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The Isolation of Polygenic Factors Controlling Bristle Score in *Drosophila melanogaster*. I. Allocation of Third Chromosome Sternopleural Bristle Effects to Chromosome Sections

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Manuscript received March 5, 1987
Revised copy accepted November 7, 1987

ABSTRACT

A single third chromosome *C*, with a high sternopleural bristle score, had been extracted from an artificial selection line. *C* was divided into five chromosomal sections by recombination with a multiply marked third chromosome *ruseca*, which had a low sternopleural bristle score. A nonuniform distribution of sternopleural bristle effect with physical length of chromosome was observed. The second section (26–44 cM) of *C* carried the most sternopleural bristle effect (10 bristles when homozygous), the first (0–26 cM) and third (44–62 cM) also carried significant sternopleural bristle effects (six and five bristles, respectively). The fourth section (62–71 cM) carried a small but significant effect (less than one bristle) while the fifth section (71–101 cM) carried little effect when alone (less than one bristle), though it did carry effects which had an epistatic interaction with those of the first and second sections.

OUR understanding of the nature and function of individual genes involved in the control of quantitative characters remains poor despite the fact that most economically important commercial traits are continuous variables. Studies of more easily manipulated characters such as bristles in Drosophila should reveal the nature of quantitative trait loci with implications for economically important traits.

What are we looking for? A polygene is defined as such because its effect is small relative to other sources of variation; if there are genes of large effect among the genes controlling a quantitative character, they must be few in number. Opinions vary as to how many genes are involved in the control of quantitative characters, MATHER and JINKS (1971) suggested that possibly hundreds of genes would be involved while THODAY and THOMPSON (1976) suggested rather few loci were involved. MATHER suggested the term "effective factor" (see MATHER and JINKS 1971) to describe a located polygenic effect which had been genetically located by recombination, granted that subsequent recombination may further divide such factors into still smaller, but linked effects. In the present report the term "factor" is used for a located polygenic effect.

The first attempt to study Drosophila bristle genes was that of KARP (1936) who used a multiple recessive marker chromosome to investigate the abdominal bristle differences between it and another third chromosome. He isolated chromosome segments and collected recombinants which he established in stocks. He concluded that there were at least six genes and these were both decreasing and increasing, appearing to more or less counterbalance one another.

SAX (1923) suggested a method of studying quantitative character factors if they were linked to markers enabling chromosomes to be followed. This was developed by BREESE and MATHER (1957) who used chromosomes carrying marker genes to divide up a *Drosophila* third chromosome into regions which could be scored for bristle effects. BREESE and MATHER (1957) analyzed abdominal bristle selection lines by manufacturing "synthetics," using multiple marker stocks. Their "synthetics" consisted of different amounts of up "H," and down "L" selected chromosomes with the possibility of a short section of marker chromosome between them. They fractionated the third chromosome into six different regions, each of which carried bristle effects, implying at least six "factors." Previous investigations of sternopleural bristle effect distribution in *Drosophila melanogaster* have had some success. THODAY (1961) was able to successfully isolate major effects involved in the control of bristle number. He combined the method of BREESE and MATHER (1957) with that of SAX (1923) who had looked at linkage between major genes and polygenes by using markers to follow chromosomes. A chromosome with a minimum of two recessive marker genes is used to analyse a homologous chromosome which has a different value for the quantitative character under investigation. The recombinant progeny from the cross of a heterozygous female

to a homozygous male are scored and assigned by their phenotype into separate classes. The rest of the genome is assumed to be homozygous. This method, though powerful, is limited by the availability of suitable markers which should be neutral in effect on the character and close enough together to allow the frequency of double crossovers between them to be ignored. Adequate progeny-testing is required to determine how many subgroups and hence how many loci are involved.

In the results from a series of studies, THODAY (1967, 1973) and THODAY and THOMPSON (1976) were able to locate a total of nine major sternopleural bristle effects situated on all three major chromosomes and to account for accelerated responses, seen during selection by recombination between these located effects.

DAVIES (1971) examined the lines of DAVIES and WORKMAN (1971) using a multiple recessive marker stock in an analysis similar to that of THODAY (1961). He assayed chromosomes that were the product of a single crossover between the selected chromosome and a multiple recessive marker chromosome, that had been made homozygous. He found factors of both directions on the selected chromosome and so there must be doubt about their location and size. His high sternopleural bristle third chromosome carried at least eight increasing factors and no decreasing factors.

LOUW (1966) detected eight effects on a selected high sternopleural bristle third chromosome using a multiple recessive marker third chromosome which carried eight markers. PIPER (1972) examined a third chromosome from a high sternopleural line from the Kaduna strain. In a high sternopleural bristle scoring background, using a multiple recessive marker stock (*spt se st*), he located at least five factors between the *se* and *st* loci.

WRIGHT (1952) proposed a method for the location of one or more relatively important factors controlling a quantitative character. The method comprises repeated backcrossing to one fixed genotype, accompanied by the appropriate selection, in order to isolate dominant effects. MOSTAFA (1963) used this method and suggested that there were a small number of polygenes with large effects on sternopleural bristles clustered on the third chromosome between 3–26.5 and 3–44 cM. This method appeared to isolate large blocks of chromosome rather than individual loci. PIPER (1972) also used this method and found a similar result. This method appears to be less powerful than that of Thoday because it isolates large chromosomal sections rather than individual loci.

SPICKETT, SHIRE and STEWART (1967) showed that by redefining a quantitative character in terms of its qualitative components, the character becomes more easily handled and understood. This approach is to break down quantitative characters into their simpler discontinuous components. SPICKETT (1963) divided the sternopleurite into four regions and counted the number of bristles in each. This enabled him to ascribe a different morphological effect to each of three previously located loci and to discover a fourth. Such an approach in combination with THODAY's (1961) techniques forms a powerful tool for detecting the more important discontinuous factors involved in a quantitative character.

JINKS and TOWEY's (1976) method of "Genotype Assay" examines the frequency of heterozygotes when two pure bred lines are crossed. The main problem with the biometrical methods are that they are unable to give chromosomal locations.

While there are powerful biometrical methods available for the detection of the components of variation in such characters (MATHER and JINKS 1971), if we are to gain a fuller understanding of continuous variation and of its evolution, it will be necessary to understand the nature and function of the individual genes involved. For this reason we wished to attempt an approach similar to that of THODAY (1961). The method used is also limited in that it can only detect those factors with direct effect (*i.e.*, not fitness genes) that are segregating in the cross. Only one chromosome can be examined at a time, giving little idea of gene frequencies and only individual factors of sufficient size can be detected and mapped.

We report the first steps in the isolation of bristle effects in this paper: the subdivision of a chromosome with a high sternopleural bristle score (*C*) into sections. In the second paper a more thorough analysis of each chromosomal section is performed (SHRIMPTON and ROBERTSON 1988) in which the distribution of bristle effects within sections is investigated.

MATERIALS AND METHODS

Conditions: Flies were kept in either 1- by 3-inch glass vials or ⅓ pint bottles at a constant temperature of 25°, except during the collection of virgin females when flies were kept overnight at a constant 18°. The fly medium used was the standard mixture (cornmeal-molasses-agar) of this laboratory.

Stocks: The "high sternopleural bristle" third chromosome, *C*, came from the extreme sternopleural selection line, CA of DA SILVA (1961). CA had been produced by the crossing together of two previously selected lines, C (25 generations at an intensity of 10/25) to A5 (22 generations at an intensity of 10/25) followed by further selection. The CA line had a final mean sternopleural bristle score of about 52. *C*, a single third chromosome was extracted from CA. The "low sternopleural third chromosome," D, was extracted from the 6171(1) line of EL SAYED OSMAN and ROBERTSON (1968). 6171(1) had been produced by the crossing together of two previously selected lines, L (30 generations at an intensity of 10/25) to a second line which had been selected for six generations at an intensity of 10/100. Seven generations without selection were followed by a

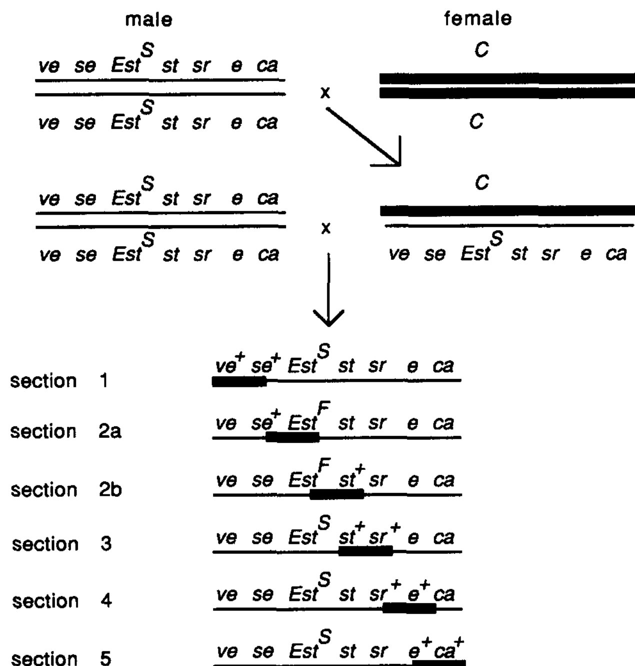

FIGURE 1.—Crosses performed in the standard background. The *C* third chromosome was considered as 5 adjacent sections. Each was then isolated in an otherwise *ruseca* chromosome and standard background. A *ruseca/C* heterozygous female was crossed to a *ruseca* male. The appropriate recombinant progeny were isolated and used to establish lines such that the 5 "sections" of *C* were isolated in an otherwise *ruseca* chromosome. Section 1 of the chromosome was from the *ve* to *se* loci, section 2 was from *se* to *st* and could be divided into two subsections using the *Est-6* locus. Sections 3, 4 and 5 lay between the *st* to *sr*, *sr* to *e*, and *e* to *ca* loci, respectively.

further 20 generations of selection at an intensity of 10/100. The 6171(1) line had a final mean sternopleural bristle score of about seven. The third chromosome was known to control half of the total difference in sternopleural bristles between the extreme high and low stocks. An isogenic high sternopleural "standard" background on chromosomes *I*, *II* and IV, in which D has a score of about 16 and *C* about 40 sternopleural bristles, was used throughout. The base population, Kaduna, from which all selection lines had been derived, had been kept in a laboratory cage, with an average population size of approximately 5,000 flies, since its capture in 1949 (see CLAYTON, MORRIS and ROBERTSON, 1957) and had a sternopleural bristle score of approximately 16 bristles.

C was analyzed using a multiple recessive marker third chromosome, *ruseca*. *ruseca* had been constructed by crossing various recessive markers into D and, like D, had a score of about 16 bristles in the standard background (PIPER 1972). The difference in score, 24 bristles, was the total effect accessible to study. *ruseca* carried the following mutations on the third chromosome (LINDSLEY and GRELL 1968) *ru; roughoid,* 0.0 cM; *ve: veinlet,* 0.2 cM; *se: sepia,* 26.0 cM; *Est-6^S: Esterase 6,* 36.8 cM; *st: scarlet,* 44.0 cM; *sr: stripe,* 62.0 cM; *e: ebony,* 70.7 cM; *ca: claret,* 100.7 cM; and, since it had as low a score as D, was unlikely to be carrying any alleles at sternopleural bristle loci with greater effect than those carried on the high scoring *C* chromosome. Since *ru* and *ve* are closely linked, in both this and the accompanying paper either *ru* or *ve* is used to represent *ru ve*.

A homozygous *ruseca* male fly was crossed to a homozygous *C* female fly and the female progeny backcrossed to the male parent. From this cross the appropriate phenotypic combinations were collected such that each separate "section" of high scoring *C* chromosome flanked by adjacent

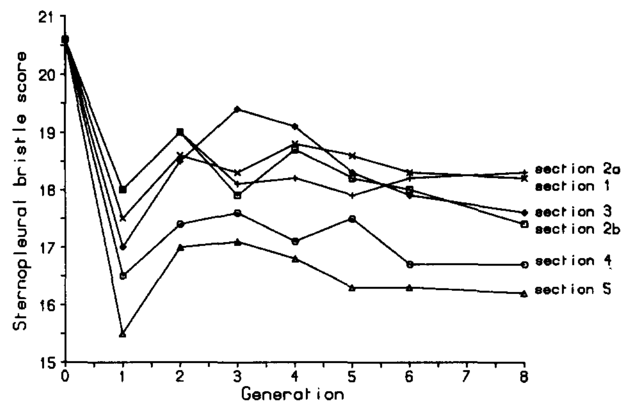

FIGURE 2.—To purify each *C* section, *ruseca*/single *C* section heterozygous females were backcrossed to *ruseca* males for 7 generations accompanied by mild selection for low sternopleural bristle score. Shown are the sternopleural bristle scores of the sections, as heterozygotes with *ruseca*, during backcrossing and selection for low sternopleural bristle score.

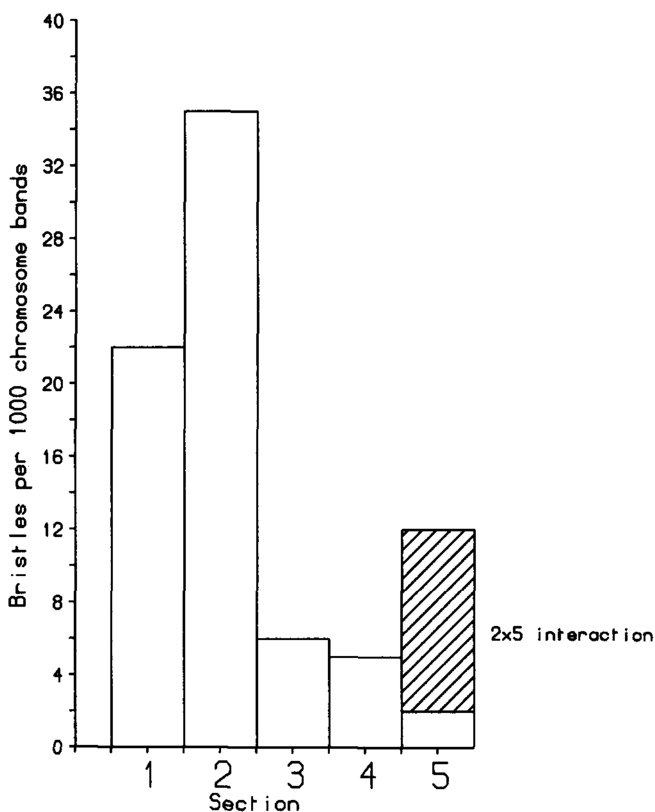

FIGURE 3.—To give a crude indication of the distribution of sternopleural bristle effect on *C*, each of the five *C* sections, in an otherwise *ruseca* third chromosome, were made homozygous and 50 flies of each sex scored for sternopleural bristles (see Table 1). The sternopleural bristle effect of each of the 5 sections is given per chromosome band in an attempt to correct for the physical size of each section. The fifth section (*e* to *ca*) alone had little effect but had an epistatic interaction with section 2 (hatched bar). The second section (*se* to *st*) appeared to carry a concentration of effect.

TABLE 1

Distribution of sternopleural bristle effect on *C* sections

Chromosomal section	Male		Female		Mean of sexes	
	Het.	Hom.	Het.	Hom.	Het.	Hom.
1 *ru-se-*	1.76	5.82	1.72	6.28	1.74*	6.05*
2 *se-st-*	3.22		2.83		3.03*	10.02*
2a *se-Est6-*	1.73	5.29	1.69	4.81	1.71*	5.05*
2b *Est6-sr-*	1.62	5.03	1.46	3.91	1.54*	4.47*
3 *st-sr-*	1.67	4.89	1.46	4.79	1.57*	4.84*
4 *sr-e-*	0.04	0.85	0.05	0.91	0.05 (NS)	0.88*
5 *e-ca-*	0.23	1.03	0.20	0.30	0.02 (NS)	0.67*
SE	±0.23	±0.25	±0.24	±0.24	±0.16	±0.18

$*P = <0.01$, NS = $P > 0.05$.
Scores were based on 50 flies of each sex and are given for sections as heterozygotes (het.) with *ruseca* and as homozygotes (hom.), as deviations from *ruseca* (male 15.64, female 16.48, mean 16.06).

TABLE 2

Interactions between chromosomal sections

C Section combinations	Expected sternopleural bristle scores if sections were additive	Observed sternopleural bristle scores	Difference
1 + 3	27.23	26.96 ± 0.44	NS
1 + 4	23.27	22.42 ± 0.45	NS
1 + 5	23.06	24.26 ± 0.36	*
2 + 4	27.22	27.06 ± 0.34	NS
2 + 5	27.03	29.84 ± 0.57	*
3 + 5	21.85	21.42 ± 0.38	NS
1 + 3 + 5	27.90	31.72 ± 0.48	*

$n = 25$ each sex, $*P < 0.05$, NS = $P > 0.05$.
There was a significant departure from additivity between sections 1 and 5, 2 and 5, and 1, 3 and 5.

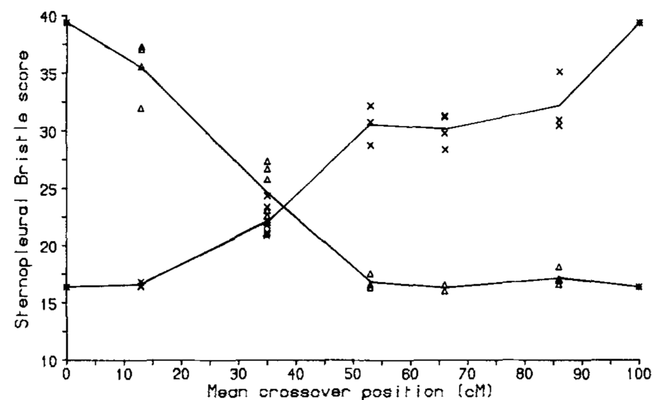

FIGURE 4.—Sternopleural bristle score along the C chromosome. Thirty-nine recombinant lines, that were the product of a single crossover event between *C* and *ruseca*, were established and 25 flies of each sex scored for sternopleural bristles (see Table 3). The more *C* chromosome they carried the higher their sternopleural bristle score; giving a crude indication of the distribution of sternopleural bristle effect differences between *C* and *ruseca*. The recombinant line mean sternopleural bristle scores are arranged in two classes according to whether their left end was from *C* and right end from *ruseca* (×) or vice versa (Δ). The *C* and *ruseca* parental scores are also represented (*). For example, there were four recombinant lines with a *ve* phenotype, thus their left end is from *ruseca*, their symbol is a Δ and their mean crossover position is at 13.5 cM.

markers was isolated in an otherwise *ruseca* chromosome (Figure 1). A "section" is defined as a chromosomal segment bounded by two adjacent recessive marker loci, *e.g.*, section 1 is the chromosomal segment between the *ru* and *se* loci and is thus 26 cM in length (section 2 is 18 cM; section 3 is 18 cM; section 4 is 9 cM; section 5 is 30 cM). A further seven generations of backcrossing to *ruseca* accompanied by downward selection of the heterozygote for sternopleural bristle score was carried out on each section (Figure 2). This was to remove "contaminating" *C* chromosome flanking the section being isolated. Each section was then made homozygous and scored (see Table 1 and Figure 3) and flies with the lowest sternopleural bristle score used to establish stocks. Nonadjacent sections could also be combined, established in stocks and scored for their sternopleural bristles (Table 2). Twenty-five flies of each combination and sex were scored. Only nonadjacent sections could be combined, as an intervening chromosomal section in which recombination could occur was required.

A similar approach was to collect single male recombinant flies which represented single crossover events between a *ruseca* and *C* chromosome. These were made homozygous and established in lines. Thirty-nine such lines were established and 25 flies of each sex were scored for their sternopleural bristle score (Table 3).

RESULTS

Bristle scores: The sternopleural bristle scores of homozygous *C* chromosome sections are given in Table 1 and in Figure 3. The section scores are given per salivary chromosome polytene band, as this, rather than recombinant distance, was considered to be the best measure of the genetic content of a section. All five sections, when homozygous, carry a significant sternopleural bristle effect. The left two sections (*ru-st*) carry a high proportion of the total *C* chromosome effect. Another indication of the distribution of effect on *C* is given in Figure 4, this and the nonadditive interactions between nonadjacent *C* chromosome sections (Table 2) indicate that section 5 (*e-ca*) carries significant effect which has a nonadditive interaction with the left end of *C* (sections 1 and 2).

TABLE 3

Bristle scores of recombinants between *C* and *ruseca*

Phenotype	Mean cross-over position (cM)	Sternopleural bristle scores	Phenotype	Mean cross-over position (cM)	Sternopleural bristle scores
+	0	39.38	*ruseca*	0	16.34
ve	13	37.06	*se st sr e ca*	13	16.40
		35.60			16.44
		37.32			16.80
		31.96			
			st sr e ca	35	24.36
ve se	35	25.80			21.02
		22.04			23.38
		22.58			20.86
		27.36			21.78
		23.08			21.12
		26.70			
			sr e ca	53	32.18
ve se st	53	16.56			28.78
		16.30			30.76
		17.52			
			e ca	66	29.80
ve se st sr	66	16.00			31.20
		16.54			28.36
					31.32
ve se st sr e	86	18.14			
		17.02	*ca*	86	30.96
		16.96			30.48
		17.06			35.14
		16.58			
		16.94	+	100	39.38
ruseca	100	16.34	$S_{\bar{x}}$ = 0.28 = square root of the error variance		

The sternopleural bristle scores of recombinant lines established from single crossover events between *C* and *ruseca*, made homozygous in the high sternopleural bristle standard background. Twenty-five flies of each sex were scored per recombinant line.

Nonadjacent *C* sections were combined. For example a homozygous section 2 fly was crossed to a homozygous section 5 fly (Table 2) and their female F_1 progeny crossed to TM3/*ruseca* males. A male progeny with the appropriate phenotype, *ve sr*, was then crossed to a Tm3/*ruseca* female and the e^+/TM3 heterozygote progeny selected to initiate a "2 + 5" stock.

Summary of sections: All sections had a significantly higher sternopleural bristle score than *ruseca* ($P < 0.01$) when homozygous. Only sections 1, 2 and 3 had scores significantly different from *ruseca* when heterozygous with *ruseca* (Table 1).

Section 2 of *C* carried the largest effect, with about 10 sternopleural bristles when homozygous. Its neighboring sections (1 and 3) also have sizeable sternopleural bristle effect (5–6 bristles) when homozygous, perhaps because of partial overlap into section 2. *C* chromosome to the right of the *sr* locus carried little sternopleural bristle effect, as shown by the low sternopleural bristle score of *ve se st* homozygous lines (Figure 4 and Table 3). The similarity of sternopleural bristle score between *sr e ca* and *e ca* lines also indicates a lack of sizeable sternopleural bristle effect in section 4. The low but significant sternopleural bristle scores of these sections when homozygous in an otherwise *ruseca* chromosome also indicated little sternopleural bristle effect, *i.e.*, section 4 scored about 0.9 sternopleural bristle and section 5 scored about 0.7 sternopleural bristle (Table 1) measured as a difference from *ruseca*. Against this one of the *ca* recombinant lines had a sternopleural bristle score intermediate between the *e ca* recombinant line scores and a *C* chromosome, indicating that section 5 did carry sternopleural bristle effect but this was detectable only when the rest of the *C* chromosome was present, presumably due to epistatic interaction. Evidence to support this was found by the combination of section 1 or 2 with section 5 (Table 2). Section 4 did not appear to have a nonadditive interaction with sections 1 or 2.

se st sr e ca recombinant lines indicated that section 1 of *C* alone carried little effect (Table 3 and Figure 4). However, the isolated section 1 of *C* had sizeable effect (Figure 3), perhaps indicating the presence of overlap with section 2 of the *C* chromosome. However

the variation in sternopleural bristle scores of *ve* recombinant lines (Table 3 and Figure 4), indicated an effect within this section, which could be detected only through interaction with the rest of the *C* chromosome.

A more detailed examination of the effects carried by these sections, and of their interactions, is given in the accompanying paper (SHRIMPTON and ROBERTSON 1988).

DISCUSSION

The aim of the present study was to make a preliminary investigation of the distribution of sternopleural bristle effects on the third chromosome. The difference in sternopleural bristle score between the two homozygotes, in a standard background, was 24 bristles (40–16).

A single chromosome, *C* was investigated using a single tester chromosome *ruseca*. Only genes which were polymorphic between these two chromosomes could be investigated, *i.e.*, only the genes responsible for the difference in their sternopleural bristle scores (24 bristles) were accessible to study. Other genes which were not polymorphic in the comparison, located on other chromosomes, or affect the character indirectly (for example fitness or environmental sensitivity genes) were not accessible to this study.

The genes which were polymorphic between *C* and *ruseca* were from two sources. First, those alleles segregating in the original Kaduna population and fixed during selection (drift during the manufacture of *C* and *ruseca* will have resulted in the loss of some of the favorable alleles). Second, new mutations arising during selection and subsequently fixed would augment those from the original Kaduna population.

The third chromosome was divided into five sections, varying in size from 9 cM (section 4) to 30 cM (section 5). These were short enough to discount the probability of a double crossover event within a section during its isolation, ensuring that the chromosome between the visible marker loci at its boundaries was of known origin. After the initial isolation of each section of *C* into an otherwise *ruseca* third chromosome, the flanking sections would be hybrid for *C* and *ruseca* chromosome. By backcrossing single section heterozygous females to *ruseca* males and selecting for low sternopleural bristle score it was hoped that the contaminating *C* chromosome would be removed from the flanking regions of the section being isolated. However, because the high sternopleural bristle alleles of the *C* chromosomes were largely recessive (Table 1), doubt must remain as to the efficiency of this process of removal, as the largely dominant *ruseca* low alleles would be masking the high *C* alleles. Chance crossovers within the flanking sections during the 7 generations of backcrossing to *ruseca* would have removed *C* chromosome but the lack of high sternopleural bristle phenotype will have reduced the effectiveness of selection. The selection of the homozygous flies with the lowest sternopleural bristle score to establish the final stocks would also have minimized section overlap.

Recombination is not uniform over the chromosome with physical distance, being reduced with proximity to the centromere and chromosome tips. There is good evidence (JUDD, SHEN and KAUFMAN 1972; HALL, MASON and SPIERER 1983) that there is approximately one chromosome band to one gene, thus the number of salivary gland chromosomal bands is an estimate of the genetic content of a chromosomal section. The sternopleural bristle scores for each of the five sections is given per chromosomal band and is clearly nonuniform (Figure 3). The left end of the chromosome (*ve-st*) carries most of the effect while the fifth section (*e-ca*) carries an effect which is largely detectable through nonadditive interaction with the left end effects, having little effect in an otherwise *ruseca* chromosome. The data from this study indicate that all five sections of *C* carry some effect. This could conceivably be due to just one or two bristle genes per section or alternatively there could be many genes of individually small effect within each chromosomal section. The results do show that even if there are many genes affecting sternopleural bristles then they are not distributed uniformally along the chromosome (as measured by the number of euchromatic bands). For example the second section clearly carries very much more effect than the fourth while having less than twice as many euchromatic bands.

There have been several previous attempts to locate sternopleural bristle genes, *e.g.*, THODAY (1967, 1973) and THODAY and THOMPSON (1976) analyzed all three major chromosomes and were able to locate nine major sternopleural bristle effects. LOUW (1966) and PIPER (1972) both analyzed a third chromosome using a multiple recessive marker tester chromosomes and concluded that there were at least eight increasing sternopleural bristle effects on their tested third chromosome. The present paper indicates that all five sections carried significant sternopleural bristle effect, indicating a minimum of five sternopleural bristle genes. A more detailed analysis of the effects located within sections is attempted in our companion study (SHRIMPTON and ROBERTSON 1988).

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