Theoretical and Applied Genetics 42, 12–15 (1972)

Selection for Six Scutellar Chaetae in *Drosophila melanogaster*

I.T. MacBean, J. A. McKenzie and **P. A. Parsons**

Department of Genetics and Human Variation, La Trobe University, Bundoora, Victoria (Australia)

Summary. 1. From a base population showing some flies with more than the normal 4 scutellar chaeta phenotype directional selection was carried out and lead to a line with many flies having 6 chaetae. 2. Selection was then practised for 6 chaetae such that the extra 2 chaetae were in the anterior left and anterior right positions on the scutellum. This lead to a line with most flies having this chaeta number and pattern, therefore showing some canalization. 3. Additive genetic activity controlling the increased chaeta number was found on all the 3 major chromosomes.

Introduction

The scutellar chaeta system differs from other bristle systems in *Drosophila*, as in normal flies it shows little phenotypic variation from four chaetae. However, selection experiments have demonstrated that considerable genotypic variability exists for the trait (Payne, 1918; Sismanidis, 1942). The limited phenotypic variability normally observed is thought to result from developmental canalization where a variety of underlying genotypes produce an equivalent phenotype (see Rendel, 1967).

Variation from the normal 4 scutellar chaetae, or "genetic leakage" (Fraser, 1963), has been reported in natural populations (for example Parsons and Hosgood, 1967) and is thought to be due to segregation of genes producing combinations whose action lies outside the range of the canalizing system, and may also occur as a concomitant to certain gene substitutions (Rendel, 1967).

Fraser (1967) concluded that the evolution of 4 scutellar chaeta number is a development of a complex system of interactions, between two systems of modifiers and their switch loci, that results in stabilization of development to produce the 4 chaeta canalization zone. Rendel (1959), from his work involving scute, suggested secondary canalization zones at 0 and 2 chaetae and, on the basis of limited data, at 6 chaetae. Rendel, Sheldon and Finlay (1966) selected for low and high variance of scutellar chaeta number with a mean of 2 chaetae. In the low variance selection line fifty generations of selection resulted in a population of which approximately 95% had 2 chaetae. In both low and high variance selection procedures the sensitivity of scutellar bristle number to temperature change was reduced, with the low variance line being the less sensitive (see also Rendel and Sheldon, 1960).

Parshad and Narda (1964) suggested a secondary canalization zone, with a threshold similar to the 4 chaeta zone, at 8 chaetae. However, Rendel (1965) concluded that there was no justification for this as probit analysis showed the 8 chaeta class to be no more canalized than any other class above the 4 chaeta level.

In view of the interest in the possibility of lines canalized at 6, 8 . . . scutellar chaetae, in this paper we will report on a line with a high frequency of 6 scutellar chaetae.

The Selection Lines

All lines were maintained at 25 °C because of the known effect of temperature on scutellar chaetae number and position (Pennycuik and Fraser, 1964; Gibson, 1969).

Line 3B

This line was established from a base population made up of a hybrid of 16 strains with different scutellar chaeta numbers (Hosgood and Parsons, 1967). Directional selection was practised up to generation 32 by taking the 10 highest scoring flies from samples of 100 of each sex to provide the next generation. At this stage 75% of females and 50%

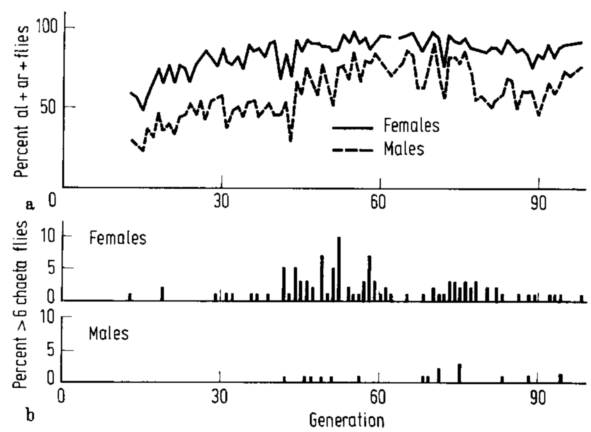

Fig. 1. Response in selection line 3B. (a) Percentage of al+ ar+ flies in 3B; (b) Percentage incidence of flies with leakage above 6 chaetae

of males had 6 chaetae (Fig. 1), mainly due to the addition of an extra anterior left and right chaeta (al + ar + flies in Fig. 2). It was then decided to see if higher proportions of such 6 chaeta flies could be obtained by selection. Thus from generation 32 the procedure was to select 10 al + ar + flies in each generation. Between generations 50 and 75 the percentage of al + ar + flies was normally in excess of 90% in females and about 75% in males. However, from generation 76 to 90 the percentage of al + ar + flies fell somewhat as did mean chaeta numbers (see also Figs. 3 and 4). This may be associated with a bacterial infection at this time as in later generations both measures returned to their former levels. This suggestion of change due to environmental variation receives support from a sudden increase in leakage above 6 chaetae associated with bacterial infection at generation 40 (Fig. 1). Crosses between 7 chaeta flies, or 7 and 6 chaeta flies carried out at these times failed to produce 7 chaeta progeny which agrees with the environmental interpretation. Crosses involving 7 chaeta flies in other generations also only produced al + ar + flies or a few flies with less than 6 chaetae.

Therefore a line with 6 chaetae has been established by selection. The effect of selection on the 3 major chromosomes of line 3B relative to 4AC, a control line highly canalized at 4 chaetae (Figs. 3 and 4), was investigated using the technique of Kearsey and Kojima (1967), and significant additive genetic activity was observed for each chromosome while dominance effects were not significant. These additive effects probably explain most of the increase from 4 to 6 chaetae.

Line 3BR

This line was set up at generation 75 by randomly selecting 10 flies of each sex from 3B and was maintained by randomly choosing parents in subsequent generations. In other words selection for only al + ar + flies was discontinued, however most flies were of course of this phenotype. Little tendency to revert away from 6 chaetae was observed.

Line 3BB

This line was established at generation 77 by selecting the 10 lowest scoring flies of each sex out of 100. Because there were relatively few of these flies, this would imply a reasonable intensity of selection. There was a rapid response back to a base level, established after 6 generations, which was not the normal canalized 4 chaeta zone. A further 14 generations of back selection did not fix the mean chaeta number at 4 but maintained it at a level (4.05 chaetae in females and 4.02 chaetae in males) similar to that of the original heterogeneous base population (Figs. 1 and 2 of Hosgood, MacBean and Parsons, 1968). In other words, it seems difficult

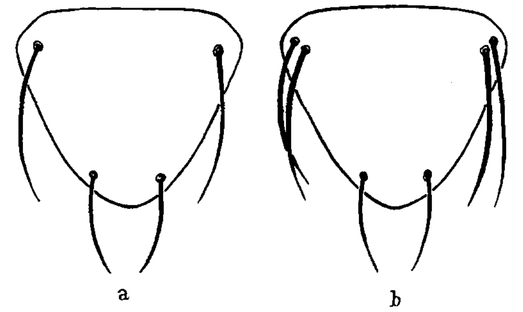

Fig. 2. Patterns of incidence of chaetae on the scutellum showing (a) normal distribution as observed in line 4AC and (b) two additional chaetae in the anterior positions (al+ ar+) as observed in line 3B

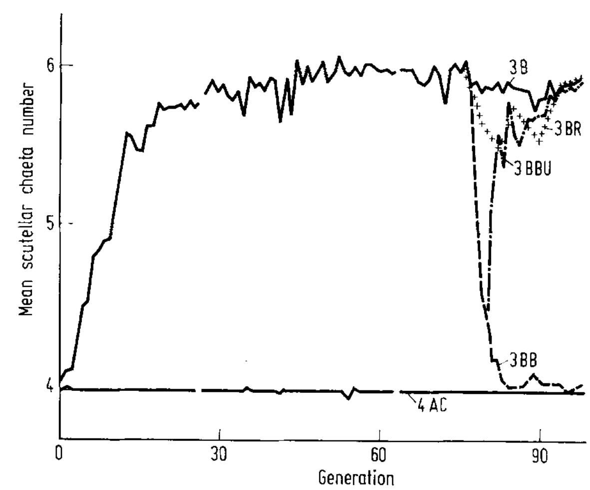

Fig. 3. Selection response in females in lines 3B, 3BR, 3BB and 3BBU relative to the control line 4AC

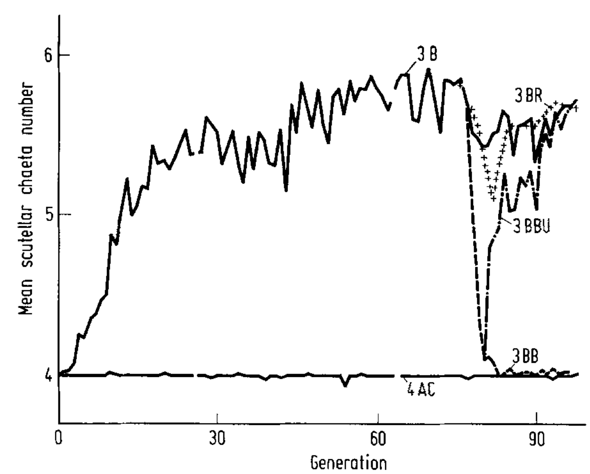

Fig. 4. Selection response in males in lines 3B, 3BR, 3BB and 3BBU relative to the control line 4AC

to reduce a strain which normally has a high level of genetic leakage above 4 chaetae to a mean of 4 chaetae, just as it is difficult to change the chaeta number of a highly canalized 4 chaeta stock. This is reasonable as Parsons and Hosgood (1967) showed that high levels of genetic leakage are under the control of additive genes.

Line 3BBU

This was established from 3 BB after 3 generations of back selection by selecting the 10 highest scoring flies of each sex. It was subsequently selected similarly to 3 B. There was a rapid response to selection, such that after 4 generations the mean returned to the 6 chaeta level of 3 B and 3 BR, and then remained at this level for a further 14 generations producing mainly al + ar + flies.

Discussion

Since 3 BR maintains the level of 3 B, there is a tendency for natural selection to maintain the 6 chaeta level. In 3 B, from generation 40 the only periods of marked leakage from 6 chaetae were at times of bacterial infection. Crosses involving the 7 chaeta flies failed to produce flies with 7 chaetae in the progeny. Environmental change may alter the expression of otherwise invariant characters, including scutellar chaeta number (Gibson, 1969), so that these observations still collectively argue for the establishment of a 6 chaeta canalization zone.

Further, the width of the 6 chaeta class, as estimated by the average probit values between generations 40 and 98, was 3.61 σ in females and 2.78 σ in males with no marked fluctuations being observed. These values compare favourably with the 2 chaeta class probit width measures of 3.65 σ and 2.75 σ for females and males respectively, after 120 generations of selection for low variance about a mean of that chaeta value (Rendel, Sheldon and Finlay, 1966). The threshold for the 6 chaeta zone is in fact about 50 percent of the highly canalized 4 chaeta zone which spans about 6.0 σ (Sheldon, Rendel and Finlay, 1964). In line 3 BR there was no decrease in the probit width of the 6 chaeta class, again indicating the stability of the 6 chaeta zone.

The response to back selection in 3 BB indicates that the 6 chaeta line is not homozygous, as potential variability is still available in 3 B after it maintained essentially the same chaeta level for 50 generations. The limits of back selection are apparently determined by the original gene pool of 3 B as after 20 generations of back selection, 3 BB showed no tendency to become canalized to 4 chaetae, but established a limit at about the level of the original heterogeneous population from which 3 B was derived. This may indicate that there has been no fixation of genes for 6 chaetae. Support from this comes from 3 BBU which shows a similar type and rate of response to 3 B from the same initial chaeta level to the canalization zone level (Figs. 3 and 4). In other words, the changes between 4 and 6 chaetae may involve gene frequency changes of scutellar chaeta determining genes, but these frequency changes must be related to the rest of the potentially interacting genetic system, as other lines derived from different constituents of the original population have yielded selection responses to produce chaeta numbers greatly in excess of the 6 chaeta level (MacBean, McKenzie and Parsons, 1971).

The 6 chaeta line involves the formation of a constant pattern (al + ar +) as well as a constant number phenotype. This is reasonable as Whittle (1969) found evidence for genes controlling chaeta patterns as well as numbers. Furthermore, there is evidence for an anterior-posterior gradient in scutellar chaeta number as observed by Fraser (1963) in natural populations, by Gibson (1968) who showed that anterior chaetae are lost first during selection for reduced chaeta number, by ourselves where in going from 4 to 6 chaetae extra anterior chaetae are added and in back selection experiments these are lost again, and finally by Pennycuik and Fraser (1964) and Parsons (unpub.) who showed the gradient to be temperature sensitive such that the frequency of additional chaetae goes from the anterior to the posterior region as temperature is increased. Therefore it seems that a line fixed at a given scutellar chaeta number will involve a pattern stability of an anterior-posterior type as there is little evidence for left-right asymmetry. Thus, in practice it should be possible to establish canalized lines at 6, 8 . . . chaetae, but whether this occurs will depend on the genes in the population under selection.

Acknowledgement

Financial support from the Australian Research Grants Committee is gratefully acknowledged.

Literature

1. Fraser, A. S.: Variation of scutellar bristles in *Drosophila* I. Genetic leakage. Genetics **48**, 497–514 (1963). — 2. Fraser, A. S.: Variation of scutellar bristles in *Drosophila* XV. Systems of modifiers. Genetics **57**, 919–934 (1967). — 3. Gibson, J. B.: Selection for the absence of scutellar bristles. Nature **217**, 188–190 (1968). — 4. Gibson, J. B.: Effects of temperature on the development of scutellar bristles. Experientia **25**, 1198 to 1199 (1969). — 5. Hosgood, S. M. W., MacBean, I. T., Parsons, P. A.: Genetic heterogeneity and accelerated responses to directional selection in *Drosophila*. Molec. Gen. Genetics **101**, 217–226 (1968). — 6. Hosgood, S. M. W., Parsons, P. A.: The exploitation of genetic heterogeneity among the founders of laboratory populations of *Drosophila* prior to directional selection. Experientia **23**, 1066 (1967). — 7. Kearsey, M. J., Kojima, K.: The genetic architecture of body weight and egg hatchibility in *Drosophila melanogaster*. Genetics **56**, 23–37 (1967). — 8. MacBean, I. T., McKenzie, J. A., Parsons, P. A.: A pair of closely linked genes controlling high scutellar chaeta number in *Drosophila*. Theoret. Appl. Genetics **41**,

227–235 (1971). — 9. Parshad, R., Narda, R. D.: Canalization and threshold effect of the extra scutellar phenotype in *Drosophila melanogaster*. Heredity **19**, 334 –335 (1964). — 10. Parsons, P. A., Hosgood, S. M. W.: Genetic heterogeneity among the founders of laboratory populations of *Drosophila*. I. Scutellar chaetae. Genetica **38**, 328–339 (1967). — 11. Payne, F.: An experiment to test the nature of the variations on which selection acts. Indiana Univ. Stud. **5**, 1–45 (1918). — 12. Pennycuik, P. R., Fraser, A. S.: Variation of scutellar bristles in *Drosophila*. II. Effects of temperature. Aust. Jour. Biol. Sci. **17**, 764 to 770 (1964). — 13. Rendel, J. M.: Canalization of the *scute* phenotype of *Drosophila*. Evolution **13**, 425–439 (1959). — 14. Rendel, J. M.: Scutellar bristles in *Drosophila*: A comment. Heredity **20**, 137–138 (1965). — 15. Rendel, J. M.: Canalization and Gene Control. N.Y. and London: Logos Press, Academic Press 1967. — 16. Rendel, J. M., Sheldon, B. L.: Selection for canalization of the scute phenotype in *Drosophila melanogaster*. Aust. Jour. Biol. Sci. **13**, 36–47 (1960). — 17. Rendel, J. M., Sheldon, B. L., Finlay, D. E.: Selection for canalization of the scute phenotype. II. Am. Nat. **100**, 13–31 (1966). — 18. Sheldon, B. L., Rendel, J. M., Finlay, D. E.: The effect of homozygosity on developmental stability. Genetics **49**, 471–484 (1964). — 19. Sismanidis, A.: Selection for an almost invariable character in *Drosophila*. J. Genet. **44**, 204–215 (1942). — 20. Whittle, J. R. S.: Genetic analysis of the control of number and pattern of scutellar bristles in *Drosophila melanogaster*. Genetics **63**, 167–181 (1969).

Received May 27, 1971

Communicated by H. Stubbe

I. T. MacBean
J. A. McKenzie
P. A. Parsons
Department of Genetics and Human Variation
La Trobe University
Bundoora 3083, Victoria (Australia)