VARIATION OF SCUTELLAR BRISTLES IN DROSOPHILA
I. GENETIC LEAKAGE

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THE number of bristles on the scutellum of Drosophila is characteristically four. Flies occur infrequently which have more or less than four bristles. PAYNE (1918) selected for increase of the number of scutellar bristles, producing, after several generations of selection, flies with many extra scutellars. This showed that there was considerable unexpressed genetic variation for number of scutellar bristles in flies with four bristles. He further showed that a major component of this variation was sex-linked.

scute alleles are characterised by a reduction of the number of scutellar bristles, but the reduction is not constant. scute flies vary in their number of scutellar bristles. RENDEL (1959) selected for increased and decreased number of scutellar bristles in scute flies, producing a low line in which almost all flies had no scutellars, and a high line in which almost all the flies had four bristles, and some had extra scutellars. Substitution of the + for the *sc* allele in the high line showed that selection for scute modifiers had affected the expression of the + allele. Wild-type flies of the high line had extra scutellars.

Both PAYNE's and RENDEL's results can be explained by the existence of a canalisation of development at four bristles (see RENDEL 1959). Canalisation of extreme phenotypes have been demonstrated and discussed by WADDINGTON (1956) and MILKMAN (1960). DUN and FRASER (1958) demonstrated that the number of secondary bristles in mice is canalised at an optimum number, using the Tabby gene to demonstrate unexpressed variability of whisker number in + mice.

On the assumption that there is a canalisation of bristle development at four bristles, then the infrequent wild-type flies with more or less than four bristles are caused by segregation of the scutellar genes producing combinations with a summed action of more or less than four bristles. This can be termed "genetic leakage" of the canalised scutellar genotype. The term is introduced to distinguish these phenomena from that of "phenodeviants" as discussed by LERNER (1954).

In this paper data are presented of genetic leakage in wild and laboratory populations, and of comparisons of scute and + variability.

Patterns of bristle position: PAYNE (1918) and RENDEL (1959) in their studies of extra-scutellars make no point of differences of position of extra or missing

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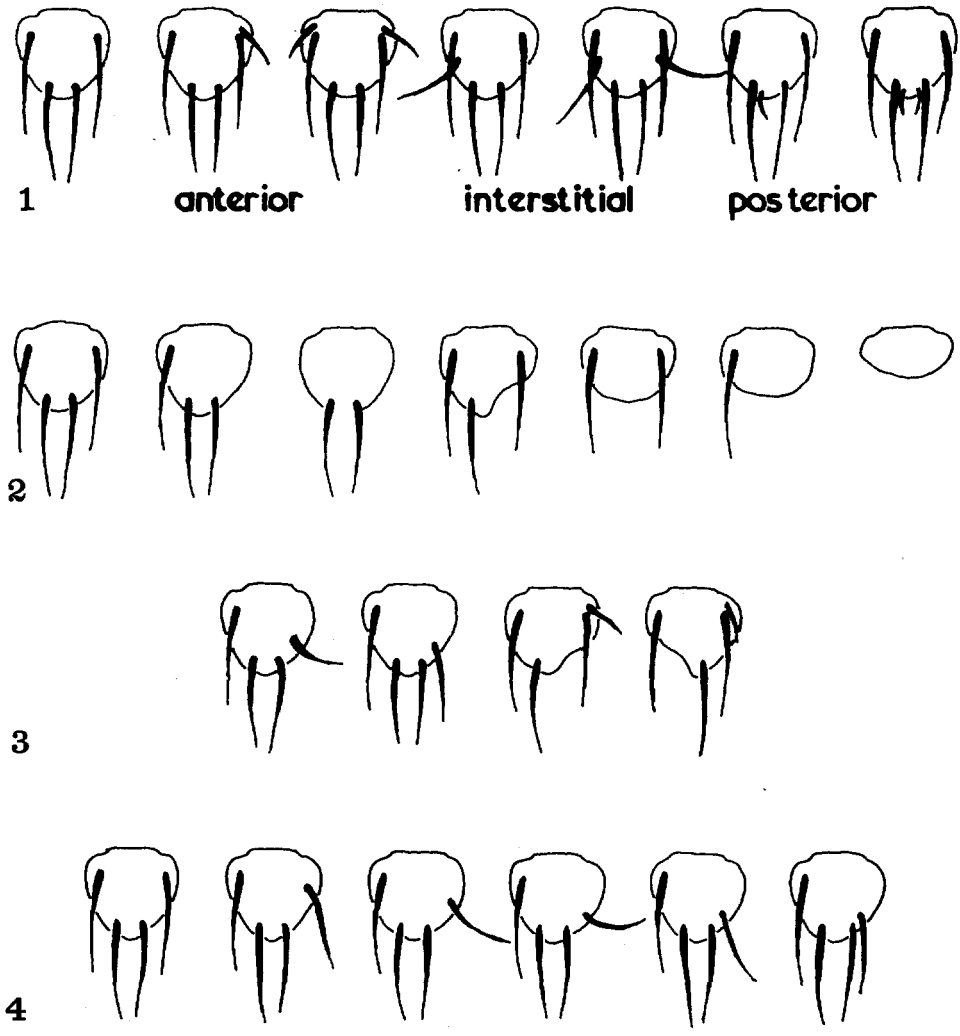
bristles. RENDEL and SHELDON (1960) found, in flies cultured at 30°C, that many had extra small bristles located posterior to the main bristles. They regarded these as genetically distinct from other types of extra scutellars. The possibility of genetic heterogeneity among extra bristles based on position has been a major feature of these researches. It became apparent very early that extra scutellars did not occur at random on the scutellum. The most frequent type found in unselected populations are smaller than the main bristles, located close to and anterior to the anterior main bristles. Extra bristles in this position are termed anterior (*a*) bristles. They are predominantly straight. Another type of bristle is rarely found in unselected populations, but it can predominate in selected populations. This type is located between the anterior and posterior pairs of main bristles, to the edge of the scutellum. Extra bristles in this position are termed interstitial (*i*). They are often markedly curved. A third type of bristle is extremely rare in unselected populations raised at 25°C. These bristles are small, curved, and located at the posterior edge of the scutellum. They are termed posterior (*p*) bristles. The three types of bristles are fairly distinct, but not completely so. In selected populations the classification of extra bristles into *a*, *i* or *p* types becomes increasingly difficult as the number of extra bristles increases. Various patterns of extra scutellars are illustrated in Figure 1.

The patterns of missing bristles are illustrated in Figure 2. The only obvious heterogeneity is whether anterior or posterior bristles are missing.

An important problem is the relation of the genetic systems controlling the subtraction and addition of bristles. Some patterns of bristles, which are extremely rare in unselected populations, indicate that it is possible simultaneously to add to, and subtract from the basic pattern of four bristles. These patterns of apparently simultaneous addition and subtraction are illustrated in Figure 3.

Addition-subtraction patterns could result from the existence of separate genetic systems for the addition of extra bristles, and the loss of main bristles. One of these "loss-addition" patterns has been shown by selection not to involve either loss of, or addition of, bristles, but instead to involve the shift of position of one or both of the anterior main bristles. Flies of this type *appear* to have lost one of the anterior main bristles, and to have an *additional* interstitial bristle located on the same side as the missing bristle. Flies of this type occurred in the second and third generations of selection lines for extra scutellars, in both *D. melanogaster* (from Rochester, New York), and *D. simulans*. Selection for this particular pattern was successful, without any concomitant increase of the frequency of flies which had extra bristles, or lacked any of the main bristles. This pattern was termed "shift," and in very few generations of selection the percentage of flies with uni- or bilateral shift increased to seven to eight percent.

A marked feature of "shift" flies, is that the bristle produced in the shifted position is often curved in a way analogous to that of extra interstitial bristles. This suggests that the curvature of interstitial bristles is a feature of their position, rather than an effect of the genetic system causing interstitial bristles—i.e., that curvature is a general feature of the interstitial position. This is supported by the straightness of the shifted bristle in flies with extreme shift. The patterns



FIGURES 1–4.—Figure 1.—(Top row.) Patterns of bristles on the scutellum. Extra bristles are most often located as shown, but there is considerable variation. Figure 2.—(Second row.) Patterns of bristles on the scutellum. Missing bristles most often result in the patterns as shown, but there is considerable variation. Figure 3.—(Third row.) Patterns of bristles which indicate a simultaneous addition and deletion. Figure 4.—(Fourth row.) "Shift" of main anterior bristles into a posterior location. Bristles which have been shifted to an intermediate position are usually characteristically curved.

shown in Figure 4 illustrate how the curvature of the bristle is at a maximum in flies with an intermediate degree of "shift."

There is no marked sex difference in the frequency of "shift." This lack of a sex difference contrasts with the marked sex difference of genetic leakage found in *melanogaster* (see RENDEL 1959, and below), supporting the hypothesis that the genetic system causing "shift" is independent of that controlling the number

of bristles. However, the occurrence of "shift" in selection lines for extra scutellars suggests that "shift" is in some way connected with the genetic system for number of bristles.

Other "loss-addition" patterns did not increase in frequency under selection, and they often occurred in cultures which included both flies with extra bristles, and other flies which lacked one or more main bristles. It would appear that it is possible for one genetic system to cause extra scutellars independently and conjointly with another genetic system causing the loss of main scutellars. This seems particularly evident from flies in which an absence of the posterior main bristle involves the indentation of the scutellum characteristic of the loss of posterior main bristles, with additional bristles occurring in the *a* position. WADDINGTON (1955) in his studies of the posterior cross-vein in Drosophila, also found addition and subtraction phenotypes; flies occurred with a break in the cross-vein combined with the addition of a piece of extra-vein. "The fact that such flies occur shows that the character *quantity* of *crossvein* is not causally homogenous." He suggests that when a just sub-threshold dosage of deficient-vein factors is combined with a just sub-threshold dosage of extra-vein factors, then the regulation of the developmental processes breaks down and both factors come into expression.

One argument against a "loss-addition" explanation of these rare bristle patterns is that their frequency is greater than would be expected from the frequencies of flies which have either lost a main bristle, or had an extra bristle. It is possible that a more determined selection program would show that the 5^a3^p pattern is the inverse to the 5^i3^a pattern—i.e., that they are due to a shift in the opposite direction.

A major feature of the morphology of bristles in *D. simulans*, and to a lesser degree in *melanogaster*, is the occurrence of incompletely formed main bristles. This deficiency of bristle formation can range from a bristle being slightly shorter than normal, to the complete absence of any sign of bristle development. A marked feature of incompletely developed bristles is their fragility. Initially it was considered that this phenomenon was independent of the normal loss or addition of bristles. However, selection for an increased frequency of "deficient bristles" showed a marked correlated response in the frequencies of additional and missing bristles. The data are shown in Figure 5.

One feature noted in the "deficient bristle" selection lines was the simultaneous occurrence of extra bristles and of "deficient" main bristles. Flies were frequently seen with all the main bristles represented only by their basal rings, and with extra *a* bristles. This adds considerable support to a hypothesis of independent loss and addition of bristles. However, the marked correlated responses shown in Figure 5 show that such a hypothesis could not have a general validity. It would appear that, *either* there are several independent genetic systems controlling the number of bristles; some of which act only to reduce the number of main bristles, *or* there is an intricate epistasis operative only in the ranges of 3–4, and 4–5 bristles. BATEMAN (1959b), in her work on the assimilation of venation phenocopies, found that a major component of the variation of deficient venation

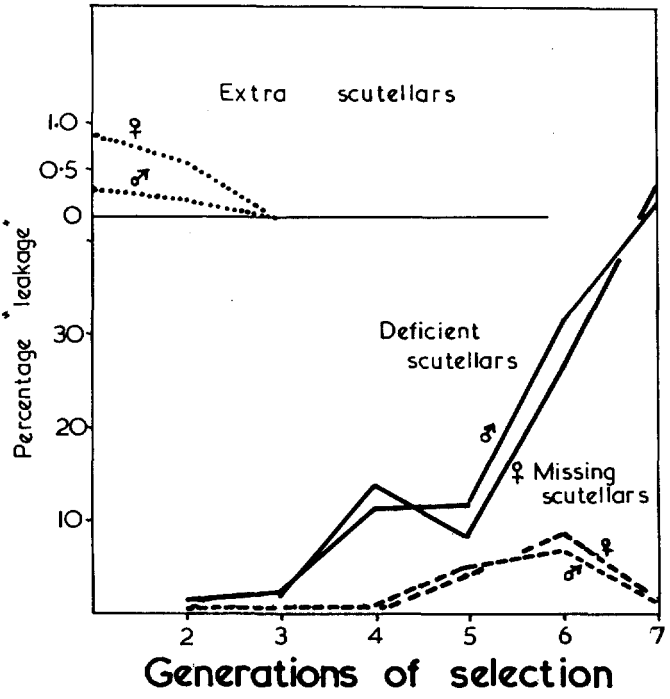


FIGURE 5.—Response to selection in *simulans* for an increased percentage of flies with one or more deficient bristles. Correlated responses in the "leakage" of extra and missing bristles are also shown.

was located on chromosome III, whereas a major component of extra venation was located on chromosome II. If these genotypic components were to any degree developmentally independent, then it would be possible to have both additions and deletions of the crossveins as found by WADDINGTON (1955). A similar system could be acting on variation of scutellar number.

Although these unusual bristle patterns are very probably of considerable importance in a complete understanding of genetic leakage they are infrequent and have been disregarded in the following analysis.

Genetic leakage in wild populations: Collections of wild Drosophila were made at three locations in Australia: Windsor, near Sydney; Surfers Paradise, near Brisbane; and Rockhampton. These are termed the W, S, and R regions. Single females from these collections were placed in vials, producing the L_1 cultures. The L_1 flies were allowed to mate in the vials, and mass cultures were set up in bottles. These are termed the L_2 cultures.

Three species were found in these cultures: *melanogaster*, *simulans* and *serrata*. Counts were made of the number of scutellar bristles of all the L_2, and most of the L_1 cultures. The complete data are given in Table 1.

The L_1 and L_2 cultures differ in the degree of inbreeding—the L_2 cultures resulted from sib-matings. The data of Table 1 are totalled to allow a direct L_1

TABLE 1

Frequency distributions of scutellar number in first and second generation progeny of wild females

		Number of scutellar bristles																							
		2	3			4	5				6									7					
			a		*p*		*a*	*i*		*p*	*aa*		*ai*	*ii*		*ap*		*pp*		*aaa*		*aai*		
Females:																									
melanogaster																									
(Windsor)	L_1					631	10	1			1														
	L_2		1		2	3060	101	3			14		4	1						1		1			
(Surfers)	L_1					119	2																		
	L_2					410	12			1	4														
(Rockhampton)	L_1					437	8				1														
	L_2					1961	14	3		2															
simulans																									
(Windsor)	L_1				1	673	2																		
	L_2		8		6	6009	62	5			7		4	3								1			
(Surfers)	L_1				1	1332	4				1														
	L_2		5		11	4772	16	1			2														
(Rockhampton)	L_1		1		1	400	1																		
	L_2	1	2		3	1189																			
serrata																									
(Surfers)	L_1					431																			
	L_2				4	2926	30	5		1	9					1		1		1					
Males:																									
melanogaster																									
(Windsor)	L_1					627	4																		
	L_2				3	3102	14			1	4		1												
(Surfers)	L_1					97																			
	L_2		1			377	3																		
(Rockhampton)	L_1				1	437	2																		
	L_2	1			3	1780	3	1																	
simulans																									
(Windsor)	L_1					610	1																		
	L_2		11		11	6292	17	4			2			1											
(Surfers)	L_1				2	1378	4																		
	L_2	2	4		2	4495	6	1																	
(Rockhampton)	L_1				1	397																			
	L_2				5	1264																			
serrata																									
(Surfers)	L_1					392	1	1																	
	L_2	1	1		3	2413	19			2	1					1									

to L_2 comparison in Table 2. There is a greater leakage in the L_2 than in the L_1 cultures, indicating that the single generation of sib-mating has either affected the variance of the "scutellar genetic system," or caused a decrease in the effectiveness of the canalisation mechanism. A series of sib-mating lines were established from the *simulans* cultures—one from each L_2 culture. A marked effect on viability became apparent after two to three generations of sib-mating, but there was no concomitant increase of scutellar leakage. Although the parents

TABLE 2

Frequencies in percentages of scutellar numbers totalled over collection sites to allow comparisons between the L_1 and L_2 generations of progeny from wild females

		3		4	5			6		n
		a	*p*		*a*	*i*	*p*	*aa*	*ai*	
Females:										
melanogaster										
	L_1	..	..	98.1	1.7	0.1	..	0.2	..	1,210
	L_2	..	..	97.1	2.3	0.1	0.1	0.3	0.1	5,595
simulans										
	L_1	..	0.1	99.5	0.3	..	..	..	..	2,417
	L_2	0.1	0.2	98.9	0.6	0.1	..	0.1	..	12,107
Overall										
	L_1	..	0.1	99.0	0.7	..	..	0.1	..	3,627
	L_2	0.1	0.1	98.3	1.2	0.1	..	0.2	..	17,702
Males:										
melanogaster										
	L_1	..	0.1	99.4	0.5	..	..	..	..	1,168
	L_2	..	0.1	99.3	0.4	..	..	0.1	..	5,294
simulans										
	L_1	..	0.1	99.7	0.2	..	..	..	..	2,393
	L_2	0.1	0.2	99.5	0.2	..	..	..	..	12,117
Overall										
	L_1	..	0.1	99.5	0.3	..	..	..	..	3,571
	L_2	0.1	0.1	99.4	0.3	..	..	..	..	17,411

were taken without reference to the scutellar number, there was a decrease of leakage in the last generations. A more complete account will be given of these sib-lines in a later paper, when the lines have reached a much greater degree of inbreeding. These preliminary results are given here because they show that inbreeding beyond L_2 did not cause any further increase of leakage; rather, it caused the reverse—i.e., the canalisation mechanism is not sensitive to inbreeding. Consequently, it can be taken that the greater leakage in L_2 than L_1 is due to a segregation of the scutellar genetic system.

The differences between L_1 and L_2 are not large, and it is reasonable to exclude this comparison by summing the L_1 and L_2 counts. The results, reduced to percentages, are given in Table 3, separately for the three species. A feature of this comparison is that there is a very marked difference between sexes in *melanogaster;* the "extra scutellar" leakage is greater in females, and the "missing scutellar" leakage is greater in males. This is not so apparent in *simulans;* there is little if any difference between males and females in the missing scutellar leakage, and although there is a greater extra scutellar leakage in females, the difference is not as great as in *melanogaster*. The third species, *serrata,* has less difference between sexes than *simulans*.

The data of Table 3 allow a comparison of *melanogaster* with *simulans*. The two features from this comparison are, that *melanogaster* shows a much greater extra scutellar leakage than *simulans*, and that *simulans* shows a greater missing

TABLE 3

Scutellar frequencies of progeny of wild females, summed over collection sites, and over L_1 and L_2 generations; expressed as percentages

	3		4	5			6		n
	a	*p*		*a*	*i*	*p*	*aa*	*ai*	
Females:									
melanogaster	. .	. .	97.3	2.2	0.1	. .	0.3	0.1	6,805
simulans	0.1	0.2	99.0	0.6	. .	. .	0.1	. .	14,524
serrata	. .	0.1	98.5	0.9	0.1	. .	0.3	. .	3,408
Males:									
melanogaster	. .	. .	99.3	0.4	. .	. .	0.1	. .	6,463
simulans	0.1	0.1	99.5	0.2	. .	. .	. .	. .	14,510
serrata	. .	0.1	98.9	0.7	. .	0.1	. .	. .	2,835

scutellar leakage than *melanogaster*. This difference can be explained *either* by the canalisation zone being located differently in the two species, *or* by the scutellar genotype having a lower value in *simulans* than in *melanogaster*. *serrata* is intermediate between *simulans* and *melanogaster* in females, but the *serrata* males have a greater extra scutellar leakage than *melanogaster*.

The three collection sites differ considerably in latitude, with Windsor in a Mediterranean climate, Rockhampton in the sub-tropics, and Surfers Paradise intermediate. The data of Table 1, are summed over the L_1 and L_2 cultures in Table 4 and expressed as percentages. The data indicate a gradient of leakage, from a maximum at Windsor, to a minimum at Rockhampton. This holds for both *melanogaster* and *simulans*, and for both males and females. Since the flies on which these observations were made were all cultured at 25°C under standard conditions, these differences cannot be regarded as directly due to the temperature differences between the regions. It is reasonable to suggest that the differences between regions, and between species are not fortuitous, but have some adaptive value. This could be due to the differences in number of scutellars, or to some underlying variation of which the variation of scutellar number is symptomatic.

Genetic leakage in laboratory populations: Scutellar leakage was measured in laboratory populations of *simulans* and *melanogaster* to complement the above data on leakage in the progeny of wild females. A random collection of cultures were scored for number of scutellars: 25 *melanogaster* stocks, and 36 *simulans* stocks. The results are given in Table 5. There is a general similarity with the results found from the wild populations. *melanogaster* has a greater extra scutellar leakage than *simulans* in females, and there is a marked difference between sexes in *melanogaster*, whereas there is no obvious difference between sexes in *simulans*. This supports the hypothesis that the difference of leakage between *simulans* and *melanogaster* is not fortuitous, but has some adaptive value.

Selection for increased genetic leakage: A large number of selection lines were established from the above cultures. Initially the selection procedure was predominantly to set up any females with extra or missing scutellars as single

TABLE 4

Scutellar frequencies, summed over L_1 and L_2 progenies, to allow comparisons between collection sites

	2	3		4	5			6		
		a	*p*		*a*	*i*	*p*	*aa*	*ai*	*ii*
Females:										
melanogaster										
Windsor	..	..	0.1	96.3	2.9	0.1	..	0.4	0.1	..
Surfers	..	..	..	96.5	2.6	..	0.2	0.7	..	..
Rockhampton	..	..	..	98.8	0.9	0.1	0.1	..	..	..
simulans										
Windsor	..	0.1	0.1	98.5	0.9	0.1	..	0.1	0.1	..
Surfers	..	0.1	0.1	99.3	0.3	..	..	0.1	..	..
Rockhampton	0.1	0.2	0.2	99.4	0.1	..	..	..	..	..
Males:										
melanogaster										
Windsor	..	..	0.1	99.4	0.5	..	..	..	..	..
Surfers	..	0.2	..	99.2	0.6	..	..	..	..	..
Rockhampton	..	..	0.2	99.5	0.2	..	..	..	..	..
simulans										
Windsor	..	0.2	0.2	99.3	0.3	..	..	..	..	..
Surfers	..	0.1	0.1	99.6	0.2	..	..	..	..	..
Rockhampton	..	..	0.4	99.6	..	..	..	..	..	..

TABLE 5

Scutellar frequecies in laboratory populations, summed over 25 melanogaster *stocks, and 36* simulans *stocks; expressed as percentages*

	3		4	5			6		*n*
	a	*p*		*a*	*i*	*p*	*aa*	*ai*	
Melanogaster									
Females	..	..	96.7	2.5	0.4	..	0.2	..	4,402
Male	0.1	0.1	99.4	0.3	0.1	..	..	..	4,242
simulans									
Female	..	0.1	98.9	0.6	0.1	0.1	0.1	..	3,108
Male	..	0.2	99.3	0.5	..	..	..	..	2,825

female cultures. No attempt was made to identify the male parents. This procedure was modified in later generations as the frequency of flies with more or less than four scutellars increased. Mass cultures were frequently used, and selection practised on the male parents. The aim was to establish a number of lines with high leakage, rather than to make a quantitative study of the effects of selection. The data, reduced to percentages, are plotted in Figures 6 and 7.

Selection for both extra scutellars and missing scutellars has been successful, showing that the leakage is, to at least some degree, genetic. There is no marked asymmetry of response between selection for increased, and decreased number of scutellars, once a response to selection has been established. No marked differences occur between *simulans* and *melanogaster* in the rate of response, if the

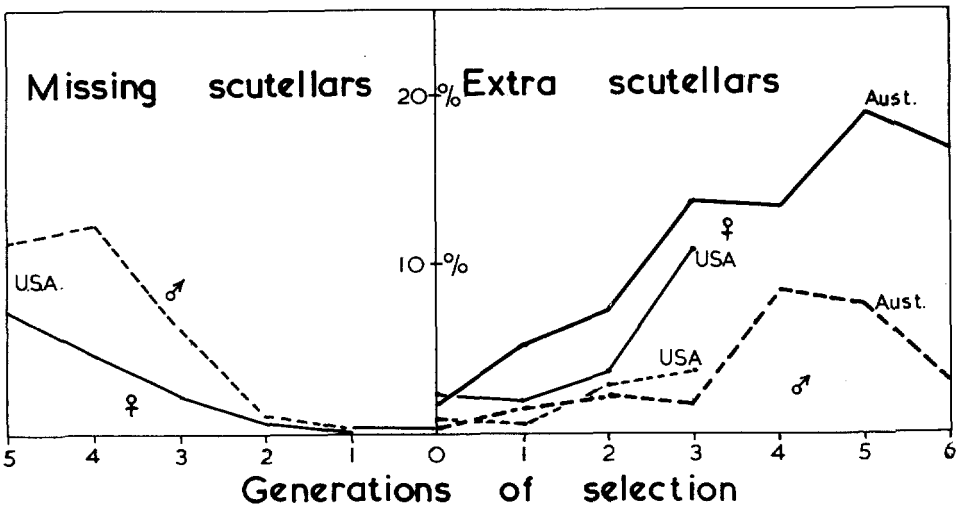


FIGURE 6.—Response to selection for increased leakage of extra and missing scutellars in *melanogaster*, averaged over all selection lines; separately for the lines derived from the Australian and U.S.A. populations.

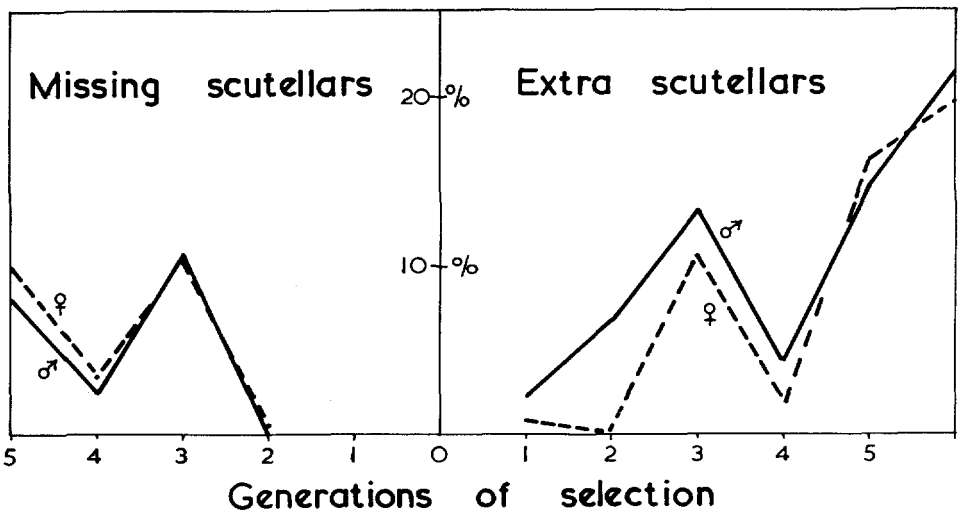


FIGURE 7.—Response to selection for increased leakage of extra and missing scutellars in *simulans*, averaged over all selection lines.

comparisons are made of female *melanogaster* with *simulans* for selection for increased scutellar number, and of male *melanogaster* with *simulans* for selection for decreased scutellar number. There is a fairly close similarity in the response to selection for increased number of scutellars between the lines originating from the Australian populations, and those originating from the American population.

The above results indicate that the increased genetic leakage is not due to a

decreased width of the canalisation zone. If it were, then we would expect the frequency of the complementary leakage to increase or stay constant, whereas it has decreased. Consequently, it is reasonable to conclude that the selection for increased genetic leakage has acted on the scutellar genetic system. The symmetry of response, and the similarities between species, and between different populations of *melanogaster*, indicate that the scutellar genetic system is predominantly additive without any marked dominance. This point needs to be verified by crossing the various selection lines. Although no such crosses have been made, a fairly extensive system of crosses was made between two laboratory stocks which had greater than normal frequencies of extra scutellars. The two lines, 70 and 71, were part of a set of backcross lines in which a series of white alleles had been crossed onto Oregon R. Line 70 carries the w allele, and line 71 carries the w^{col} allele. The two lines were crossed to give an F_1. This was sibmated to give an F_2, and also backcrossed to both parents. The BCF_1 flies were then backcrossed once more to give the backcross F_2.

The parental strains showed high degrees of extra scutellar leakage. Line 70 had 25.3 percent and Line 71 had 15.3 percent of females with extra scutellars. This leakage was very markedly different in type between the two lines: in Line 70 the extra bristles were of both the anterior and interstitial types, whereas in Line 71, the extra bristles were all of the anterior type.

The F_1 between these two lines showed a very marked reduction of leakage: to 3.0 percent in females, and 0 percent in males. This demonstrates that a marked degree of non-additivity exists for the scutellar genetic system.

The F_2 did not show any marked increase of leakage: from 3.0 to 3.7 percent in females, and from 0 percent to 0.9 percent in males, indication that a fairly large number of genes are concerned. In the F_2 males, three had less than four scutellars. No flies with missing bristles had been found in 2048 males of the parent lines.

A further demonstration of non-additivity came from the occurrence (in the backcrosses to Line 70) of flies with posterior extra bristles. No flies with this type of bristle had been found in the parent lines. In addition, the Line 70 backcrosses showed a much wider range of combinations of extra bristles.

A series of selection lines were started in which selection was concentrated on extra scutellars of one type; these are termed the *a*, *i* and *p* lines respectively. Some of these lines originated from the 70 and 71 lines; others from the crosses between them. Other *a*, *i*, *p* lines originated from the progeny of wild females. In these lines the initial selection was based on flies with extra *a* bristles, since extra *i* and *p* bristles are very rare in unselected lines. Once flies were produced with *i* or *p* bristles, then selection was concentrated on one type: *a*, *i* or *p*. The results are given in Table 6 for the last generation of selection. A more detailed analysis of these selection experiments will be presented in a later paper. The results given in Table 6 show that selection for *a* bristles can result in an increased leakage which is predominantly of *a* extra bristles. Selection for *i* bristles has resulted in an increased leakage, but this includes an appreciable fraction of *a* bristles. Selection for *p* bristles similarly, resulted in an increased frequency of

TABLE 6

Scutellar frequencies, calculated separately for the a *and* i *types of extra bristles, for the* a *and* i *selection experiments. Only the data from females are given*

	not *a*	5^{a}	6^{aa}	7^{aaa}	not *i*	5^{i}	6^{ii}
Selection in *simulans*							
for *(i)*	64.3	30.0	5.7	...	22.9	32.9	44.3
for *(a)*	51.0	37.2	11.8	...	88.3	8.4	3.3
Selection in *melanogaster*							
for *(i)*	68.1	26.7	5.2	...	44.0	30.5	25.3
for *(a)*	27.9	46.5	15.5	0.1	89.3	10.0	0.7

both *a* and *p* bristles. It appears that there is a genetic relationship between the *a* and *i* and the *a* and *p* types, but not a very marked relationship between the *i* and *p* types. It appears that the expression of genes affecting the formation of *i* or *p* bristles, is dependent on the presence of genes producing *a* bristles. This hypothesis cannot be taken as more than a basis for further work, because flies with either *i* or *p* bristles, but without *a* bristles occur frequently. It is possible that the *a* genotype has an incomplete penetrance both in the production of *a* bristles, and in its reaction with the *i* or *p* genotypes.

Two phenotypic differences appeared in the selection lines in *simulans*. These have been termed "scutellar microchaetae" and "Bare." The *smc* phenotype involves the formation of typical microchaetae on the scutellum. These are located in the anterior part, and are indistinguishable from the microchaetae of the dorsum. *smc* individuals were not found in any of the immediate progeny of wild females. They were first found in the second and third selection generations, but were not taken as a basis for selection until the fourth and fifth generations. There was a very rapid increase in frequency indicating that this phenotype has a simple genetic basis.

The "Bare" phenotype involves the absence of micro- and macrochaetae. Characteristically this includes areas of the dorsum lacking microchaetae. This phenotype was not noticed in the direct progeny of wild females, appearing first in the third and fourth generations of selection. Crosses were made of the "Bare" phenotype to the Low selection line—it segregated as a simple dominant, with a wide range of expression, from missing scutellars, dorso-centrals, and dorsal microchaetae, to just a single dorso-central missing. In crosses of "Bare" to unselected lines it behaved as a simple recessive, reappearing only in the F_2. "Bare" individuals in these crosses had a markedly reduced expressivity. In further backcrosses of "Bare" to unselected lines, there has been a decrease in the penetrance as well as the expressivity.

It hardly seems fortuitous that "scutellar microchaetae" appeared in the selection line for extra-scutellars, and that "Bare" appeared in the selection line for missing scutellars. LATTER (personal communication) has found *smc* individuals in his selection line for extra-scutellars in *melanogaster*. The simplest hypothesis to relate these facts is that the phenotypic expression of the "Bare" and *smc*

genotypes is dependent on the summed action of the basic scutellar genes. This summed action needs to exceed some threshold before the *smc* genotype is expressed, and it needs to be less than some threshold before the Bare genotype is expressed.

Correlation of scutellar leakage with "scute" variability: The results from the Tabby selection experiment (see FRASER and KINDRED 1962) and the scute selection experiment (see RENDEL and SHELDON 1960) have shown the value of correlating variation at one genetic level with that at another level. In the present researches comparisons of the number of scutellar bristles in $+^{sc}$ and scute flies were made in two stocks: an unselected population segregating for $+^{sc}$ and *sc*, and in three backcross populations in which *sc* was backcrossed into the 70 and 71 stocks discussed in the previous section. In addition, a third stock, the 73 stock, characterized by a small amount of leakage was included. The *sc* allele was the same in both the unselected and backcross lines, but the original cross to introduce *sc* into the 70, 71 and 73 lines was with the *DOWN* selection line (RENDEL 1959). In both stocks the w^{blood} allele was kept linked to *sc*.

A series of single females were set up from the unselected population. The females were all heterozygous for *scute* and w^{bl}, but some of the male parents were *sc*, others were $+^{sc}$. The results are given in Table 7 separated into two groups. In one group there was no leakage in the + flies, and in the other group there were + flies with extra scutellars. These data show that the scute flies of the *no* leakage cultures have less scutellars than those of the *leakage* cultures; the genes causing extra-scutellars in + flies have an analogous effect in *sc* flies.

The data for the backcross lines are also given in Table 7. There is a clear correlation of the degree of leakage in the + flies of the 70, 71, 73 lines, with the number of scutellars in the *sc* flies of the backcross lines. Although the leakage in + flies of the "unselected" line is far less than that in the 70, 71 lines, the number of scutellars in *sc* flies is less in the backcross lines. This difference is shown in Figure 8.

This difference between the unselected and backcross lines almost certainly has its basis in the use of the Down selection line as the source of the scute allele.

TABLE 7

Scutellar numbers in sc *and* + males *of the "backcross" and "unselected" lines, to allow comparison of leakage in + flies, with mean scutellar number in* sc *flies*

		sc males					+ males			
	Line	0	1	2	3	4	3	4	5	6
Backcross										
	73	189	14	1	..	..	..	637	..	..
	71	186	39	12	..	..	..	455	3	..
	70	137	63	44	3	1	..	507	59	4
Unselected										
	No "leakage"	267	303	244	2	..	..	846	..	..
	"Leakage"	171	271	257	6	1	1	708	18	..

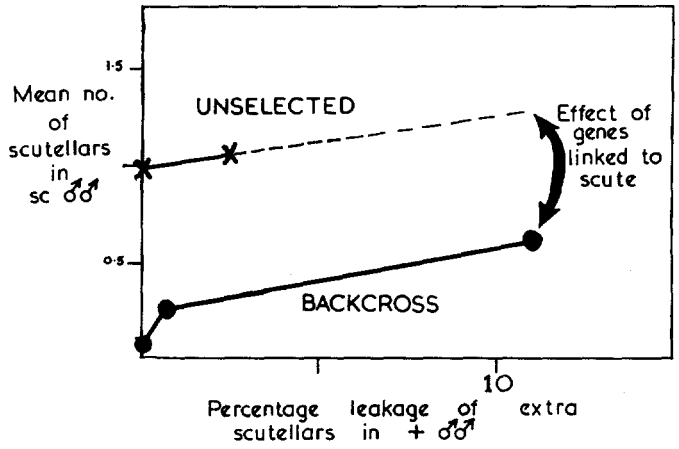


FIGURE 8.—The relationship of the leakage of extra scutellars in the ± males, with the mean number of scutellars in *sc* males. The difference between the "unselected" and "backcross" regressions can be explained by the linkage of negative modifiers to scute in the backcross lines.

It is reasonable to suggest that the selection of the Down line had accumulated negative modifiers of scute located at the same end of the X. (PAYNE 1918, came to the same conclusion). Since *sc* and w^{bl} have been kept linked through the backcrosses, this has ensured that a minimum of 1.5 percent of the X chromosome from the Down line has been carried with scute through all the backcrosses. Five backcrosses were made, and, therefore, it is likely that some ten units of the X chromosome still are identical with the original X chromosome from the Down line.

In later generations of backcrossing scute onto the 70, 71 lines, a separation was made on the basis of crossovers between *sc* and w^{bl}. No such separation was possible for the 73 line which itself carries w^{bl}. The results are shown in Table 8. The noncrossover males have less scutellar bristles than the crossover males. This result is expected if the Down selection practiced by RENDEL had accumulated low scutellar modifiers on the X chromosome near to the *sc* w^{bl} region. The modifiers do not act specifically on the scute action—the same difference can be seen in +/*sc* females.

GREEN (1960) has shown that rearrangements of specific X-located heterochromatin segments modify the expression of the "hairy" locus, as diagnosed by the occurrence of extra microchaetae on the wings, halteres, and scutellum. This suggests a possibility that the scute allele of RENDEL's Down line has, during the selection experiment, become involved in a heterochromatic rearrangement.

RENDEL (personal communication) states that in crosses between the "Down" and "Up" selection lines no evidence could be found of a major sex-linked component of the genetic variation of scutellar number. A possible explanation for this discrepancy could be that the 70, 71 lines contain a genetic component which shows a marked interaction with a sex-linked component.

TABLE 8

Frequency distributions as percentages of the scutellar number in the backcross stocks of scute onto the 70, 71 lines, separated into the crossover and non-crossover lines established after five generations of backcrossing

	Number of scutellar bristles, as percentages							
	0	1	2	3	4	5	6	*n*
Line 70								
Noncrossover								
$+^{sc}$ *w*/*sc* w^{bl}	...	...	...	...	96.6	2.8	0.6	507
$+^{sc}$ *w*	...	...	...	...	98.2	1.4	0.5	222
sc w^{bl}	55.9	25.7	18.0	0.4	...	...	...	245
Crossover								
$+^{sc}$ *w*/*sc w*	...	...	...	...	93.4	5.6	1.0	301
$+^{sc}$ *w*	...	...	...	...	98.2	1.2	0.6	163
sc w	31.0	27.5	35.2	6.3	...	...	...	142
Line 71								
Noncrossover								
$+^{sc}$ w^{col}/*sc* w^{bl}	...	...	...	0.6	94.7	3.7	1.0	508
$+^{sc}$ w^{col}	...	...	...	0.4	96.4	2.8	0.4	281
sc w^{bl}	78.8	16.1	5.1	...	...	...	...	236
Crossover								
$+^{sc}$ w^{col}/*sc* w^{col}	...	...	...	...	90.6	8.2	1.2	341
$+^{sc}$ w^{col}	...	...	...	...	97.6	2.4	...	206
sc w^{col}	28.8	36.8	33.7	0.6	...	...	...	163

DISCUSSION

The above data can best be explained by a canalisation of the number of scutellar bristles at four. This involves two systems: the "scutellar" system, which determines the potential number of bristles, and the "canalisation" system, which modifies the effect of a part of the range of actions of the "scutellar" system. The results given above, and those of PAYNE (1918) and RENDEL (1959) are consistent with the "scutellar" system being polygenic and highly heterozygous.

The term "genetic leakage" has been used in this paper for the occurrence of individuals with other than the standard four bristles. Such individuals could be termed "phenodeviants," following LERNER (1954), but it can be argued that the rare scutellar abnormalities have a different genetic basis from the rare abnormalities discussed by LERNER (1954). His primary hypothesis is based on homozygosity being the cause of the abnormalities, rather than the summed genetic effect. Consequently, the frequency of such abnormalities will be primarily dependent on inbreeding causing homozygosity. Selection will only be effective insofar as it causes an increased homozygosity. It follows then that heterozygosity has a reproductive advantage. The hypothesis of genetic "leakage," on the other hand, does not involve any direct reference to homozygosity or heterozygosity. The "scutellar" system is considered to be a polygenic system which only differs from the more usual quantitative system in that the

mean of the genetic system is located at a value where a wide range of summed genetic values all lead to the same phenotypic effect. If the mean of the genetic system is shifted to a value outside the range of the canalisation system, then the genetic variability is fully expressed. Genetic leakage is caused by segregation of the scutellar system producing genotypes whose summed actions lie outside the range of the canalisation system. Consequently, selection will be effective without reference to inbreeding. In fact, it is probable that intensive prolonged inbreeding would decrease the effectiveness of selection for increased genetic leakage. In unselected populations, the amount of leakage will be dependent on the deviation of the scutellar system from the center of the canalised zone.

There is the possibility that aberrant phenotypes could be caused by a decrease in the effectiveness of canalisation. If the width of the zone is decreased, then there will be an increase of leakage. This can be detected by reference to the mean and variation of the number of bristles in scute flies. If two lines differ in the leakage of + flies, due to a difference of canalisation width, then no difference would be expected between the lines in the means of *sc* flies. The term "canalisation disruption" is suggested for this phenomenon, which has not yet been observed.

A rare, aberrant phenotype can then have four different causes. (1) mutation, or segregation of major mutants (oligogenes), (2) homozygosity of a genetic homeostatic system—i.e., LERNER's "phenodeviants"—(3) genetic leakage of a canalised polygenic system, and (4) genetic disruption of a canalisation system.

An important feature of the survey of leakage in wild populations is the difference between *simulans* and *melanogaster*. In essence, *melanogaster* has a greater leakage of extra bristles, whereas *simulans* has a greater leakage of missing bristles. If we assume that the effectiveness of canalisation is identical in the two species, then the means of the scutellar system are differently located in the two species; *melanogaster* has a greater mean than *simulans*. The assumption of an identical canalisation is, however, not valid. This is shown by the much greater frequency of "deficient" bristles in *simulans* than in *melanogaster*. The development of a main bristle is not as well regulated in *simulans* as it is in *melanogaster*. Development of a bristle appears to have a greater ability to proceed completely in *melanogaster* than in *simulans*. It is probable that more intensive studies will show that bristle development has two components: that determining the initiation of a bristle's development, and that determining the degree of regulation of such development.

However, even allowing for *simulans* having a narrower canalisation zone, such that there is greater leakage of missing bristles, this does not explain why *simulans* has less leakage of extra bristles than *melanogaster*. It could be that selection against extra scutellars is more intense in *simulans* than in *melanogaster*. This will result in the mean of the "scutellar" system being lower in *simulans* than in *melanogaster*. On this scheme, selection operates only on the phenotypically expressed fraction of the scutellar genotype—i.e., it operates only against leakage. An alternative possibility is that the scutellar genes have pleiotropic effects which are not canalised, and selection operates on these pleiotropic

effects such that *simulans* has a lower mean value than *melanogaster*. Selection, on this scheme, acts on the whole of the "scutellar" system, not just on the fraction which causes extra scutellars. RENDEL (personal communication) has shown that the "scutellar" genes affect the number of abdominal bristles, which are not noticeably canalised. It is feasible that the optimum number of abdominal bristles is different in *simulans* than in *melanogaster*. This second alternative is supported by the occurrence of "Bare" and "scutellar microchaetae." The "Bare" and *smc* phenotypes are, very probably, due to single genes. In unselected populations it is suggested that these genes are effectively iso-allelic with their alternatives. Selection for extra scutellars modifies the effect of *smc* such that it is no longer iso-allelic with its normal allele. Similarly, "Bare" is iso-allelic with its normal allele in unselected populations, but selection for missing scutellars modifies the effect of "Bare" such that it is no longer iso-allelic. Both genes produce major changes of the bristle pattern which are probably deleterious, and, consequently, it is reasonable to postulate that selection would operate on the "scutellar" system to minimize the effects of "Bare" and *smc*. This postulate effectively gives the "scutellar" system a role as a modifier of these two genes, and, therefore, allocates a fitness function to a pleiotropic effect of the scutellar genes. This model has a canalisation mechanism modifying the effects of the "scutellar" genes on the number of scutellars, and a secondary effect of the scutellar genes modifying the effect of the "Bare" and "microchaetae" genes on a wider range of bristles.

BATEMAN (1959a) in her assimilation experiments with the "dumpy" phenotype, and WADDINGTON (1956) with the bithorax assimilation similarly found major segregations which occurred in two separate selection lines. Although both workers argue for a mutational origin of the major segregants during the course of their experiments, it is plausible to suggest that their selection had changed the genetic background such that the effects of the major genes became clearly distinguishable from those of the + allele. This hypothesis clearly accounts for the major segregants found in the "crossvein" experiments of BATEMAN (1959b). In effect, the selection pressure produces a genetic climate allowing iso-alleles to be distinguished.

A further complication comes from the genetic independence of the *a*, *i* and *p* types of extra bristles. The relationship of "microchaetae" and "Bare" to the scutellar genotype, and that of the *i* and *p* genotypes to the *a* genotype, show that the canalisation of scutellar number cannot be regarded as a simple two dimensional system. It will be necessary to consider the genetics of scutellar number as a multi-dimensional system, on the lines of the model devised by FRASER and KINDRED (1960) to describe the canalisation of hair growth in the mouse.

Although a considerable information has been collected on the "scutellar" system, very little is known of the "canalisation" system. RENDEL (1963) has compared the genetic widths of the various bristle classes—e.g., he has shown that the genetic widths of moving from zero to three, and from three to five bristles are 3.5 and 8.5 approximately. This description is based on the assumption that the "scutellar" system has no function in the canalisation. FRASER and

KINDRED (1960) based their discussions of the canalisation of whisker number on the same assumption. The present researches indicate that this assumption is not completely valid. The modification of the "scutellar microchaetae" and "Bare" genotypes by the scutellar system, and the modification of the expression of the *i* and *p* genotypes by the *a* genotype, show that the scutellar system is itself an inhibitor of the expression of genetic variation. In addition, M. M. GREEN (personal communication) studying a series of mutational reversions of *sc* to $+^{sc'}$, has found that some of these reversions have a markedly greater variability of scutellar number than is usual for $+^{sc}$.

SUMMARY

Comparisons of the frequencies of extra and missing scutellar bristles are given for *Drosophila melanogaster*, *simulans* and *serrata*, between wild and laboratory populations. Selection on scutellar number was practiced in *melanogaster* and *simulans*. Correlations have been established between the genetic system controlling the occurrence of extra scutellars, and the genetic system modifying the expression of the "scute" locus.

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