+0.31	(2.47)	0.84	1.02	1.02	0.52					
6(b)	18	+0.25	2.49	0.73	1.01	0.67	0.34	0.24				
6(c)	18	+0.32	(2.45)	0.70	1.05	0.85	0.49					
7	18	+0.37	2.62	0.72	0.95	0.53	0.30	0.05	0.46	0.09	0.33	
8	18	+0.71	(2.10)	0.68	0.71	0.70	0.62		0.24	0.08	0.49	
8(a)	18	+0.03	(2.72)	0.69	0.62	0.33	0.09	0.14	0.08			
9	18	+0.59	(2.24)	0.57	0.67	0.47	0.61	0.15	0.15	0.17	0.07	

* Base population (two values are from Caltech samples 1 and 2 in Table 1).

values differ from the ones given in Table 6). In the figure, generation 0 represents a pool of the two base population estimates in Table 2, generation 6 is a pooled estimate from the three subsamples (a), (b), and (c), and the 4-bristle zone in generations 8 and 9 is shown as the mean of generations 6 and 7 as it was not measurable in genera-

tions 8 and 9. The probit width of the 4-bristle class in males seems to be fairly stable at about 2.6σ from generation 5 onwards, after which the mean begins to increase.

A further point from Table 5, comparing data for generation 5 at 25 and 30°C with data in Table 1, is that the frequency of flies with *p.c.* bristles did not increase

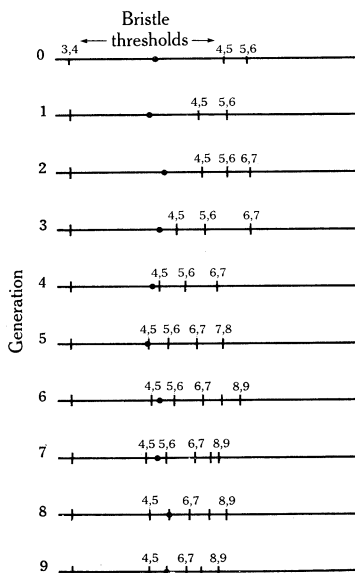


Fig. 2.—Response to selection in the high selection line expressed on the probit scale.

● Mean values.

in this line. Apart from those shown in Figure 1, the positions of extra bristles are shown in Figure 3, though no exact recording was made of the frequencies of the different types. A probable increase in the overall variance, reflected in the narrowing of the probit width of most bristle classes as selection progressed, should also be noted. Finally, after only five generations of selection, the population was quite sensitive to temperature changes (Table 5). This is to be expected, as either the canalization system is disrupted or the mean phenotype of the population moves outside the influence of the canalizing mechanism.

(d) Selection for Low Bristle Number

A low selection line, cultured on Caltech medium, was begun from generation 1 of the disruptive selection line. Random matings of 50 females and 50 males of this generation were cultured at 30°C to form a base population for low selection. From this, two cultures with selected parents were set up: (1) 5 males with 3 bristles \times 20 females with 4 bristles, and (2) 5 males with 4— bristles \times 20 females with 4 bristles; and also four cultures with random parents, about 10 females and 10 males per culture. The parents of all six cultures were transferred to fresh bottles after a few days to give a replicate batch. From the resulting generation 1, 7 females with 3, 10 with 4—, and 20 with 4 bristles were pooled in a mass mating with 5 males having 3 bristles and 20 males with 4— bristles. Several days later these parents were randomized over six bottles and later transferred as before to give a generation 2 replicate. Generation 3 was produced in 10 bottles of random parents (10 pairs to each) and five bottles set up from a pool consisting of 3 females with 3, 13 with 4—, and 15 random; and 1 male with 3 and 30 with 4—. The latter selected parents also yielded a replicate batch of cultures. Generation 4 consisted of four bottles, the parents coming from a pool of 9 females with 3 and 35 with 4— bristles, and 20 males with

3 and 9 with 4— bristles. The line was then relaxed. All generations were cultured at 30°C on Caltech culture medium. Replicate batches of cultures have been pooled within generations in presenting the results.

The frequency distributions of bristle numbers in this selection line are given in Table 7, which also includes the unselected Oregon-RC distributions at 30°C from Table 1. The high frequency of males with 2 or 3 bristles in sample 2 of Oregon-RC is due to the presence of a new mutant. This sample was raised in large numbers in order to establish a second low selection line with a much bigger initial selection differential. Unfortunately at least one-quarter and possibly more of the males with 2 or 3 bristles in sample 2 proved to be carrying a new, recessive, sex-linked mutation, and presumably all came from one or two heterozygous females. Because of this the second low selection line was abandoned. This mutation, which is not at the *scute* locus, removes bristles from the scutellum mainly in the anterior position, and many flies have a large black pigment spot within the cuticle at or near the missing bristle site.

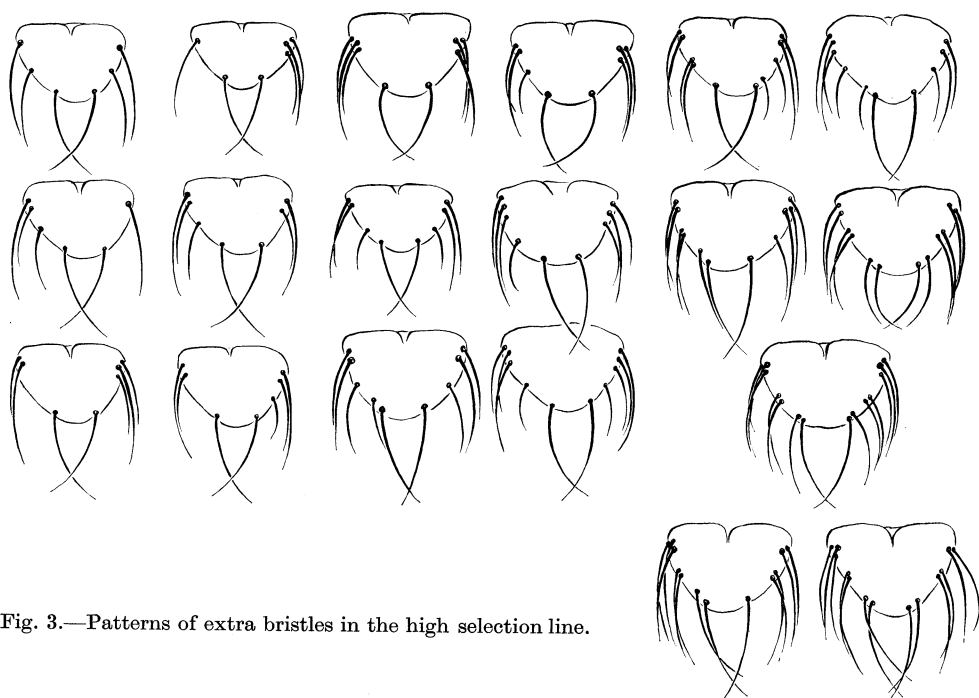


Fig. 3.—Patterns of extra bristles in the high selection line.

After allowance is made for this feature of sample 2, few trends can be discerned in the data of Table 7. The frequencies of flies with 2, 3, 5, and 6 bristles show no change but the frequency of the 4— class increases and the frequency of *p.c.* bristles declines as compared with the unselected samples of Oregon-RC in Table 1. However, the latter can hardly be attributed to the effects of low selection, as the base population and generation 1 were already as low as the following generations. The increase in the 4— class is therefore the only unambiguous result of selection. The selection run was too short to allow any conclusion on correlation between the 4— condition and missing bristles.

The data were transformed to the probit scale as previously in this paper. However, a certain amount of difficulty arises over how to handle the 4— and the *p.c.* classes. It seems reasonable that the 4— class should be treated as a separate class, below the normal 4-bristle class, when taking probits. Providing that any change that has occurred in the width of the 4-bristle class has been at the upper (4,5) threshold, the increase in frequency of the 4— class from 0.4 to 1.6% in females will mean a drop of about 0.5σ in the mean on the probit scale. Similarly a change from 0.5 to 2.3% in males corresponds to a drop of about 0.6σ . The *p.c.* bristles can be ignored when estimating probits because their specific response to increased temperature and their nature as micro- rather than macrochaetae indicate that they are uncorrelated or poorly correlated with the canalization system controlling the main bristle pattern on the scutellum. If this is done, as was done in the paper

TABLE 7
FREQUENCY DISTRIBUTIONS OF BRISTLE NUMBERS IN THE LOW SELECTION LINE RAISED AT 30°C
A question mark indicates that this class was not scored separately in this sample

Generation	Bristle Class							
	2	3	4—	4	4+1 <i>p.c.</i>	4+2 <i>p.c.</i>	5	6
Females								
Oregon-RC 1	—	2	?	327	75	10	—	—
Oregon-RC 2	—	10	43	9021	840	80	36	1
0*	—	—	—	1798	92	6	12	—
1	—	7	10	3985	186	11	17	4
2	—	3	13	1923	124	5	9	—
3	—	9	35	6272	336	19	23	—
4	—	2	24	1444	61	3	7	1
Males								
Oregon-RC 1	—	1	?	375	26	1	—	—
Oregon-RC 2	5	45	53	9589	142	1	26	—
0*	—	5	5	1847	9	—	3	—
1	—	5	20	4261	9	1	13	—
2	—	1	33	1993	20	—	3	—
3	—	20	99	6504	39	1	13	—
4	1	4	34	1451	12	—	1	—

* Base population from disruptive selection line, generation 1.

by Rendel and Sheldon (1960) and in obtaining the estimates in Table 2, it can be seen that the canalization span of the 4-bristle class is reduced very slightly, and that the mean is reduced by about 0.4σ , in the present low line. This is shown in Table 8. Alternatively the *p.c.* bristles can be regarded as an integral part of the main scutellar bristle system and treated as separate classes when calculating probits. The results of this procedure are also given in Table 8. The position of the mean relative to the lower threshold is not affected by the different treatment of the *p.c.* bristles. The probit widths of the 4 class are much reduced when *p.c.* bristles are classified separately. However, the slight decrease in width of the 4 class when the *p.c.* class is included is not evident in the data when this class is considered separately because of the fewer flies with *p.c.* bristles in the selection line relative to the unselected Oregon-RC sample.

Some information on selection for 4- type alone was obtained by mating the 43 females and 53 males of this class from the Oregon-RC sample 2 in Table 7. The F_1 was raised at 30°C, then approximately the same number of random F_1 flies were used to produce an F_2 , also raised at 30°C. The F_1 and F_2 were raised on Caltech medium and their scores are given in the following tabulation:

	Females							Males				
Bristle class	3	4—	4	4+1 <i>p.c.</i>	4+2 <i>p.c.</i>	5	6	3	4—	4	4+1 <i>p.c.</i>	5
No. of flies in F ₁	1	2	478	16	1	1	—	3	5	354	3	—
No. of flies in F ₂	—	10	1141	156	13	3	1	4	8	1215	36	4

The data give no more than an indication of an increase in the frequency of 4- and show no increase in frequency of flies in the 3-bristle class but show again the big variation in frequency of flies in the p.c. class in different samples. No further selection was possible at this time on 4-, but would seem desirable in any attempt to examine the correlations between the number and position of scutellar bristle sites and amount of bristle formed per site.

TABLE 8

POPULATION MEANS AND WIDTHS OF THE CANALIZED 4-BRISTLE CLASS, OBTAINED BY PROBIT TRANSFORMATION OF THE DATA GIVEN IN TABLE 7 FOR THE LOW SELECTION LINE

Values in parentheses as in Table 6

Generation	Distance of Mean above 4-, 4 Threshold	Width of 4-Bristle Class*	Width of 4-Bristle Class†	Distance of Mean above 4-, 4 Threshold	Width of 4-Bristle Class*	Width of 4-Bristle Class†
	Females			Males		
Oregon-RC 2	2.56	5.24	3.87	2.31	5.10	4.43
0‡	(3.29)	(5.78)	(4.87)	2.55	5.50	5.04
1	2.65	5.23	4.28	2.52	5.27	5.08
2	2.42	5.05	3.92	2.13	5.10	4.41
3	2.48	5.19	4.06	2.10	4.99	4.51
4	2.12	4.68	3.80	1.87	5.13	4.32

* Posterior centrals included in 4-bristle class.

† Posterior centrals classed separately.

‡ Base population.

(e) Selection for p.c. Bristles

This selection line was also begun from the Oregon-RC sample 2 in Table 7. About 106 females with 1 or 2 p.c. bristles were mated to 100 males with 1 p.c. bristle, divided among 10 bottles. From generation 1 about 50 random females and 50 random males were used to produce generation 2. Parents of generation 3 were 11 females with 2 p.c. bristles, 10 females with 1 p.c. bristle, 8 males with 1 p.c. bristle and 10 other males, selected at random but with no p.c. bristle. Generation 4 was produced from random parents, 50 of each sex. The 40 female parents of generation 5 all had 2 p.c. bristles, and were mated to 38 males with 1 p.c. and 1 male with 2 p.c. bristles. Female parents of generation 6 mainly had 1 p.c. bristle. There were about 75 of these, and also 5 females with 2 p.c. bristles, and 16 males with 1 p.c. bristle. The line was relaxed at generation 6. All generations were raised at 30°C, and on Caltech culture medium.

The results of this selection for p.c. bristles are given in Table 9. At first sight it appears that an increase in frequency of p.c. bristles has occurred, though the fluctuations from generation to generation are very large. However, the values for

the base population in the above tabulation are only one out of the three different sets on unselected Oregon-RC at 30°C which were given in Table 1. Over all three samples, the range of frequencies of females with 1 or 2 *p.c.* bristles was 9.2–20.5% and of males was 1.4–6.7%. A real but small percentage increase in the females but not in the males of the line has probably occurred. No strong correlated response can be seen, but the frequency of flies with 3 bristles in the selection line seems to be running slightly below the average level in the four sets of results for Oregon-RC flies at 30°C in Table 1. The frequency of the 4– class tends to be a bit lower in females but a bit higher in males than in the base population. The frequency

TABLE 9

FREQUENCY DISTRIBUTIONS OF SCUTELLAR BRISTLES IN THE LINE SELECTED FOR FINE POSTERIOR CENTRAL BRISTLES AT 30°C

Generation	Bristle Class							
	2	3	4–	4	4+1 <i>p.c.</i>	4+2 <i>p.c.</i>	5	6
Females								
0*	—	10	43	9021	840	80	36	1
1	—	1	2	617	74	7	3	—
2	—	—	—	376	142	23	3	—
3	—	1	1	321	55	17	1	—
4	—	1	7	659	176	45	7	—
5	—	1	2	1241	98	6	2	—
6	—	—	—	537	156	28	4	—
Males								
0*	5	45	53	9589	142	1	26	—
1	—	1	3	640	13	—	—	—
2	—	1	—	471	19	—	1	—
3	—	—	3	334	5	—	—	—
4	—	1	12	831	38	1	1	—
5	1	1	9	1301	16	—	3	—
6	—	1	3	722	46	3	—	—

* Base population.

of flies in the 5- and 6-bristle classes is rather lower than in the four sets of results for Oregon-RC flies at 30°C. There is some possibility, therefore, that the slight increase in number of *p.c.* bristles was obtained partly at the expense of the normal 5- and 6-bristle classes, perhaps by selecting a slight posterior shift in the normal anterior-posterior gradient of precursor, substrate, etc. involved in this developmental process.

(f) *Effects of Relaxing Selection*

All lines were scored after 20 generations of relaxation and some of them after a further 25 generations. Cultures were on Sydney standard medium and were raised at 25°C. The frequency distributions for the different lines are given in Table 10.

The disruptive line still has a mean bristle number slightly higher than the unselected Oregon-RC flies (cf. Table 1) but canalization at 4 bristles appears to have returned to normal. The probit width of the 4 class is 5.1 σ in females and 5.7 σ in males in the sample taken after 45 generations of relaxation. This now shows a slight

increase in frequency of *p.c.* bristles over the unselected level at 25°C, whereas an increase in *p.c.* bristles was not evident in the selection line itself at 30°C (Table 3).

The relaxed high lines have regressed from the selected level, where over 40% of females had more than 4 bristles at 25°C, to a level where only 5–10% of females have more than 4 bristles. However, this is still considerably higher than the unselected level of 1–2%. It is interesting that the relaxed line which had undergone a slightly longer period of selection still has a higher mean bristle number than the

TABLE 10

FREQUENCY DISTRIBUTIONS OF SCUTELLAR BRISTLE NUMBER IN THE SELECTION LINES AFTER COMPLETE RELAXATION OF SELECTION PRESSURE

Line	No. of Generations of Relaxation	Bristle Class						
		3	4—	4	4+1 <i>p.c.</i>	5	6	7
Females								
Disruptive selection	20	—	—	164	3	11	1	—
	45	1	2	2338	10	88 ^a	10	—
High selection*	20	—	—	155	6	5	—	—
	45	—	—	1571	—	121 ^b	9	1
High selection†	20	—	—	129	1	8	1	—
	45	—	—	1603	4	146 ^c	13	1
Low selection	20	—	—	151	—	—	—	—
	45	—	1	2620	9	32 ^d	1	—
Selection for 4—	20	—	—	316	2	4	—	—
Selection for <i>p.c.</i> 's	20	—	1	328	4	9	—	—
Males								
Disruptive selection	20	—	—	222	—	2	—	—
	45	2	1	2597	4	13	1	—
High selection*	20	—	1	237	1	1	—	—
	45	10 ^e	1	1755	—	14 ^f	—	—
High selection†	20	—	—	156	1	2	—	—
	45	1	—	1644	1	29 ^g	6	—
Low selection	20	—	—	241	—	—	—	—
	45	3	2	2820	—	4 ^h	—	—
Selection for 4—	20	—	—	367	—	—	—	—
Selection for <i>p.c.</i> 's	20	—	—	325	—	—	—	—

* Relaxed after six generations of selection.

† Relaxed after nine generations of selection.

^a 85*a*, 3*i*. ^b 100*a*, 20*i*, 1*p*. ^c 138*a*, 8*i*. ^d 28*a*, 4*i*. ^e 10*a*. ^f 11*a*, 3*i*. ^g 26*a*, 3*i*. ^h 4*a*.

relaxed line which had a shorter period of selection. Taking the disruptive line also into account, it is seen that the levels of these three relaxed lines bear the same rank relationship to each other as the selection lines from which they were derived. Unfortunately, with respect to the relaxed high selection lines, absence of flies with less than 4 bristles in two of these samples meant that strength of canalization at 4 bristles could not be measured. Hence it is not certain whether their higher mean bristle number is due to canalization at 4 bristles still being weaker than in unselected lines, or due to a higher mean on the underlying scale, strength of canalization having recovered, as in the disruptive line, back to the unselected level.

The relaxed low line is practically indistinguishable from unselected Oregon-RC flies. The frequency distributions of bristle classes are the same, except for a slightly higher frequency of *p.c.* bristles in the females, and the strength of canalization is normal, the probit widths of the 4 class being about 6.0σ in males and 5.5σ in females. The low line did not move far under selection so it is not surprising that the small increase in frequency of the 4— type and the small reduction in strength of canalization have been lost under prolonged relaxation.

The data on the 4— and *p.c.* relaxed selection lines are too scanty for any definite conclusions. The 4— line has lost part or all of its higher frequency of 4— type, but the *p.c.* line may have retained at 25°C some of its higher frequency of *p.c.* type which had occurred in females under selection at 30°C.

If the response to selection in the disruptive and high lines was due mainly to a narrowing of the 4-bristle canalization zone, as suggested previously, then regression towards unselected levels on relaxation could be due to recovery of the canalization genotype by natural selection. The slightly higher-than-unselected mean bristle number remaining in these three relaxed lines might then reflect that small part of the original response which was achieved by a change in genotype independent of the canalization genotype and not otherwise negatively correlated with fitness.

III. DISCUSSION

The results of the disruptive selection and high selection lines bear directly on the question of whether selection pressure directed primarily at the mean phenotypic expression of a canalized character is likely to affect the genetic system governing the canalization mechanism. Rendel's (1959*a*) original study on the scutellar bristle character concluded that the canalization genotype was not affected by the mutant scute (*sc*) or by selection primarily on *sc* flies in a population segregating for *sc* and *sc*⁺. The mutant or selection merely moved the population to different parts of the one sigmoid curve of relationship between genotype and phenotype. Rendel (1959*b*, 1962) maintained the same position in subsequent studies but in a later paper (Rendel 1963) allowed doubts about its validity when *sc* flies in a high line showed a lower degree of canalization at 4 bristles than *sc*⁺ flies normally do. Dun and Fraser (1959), in their similar experiments with tabby (*Ta*) mice, preferred the view that the mutant directly disrupts the canalizing genotype and that selection response followed different dose-response curves for the different genotypes. However, Fraser and Kindred (1960) rejected this view and accepted Rendel's when canalization at 18–19 vibrissae became evident in the *Ta*/+ segregants of their high line. Kindred (1963) returned to the earlier viewpoint when she was able to show that degree of canalization at 19 vibrissae was less in *Ta*/+ than in +/+ mice.

If a reduction in the proportion of the population falling in the canalized class, or, more strictly, a reduction in the probit width of the canalized class, is taken to mean a disruption or weakening of canalization, the present study leads to the conclusion that selection on bristle number in wild type can reduce the degree of canalization at 4 bristles. The actual response in bristle number in the disruptive and high lines is seen then partly as a result of change in a basic bristle number genotype and partly a result of change in the canalization genotype, the emphasis in

the early stages of selection being on the latter. However, if the interpretation of the results of a later experiment by Rendel, Sheldon, and Finlay (1965) is correct, this view is no longer acceptable. This report proposed that canalization at 4 bristles is effected by regulation of the gene at the scute locus. Each individual's bristle number is determined by a contribution from a basic genotype of minor genes and a contribution from the major gene at the scute locus, plus environmental effects. Depending on the contribution from minor genes, the major gene is switched off earlier or later in different individuals as total activity reaches a level sufficient for 4 bristles. In the unselected base population only a few individuals have a high enough minor gene contribution which, together with a minimum uncontrollable contribution from the major gene and the environmental contribution, is sufficient for 5 or 6 bristles. As the minor gene contribution rises in the disruptive and high selection lines, the number of individuals with minor gene plus uncontrollable major gene plus environmental activity high enough to make more than 4 bristles increases and the probit span of the 4-bristle class falls. About 4σ of the initial probit value of $5.5-6\sigma$ in the base population represents activity of the sc^+ gene which can be controlled out as the level of minor gene activity rises. In this view, the canalization genotype, the regulator genes specific for the scute locus, has not been touched by selection. Variation from the normal 4 bristles has been brought about not by change in the canalization genotype but because the canalization genotype is specific for the scute locus and exerts no control over the activity of the minor genes. The relaxed disruptive and high lines also support this view.

Another way in which bristle number could be increased would be for selection to pick out wild-type isoalleles of sc^+ which are not well controlled by the usual regulator genes. Alternatively some or all of the regulator genes may have been replaced by inefficient regulator alleles or non-regulator alleles. In either case a reduction in probit width of the 4-bristle class could occur, though not necessarily, so they cannot be invoked exclusively to explain the present results. However, Payne's (1918) selection line showed a complete absence of flies with less than 4 bristles right from the beginning. The population size was such that if the probit width of the 4 class were decreasing, a few flies with 3 bristles should have occurred in the early generations. It is possible, therefore, that in Payne's line one or both of these alternative mechanisms may have occurred. A scheme of full brother-sister matings, which Payne used, would tend to favour rapid fixation of either a poorly regulated sc^+ allele or an inefficient allele at a regulator locus. His back selection line begun at the 11th generation and showing only minor response over 25 generations gives some support to this idea. The virtual absence of flies with less than 4 bristles in all of Sismanidis' (1942) high lines leads to similar conjecture. In Fraser's selection lines (Fraser 1963) it is not clear to the reader what happened as the frequency distributions were not given. However, he stated that the probit width of the canalization zone did not decrease, since the frequency of flies with less than 4 bristles decreased as the frequency of those with more than 4 increased. His results therefore could be similar to those of Payne (1918) and Sismanidis (1942). Fraser's lines had a narrow genetic base, being each derived from single females, but the inbreeding was not as severe as with the other two authors. Comparison with Latter's (1964, 1966) results from this point of view is not possible from his published material.

The effects of temperature on bristle number and probit width of the 4 class are not entirely consistent with the model of regulation of the scute locus. If low temperature (15–20°C) increases the amount of activity of the minor genes so that the *sc*⁺ allele is switched off earlier, then the probit width of the 4 class will be smaller than at 25°C, just as in the high selection line it is smaller than in the base population. This is what happened in most experiments (Tables 2, 4, and 6). If high temperature (30°C) decreases the amount of minor gene activity then the probit width of the 4 class should increase. This occurred in the high selection line (Table 6), where the minor gene activity was already much higher, but not in unselected material (Table 2). One reason for this apparent departure from the model may be that at 30°C the total activity of the *sc*⁺ allele is also reduced so that a few more individuals in the population do not reach the 4-bristle level. But the frequency of flies with 5 or 6 bristles (not *p.c.* bristles) in unselected material was not reduced in all samples at 30°C (Table 1). Similarly the frequency of flies with 2 or 3 bristles was not reduced in the majority of samples at low temperature. It seems likely, therefore, that the temperature effect on probit width of the 4 class is at least partly the result of an increase in variance of bristle *make* at both high and low temperatures.

Some further comparison with Fraser's (1963) description of variation in scutellar bristles can be made. With respect to frequency of flies with other than 4 bristles in unselected material, the *D. melanogaster* stock used here was similar to his *D. melanogaster* stocks. However, it had a slightly different distribution, more flies with 3 and less with 5 and 6 bristles. It also differed in the position of extra bristles, a much higher proportion of them being in the intermediate or interstitial (*i*) position than in Fraser's material. The frequency of the *p.c.* type was about the same, and also the tendency for bristles to be missing at the posterior sites rather more frequently than at the anterior sites. The probit width of the 4-bristle class, the so-called index of strength of canalization, was only slightly less in Fraser's unselected *D. melanogaster*, though he did not analyse his data by this method. With respect to selected material, the main difference was that the high line in the present study had twice the frequency of flies with extra scutellar bristles at 25°C compared with the average of Fraser's high lines selected from wild-type *D. melanogaster*. The present high line was developed by mass selection using a large number of parents per generation, and at 18°C, while Fraser's lines were developed originally from single female cultures, with a much smaller number of parents per generation, and little selection differential on the males. It is not possible to say that the greater rate of response here was due to the different mating scheme or to the selection being done at a temperature which tends to push the character in the required direction to begin with. It is clear though that selection at 18°C was very effective in obtaining a response at 25°C and thus may have been partly responsible for the bigger response compared with Fraser's, not only by increasing the male selection differential but by exposing additional genetic variation for selection. After selecting for extra scutellars at specific sites — anterior, intermediate, or *p.c.* — Fraser put forward the hypothesis of a genetic relationship between the three types of bristle such that the expression of genes affecting the formation of intermediate or *p.c.* bristles is dependent on the presence of genes affecting anterior bristles. This is not supported by the present results, since in the disruptive and high selection lines no increase in *p.c.*'s occurred,

and in the *p.c.* selection line no increase in anterior or intermediate bristles. The dependence of development of *p.c.* bristles on high temperature, shown by Rendel and Sheldon (1960) and confirmed in this study, appears to be a highly specific phenomenon, since Pennycuik and Fraser (1964) obtained this effect in only one of the three lines they studied. A further difference between the present study and that of Pennycuik and Fraser was in the results on enriched medium. They found a big reduction in the frequency of flies with extra scutellars when they were raised on enriched medium, the reduction being similar for both anterior and intermediate bristles. The present study found no difference in total frequency of flies with extra bristles, but on enriched medium there was a much higher proportion of anteriors. It is impossible to generalize on temperature or culture effects until more populations of different origin have been studied.

IV. ACKNOWLEDGMENTS

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