

The Exploitation of Genetic Heterogeneity among the Founders of Laboratory Populations of *Drosophila* Prior to Directional Selection

PARSONS and HOSGOOD¹ described experiments where a number of strains of *Drosophila melanogaster* set up from single inseminated females collected in the wild from the same locality (Leslie Manor, Victoria), were scored for scutellar chaetae. In a first experiment the incidence of flies with more than the normal 4 scutellar chaetae (i.e. additional chaetae) was followed for 45 generations at 25°C in 3 strains collected at the same time. Each strain had a characteristic incidence of additional chaetae over this time. One strain had 15–30% of females and 3–10% of males with additional chaetae, the second had 2–5% of females and 0–4% of males, and the third had very few flies with additional chaetae. A diallel cross at the 24th generation in the laboratory confirmed that the differences between strains are genetic in origin, presumably arising from genetic differences between the 3 inseminated founder females. In a further experiment, where 15 strains from the same locality were followed for 9 generations, each strain again maintained a characteristic incidence of additional chaetae. Similar evidence has been found for mating speed in *D. pseudoobscura*².

The heterogeneity between strains for additional chaetae leads one to ask whether, if the strains are subjected to directional selection, the response may depend on the incidence of additional chaetae before selection. Thus to obtain a rapid response to selection for additional chaetae, it may be advantageous to base selection on those strains having high incidences of additional chaetae. Such an experiment will be reported here. From 16 of the strains discussed above, 4 replicated selection lines were derived

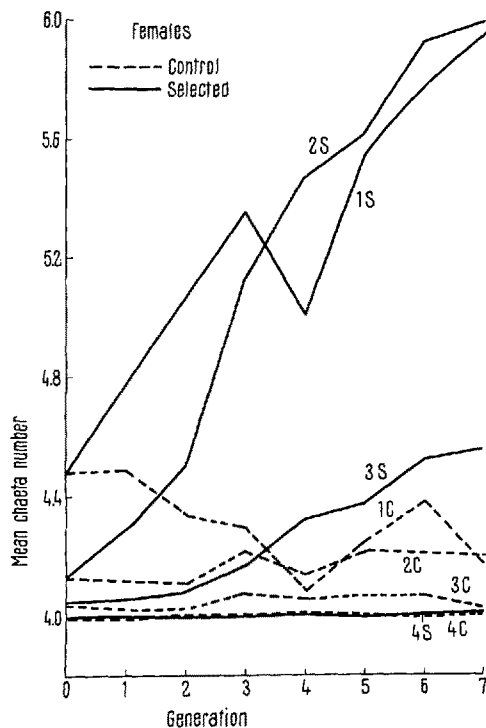


Fig. 1. The mean chaeta number in the 4 selection lines (S) and control lines (C) set up from populations as described in the text (females).

as follows: (1) the strain having the highest incidence of additional chaetae; (2) a hybrid population derived from the 4 strains having the highest incidence of additional chaetae; (3) a hybrid population derived from all 16 strains, and (4) the strain having the lowest incidence of additional chaetae. In these lines, directional selection was carried out each generation by selecting from the 100 flies of each sex scored, the 10 of each sex having the highest numbers of scutellar chaetae to provide the next generation.

The results for the selected and control lines over the first 7 generations of selection after combining replicates, are given in Figure 1. Throughout, the incidence of additional chaetae is higher in females than in males as is usual in most work on scutellar chaetae. The incidence of additional chaetae in the controls in general is in the sequence (1) > (2) > (3) > (4), as would be expected from the incidences of scutellar chaetae in the 4 base populations, and this is generally maintained over the 7 generations as expected from the results of PARSONS and HOSGOOD¹. The response to selection was very rapid in (1) and (2), slow in (3) and absent in (4). At generation 7, the percentage response (see Table) in (2) was greater than in (1), no doubt because (2) was based on a hybrid population of 4 strains, so providing a greater level of heterogeneity for additional chaeta genes than in (1). Thus, selection of favourable strains before selecting for chaeta number has led to a dramatic response to selection in (1) and (2).

These results have certain implications in selection experiment theory. They indicate that heterogeneous and unrepeatable responses to selection often reported in the literature could be partly due to the exact nature of the population before selection. Selection experiments usually begin with a rather heterogeneous base population as in (3) where the response is far slower than in (1) and (2). In many strains, the number of scutellar chaetae is rigidly canalized to 4, as shown by experiments of RENDEL³ who found that the normal number of 4 scutellar chaetae was so tightly controlled developmentally that no change in visible phenotype occurred for a considerable amount of gene substitution. Once the trait was moved away from the normal phenotype it became easier to modify it further. The initial selection of strains with poor canalization to 4 chaetae has led to a dramatic response to selection in (1) and (2) because at the outset, populations were taken in which canalization was not rigid. There is rigid canalization to 4 chaetae in line (4) and thus there is little phenotypic variability on which to select. Therefore it is not surprising that there was no response to selection.

Application of the results in laboratory experiments will enable a more rapid response to selection for scutellar

Percentage increase in scutellar chaeta number over 7 generations of selection

Selection line	(1)	(2)	(3)	(4)
Females	31	46	13	0.25
Males	25	31	5.5	0.25

¹ P. A. PARSONS and S. M. W. HOSGOOD, *Genetica* 38, in press.

² P. A. PARSONS and D. KAUL, *Experientia* 23, 131 (1967).

³ J. M. RENDEL, *Evolution* 13, 425 (1959).

chaeta number, and probably for chaeta number elsewhere on the fly. Chaeta number traits seem to be controlled by polygenic activity mainly restricted to specific parts of the genome^{4,5}. Thus it is necessary to commence with strains having the appropriate genes. Traits such as viability and fecundity are probably influenced by an enormous number of genes so that polygenic activity

controlling them may be expected to be ubiquitous and less localized, leading perhaps to less heterogeneity and hence less variability in the response to directional selection. There is evidence that the genetic architecture of such traits, which in nature are mainly subject to directional selection, differs from those such as chaeta number which are subject to stabilizing selection^{6,7}, so that artificial directional selection will be expected to be less effective for traits normally subject to directional selection than those subject to stabilizing selection⁸.

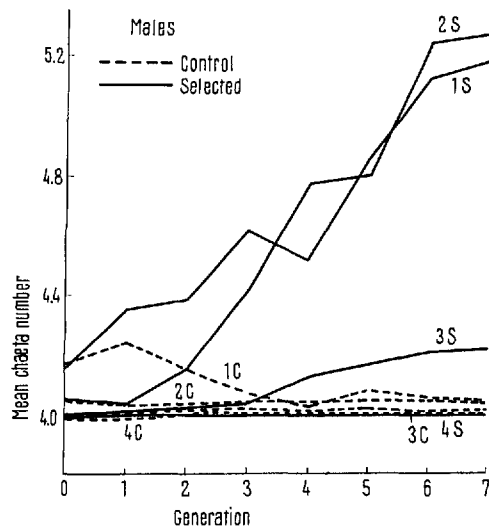


Fig. 2. The mean chaeta number in the 4 selection lines (S) and control lines (C) set up from populations as described in the text (males).

Résumé. Chacune de 16 souches, filiations de femelles uniques, et fécondées dans la nature, montrait une proportion caractéristique de mouches ayant plus de 4 soies scutellaires (soies supplémentaires). La sélection pour soies supplémentaires allait à une vitesse bien plus grande chez les lignées portant un haut niveau de soies supplémentaires que chez les lignées où ce niveau était plus bas. Ces résultats ont une répercussion importante sur la théorie des expériences de sélection.

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School of Biological Sciences, La Trobe University, Bundoora, Victoria (Australia), 17 April 1967.

⁴ J. M. THODAY, *Nature* 191, 368 (1961).

⁵ D. MILLER, L. ERWAY and A. FRASER, *Genetics* 54, 348 (1966).

⁶ E. L. BREESE and K. MATHER, *Heredity* 14, 375 (1960).

⁷ K. MATHER, *Proc. R. Soc. B* 164, 328 (1966).

⁸ This research was supported by the Australian Research Grants Committee. One of us (S.M.W.H.) was supported by a Commonwealth of Australia Postgraduate Award.

Observations on the Centromere Area of Human Chromosomes

Uncertainty over the exact function and structure of the centromere area of chromosomes persists¹⁻⁵. The area adjacent to the centromere often has a particularly bright, clear, slightly refractile appearance (Figure). GERMAN independently has made the same observation and commented that the chromatids in the area of exchange in somatic crossing over were at times distorted by a material similar in appearance to that which normally indents the centromere⁶. This appearance of the centromere area has not otherwise been commented upon or studied intensively. The term centromere area will be used to describe this area adjacent to the centromere and the term centromere will refer to the narrowed portion of the chromosome itself. It is the purpose of the present report to record certain observations on the behavior and appearance of the centromere area in cultured human lymphocytes.

Methods. The observations were made primarily by phase microscopy on air-dried human leucocytes stained with aceto-orcein after a culture period of 3 days as previously described⁷. Exceptions are included under observation. Acridine orange staining for RNA was carried out as described by GLUCK et al.⁸ and DDD staining for SH groups as described by BARNETT et al.^{9,10}

Monochromatic light was obtained with a green filter and a Zeiss mercury arc UV-light source.

Observations. A bright, clear, well-demarcated circle was present at nearly every centromere area in some cells (Figure a), and at few or none in other cells. Clear areas have been seen at the centromere of every chromosome, and although usually present bilaterally, at times may be either less evident or absent at 1 of the 2 centromere areas of a chromosome (Figure a). They were best seen by phase microscopy, but were also present on bright field examination as well as when observed with monochromatic light. When the bright appearance was present a

¹ A. LIMA-DE FARIA, *Hereditas* 42, 85 (1956).

² D. MAZIA, *The Cell* (Academic Press, New York 1961), vol. 3, p. 80.

³ M. GIMENEZ, *Experientia* 21, 391 (1965).

⁴ B. R. BRINKLY and E. STUBBLEFIELD, *Chromosoma* 19, 28 (1966).

⁵ P. GEORGE, L. J. JOURNEY and M. N. GOLDSTEIN, *J. natn. Cancer Inst.* 35, 355 (1965).

⁶ J. GERMAN, *Science* 144, 298 (1964).

⁷ H. LUBS, *New Engl. J. Med.* 267, 326 (1962).

⁸ L. GLUCK and M. V. KULOVICH, *Science* 138, 530 (1962).

⁹ R. J. BARNETT and A. M. SELIGMAN, *J. natn. Cancer Inst.* 13, 215 (1952).

¹⁰ R. J. BARNETT, *J. natn. Cancer Inst.* 13, 905 (1953).