

VARIATION OF SCUTELLAR BRISTLES IN *DROSOPHILA*

IV. EFFECTS OF SELECTION*

By A. S. FRASER,† W. SCOWCROFT,† R. NASSAR,† H. ANGELES,† and G. BRAVO†

[Manuscript received September 22, 1964]

Summary

A series of experiments of selection of scutellar bristles in *D. melanogaster* is described. The evidence suggest that there are three levels at which artificial selection is relatively ineffective and that these levels are not necessarily a function of homozygosity but rather of natural selection maintaining the line at a new equilibrium value. Crosses between the initial set (A set) of selection lines led to the conclusion that there is a consistent dominance of the parent with the lower scutellar value.

Inversion-marked chromosomes were used to determine the location of selection advance on chromosomes I, II, and III. In the lines which had reached the highest level of selection advance the most effective chromosomes were chromosomes I and III or a combination of each of these. The lines which had reached the second level showed a marked heterogeneity of response, which included large negative components resulting from interchromosomal interactions.

I. INTRODUCTION

Drosophila normally have four scutellar bristles, but this constancy is not consequent from a lack of genetic variability. Payne (1918) and Sismanidis (1942) have shown that selection for extra scutellars can result in lines whose number of scutellars far exceeds the norm of four. The normal constancy of scutellar number must be due to inhibition of the expression of genetic variability. Mather (1942) proposed that this genetic variability is not normally expressed because it is present in the form of balanced polygenic combinations. This suggestion is not tenable as a complete explanation—the variability of scutellar number increased in the lines selected for increased number and only a small proportion of this variability was genetic—the majority of the variability was due to environmental effects (Rendel 1959; Fraser 1963). The polygene hypothesis cannot explain the normal lack of expression of environmental variability, since the existence of the scutellar genes in balanced combinations will only reduce the variability by the amount due to genetic segregation and recombination.

Reeve and Robertson (1953) have suggested that selection can modify isoalleles into oligogenes by changing the background genotype. Fraser (1963) demonstrated the validity of this suggestion. He found that selection for decreased scutellar number in *D. simulans* changed a gene, *Bare*, from an isoallele into a fully penetrant dominant with an extreme effect. The same objection to this explanation can be made as has been made to the polygene explanation; that it only applies to the genetic component of the variability.

* Supported, in part, by National Institutes of Health Grants Nos. 10646 and 11778.

† Department of Genetics, University of California, Davis, California.

Rendel (1959), following Dunn and Fraser's (1959) approach, showed that selection for both increase and decrease of scutellar number was effective in *scute* stocks. The *scute* gene causes both a decrease of scutellar number, and a marked increase of variability. Only a proportion of this variability is genetic, and Rendel found that in the line selected for increased number there was a very marked decrease of the variability as the mean approached the norm of four scutellars. He proposed an explanation of "developmental canalization" which could be represented by a non-linear relation of the actions of the scutellar genes to their effects on scutellar number. This is shown in Figure 1.

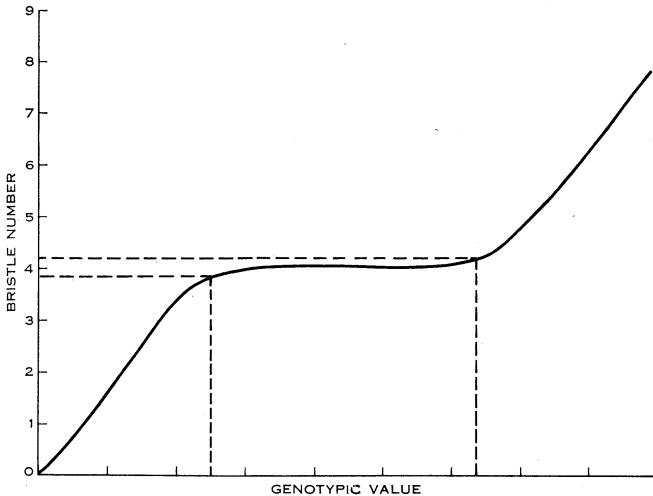


Fig. 1.—Hypothetical relationship of the phenotype to the genotype, for canalization at an intermediate phenotype.

A major feature of this hypothesis which distinguishes it from both the "poly-gene" and the "isoallele" hypotheses is that the mechanism of canalization can act on both genetic and environmental components of the variability (see Waddington 1953). It is implicit in the statements of this hypothesis that the same set of genes is responsible for variation both in mutant and wild-type stocks (see Dunn and Fraser 1959; Rendel 1959). Haskell (1943) gives data which do not show such a correlation of mutant and wild-type expression. Further, Fraser and Green (1964) have shown that selection for extrascutellars in wild-type stocks does not affect the expression of *scute*. Conversely, they found a very marked effect on the expression of *scute* of selection for missing scutellars in wild-type stocks, which suggests that there are two systems affecting the number of scutellars; one operating when development is above the norm, the other operating when development is below the norm. It appears that the hypothesis of developmental canalization of scutellar number as stated by Rendel (1959) is an oversimplification. Another aspect of the canalization hypothesis which is proving to be an oversimplification is that the canalized genotype is genetically simple, being mainly additive. The occurrence in unselected populations of individuals with other than the normal four scutellars is, on this hypothesis, due simply to the segregation of extreme combinations. Fraser (1963) proposed the term

“canalization leakage” for this phenomenon to distinguish it from “phenodeviance.” Lerner (1954) showed that the effectiveness of selection for a number of characters which are conditioned in their expression by some form of a threshold is positively related to the degree of inbreeding. He emphasized the role of “overdominance” in maintaining genetic variability but did not exclude interactions as an explanation. He suggested that inbreeding, by reducing heterozygosity, causes a decrease of developmental stability, and a consequent increase of the frequency of “phenodeviants.” Fraser (1962) differed with this hypothesis, concluding from computer simulations of normalizing selection that selection for phenotypic constancy is extremely inefficient and, therefore, that heterozygosity is the expected feature of any genetic system in the absence of inbreeding. He concluded that the genetical variability of a canalized genotype is a residual which selection is ineffective in reducing. On this model, the canalized genotype would be expected to be genetically simple. Fraser (1963) showed that the canalized genotype can be complex: the modification of the *Bare* isoallele into a dominant with major effects is an example of this. Another example comes from crosses between unselected strains in which the frequency of extrascutellars was reduced—continuation of these crosses to the F_2 did not show any segregation of extrascutellars.

Clearly there are a number of problems requiring resolution in the understanding of the determination of scutellar number, and a number of us have cooperated in an analysis of the effects of selection on scutellar number. Many aspects of the results presented below will later be considered in more detail, but a comprehensive discussion over the whole range has value as a focus for the other papers.

II. MATERIALS AND METHODS

The A set of selection lines was derived from a survey for scutellar leakage (Fraser 1963). Initially selection was practised on a very large number of lines, each originating from the progeny of a single female. Many of the lines were discarded at the third to fourth generations and some selection was practised between lines. A considerable fraction of the remaining lines were later discarded because of reduced viability. The A set of lines has, therefore, been selected inter- and intraline for both scutellar number and viability. In all lines no attempt was made to maintain constant selection differentials, and selection was restricted primarily to females; about 30–60 flies were scored each generation, from which two to five females were selected—whenever males with extrascutellars occurred, these were placed with the selected females, but since no attempt was made to collect virgin females, it is unlikely that this selection of males was effective to any significant degree. The results given below are for females only, unless otherwise specified. The majority of the A lines originated from stock 70, and from crosses of stock 70 with stock 71 (see Fraser 1963). A few of the A lines originated from wild females (lines A15, A42, A27). Three types of selection were practised: high, low, and for extrascutellars occurring at specific locations. [Fraser (1963) classified extrascutellars into anterior (*a*), interstitial (*i*), and posterior (*p*), and selection was practised on the occurrence of one or other of these types without reference to the occurrence of extra bristles at other locations.] The origins of the A lines are listed in Table 1.

Approximately one year after the initiation of the A lines, a second set of lines (the B set) was derived from the base stocks which figured prominently in the origins of the A lines, namely stocks 70 and 71. Selection was for high bristle number, and no selection was practised between lines after the first generation. After several generations each line was split into three replicates which were then maintained as separate selection lines. The lines were split into three replicates after seven generations, in order that a measure could be gained of the amount of variability retained

TABLE 1

ORIGINS OF THE A SET OF SELECTION LINES AND TYPE OF SELECTION PRACTISED DURING THE FIRST 15 GENERATIONS OF SELECTION

After 15 generations of selection all lines were selected for increased number of scutellar bristles regardless of their position. Extensive counts of scutellar number, made on these lines at the 40th generation, are given. Counts of unselected stocks (70, 71, 73) made at the same time are also given

Selection Line	Origin	Type of Selection	Frequency Distribution of Scutellar Number									
			3	4	5	6	7	8	9	10	11	$\bar{x}$
A1	70 × 71 × 70	<i>a</i>	—	7	32	232	392	241	71	20	5	7.15
A9	70	High	—	—	6	98	293	395	154	46	8	7.76
A18	70 × 71	High	—	3	52	370	377	155	33	9	1	6.77
A4	70	<i>i</i>	—	383	349	198	52	16	2	—	—	4.98
A6	70	<i>a</i>	—	268	445	268	19	—	—	—	—	5.04
A15	Wild	<i>a</i> and <i>p</i>	—	65	248	503	164	20	—	—	—	5.83
A21	70	<i>a</i>	—	451	396	137	16	—	—	—	—	4.72
A27	Wild	<i>p</i>	—	505	303	187	5	—	—	—	—	4.69
A30	70	<i>i</i>	—	364	419	190	25	2	—	—	—	4.88
70	—	—	1	305	298	12	—	—	—	—	—	4.09
71	—	—	—	499	16	—	—	—	—	—	—	4.03
73	—	—	1	797	2	—	—	—	—	—	—	4.00

after the seven generations of inbreeding as a result of the small number of matings used. The number of flies scored and selected were the same as in the A set. Two further lines (the C set) were initiated from stock 70, about 6 months after the initiation of the B set. These lines were maintained by selection of a minimum of eight females. The C set of lines were initiated to determine whether the responses to selection found in the A and B sets of lines were a result of the high rate of inbreeding in these lines.

The D set of lines was initiated from a number of wild-type stocks maintained at the Department of Genetics, University of California, Davis. Each line was split into separate replicates after several generations. Selection was as in the B set.

Results are mostly given as the mean scutellar number. The percentage of females with extrascutellars (the scutellar leakage) is also given for some analyses of the data. The data is far too extensive to allow a complete representation and the original protocols will, therefore, be kept available on file at this Department.

III. RESULTS

(a) *The A Set of Selection Lines*

The results for the A set of selection lines are given in Figure 2, in which the mean scutellar number is plotted against generations of selection. There is a considerable heterogeneity of rate of advance; response was slow or zero in some periods and in other periods it was extremely fast.

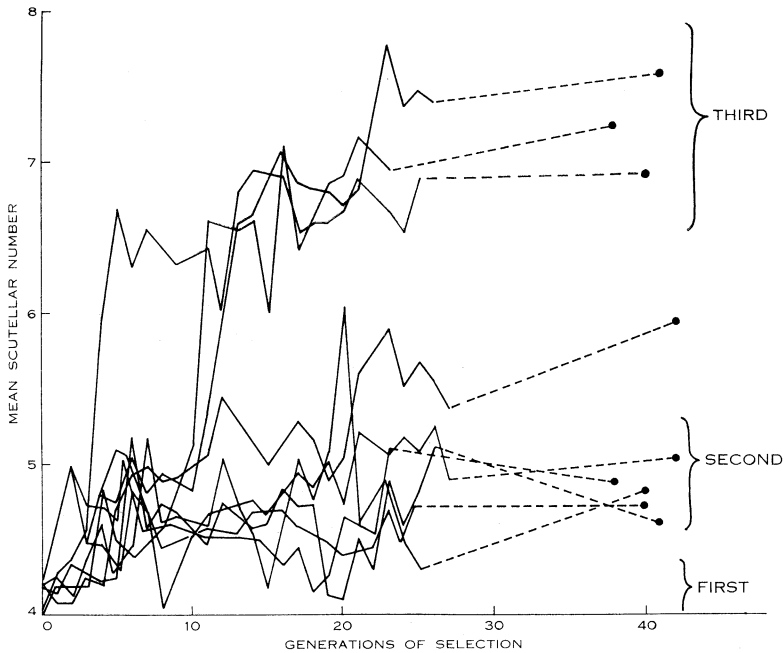


Fig. 2.—The A set of selection lines. Mean scutellar number of females plotted against generations of selection. Solid lines represent progress under selection. Broken lines represent maintenance by mass-mating. Groups designated as first, second, and third refer to levels at which selection was relatively ineffective.

Fraser (1963) has described the normal variation of scutellar number. This will be called the “norm” or first level. Two other levels can be distinguished at which selection is *relatively* ineffective. These are: (1) the level reached by the majority of the lines, which was in the range 4.5–5.5 bristles (termed the second level); and (2) the level reached by a small proportion of lines, which was in the range 6.5–7.5 bristles (termed the third level). Line A9 (see Fig. 3) illustrates the distinction between the second and third levels. In this line the mean scutellar number was 4.18 in the initial population; it advanced to 4.9 in two generations, and then fluctuated about 4.8 for nine generations, when a rapid advance occurred to more than 6.0. A slow advance then occurred to about 7.0.

The distinction between the first, second, and third levels is not claimed to be more than a rough separation which is considerably confounded by long-term slow advances and regressions. Line A15, for example, showed an initial period of 4–5

generations at the first level; it then advanced in a few generations to about 5 bristles, and has over the next 18 generations of selection advanced to nearly 6 bristles (see Fig. 3). If all of the lines are considered as a whole there is a real distinction between the three levels. Data are given in Table 1 to show the distinction.

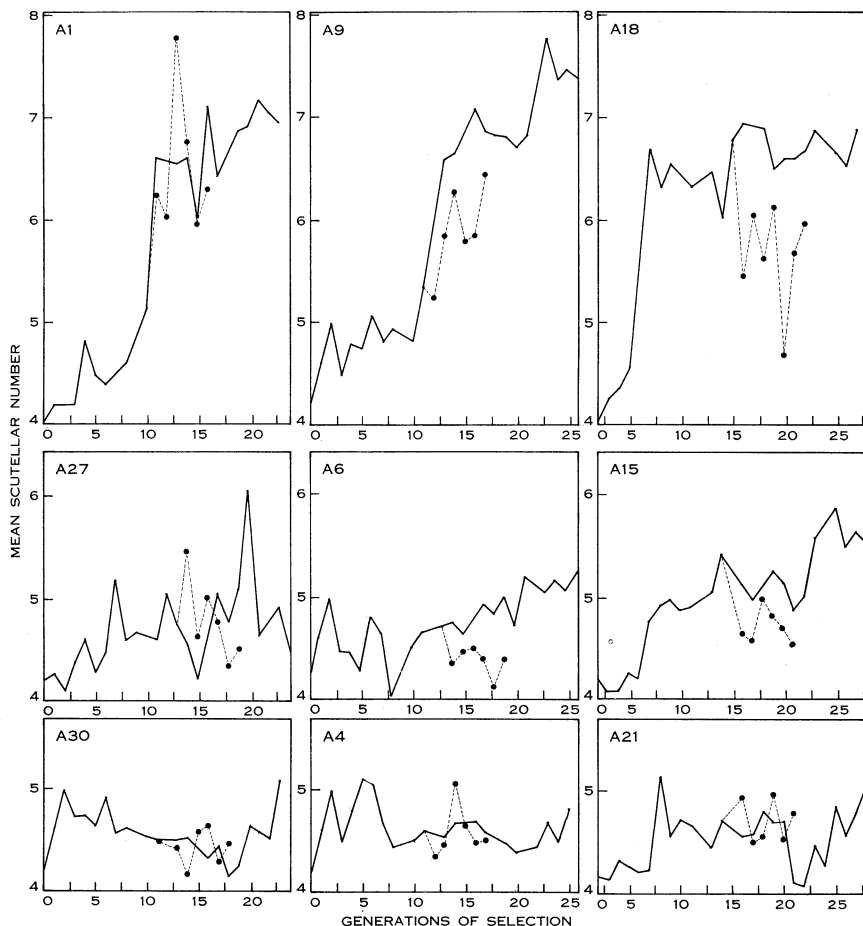


Fig. 3.—Individual lines of the A set of selection lines. Solid lines represent positive selection. Broken lines represent reverse selection.

Reverse selection lines were initiated to determine whether the relative ineffectiveness of selection at levels 2 and 3 was due to the exhaustion of genetic variability. Females with bristle numbers of 4, or closest to 4, were selected as parents. The results are shown in Figure 3. Reverse selection has been successful at both the second and third levels in at least some of the lines, showing that lack of response to positive selection is not necessarily due to a lack of genetic variability. A very interesting feature of some of the reverse selection lines is shown in lines A1 and A9. These reverse selection lines were fortunately initiated just as the lines started a rapid advance from the second to the third levels. The reverse selection lines also

advanced to the third level, suggesting that the selection for extrascutellars has disturbed an equilibrium, and that this disturbance is such that natural selection then shifts the line to another equilibrium region, regardless of the direction of the artificial selection.

The heterogeneity of response between lines could be due to the different types of selection which were practised, since some of the lines were selected for extrascutellars occurring in specific positions whereas others were selected for extrascutellars without reference to position. Selection for specific types was successful (Fraser 1963), but this does not appear to be related to the overall response. Five lines reached the third level: three of these were high lines, one was an *a* line and the other was an *i* line. Seven lines reached and stayed at the second level: one was a high line, two

TABLE 2
FERTILITY AND FECUNDITY OF THE A LINES AT GENERATION 22

Ten males for each line were each mated to five females. Male fertility is the percentage of males which produced offspring in at least one mating. Female fertility is the percentage of females mated to fertile males which produced offspring. Fecundity is the mean number of progeny from the fertile matings. Vials were used

Line	Male Fertility (%)	Female Fertility (%)	Fecundity	Mean Scutellar Number
A27	90	70	47	4.66
A15	80	72	52	5.31
A42	50	84	52	3.96
A1	30	40	42	6.20
A4	100	78	29	4.63
A6	30	46	56	4.89
A9	80	80	45	7.12
A18	90	58	28	6.37
A21	30	53	60	4.47

were *a* lines, two were *i* lines, and two were *p* lines. There is only a slight correlation of the type of selection with the response achieved. These results also indicate that the number and location of extrascutellar bristles are separately determined.

Another possible explanation of the heterogeneity of response between lines is that they had different origins. Of the five lines which reached the third level, four originated from crosses between stocks 70 and 71—the fifth came from stock 70. Four of the second-level lines came from stock 70 and three from progeny of wild-type females. Advance from the second to the third level appears to be more probable in lines originating from crosses of stocks 70 and 71, but it can occur from stock 70 alone.

The existence of the second and third levels could be due to subsidiary zones of canalization, which make selection less effective by reducing the phenotypic expression of genetic variability. There were no indications of such secondary zones of canalization—the variability of the second-level lines is considerably greater than

that of the first-level lines, and that of the third-level lines is greater than that of the second-level lines. Characteristic frequency distributions of scutellar number are given in Table 1.

There have been periods in almost all of the selection lines when the fecundity or viability decreased, and it is possible that the decreased response to selection is due to a lowered reproductive fitness. Tests were made at generations 28–32 to determine

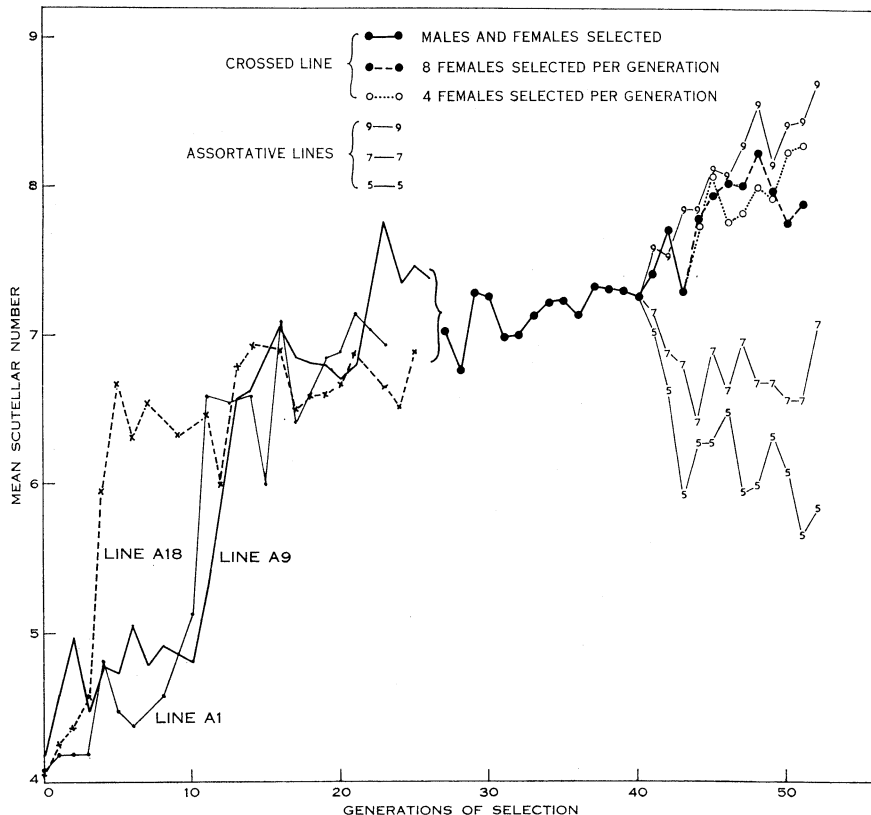


Fig. 4.—The A set of selection lines. Selection response of lines shown prior to generations 22–24 as in Figure 2. Solid circles represent selection response of a population established by intercrossing the three A lines which reached the third level.

fecundity and viability. Ten males from each line were each mated to five females, which were then set in single vials, and counts were made of the progeny, and of the occurrence of extrascutellars. The results are given in Table 2. A feature of these data is that there is no correlation of fertility or number of flies per vial with amount of advance, which agrees with a general observation that the loss of lines due to decreased viability was not correlated with the scutellar number.

Several lines which reached the second level have shown a regression against selection, toward the first level. In some but not all of these lines the regression has

been correlated with a decreased viability. Similar regressions against selection have been observed in the B and D set of lines.

Stock 70 has shown a decrease of scutellar leakage. Initially this stock showed about 25% of females with extrascutellars (see Fraser 1963; Pennycuik and Fraser 1964). About one year later this had decreased to 10%, and 6 months later it had dropped to 8%. This decrease was also found in replicate cultures of stock 70 maintained at Michigan, and a similar decrease has been reported in the cultures of

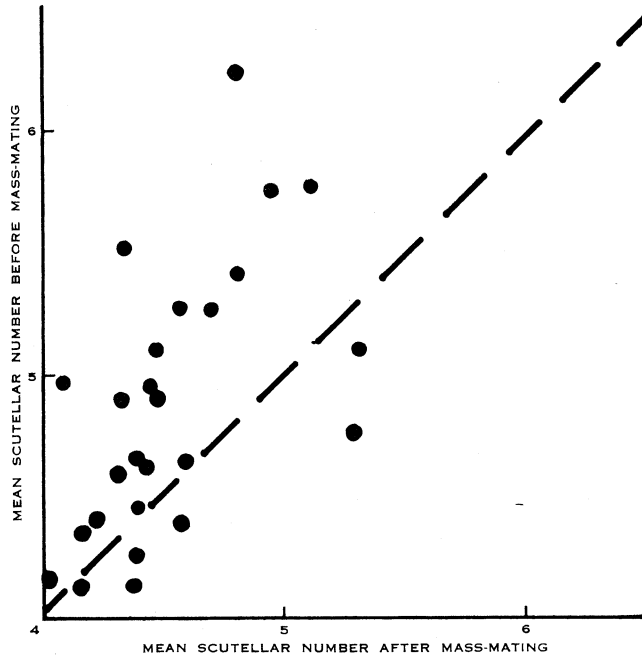


Fig. 5.—Scutellar number of non-*scute* flies in segregating populations of *scute*¹-substituted A selection lines, immediately after substitution of the *scute*¹ allele as a function of scutellar number after 5–7 generations of mass-mating.

stock 70 maintained at Sydney, Australia. Clearly, natural selection has been operating against extrascutellars in line 70. Many of the features of the above data can be reconciled if the occurrence of extrascutellars is closely correlated with a major determinant of reproductive fitness. Once selection for extrascutellars has modified the equilibrium mechanism then natural selection will operate either to return to the initial equilibrium value, or to move to another equilibrium value. The justification for this model is considerably strengthened by the phenomena found in the B set of lines (see Fig. 8).

Five lines reached the third level, but selection was only continued on three of these: lines A1, A9, and A18. They showed a slow rate of response. These three lines were crossed together to increase the genetic variability, and selection was practised on both males and females to increase the selection differential. The rate of response

in this "crossed" line was not noticeably different from that which had been found in the three parent lines.

At the time that the three third-level lines were crossed to produce the crossed line, selection was discontinued on these lines which were then maintained by mass-mating in four separate replicates. The mass-mated lines from A1 and A18 showed an increase of scutellar number between generations 25 and 37 which was of the same order as that found in the crossed line. The mass-mated lines from A18 did not show such an increase.

These complicated results can be explained if natural selection operating on lines A9, A1, and the crossed line maintained an equilibrium which was slowly moved to a new value. The similarity of the response of the crossed line, and of the mass-mated lines indicate that the artificial selection practised in the crossed line was not the major determinant of the advance of this line.

A further change of the selection scheme was initiated at generation 40. Selection in the crossed line was restricted to females, and two replicate lines were maintained—in one the line was maintained by selecting the eight females per generation with the greatest scutellar number; in the other, the line was maintained by selecting four females per generation with the greatest scutellar number. These lines showed a marked response to selection which was continued until the populations reached a mean of approximately 8 bristles. It is not certain whether the advance was consequent upon the change of the mode of selection; the advance is, however, diagnostic of the crossed line containing realizable variability.

Another set of lines was initiated from the crossed line to further determine whether this line contained genetic variability which could be affected by selection. These lines were maintained by selecting females of a single scutellar value. Lines for 5, 6, 7, 8, 9, and 10 bristles were established. The results of the 5, 7, and 9 scutellar lines are shown in Figure 4. Clearly, there is a considerable genetic variability in the crossed line which can be realized by selection. This same variability must have previously existed in a non-realizable form. An interesting feature of these lines is that the lines for 9 and 10 bristles have shown an advance which continued for several generations before decreasing. If the main crossed lines and the 9 and 10 scutellar lines are considered together, there is an indication that they are moving into a fourth stasis level at about 8 bristles. The lines for 5, 6, and 7 bristles have also shown an initial period of fast response after which they have shown little, if any, response to selection. It is probably not fortuitous that the "5, 6, and 7" lines reached stasis at values of the same order as that reached by the initial accession of the A1, A9, and A18 lines to the third level. This suggests that the same natural selection systems, which effected the shift from the second to the third levels, also operate against artificial selection directed from the third back to the second levels.

The *scute*¹ gene and three derived-Y translocations were separately substituted into the A set of lines. The *scute*¹ stocks were maintained in segregation for *sc*¹ and *sc*⁺, without any selection for scutellar number, and the derived-Y stocks were maintained by mass-mating. All of these substituted lines were scored first, shortly after formation, and then after 5–7 generations of mass-mating [see Fraser and Green

(1964) for original data]. The correlations between these scores for the sc^+ segregants are shown in Figure 5. There has been an appreciable regression toward a lower scutellar number in many of the lines. This contrasts with the absence of any regression towards a lower scutellar number in the A selection lines after they have been maintained by mass-mating for several generations (see Figs. 2 and 4). The substitutions of the sc^1 and derived-Y translocations into the selection lines did result

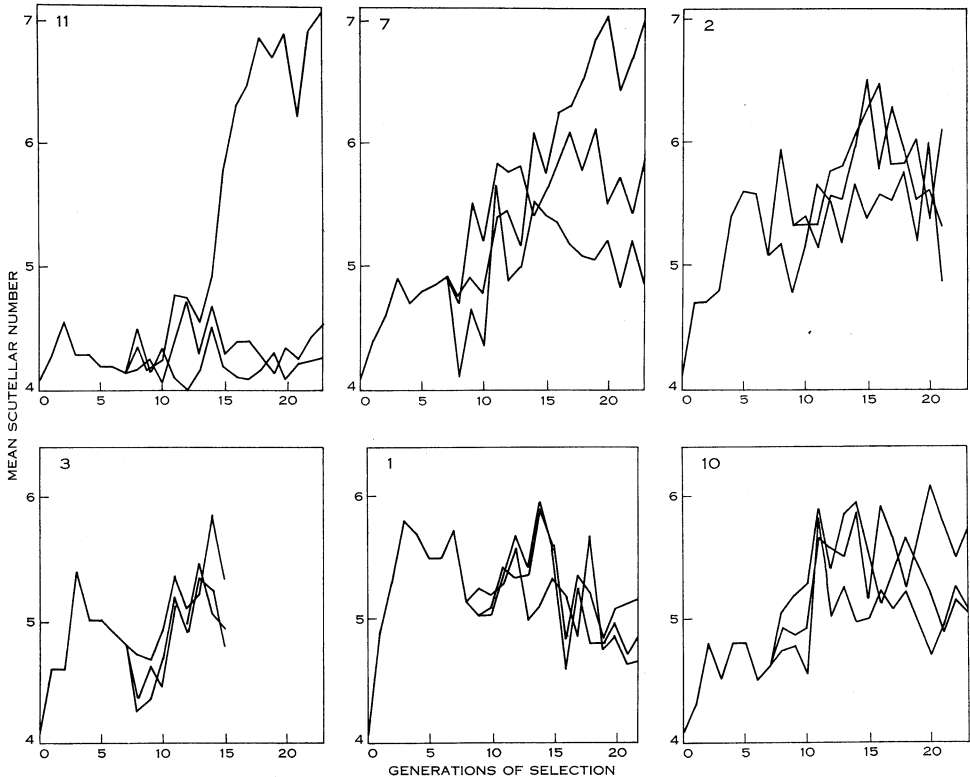


Fig. 6.—The B70 set of selection lines. Mean scutellar number of females plotted against generations of selection for lines originating from stock 70.

in a small but not negligible loss of the advance gained by selection, and it is reasonable to suggest that the introduced genetic material which caused this loss has resulted in the equilibrium reached under selection being disrupted; enough to allow natural selection to cause a regression to a lower scutellar number.

The restriction of the advances reached by selection to two main levels confirms the suggestion by Sismanidis (1942) that there were a restricted number of levels at which selection was ineffective. This cannot be satisfactorily explained on a simple hypothesis of recombination within "polygenes", using the term polygene in the original sense of Mather (1942).

(b) The B and C Set of Selection Lines

A second set of selection lines (the B set) was initiated from stocks 70 and 71. A number of fertilized females from each of these stocks were scored for scutellar number, and set up singly in vials. Fifty such cultures were set up from stock 70, and

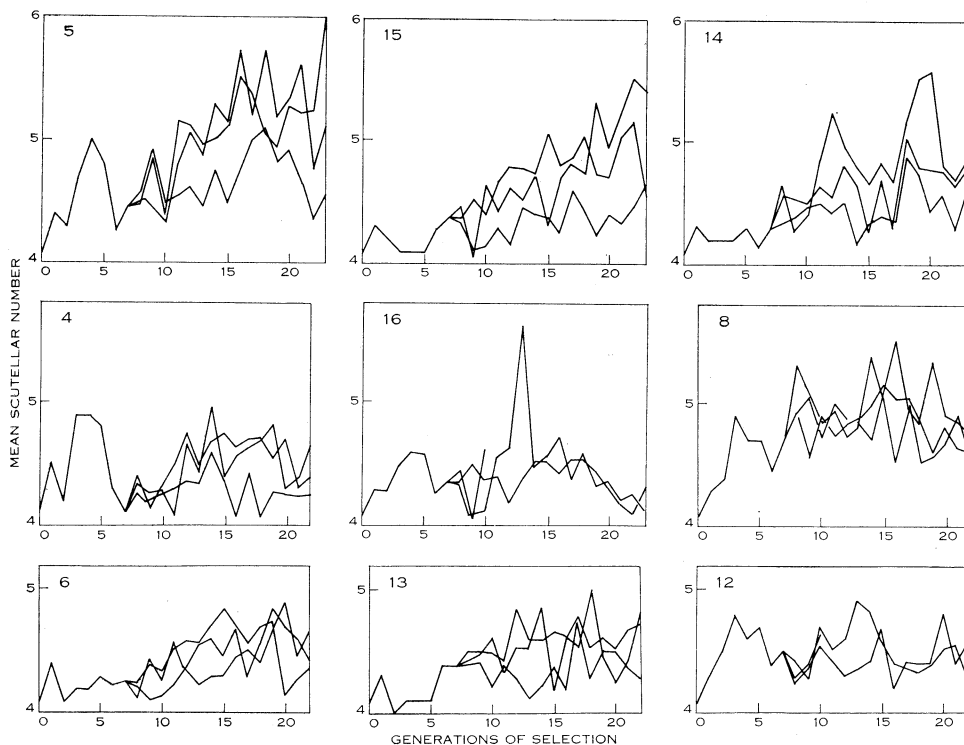


Fig. 7.—The B70 set of selection lines. Mean scutellar number of females plotted against generations of selection for lines originating from stock 70.

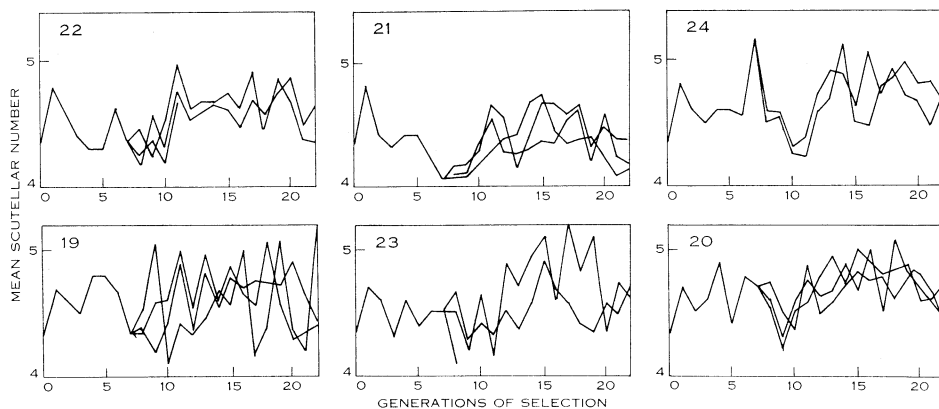


Fig. 8.—The B71 set of selection lines. Mean scutellar number of females plotted against generations of selection for lines originating from stock 71.

a single selection line was initiated from each of the 15 cultures with the greatest scutellar number (the B70 set). Twenty-six cultures were similarly set up from stock 71, and selection lines were initiated from each of the top six cultures (the B71 set). The results are shown in Figures 6, 7, and 8, and also in Figure 9 for a representative group of the B70 lines after simplification to reduce variability; this consisted of taking a running average over three generations. Figure 9 covers more generations of selection.

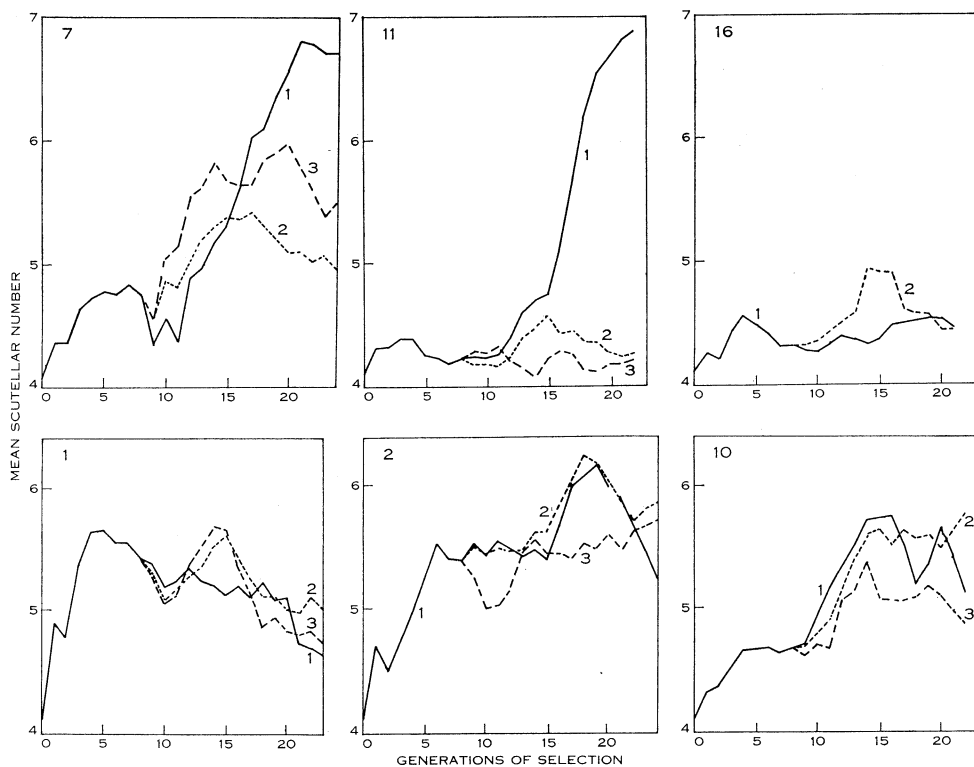


Fig. 9.—The B70 set of selection lines. Mean scutellar number as a running average over an interval of three generations (1, 2, and 3).

The results obtained in the B70 lines show some similarities with the A lines. A small proportion of the lines showed a rapid response to a high level, the majority showed an advance to an intermediate level, and several of the lines remained at a low level. It is not unreasonable to conclude that a similar trilogy of stasis levels to that found in the A set also occur in the B70 set. Selection in the B71 lines produced an immediate response which was then followed by a regression against selection pressure. The differences between the B70 set suggests that the heterogeneity of advance found under selection in the A lines is primarily a feature of the 70 stock. Estimates of the probit intervals for the different bristle classes have been made for several trios of the B selection lines—these do not show any consistent relation with the lines reaching or leaving a stasis level, confirming the suggestion from the A lines

that the occurrence of periods when selection is ineffective is not due to there being secondary zones of canalization.

Two further lines (the C set) were set up from stock 70 about 6 months after the initiation of the B lines. The number of female parents was kept in excess of 8 throughout the experiment. These lines are shown in Figure 10. They were similar in their response to selection; both showing a similar decrease of the effectiveness of selection after 10 generations of response. These lines indicate that the occurrence of "stasis" at the second level is not a consequence of lines being based on a single female, and being maintained by a small number of parents. Further experiments based on larger numbers of parents are needed to confirm this indication.

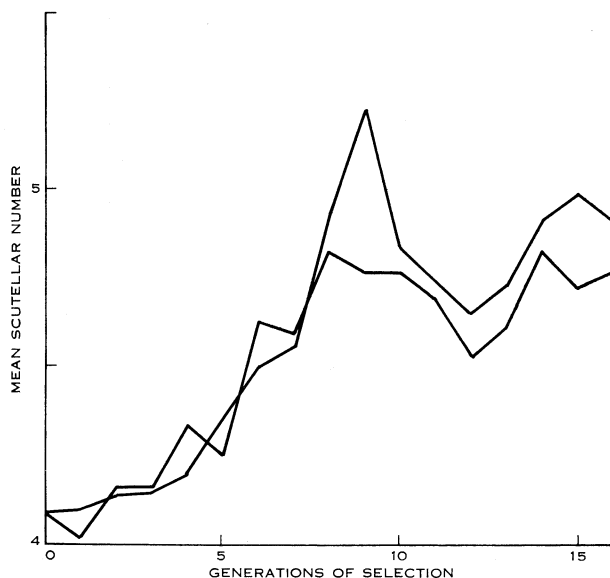


Fig. 10.—The C set of selection lines. Mean scutellar number of females plotted against generations of selection. The number of parents per generation was in excess of 10.

The results for the D set of lines are shown in Figure 11. In one replicate a marked and fast advance occurred after 20 generations of selection (line D3·3), showing that the patterns of response to selection found in the lines initiated from stock 70 are not unique to that stock, since the D lines were formed from unrelated laboratory stocks.

(c) Crosses between the A Lines

A series of crosses were made between several of the A set of selection lines, with the aim of determining whether segregation occurred for the advance to the third level. Crosses were of four females with four males to give the F_1 's, which were then mass-mated to give the F_2 's. These crosses were made when the lines were at the seventh to tenth generation of selection. The mean scutellar number of the F_2 's are given in relation to the mid-parent value in Figure 12. There is a marked

dominance of the lower parent, which can also be interpreted as a regression towards the initial norm of 4 scutellars. There was a slight increase of scutellar number in the

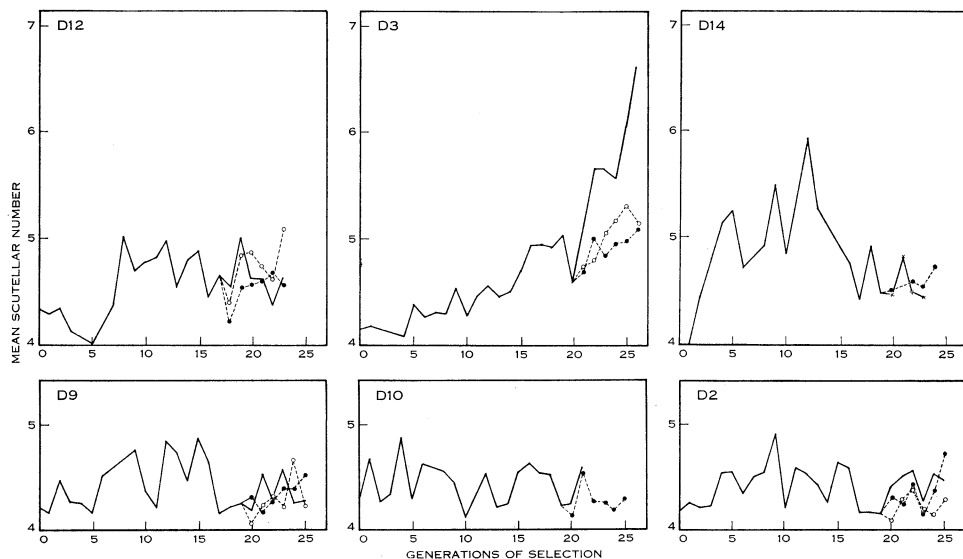


Fig. 11.—The D set of selection lines. Mean scutellar number of females plotted against generations of selection.

F_2 's over the F_1 values but no detectable segregation of major factors, suggesting that the advance to the third level is not genetically simple. Three more sets of crosses

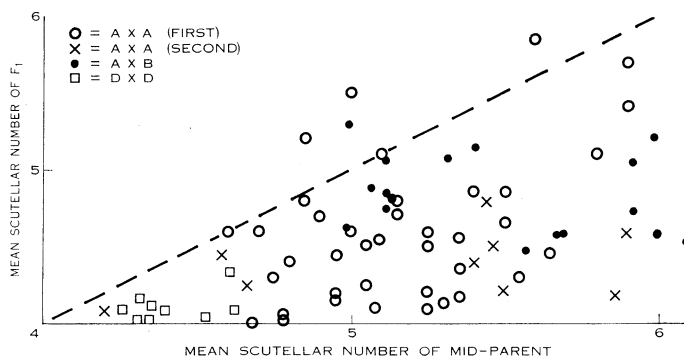


Fig. 12.—Mean scutellar number of F_1 's from crosses between the A lines, between the A and B lines, and between the D lines plotted against the mid-parent expectation. Broken line represents the expected regression based on an additive model.

were made: between the A lines, between the A and B lines, and between the D lines at generations 20–25. The results from these crosses are also shown in Figure 12. There is a consistent dominance of the lower parental value.

Crosses were made of the A lines at the seventh to tenth generation of selection to the unselected stocks 70, 71, 73. These stocks formed a series of decreasing scutellar leakage, with 70 showing about 25% of females with extrascutellars; 71 showing about 10%, and 73 showing a negligible percentage of females with other than 4 scutellars. Crosses were also made to line A42. This line which was selected for decreased number of scutellars, originated from a stock held at Rochester, New York. Although many attempts were made from different stocks to select for missing scutellars, such selection was only effective in line A42. The percentage of flies with missing bristles in line A42 fluctuated from generation to generation, averaging about 20% in males and about 5% in females. The results of the crosses between the A lines and stocks 70, 71, 73, and line A42 are given in Figure 13. Although there is a

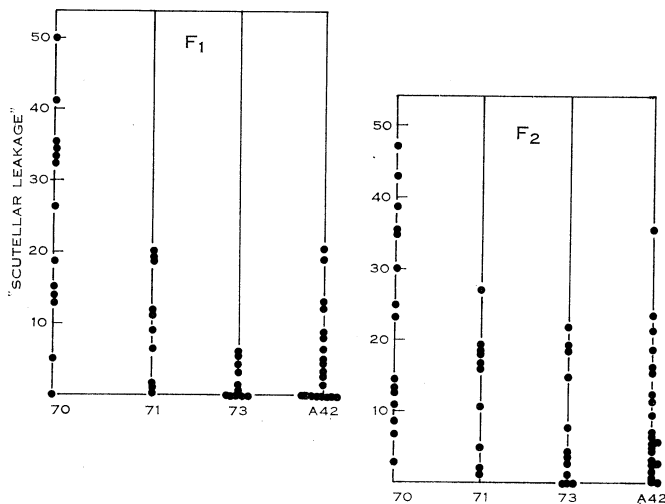


Fig. 13.—The F_1 and F_2 mean scutellar leakage for crosses of each of the A selection lines with stocks 70, 71, 73, and the low scutellar selection line A42.

wide variability, the means of the three sets of F_1 's correspond to that of the unselected parents. There is a dominance of the unselected stock. A very interesting feature of these crosses is that the F_1 's involving lines A42 did not show as marked a regression as those involving stock 73. This further supports the suggestion that genes for missing scutellars are not complementary to those for extrascutellars.

(d) Location of the Scutellar Genotype

Mather (1942), and Reeve and Robertson (1953) have used "inversion-marked" chromosomes to identify the chromosomal location of selection advances. A similar analysis has been made of several of the A set of selection lines at generation 27, and of the B11 and D3 trios of selection lines at generation 26. These results are presented in summary in Figures 14 and 15. Two different X-chromosome balancers were used: C1B and w^{m4} . Balancers for chromosomes II and III were *Cy* and *Ubx*. The w^{m4} chromosome could be used because most of the selection lines contain the w^h allele. Figure 16 shows the mean scutellar number for the different genotypes in replicate

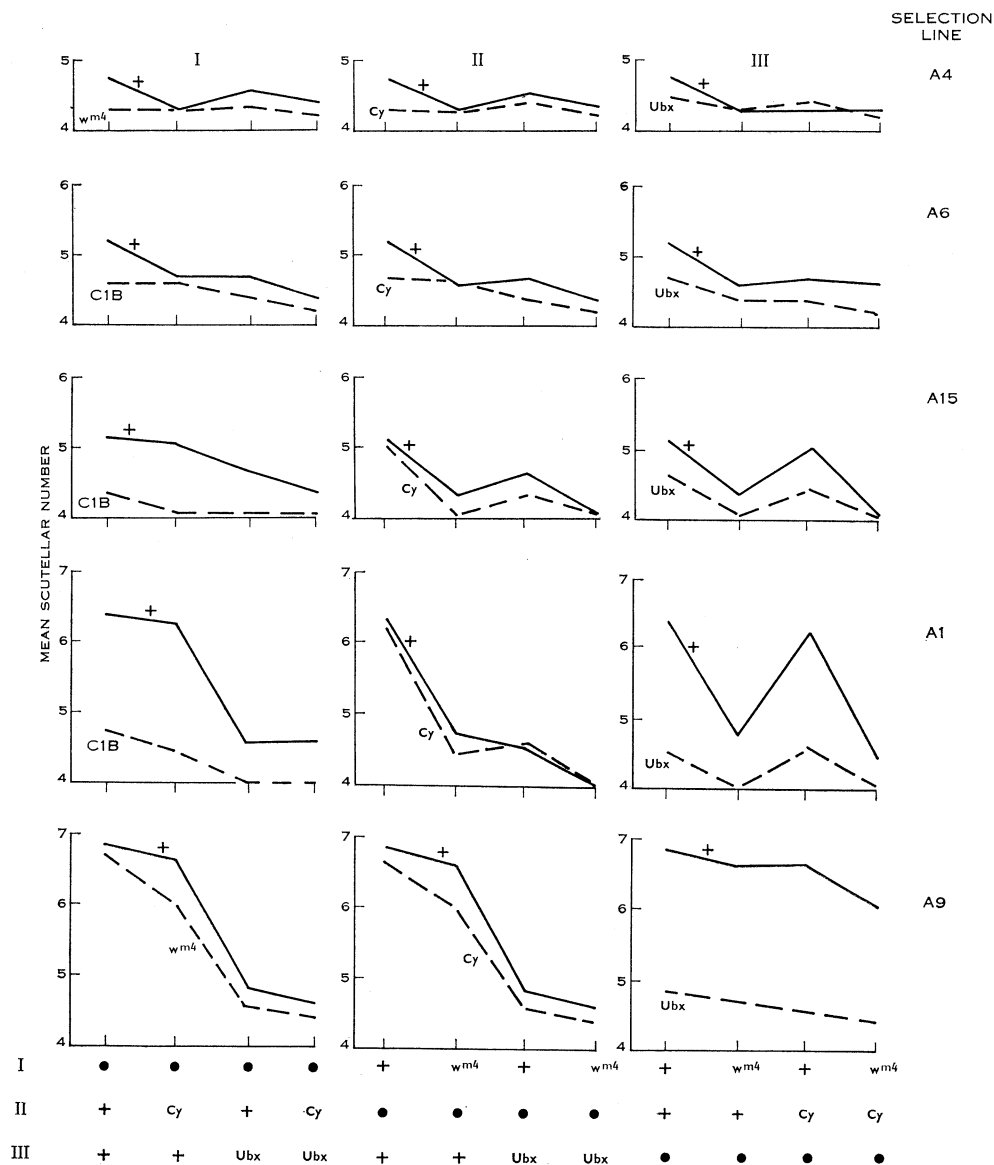


Fig. 14.—Chromosomal analysis of the A set of selection lines. A4, A6, and A15 are second-level lines; A1 and A9 are third-level lines. I, effect on scutellar number of homozygosity for chromosome I extracted from the selection line (—) compared with the effect on scutellar number of heterozygosity for marked chromosomes extracted from the selection line (---). The “inversion-marked” chromosome used in each case is indicated. The comparison is over all combinations for chromosomes II and III, and likewise for chromosomes II and III with respect to the other two chromosomes.

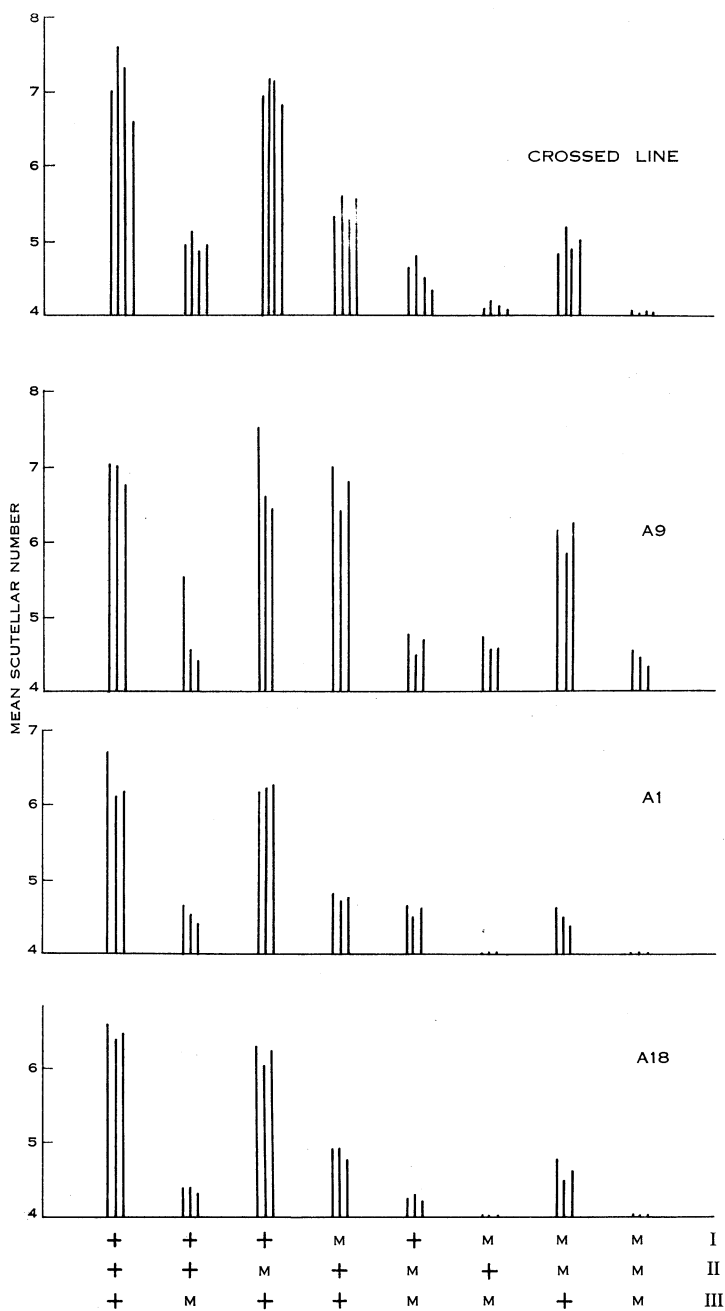


Fig. 16.—Mean scutellar numbers of the eight genotypes which occur in chromosomal analyses of the A1, A9, A18, and crossed lines. Results of four replicate analyses are given for A1, and of three replicate analyses for the other lines.

The lines which reached and stayed at the second level (A4, A6, A21, A15, and D3·2) showed a marked heterogeneity between their respective components of selection advance. The D3·2 line possessed a major component on the first chromosome with positive interactions between the first and third chromosomes contributing the remainder of the advance. A similar pattern was obtained with line A15. A major feature of the remaining lines is the relatively large negative component resulting from interchromosomal interaction. These negative effects nullify the majority of the positive selection advance manifested by the separate chromosomes. The negative interactions in these lines often involved chromosomes which had a positive determinant of the selection advance considered in isolation, but which in combination with other chromosomes had a negative effect. The negative interactions are concerned with the lower limit of normal bristle number and if it were possible to assign meaningful values below the threshold for genotypes which have values at or near the norm, then it is possible that the negative interactions found from the untransformed data would prove to be simply due to existence of a threshold at 4 scutellars. This possibility will be examined in a later paper by application of the probit method which has been used to considerable advantage by Rendel (1959).

IV. DISCUSSION

Our results are in close agreement with those obtained by Payne (1918) and Sismanidis (1942), showing that the phenomena are general, and not a fortuitous circumstance of the stocks which were used—selection for extrascutellars involves periodic reductions of the effectiveness of selection—these have been termed stasis levels. Mather (1943) based his deduction of the existence of polygenes (linked groups of minor genes) on two features of the effects of selection. These were (1) the alternation of periods of slow and fast response in both his selection lines, and in those of Payne and Sismanidis, and (2) on the considerable advances beyond the range of the parent populations which could result from selection experiments initiated from the progeny of single females. Our results cast considerable doubt on the pertinence of the first point to the polygene concept—the stasis levels appear to be more usefully considered as equivalent to Wright's (1932) adaptive peaks. This is particularly evident from the negative responses to reverse selection found in lines A1 and A9 (see Figs. 14 and 15), which demonstrate that the advance from one stasis level to another is primarily determined by natural selection. The advance from one stasis level to another appears to be *effected* by natural selection, but there is little doubt that the advance is *initiated* by the selection practised for scutellar number. It appears that this artificial selection causes a change of the genetic constitution of the population, such that this moves against natural selection from one peak into a trough between peaks. Once at this point then natural selection reinforces the artificial selection, moving the population to the next adaptive peak. This hypothesis is clearly an oversimplification, but it is sufficiently indicated by our data to be taken as the major working hypothesis. The three replicate lines of B2 show the existence of a stasis level at 5·5 bristles (see Fig. 9). This level was reached by the original single line, which was then separated into three replicates—two of these stayed at the stasis level for several generations before advancing. They showed a considerable

advance and then regressed to the stasis level. The third replicate regressed immediately to a mean of 5.0, and then advanced until it reached the stasis level, at which it stayed for several generations. The concept of peaks of fitness cannot be considered as one of specific phenotypes being consistently more fit than others. The shapes and means of the adaptive peaks seem to move. Another trio of lines, the B1 trio, shows a general regression after an initial advance. The three replicates advance from and regress to this line of regression, indicating that the stasis level is not a fixed phenotype, but rather a mean phenotype which after the initial advance regressed back towards the norm.

The chromosomal analyses have shown that the chromosomes I and III can, separately or conjointly, be responsible for the advance to the same third level. This argues against a simple polygenic explanation of the phenomena. Chromosome II has very noticeably never contained a major positive component of the advance, differing from Sismanidis (1942) who found a positive component of chromosome II in his lines. There is a strong indication that some of the chromosomes which contain a positive component may have negative components in conjunction with other chromosomes. This very interesting phenomenon can be termed "compensative interaction" and it could explain many of the complex features of our data, but more detailed analyses will be needed before its utility as an explanation can be fully examined.

The second, and more important, effect of selection which was considered by Mather (personal communication) to be diagnostic of the existence of balanced polygenes was that selection produces responses beyond the range of the initial population in lines initiated from the progeny of a single female. The majority of our experiments were each initiated from the progeny of a single female, and yet a large proportion of the lines showed a long-continued response to selection, demonstrating that a considerable variability must have been present in the form of relationally balanced polygenes. Some analyses which we have made indicate that one such polygene is located in the left end of chromosome I between the *scute* and *white* loci. It will be necessary to follow Thoday and Boam (1959) in their explicit localization of the loci concerned in the effect of selection on sternopleural number. Given such localizations it will then be possible to determine patterns of interaction between loci for comparison with those found for whole chromosomes.

The distinction between "phenodeviance" and "canalization leakage" has been made very tenuous by our results. It is now clear that the genetic system responsible for variation of scutellar number involves a considerable degree of complexity, with natural selection playing a major role in the maintenance of heterozygosity. It appears that compensative interactions are involved, but this term is no more explanatory than the term "overdominance". Both raise more problems than they resolve. However, it would appear more reasonable to consider different genes being combined in polygenes such that compensative interactions evolve, rather than to propose that heterozygosity *per se* has such a compensatory role. Overdominance has rarely been demonstrated for identified genes, whereas specific interactions of one locus with another are not rare.

It is necessary to account for the positive correlation of efficiency of selection with inbreeding which has been emphasized by Lerner (1954). If the constancy of the normal phenotype is maintained by a system of compensative interactions, then there will be an inherent resistance to selection; artificial selection will be countered by natural selection. Inbreeding, if intense enough, can counter the natural selection, disrupting the balance of interactions, and reducing the genetic variability such that the artificial selection instead of being dissipated over a large number of interacting polygenes can be focused on a smaller part of the genotype; one or two polygenes. This hypothesis can be tested by comparing the effects of selection between stocks in which all the chromosomes are varying, and stocks which have been made isogenic for all but one or a part of a chromosome. One of us (R. Nassar) has such an experiment in progress, and the results show that selection where only one of the three main chromosomes is segregating is qualitatively more efficient than in our experiments where all these chromosomes were segregating. He has found that selection in lines which are isogenic for chromosomes I and II, but which are variable for chromosome III, can produce advances to the high scutellar levels in a high percentage of lines (approximately 70%). His experiment shows that a reduction of the total genetic variability can lead to a very marked increase in the effectiveness of selection. Such experiments are predicted from our results, and further work on this problem should be along this line.

Latter (1964) has found that the genetic determination of scutellar number is fairly simple. His selections were based on large populations, supporting our conclusion that the rapid selection advances found in our experiments are a consequence of the conjoint effects of inbreeding and selection. The researches of Thoday, Gibson, and Spickett (1964) on selection for sternopleural chaetae number gave very similar results to those found by us, but their explanation differs in that they found a linkage of two loci whose recombination could account for the rapid advances.

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