

The Isolation of Polygenic Factors Controlling Bristle Score in *Drosophila melanogaster*.

II. Distribution of Third Chromosome Bristle Effects Within Chromosome Sections

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ABSTRACT

In the present study an attempt has been made to characterize the genetic "factors" controlling quantitative characters, bristle numbers, in *Drosophila melanogaster*. A low sternopleural bristle multiple recessive marker third chromosome was used to analyze a high sternopleural third chromosome, in a high sternopleural bristle background. An attempt was made to estimate the minimum number of "effective factors" involved in the difference in bristle score between the tested and marker chromosomes. Apart from sternopleural, scutellar and ocellar bristles, a new character, subprimal bristles, was also scored. The unselected characters were used to help in the factor locations, and an attempt made to detect epistasis. Concentrations of bristle effects were found, as were a few 'factors' of large effect. At least 17 sternopleural bristle factors are required to account for the difference in bristle score between the high tested third chromosome and the low tester third chromosome. There was an ascertainment problem for polygenes with effects of less than about 0.6 phenotypic standard deviation. Only an estimate of the minimum number of factors and approximate locations can be given with any degree of certainty. The results are compatible with the hypothesis (among others) that quantitative characters are under the control of a few major genes supported by numerous genes with smaller effect.

FOR a fuller introduction, see our companion study (SHRIMPTON and ROBERTSON 1988) in which a high sternopleural bristle third chromosome (*C*) was divided into five sections, each of which were isolated in an otherwise low sternopleural bristle chromosome (*ruseca*). In the present study these sections of *C* in an otherwise *ruseca* chromosome are further subdivided to determine whether each section carries more than one gene and to estimate the minimum number of factors and their locations within sections.

The separation of closely linked polygenes requires the occurrence of a recombination event between them. The closer they are linked, the rarer such an event. The more recombinant lines collected, the greater the chance of breaking down linked polygenes become. However, for the same amount of work (number of flies scored), fewer flies per recombinant line could be scored. Thus the minimum size of effect that could be detected would be increased. The optimum strategy regarding how, for a given total number of flies, the number of lines *vs.* the number of flies per line should be distributed depends on the *a priori* unknown distribution of effects (McMILLAN and ROBERTSON 1974).

The approach used in the present investigation,

using the Studentized Range Test, is based on the assumption that there is at least one gene present having an effect on the character under consideration. The data are examined to determine a minimum number of independent groups and therefore number of genetic factors present. An alternative approach, not used in this study would be to assume that there is a uniform distribution of a large number (infinite) of genes with equal and individually very small effect. For example the effect present might be proportional to the amount of genetic material present from the high line. If the recombinant lines are ranked solely on their sternopleural bristle score, departure from the above model would be determined by significant gaps, the size of which would be used to estimate the size of the factor present. The significance of the size of gap could be determined empirically and the interpretation of the data would be to invoke a finite number of factors with large effect plus an infinite number of genes accounting for the remainder. This would perhaps be a more realistic model but was not used as it was too conservative. The method used in the present study, by its very nature, accounts for most of the effect present and gives a minimum number of factors, without a remainder effect.

MATERIALS AND METHODS

The origins, culture conditions and derivation of the lines used in this investigation are given in the previous paper (SHRIMPSON and ROBERTSON 1988). Usually 25 flies of each sex were scored for four bristle (sternopleural, scutellar, subprimal and ocellar) characters and a further 25 flies of each sex for sternopleural bristles only. Subprimal bristles do not appear to have been described previously in the literature. They consist of a group of small bristles located under the first pair of legs, on the sternopleura but quite separate from the sternopleural bristles. They were not easy to count, usually being hidden by the coxae of the first pair of legs. *C* is a high sternopleural third chromosome, extracted from an artificially selected line; *ruseca* a multiple marked low sternopleural third chromosome.

Sections of *C* in an otherwise *ruseca* chromosome had already been isolated (SHRIMPSON and ROBERTSON 1988). A "section" is the chromosome between two markers, e.g. the second section is the chromosome between the *se* and *st* loci.

To investigate a section, a series of further single recombinants between an isolated *C* chromosome section and a *ruseca* chromosome were collected. The two reciprocal classes of recombinants were made homozygous, multiplied up and scored; for example see the mating scheme for the fifth section (Figures 1 and 2). Usually, for each reciprocal class of each section examined, *n* flies of each sex for each of *N* recombinant lines collected, were scored for four bristle characters. A three-way analysis of variance, sex, line and replicate (occasion), was performed for each character. Since the "sex by line" interaction item did not account for more than 5% of the total sum of squares, usually being insignificant, all further analyses were performed on the mean of the two sexes. The analysis of variance also indicated whether or not there was a significant genetic component involved in the difference in sternopleural bristle score between the recombinant lines from a section, the investigation only continuing if the line component was significant. A correction factor was derived from the "line by replicate" interaction component. For each bristle character the additional variance from this component was assessed. This was 1.5 for sternopleurals and 2 for subprimal and ocellar bristles and included the extra variance due to collecting from different vials on different occasions, thus providing a better estimate of the error variance component.

Studentized range test: The sequential studentized range test (see SNEDECOR and COCHRAN 1967) was used to compare the recombinant line bristle score means in each section and to separate them into groups of homogeneous scores. The number of groups minus one represents the minimum number of bristle factors. The difference in group means estimates the factor sizes. The mean scores of the recombinant lines were arranged in increasing order of magnitude for their sternopleural bristle score. The lowest and highest means were tested using the *Q* statistic adjusted for the number of means being tested and, if significantly different from one another, the smallest and second largest mean values were tested (using a new *Q* statistic adjusted for the one fewer mean being tested), sequentially, until the remaining means were not significantly different from one another, forming an homogeneous group. The process was repeated using the lowest value not included in the previous group and the highest mean, until all line means had been assigned to one, and only one, group. The number of recombinant lines in each group was used to estimate

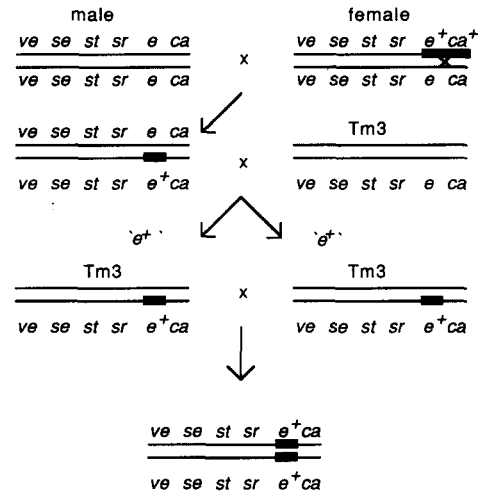


FIGURE 1.—The isolation of e^+ recombinants from the fifth section. $e^+ ca$ male recombinant flies were collected from a "section 5"/*ruseca* heterozygous female to *ruseca* male cross, and in turn crossed to Tm3/*ruseca* females. The Tm3/recombinant heterozygotes could be distinguished from the Tm3/*ruseca* heterozygotes as both Tm3 and *ruseca* carry e .

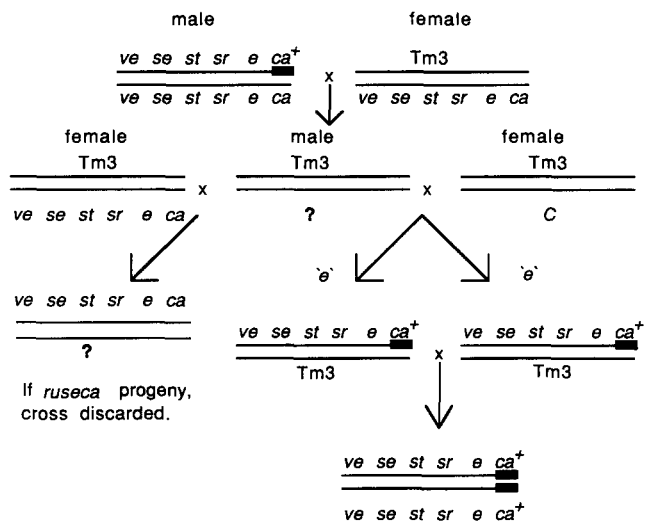


FIGURE 2.—The isolation of ca^+ recombinants from the fifth section. Individual Tm3 male progeny from $e ca^+$ male recombinant flies crossed to Tm3/*ruseca* females were crossed individually to Tm3/*ruseca* and Tm3/*C* heterozygous females. The purpose of the first cross was to determine the genotype of these males. Collection of *ru e*/Tm3 heterozygotes from the second cross established an $e ca^+$ recombinant stock.

the factor locations. In some cases there were good reasons to start from a different mean value other than the lowest; for example using the *Esterase 6* locus to identify whether or not recombinant lines could be placed in the same homogeneous group.

Recombinant line bristle scores were used to form homogeneous groups using 95% confidence limits and since this applied to each group, the overall confidence limits would be greater than this, as it does not allow for overlapping groups. There would thus be more genes actually present than factors detected and a conservative estimate of the minimum number of factors obtained. An obvious

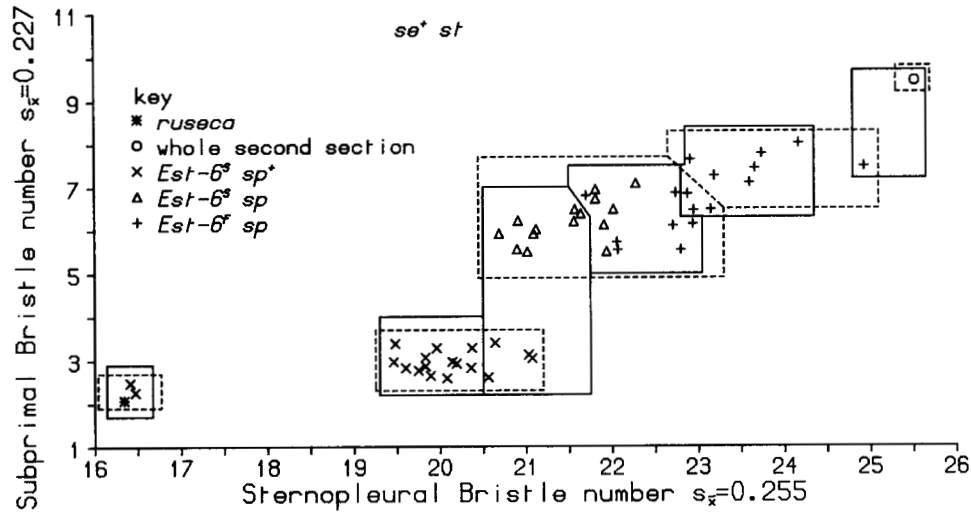


FIGURE 3.—Section 2. $se^+ st$ recombinant lines grouped into homogeneous groups using the Studentized Range Test. Recombinant lines within solid lined boxes form homogeneous groups for their sternopleural bristle scores whilst recombinant lines within dashed boxes form homogeneous groups for their subprimal bristle scores. For example *ruseca* and the two lines with the lowest sternopleural bristle scores form a homogeneous group for both their sternopleural and subprimal bristle scores. Twenty-five flies of each sex were scored for subprimal bristles and 50 flies of each sex for sternopleural bristles.

error would be the accumulation of small effects into a major locus.

The lines were ranked according to their sternopleural bristle score, their position in the ranking estimating the position of the crossover event between *C* and *ruseca* that gave rise to them. This of course depends upon the assumption that the *C* chromosome carries only increasing sternopleural bristle effects compared with the *ruseca* chromosome. Error variances were minimized by ensuring careful environmental control, large sample sizes and using genetically homogeneous material.

In reality, the amount of effort expended on bristle scoring largely determines the detection efficiency and thus the number of factors detected. Failure of the assumption of only positive sternopleural bristle effects on *C* vs *ruseca* may be detected by the occurrence of recombinant lines with sternopleural bristle scores outside the parental range. However, if the negative factor was located between positive factors it may not cause recombinants to lie outside the parental range. The negative factor could invalidate the result and remain undetected. Small effects in the opposite direction which have been fixed by chance during selection, are responsible for a limit to the detection of effects.

Secondary characters: Secondary characters were scored in the hope that they would also be polymorphic and thus provide additional markers for the further subdivision of sections. (Secondary characters were used to help discriminate between alternative sternopleural bristle groupings, not to provide additional sternopleural bristle groups.) If a section contained an easily mappable factor (*i.e.*, of large effect) affecting a secondary character it could be used to help rank the recombinant lines from that section. Three other bristle characters, ocellar, scutellar and subprimal bristles were also counted. Within the framework of sternopleural bristle score groups, the lines were then arranged according to their secondary bristle characters in such a way that the interpretation gave the minimum number of factors, when considering all characters at once. At no time was an interpretation made that required the *C* chromosome to carry negative sternopleural bristle effect. Often there was no unambiguous interpretation, in which case the most likely interpretation is presented, using the information from the secondary bristle characters to help rank

the sternopleural bristle scores and discriminate between alternative groupings.

As they do not have a normal distribution, scutellar bristles were analyzed differently. Since most flies had a score of four scutellar bristles, flies were allocated to two classes, one with four or fewer scutellar bristles and the other with more than four. Lines were then analysed using the χ^2 values adjusted by PIPER (1972) from the adjusted "t" values from Table A15 of SNEDECOR and COCHRAN (1967). Although this necessitated the loss of information it enabled an analysis comparable to that performed on the other bristle characters. Subprimal and ocellar bristles were also scored.

An example: Consider the 51 $se^+ st$ recombinants of section 2 (Figure 3 and Table A4). Since *C* and *ruseca* carry the *Est-6^F* and *Est-6^S* alleles, respectively, the recombinant lines were assayed for their *Esterase 6* genotypes. This enabled the use of the *Esterase 6* locus as an additional marker within the second section. The recombinant lines were ranked by their sternopleural bristles scores within the *Esterase 6* groupings. For example line E45 had a sternopleural bristle score (22.28) higher than that of line E15 (21.70) but by virtue of its *Esterase 6* genotype (*Est-6^S*) must carry less *C* chromosome than E15 (*Est-6^F*). The homogeneous groupings were made within this constraint.

The first comparison was that of the highest recombinant line, E6, with *ruseca* (using the Studentized Range Test). This range was too great ($P < 0.05$) so the next range tested was that of E12 to *ruseca*, and so on until a nonsignificant range was found. In this case E49, E50 and *ruseca* form a homogeneous group and so are in a solid line box in Figure 3. The next range tested was that of E51 to the second section homozygote (2/2). Again this was too great and so E51 was compared with E6 and so on until a homogeneous group formed, in this case it was from E51 to E31. The process was repeated until all lines were incorporated into homogeneous groups.

At the same time and within the constraints of the sternopleural bristle groupings, the secondary bristle character scores were also considered. They were similarly treated to produce homogeneous groups. The exceptional secondary character major gene, *subprimal* (*sbp*; III 32.9 cM, not previously described) was used as an additional

TABLE 1
Summarized locations of bristle factors in sections 1, 3 and 5

Bristle character	Section of C	Phenotype	Factor	Location (cM)	Phenotype	Factor	Location (cM)	
Sternopleural	1	<i>ve⁺ se</i>	0.6	23.4	<i>ve se⁺</i>	1.0	15.0	
			5.0	26.0		5.1	26.0	
		<i>ve⁺ se</i>	0.6	3.4	<i>ve se⁺</i>	5.1	26.0	
			5.1	26.0				
		<i>ve</i>	1.1	3.7				
			1.9	14.9				
	3	<i>st⁺ sr</i>	2.2	44.0	<i>st sr⁺</i>	1.3	44.0	
			1.7	47.6		0.8	44.6	
			1.2	52.6		1.0	47.6	
		<i>st⁺ sr</i>			<i>st sr⁺</i>	1.1	49.4	
						1.0	59.6	
						1.3	44.0	
		5	<i>e⁺ ca</i>	1.7	73.7	<i>e ca⁺</i>	1.3	79.7
				1.1	79.7		1.0	82.7
				1.4	84.7		1.0	84.2
1.3	91.7			1.3	85.7			
0.7	93.7			1.1	93.2			
Subprimal	1	<i>ve⁺ se</i>	3.7	26.0	<i>ve se⁺</i>	3.5	26.0	
	3	<i>st⁺ sr</i>	1.8	44.9	<i>st sr⁺</i>	0.7	44.0	
			1.7	53.0		2.8	45.4	
			1.0	58.4		1.1	53.7	
	5	<i>e⁺ ca</i>	1.8	88.7	<i>e ca⁺</i>	1.5	90.2	
Scutellar	1	<i>ve⁺ se</i>	0.2	23.5	<i>ve se⁺</i>	0.8	0.0	
			0.8	26.0		0.2	20.8	
Ocellar	1	<i>ve⁺ se</i>	-0.5	13.4	<i>ve se⁺</i>	-0.5	16.9	
3	<i>st⁺ sr</i>	1.0	58.4	<i>st sr⁺</i>	1.0	44.0		
		-1.1	59.3		-0.6	57.8		

Factor sizes are given in bristles; positions in cM.

marker similar to *Esterase 6*, i.e. C carried a high and *ruseca* a low subprimal bristle allele at this locus. In Figure 3 the sternopleural and subprimal bristle scores are shown and the homogeneous groups placed in boxes.

RESULTS

Recombinants: The two reciprocal classes of recombinants were collected from each of four sections (1, 2, 3 and 5). [Section 4 was not examined as it did not carry much sternopleural bristle effect (SHRIMPSON and ROBERTSON 1988).] For example, the two reciprocal classes of recombinant lines from the second section were (1) lines which were *se⁺ st* and (2) lines which were *se st⁺*. A C chromosome derived bristle gene will be examined twice, once per reciprocal class of recombinants. If it is located near one of the markers (i.e. toward the edge of a section) then in one reciprocal class it will be detected when comparatively little of the rest of the C derived chromosome is present; and once when most of that section is derived from C chromosome. In contrast a centrally located gene will, in both reciprocal classes,

have about the same amount of C derived chromosome present. In the latter case the effect would be less likely to be implicated in epistatic interactions within the section. Because section 2 (*se* to *st*) contained more sternopleural bristle effect than the other sections, it will be considered in greater detail, the summarized results of the remaining sections are in Table 1.

Section 2 (III; *se* 26 to *st* 44 cM): Fifty-one recombinant lines which were *se⁺ st* (Table 8) and 54 recombinant lines which were *se st⁺* (see Table 11) were collected. All lines were assayed for *Esterase 6*; the ratios of fast to slow lines agreeing well with expectation from the known position of *Est-6* (36.8 cM).

Sternopleural bristle score: As an example of the mapping of bristle factors, consider the two reciprocal classes of section 2 (Figures 3 and 4; see Tables 8 and 11). The recombinant lines formed the homogeneous groups shown in Table 2.

For example, combining the data from the two reciprocal classes would estimate a sternopleural bris-

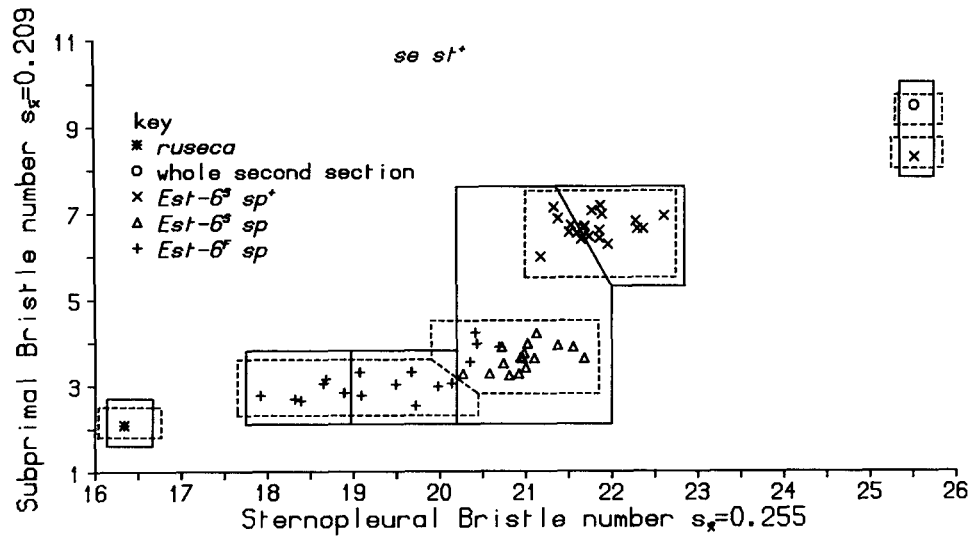


FIGURE 4.—Section 2. *se st*⁺ recombinant lines grouped in homogeneous groups using the Studentized Range Test. Recombinant lines within solid lined boxes have homogeneous sternopleural bristle scores whilst those within dashed boxes form homogeneous groups for their subprimar bristle scores. Twenty-five flies of each sex were scored for subprimar bristles and 50 flies of each sex for sternopleural bristles.

TABLE 2

Homogeneous groupings of sternopleural bristle scores from section 2

Genotype	No. of lines	Mean score	Difference in score	Location	Position (cM)
<i>se</i> ⁺ <i>st</i>	2	16.41			
	13	19.93	3.52	2/51	26.7
	13	21.06	1.13	12/51	31.3
	13	22.21	1.15	28/51	35.9
	9	23.37	1.16	41/51	40.5
	1	25.23	1.86	50/51	43.7
<i>se st</i> ⁺	0	16.41			
	6	18.34	2.14	54/54	44.0
	7	19.60	1.11	48/54	42.0
	27	21.04	1.44	41/54	39.7
	13	21.99	0.95	14/54	30.7
	1	25.52	3.53	1/54	26.3

Groupings of homogeneous sternopleural bristle scores of recombinants from section 2, providing estimates of sizes and locations of effects.

tle factor of $3\frac{1}{2}$ bristles at $26 + 3 (44 - 26)/105 = 26.5$ cM (± 0.3 cM), possibly an allele of the hairy locus (*h*: 26.5 cM). Both reciprocal classes indicated that there were at least 5 increasing factors in this section. Although the exact location and size of factors were not the same in each class, they were in fair agreement.

Subprimar bristle score: The *C* chromosome differed from the *ruseca* chromosome by carrying increasing subprimar bristle effects (no negative subprimar bristle effects were found on any of the four *C* vs *ruseca* sections examined) the high correlation between sternopleural and subprimar bristle scores perhaps indicating pleiotropy. Both reciprocal classes of recombinants (see Tables 8 and 11) gave an estimate of a large subprimar bristle factor; the *se*⁺

st class estimate of a factor of 3.5 bristles at 32.7 cM and the *se st*⁺ class of 3 bristles at position 33.0 cM.

Combining the data from the two reciprocal classes gives an estimate of $3\frac{1}{4}$ bristles at $26 + 40 (44 - 26)/105 = 32.9$ cM (± 0.9 cM), and is given the symbol *sbp* for *subprimar*. There were at least four other increasing factors within this section of the *C* chromosome. Comparing the two reciprocal sets of data (Tables 8 and 11) indicated that there were epistatic interactions between the subprimar factors within this section.

The *subprimar* and *Esterase 6* loci were used to give more accurate locations of the crossover events during the formation of recombinant chromosomes. There was a general increase in subprimar bristle score with increase in sternopleural bristle score, indicating a preponderance of increasing subprimar factors on the *C* chromosome. One of the subprimar factors was located at the same site as the large sternopleural bristle factor, at or close to the *h* locus (Figures 3 and 4) perhaps indicating pleiotropy.

Ocellar bristle scores: The ocellar bristle score of line C23 (Table 11) is too high for its sternopleural bristle score for a simple model of a single increasing factor within the section. If both C23's sternopleural and ocellar bristle scores are correct then an alternative model with an additional two equal and closely linked ocellar bristle factors of opposite direction would be required. C23's ocellar bristle score could be then explained by a rare crossover between the two closely linked equal sized ocellar factors of opposite direction. An alternative and more likely explanation was that C23 may have a false sternopleural or ocellar bristle score, especially as C23's scutellar bristle score also appeared to be high. This line was lost before repeated measurements could be made.

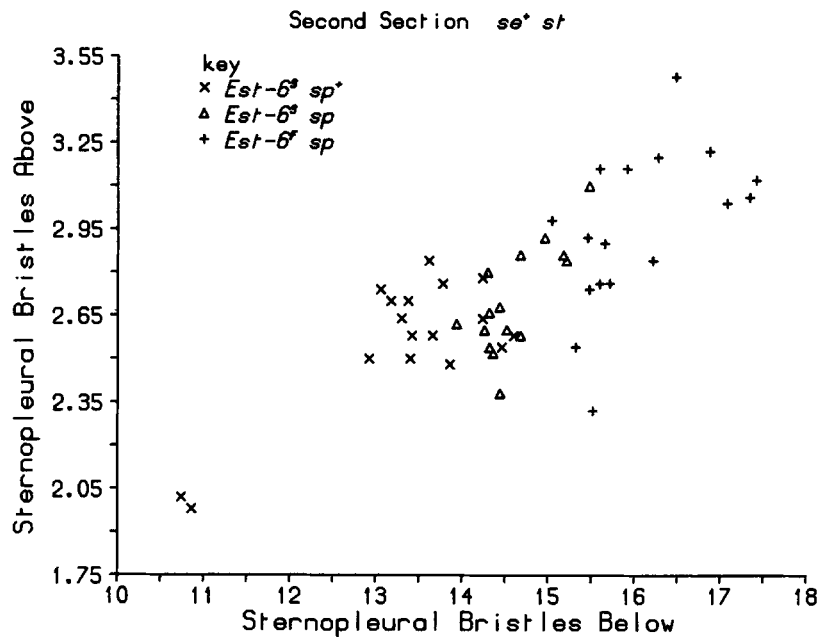


FIGURE 5.—Twenty-five flies of each sex were scored for their sternopleural microchaetae according to whether they were above or below an imaginary line drawn between the two macrochaetae on each side of the fly. Only the *se⁺ st* recombinant lines from the second section of *C* were scored in this way. There were no obvious new groupings to indicate the segregation of a major effect that influenced the pattern of bristles on the sternopleurite.

TABLE 3

Isolation of sternopleural bristle effect associated with the *se* locus^a

Line	Sternopleural bristle score	Sternopleural bristle score as difference from <i>ruseca</i>
<i>ve se⁺</i> (line U12)	23.26 ^b	6.92
<i>ruseca</i>	16.34	
<i>se h st</i>	33.86	17.52
Recombinants		
<i>se1</i>	19.39 ^b	3.05
<i>se2</i>	18.90	2.56
<i>se3</i>	18.83	2.49
Mean	19.04	2.70

^a A *se h st* stock which had an otherwise low sternopleural bristle third chromosome and the standard background was used to investigate the sternopleural bristle effect associated with the *se* locus from section 1. The technique takes advantage of the close linkage between *se* and *h* to map more precisely any linked effects. *n* = 50 each sex.

^b *n* = 75 each sex.

Scutellar bristle scores: The two reciprocal classes exhibited a pronounced difference in results and so need to be dealt with separately.

1. *se⁺ st*. Since there were a couple of lines with scores outside the parental range it was necessary to invoke effects of both directions. There appeared to be a preponderance of increasing bristle effect on the *C* chromosome; a model with two increasing and one decreasing factor was adequate.

2. *se st⁺*. Although none of the lines had a score significantly different from *ruseca*, their distribution pattern indicated that there were two increasing factors within the section. However, there was no

TABLE 4

Location of sternopleural bristle effect on *C*

Source	Sternopleural bristle score	Minimum no. factors
<i>ve</i> locus (<i>fap</i>)	15 → 16	1
Section 2	→ 25	5
Interaction between section 2 and section 5	→ 30	5
Section 3	→ 34	4
Section 1	→ 36	1
Interaction between section 1 and the rest of the <i>C</i> chromosome	→ 40	2
Total		18

The difference in sternopleural bristle score between *C* and *ruseca* could be accounted for by effects located within the four sections and their interactions. At least 17 factors are required. Both *ruseca* and *C* carried the same allele at *fap*, Female abdomen pigment, located at III 0.0 cM which is known to be associated with a sternopleural bristle effect (data not given). The → indicate the change in sternopleural bristle score accounted for by the separate chromosomal sections.

indication of the increasing and decreasing factors located to the left of the *st* locus, as detected by the *st se⁺* class, perhaps because no suitable crossover event had occurred in this class. One explanation of the two sets of lines was that there was a factor at or very close to the *se* locus which had an epistatic interaction with the rest of the section, inflating their scores.

Summary of the second section: The presence of factors of both directions for secondary bristle characters complicated the interpretation. For example, it might be possible to alter the above interpretation

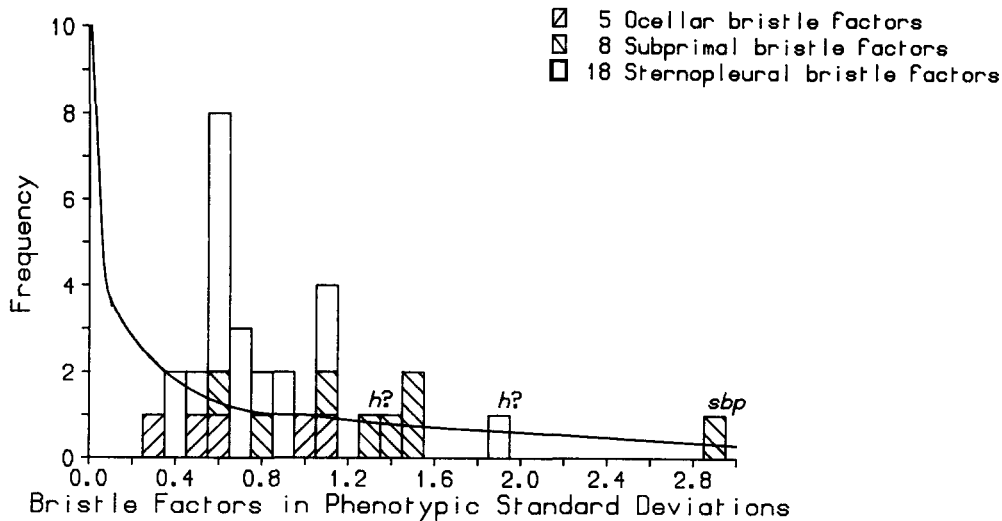


FIGURE 6.—A histogram of the frequency of bristle factors (sternopleural, subprimal and ocellar) in phenotypic standard deviations summarised from the data collected from the *C* chromosome. The largest factor was the subprimal bristle effect at *sbp*; the second largest effect was the sternopleural bristle effect located close to *h* at which was also found a subprimal bristle factor of about 1.6 bristles. Three subprimal bristle factors of about 1.8 bristles were located at approximately 45.1, 53.3 and 89.6 cM. The curve is a hypothetical frequency distribution of bristle genes, since there is an ascertained problem in detecting those effects of less than about 0.6 phenotypic standard deviation.

by invoking one fewer subprimal factor, but only at the expense of having to increase the number of factors controlling one of the other characters. The above model is the simplest.

Test for epistasis: The degree of agreement between the distribution of bristle scores of the two reciprocal classes can indicate the presence of epistasis. Sternopleural and ocellar bristle patterns were in good agreement with each other across reciprocal classes. Subprimal bristles showed a pronounced difference, indicating epistasis for this character within the section. There appeared to be a scale effect, the higher the score the greater the increase in score by the addition of a further increasing factor, *i.e.* the effects were not additive. Scutellar bristles were interpreted to be controlled by a pronounced interaction of all the effect in the section with a factor at or close to the *se* locus. In its absence very little scutellar bristle effect was detected.

Test for change in bristle distribution: The bristles were divided into two groups by an imaginary line drawn between the two major bristles. Twenty-five flies of each sex were scored for 50 of the *se*⁺ *st* lines, the scores being recorded according to the number of bristles above and below the line (see Table 9). There were, however, no obvious previously undetected gaps in the distribution of scores (indicating the segregation of a major pattern effect) when the number above and below were plotted against each other (Figure 5). The factors within this section appeared to be having their effect through a general increase in sternopleural bristle number rather than through more specific effects on particular bristles (see SPICKETT 1963). The correlation between the

two subcharacters was $r = 0.67$ if E49 and E50 are not considered and $r = 0.77$ with their inclusion. More work may have revealed bristle pattern effects.

Further investigation of the *se* locus linked factors: A *se h st* stock was used to investigate the sternopleural bristle factors associated with the *se* locus. This stock (*se: sepia*, 26.0 cM; *h: hairy*, 26.5 cM; *st: scarlet*, 44.0 cM) carried three recessive markers in a low sternopleural bristle third chromosome in the standard background. A *ve se*⁺ recombinant (line U12) from section 1, was used as the source of the *se* locus associated effect (Table 3). Male recombinants produced by a crossover event between the *se* and *h* loci in a *se h st*/line U12 heterozygous female crossed with a *se h st* male, were collected. Because *h* greatly increases bristle score, only recombinants from the *se h*⁺ recombinant class (and not the *se*⁺ *h* class) were collected (3 lines). These were made homozygous, multiplied up and scored to reveal that some effect (2.7 bristles) mapped to the right of the *se* locus (possibly at *h*). Almost certainly this is the factor at or close to the *h* locus detected earlier in the second section investigation (3.5 bristles), the difference in estimates of the size of this effect probably reflects differences in time and isolation procedure. The remaining effect is probably located to the left of the *se* locus as it was not found during the investigation of section 2. During the isolation of section 2, the effect to the left of the *se* locus must have been removed; while during the isolation of section 1, the closely linked effect associated with the *h* locus remained.

Summary of *C* chromosome: Section 2 contained the main effect of about nine sternopleural bristles

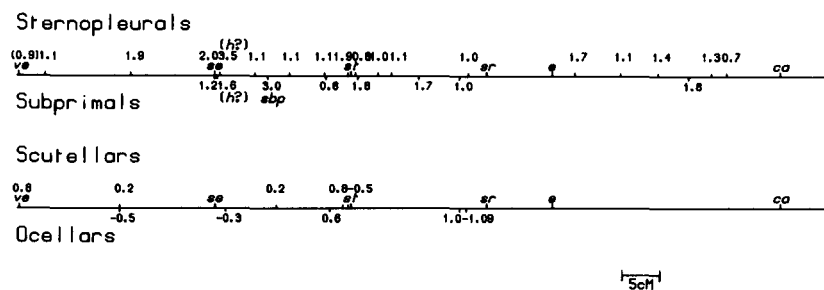


FIGURE 7.—A map showing the distribution of bristle effect differences between *C* and *ruseca*. The bristle positions and magnitudes are selected from the data to indicate one possible interpretation.

which proved to be due to at least five sternopleural bristle factors; section 5 contained very little effect alone, but a sizeable effect when section 2 from *C* was also present, accounting for a further five sternopleural bristles and requiring at least five factors. Section 3 contained at least a further four factors responsible for a further four sternopleural bristles and section 1 contained at least three factors accounting for a further six sternopleural bristles.

The difference in sternopleural bristle score between *ruseca* (16.3) and *C* (about 40) has thus been shown to be due to at least 17 factors. All factors being positive, so no departure from the assumption that the *C* chromosome carried only increasing bristle effects relative to *ruseca*, was detected. This is a conservative estimate (as it does not allow overlapping groups) of the number of factors present and has little meaning outside the conditions of this investigation. Most of the difference in sternopleural bristle score (24 bristles) can be accounted for with approximate locations of effect (Table 4). Examples of models that would account for the data are given in Figures 6 and 7.

DISCUSSION

The prediction of responses to selection, if only a comparatively few loci are involved, requires the description of genetic variance in terms of individual loci. This approach requires the knowledge of the type of gene action, the size of effect, linkage relationships with other genes and gene frequencies.

The aim of the present study was to estimate the number of loci with direct effect on the difference in bristle score between the tested *C* and tester *ruseca* third chromosomes. The number of factors detected was largely determined by the amount of effort given to their detection. The more recombinant lines collected, the more likely the factors will be separated from each other and the more flies counted per line the lower the detection threshold value becomes. Some, perhaps most, of the factors detected are probably really more than one linked gene with small effect. One limit to detection is that eventually the detection threshold value would reach the level at which alleles of small enough effect would not have been fixed during selection and would invalidate the

results by being present on the wrong chromosome. All errors in estimation of the number of factors are toward under-estimating the number; an estimate of the minimum number of factors involved is thus expected to be conservative.

One of the assumptions of the biometrical methods of estimating the number of polygenes is that they are of equal effect (MATHER and JINKS 1971). Figure 6 shows that this is not found for the bristle characters examined in this investigation, as the located factors are not all the same size. *C* would be expected to carry only increasing sternopleural effects and if there were a large number (>100) of equal sized polygenes controlling sternopleural bristle score, each would have only a small individual effect. As discussed in the previous paper (SHRIMPTON and ROBERTSON 1988) the best measurement of the genetic content of a section of DNA is the number of salivary gland chromosome bands it contains. In Figure 3 of SHRIMPTON and ROBERTSON (1988) it is seen there is no indication of a correlation between sternopleural bristle score and the size of a chromosomal section measured in this way. This would indicate that either the effects are not numerous, are not distributed uniformly or are not of equal size.

Examination of Figure 6 shows that there is a peak of detected factors with estimated sizes of 0.6 phenotypic standard deviation. The statistical technique used was not capable of detecting factors with effects of less than about 0.3 phenotypic standard deviation. There appeared to be a detection threshold value of about 0.6 phenotypic standard deviation; genes with effects of less than this being grouped into larger factors. About a third of the difference between *C* and *ruseca* has been accounted for by three or four factors with effects of one phenotypic standard deviation or more. A truer gene size distribution might be that indicated by the hypothetical curve drawn in Figure 6. The results from this study are comparable with the view that quantitative characters are controlled by a few major effects supported by a host of smaller effects of diminishing influence on the character. The implication is that there are probably genes controlling commercially important quantitative traits, of sufficient effect for their profitable use in genetic engineering.

PIPER (1972) investigated a high but unselected

sternopleural bristle third chromosome, K13, also isolated from the Kaduna stock. K13 carried as much effect as *C* in its second section (PIPER's data in Table 10), showing that this particular concentration of increasing sternopleural bristle effect existed prior to selection. This in turn would suggest that only a small number of loci were responsible for this concentration of effect. Both his results and some data collected by D. BRISCOE in 1973 (Table 10) indicated that there were at least 5 sternopleural and 2 scutellar bristle factors present in section 2 of the third chromosome, all three investigations producing very similar results. The difference between *C* and K13 would seem to be accounted for by the effects in the rest of the chromosome rather than the preexisting concentration of high sternopleural bristle effects in section 2. For example the section 5 effects which are largely detectable through their epistatic interaction with sections 1 and 2 of *C*. Interestingly the second section of the third chromosome has been found to be the source of response for sternopleural bristle score in other stocks; SPICKETT (1963) located two effects at 30.2 cM (*Pl(3)Spt1*) and 32.6 cM (*Pl(3)Spt2*), whilst more recently SCHNEE and THOMPSON (1984) found a major effect *Pl(3)Sp^s* at 32.6 ± 2.3 cM. The similarity of these findings is striking and would seem to indicate that there is a limited number of loci which respond to selection for this character. WOLSTENHOLME and THODAY (1963) on the other hand located two effects at 49 and 51 cM on the third chromosome, linked but clearly different sites to the above. CALIGARI and MATHER (1975) also found that the third chromosome had a large effect on sternopleural bristle score.

The interpretation of the results gave no additional consideration to discriminating between pleiotropy and linkage. Examination of the data in such a way that the estimate of the minimum number of factors involved was not the most important consideration, would be required to examine pleiotropy. For example the section 2 *se st⁺* (Table 11) recombinant lines have sternopleural, subprimal and ocellar bristle factors mapping to the same site (as indicated by the line drawn between C37 and C19). However the interpretation of the *se⁺ st* reciprocal recombinant lines (Table 8) invokes a model with slightly different positions for the three bristle factors. DAVIES and WORKMAN (1971) were largely able to separate abdominal and sternopleural bristle effects. Given the conservative nature of the statistical technique used, it seems likely that there are more factors present than detected and so the chances of pleiotropy

greater. Pleiotropy was indicated on occasions and could have been invoked on many.

Another refinement to this type of investigation would be the inclusion of the use of dispersed repetitive DNA probes to hybridize *in situ* to the salivary glands of recombinant lines. Assuming that the *C* and *ruseca* chromosomes would be polymorphic for some of the sites of labelling (STROBEL, DUNSMUIR and RUBIN, 1979), each polymorphic site would act as a new marker enabling a more accurate ranking of the recombinant lines, in a similar fashion to the attempted use of large secondary characters factors as markers.

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APPENDIX

The mean bristle scores of recombinant chromosome lines are given in Tables 5-14. Each data point is usually the mean of at least 50 flies, 25 flies of each sex, summed over both sides of the fly. The uncorrected error variance is also given. The horizontal lines drawn between lines means indicate homogeneous groups. Recounts on some of the extreme lines were performed to check the repeatability of the bristle scores.

TABLE 5
First section recombinants

<i>ve⁺ se</i>		<i>ve se⁺</i>				Repeat scores		
Line	St	Line	St	Line	St	Line	Old	New
"ruseca"	16.34	"ruseca"	16.34			U8	20.33	20.89
P28	15.92	U8	20.61 ^a	6	22.34	31	20.79	21.11
23	15.93	31	20.79 ^a	21	22.44	7	20.97	21.30
9	16.00	7	21.14 ^a	4	22.45	3	21.32	21.07
29	16.13	3	21.20 ^a	36	22.54	30	21.87	21.24
24	16.17	17	21.28	11	22.59	23	21.60	22.92
4	16.26	22	21.48	16	22.60	5	21.06	22.94
10	16.39	9	21.54	24	22.71	10	22.59	23.42
12	16.41	30	21.56 ^a	35	22.83	U12	23.05	23.46
2	16.42	25	21.69	18	22.88	Recounts on <i>ve se⁺</i> lines		
27	16.45	19	21.70	10	23.01 ^a			
11	16.48	28	21.71	33	23.02			
26	16.48	1	21.82	U12	23.26 ^a			
7	16.60	2	21.85	1/1	21.97			
1	16.62	13	21.96					
6	16.67	23	21.99 ^a					
22	16.68	5	22.00 ^a					
16	16.74	34	22.02					
5	16.78	29	22.08					
14	16.98	14	22.11					
P13	17.00	27	22.13					
1/1	21.97	32	22.32					

$S_{\bar{x}} = 0.30$
 $N = 33$

$S_{\bar{x}} = 0.183$
 $N = 20$
 $n = 50$
^a $n = 100$

Abbreviations: n = No. of flies per sex per line, N = No. of lines, St = sternopleurals, Sp = subprimals, Oc = ocellars, Sc = scutellars, and $S_{\bar{x}}$ = square root of the error variance.

TABLE 6
First section recombinants

<i>ve⁺ se</i>					<i>ve se⁺</i>				
Line	St	Sp	Oc	Sc	Line	St	Sp	Oc	Sc
"ruseca"	16.34	2.08	7.50	4.02	"ruseca"	16.34	2.08	7.50	4.02
V24	15.92 ^a	2.34	6.92	4.04	S23	21.24	5.46	7.42	4.12
25	16.20	1.78	6.82	4.12	9	21.42	6.30	7.56	4.04
10	16.28	1.98	6.88	4.08	8	21.70	5.86	7.30	4.06
15	16.36	2.16	7.12	4.04	2	21.80	6.00	7.28	4.10
28	16.44	1.92	7.34	4.14	18	21.16	5.60	7.60	4.22
7	16.46	2.08	7.08	4.02	22	21.24	5.78	7.42	4.14
21	16.48	2.04	6.92	4.04	20	21.62 ^a	5.82	7.42	4.26
19	16.58	1.92	6.94	4.02	15	20.31 ^a	4.96	6.54	4.16
14	16.66	1.64	6.84	4.14	5	20.87 ^a	5.30	7.06	4.28
5	16.70	2.12	7.44	4.08	21	20.94	5.40	7.16	4.24
6	16.72	2.34	7.42	4.06	3	21.00	5.22	6.76	4.30
20	16.72	1.74	6.86	4.12	14	21.22	5.82	6.80	4.40
31	16.72	1.98	7.20	4.04	7	21.30	5.86	6.60	4.22
12	16.80	2.20	7.38	4.10	10	21.34	5.64	6.82	4.32
8	17.00	2.08	7.08	4.02	19	21.52	5.28	6.82	4.26
16	17.16	1.92	7.24	4.20	13	21.56	5.96	7.08	4.14
11	16.36	1.86	6.50	4.18	6	21.90	5.64	7.16	4.32

TABLE 8

se⁺ *st* recombinants from the second section

<i>n</i> . . . Line . . .	50 St	25 Sp	25 Oc	25 Sc
"ruseca"	16.34	2.08	7.50	4.02
E49	16.41	2.48	7.90	4.06
50	16.47	2.26	8.20	4.06
51	19.48	3.38	7.50	4.16
18	19.46	2.96	7.64	4.01
1	19.60	2.82	7.44	4.23
10	19.75	2.76	6.94	4.00
33	19.83	3.06	7.34	4.12
40	19.83	2.86	7.34	4.22
24	19.89	2.64	7.82	4.24
13	19.96	3.28	7.22	4.15
32	20.08	2.58	8.02	4.26
30	20.14	2.96	7.22	4.15
22	20.19	2.92	7.38	4.13
26	20.36	2.82	7.78	4.14
31	20.37	3.28	7.30	4.42
34	20.56	2.60	7.56	4.16
35	20.64	3.40	7.22	4.07
37	21.03	3.12	7.60	4.17
"sbp" 21	21.07	3.04	7.92	4.40
53	20.69	5.92	7.58	4.33
14	20.90	5.56	7.28	4.21
25	21.02	5.50	7.52	4.28
37	21.09	5.92	7.58	4.08
43	20.91	6.22	7.46	4.51
2	21.12	6.02	7.70	4.36
56	21.56	6.20	7.18	4.41
8	21.57	6.48	7.36	4.64
27	21.64	6.38	7.10	4.17
4	21.91	6.12	7.34	4.55
44	21.94	5.50	7.74	4.29
46	22.02	6.48	7.80	4.47
9	21.81	6.72	7.28	4.35
42	21.81	6.94	7.58	4.31
"Est-6 ^S "45	22.28	7.08	7.34	4.38
15	21.70	6.80	7.56	4.16
"Est-6 ^F "23	22.74	6.86	7.78	4.48
5	22.88	6.84	7.88	4.20
36	22.06	5.72	7.44	4.35
16	22.07	5.54	7.36	4.18
38	22.71	6.10	7.44	4.68
28	22.80	5.54	7.36	4.34
54	22.94	6.14	7.74	4.44
41	22.95	6.46	7.20	4.50
17	23.15	6.48	8.26	4.47
3	22.91	7.64	7.78	4.34
58	23.19	7.26	7.92	4.35
55	23.60	7.10	8.10	4.57
47	23.74	7.78	8.50	4.21
48	23.66	7.44	8.00	5.30
12	24.17	8.02	8.18	5.09
E6	24.93	7.48	7.88	4.74
2/2	25.52	9.46	8.13	4.67
<i>S_x</i>	0.255	0.227	0.189	
<i>N</i> = 51				

TABLE 9

se⁺ *st* recombinants from the second section

Line	Sternopleurals	
	Below	Above
E49	10.86	1.98
50	10.74	2.02
51	13.30	2.64
18	12.92	2.50
1	13.42	2.58
33	14.24	2.64
40	13.18	2.70
24	13.38	2.70
13	13.40	2.50
32	13.06	2.74
30	13.66	2.58
22	13.86	2.48
26	13.78	2.76
31	13.62	2.84
34	13.78	2.76
35	14.46	2.54
57	14.24	2.78
"sbp" 21	14.60	2.58
53	14.44	2.38
14	13.94	2.62
25	14.32	2.54
37	14.32	2.66
43	14.26	2.60
2	14.36	2.52
56	14.44	2.68
8	14.30	2.80
27	14.68	2.58
4	14.96	2.92
44	14.68	2.86
46	15.48	3.10
9	14.52	2.60
42	15.22	2.84
"Est-6 ^S "45	15.18	2.86
15	15.52	2.32
"Est-6 ^F "23	15.48	2.74
5	16.22	2.84
36	15.32	2.54
16	15.04	2.98
38	15.66	2.90
28	15.60	2.76
54	15.60	3.16
41	15.72	2.76
17	16.28	3.20
3	15.46	2.92
58	15.92	3.16
55	17.08	3.04
47	16.48	3.48
48	16.88	3.22
12	17.42	3.12
E6	17.34	3.06
<i>n</i> = 25		
<i>N</i> = 50		

Twenty-five flies of each sex from each of 50 *se*⁺ *st* recombinant lines from the second section were scored for their sternopleural microchaetae above and below an imaginary line drawn between the two macrochaetae.

TABLE 10

se⁺ *st* recombinants from the second section

<i>D. Briscoe's 1973 data</i>			<i>L. Piper's 1972 data K13</i>		
<i>n</i>	45	25	<i>n</i>	30	100
Line	St	Sc	Line	St	Sc
8	15.5	4.04	<i>sp se st</i>	15.44	4.06
12	19.1	4.20	5	19.61	4.22
42	20.7	4.20	6	19.67	4.25
2	20.0	4.28	17	19.92	4.24
11	20.1	4.36	10	20.59	4.47
43	20.3	4.40	18	21.48	4.47
19	20.4	4.24	11	21.66	4.39
29	20.6	4.24	14	21.71	4.28
41	20.6	4.52	8	22.01	4.40
40	20.6	4.30 ^a	20	22.45	4.41
38	20.8	4.36	7	22.45	4.72
35	20.8	4.23 ^b	4	22.85	4.46
1	21.1	4.34	19	23.41	4.36
44	21.4	4.40	12	23.68	5.25
17	21.7	4.32	9	24.14	4.83
16	21.8	4.30	2	24.47	5.10
18	22.2	4.58	13	25.09	5.09
30	22.2	4.86	16	25.29	5.22
24	22.8	4.55 ^a	1	26.23	4.97
"Est-6 ^S "33	23.2	4.50	3	27.00	5.12
45	21.8	4.80			
"Est-6 ^F "37	22.0	4.34			
10	22.1	4.62			
46	22.4	4.67 ^b			
34	22.8	5.16			
7	22.8	5.00			
32	22.9	5.42			
25	23.4	5.80 ^a			
31	23.6	5.66			
21	23.6	5.48			
22	23.6	5.30			
36	23.6	4.60 ^a			
26	23.7	5.62			
28	23.8	5.04			
14	24.9	4.78			
20	24.9	4.65 ^a			
27	26.2	5.42			

$S_{\bar{x}} = 0.286$
 $N = 19$

$S_{\bar{x}} = 0.334$
 $N = 37$

^a *n* = 5 or 10
^b *n* = 15 or 20

TABLE 11

se st⁺ recombinants from the second section

<i>n</i>	50	25	25	25
Line	St	Sp	Oc	Sc
"ruseca"	16.34	2.08	7.50	4.02
C10	17.92	2.76	6.94	4.00
29	18.32	2.68	7.42	4.04
22	18.39	2.64	7.48	4.00
1	18.65	3.04	7.38	4.02
23	18.68	3.14	8.92	4.14
50	18.89	2.82	7.34	4.00
59	19.07	3.30	7.32	4.02
8	19.09	2.76	7.72	4.00
27	19.49	3.02	7.50	4.00
7	19.67	3.30	8.00	4.00
36	19.72	2.52	7.28	4.00
35	19.98	2.97	7.12	4.00
37	20.14	3.04	7.62	4.00
19	20.35	3.54	8.74	4.02
6	20.42	4.22	8.00	4.00
28	20.43	3.96	8.30	4.00
"Est-6 ^S "40	20.69	3.88	8.20	4.02
48	20.27	3.26	7.96	4.00
"Est-6 ^F "60	20.58	3.26	8.14	4.00
58	20.72	3.88	8.02	4.02
30	20.74	3.50	8.60	4.02
33	20.81	3.22	8.08	4.06
12	20.92	3.26	8.18	4.02
38	20.94	3.64	8.30	4.10
44	20.96	3.62	8.08	4.04
14	20.98	3.74	7.94	4.06
15	21.00	3.40	8.54	4.04
43	21.02	3.96	8.54	4.06
20	21.10	3.62	8.18	4.02
13	21.13	4.20	8.76	4.04
2	21.37	3.92	8.20	4.18
21	21.55	3.88	8.52	4.12
"sp" 52	21.68	3.62	8.06	4.00
53	21.18	5.98	8.36	4.12
51	21.33	7.12	8.36	4.08
45	21.38	6.86	7.90	4.08
57	21.51	6.54	7.92	4.10
46	21.53	6.70	8.12	4.12
5	21.60	6.52	8.30	4.06
16	21.65	6.38	8.16	4.18
17	21.68	6.64	7.96	4.06
39	21.69	6.68	8.44	4.02
25	21.74	6.44	8.18	4.04
9	21.77	7.04	7.90	4.18
47	21.86	6.58	7.72	4.16
11	21.87	7.16	7.88	4.20
32	21.89	6.96	8.30	4.08
56	21.96	6.26	7.96	4.08
26	22.28	6.80	7.92	4.08
42	22.30	6.62	8.24	4.16
41	22.37	6.62	8.50	4.18
31	22.61	6.92	8.16	4.12
54	21.86	6.40	8.26	4.32
C3	25.52	8.26	8.54	4.28
2/2	25.52	9.46	8.13	4.67

$S_{\bar{x}} = 0.255$ 0.209 0.210
 $N = 54$

TABLE 12

Recombinants from the third section

<i>st sr⁺</i>		<i>st⁺ sr</i>	
<i>n</i>	50	<i>n</i>	50
Line	St	Line	St
"ruseca"	15.86	"ruseca"	15.86
T30	15.51	R7	17.61
8	15.68	24	17.81
2	15.85	5	18.05
23	16.06	21	18.06
4	16.37	17	18.52
12	16.45	12	19.12
3	16.47	4	19.32
25	16.47	16	19.38
14	16.54	3	19.80
15	16.61	25	19.82
24	16.66	23	20.03
26	16.77	20	20.21
21	16.80	9	20.30
7	16.86	1	20.47
1	16.88	8	20.53
29	16.95	19	20.60
13	17.06	10	20.70
17	17.15	22	20.75
18	17.19	13	20.77
5	17.37	11	20.79
9	17.39	6	20.96
27	17.66	14	20.99
20	17.91	15	21.25
28	18.03	2	21.25
19	18.70	R18	21.30
4	18.83	3/3	20.99
22	18.95		
6	19.02		
16	19.05	$S_{\bar{X}}$	0.255
T11	19.71	$N = 25$	
3/3	20.99		
$S_{\bar{X}}$	0.206		
$N = 30$			

TABLE 13

Recombinants from the third section

<i>st⁺ sr</i>					<i>st⁺ sr⁺</i>				
<i>n</i>	50	25	25	25	<i>n</i>	50	25	25	25
Line	St	Sp	Oc	Sc	Line	St	Sp	Oc	Sc
"ruseca"	15.81	1.94	7.72	4.00	"ruseca"	15.81	1.94	7.72	4.00
T64	17.36	2.50	8.34	4.12	R71	15.97	1.58	7.78	4.00
62	17.01	3.50	8.26	4.04	62	16.00	1.54	7.72	4.02
55	17.59	4.04	8.48	4.10	70	16.25	1.38	7.60	4.02
79	18.83	4.00	7.58	4.00	64	16.27	1.64	7.32	4.00
72	19.51	3.90	8.24	4.02	60	16.33	2.12	7.22	4.00
65	19.69	4.82	8.80	4.02	68	16.66	1.70	7.16	4.04
69	19.91	3.64	8.16	4.00	51	16.65	3.30	6.82	4.02
80	20.17	4.76	7.70	4.00	53	16.74	2.88	6.54	4.00
59	20.42	3.70	8.08	3.98	58	17.33	2.74	7.20	4.02
81	20.59	3.70	8.50	4.06	59	17.52	2.36	7.32	4.04

TABLE 13—Continued
Recombinants from the third section

<i>st⁺ sr</i>					<i>st⁺ sr⁺</i>				
<i>n</i>	50	25	25	25	<i>n</i>	50	25	25	25
Line.....	St	Sp	Oc	Sc	Line.....	St	Sp	Oc	Sc
56	20.18	5.94	8.04	4.00	63	17.67	2.46	7.46	4.00
67	20.37	5.18	8.48	4.00	65	<u>17.82</u>	<u>3.02</u>	7.46	4.00
77	20.55	6.10	8.12	3.98	R52	<u>19.67</u>	<u>5.60</u>	<u>6.94</u>	4.00
82	20.62	5.16	8.22	4.02	3/3	20.99	6.30	8.18	3.98
71	20.64	5.88	8.30	4.00					
58	20.76	5.88	<u>8.20</u>	4.00	<i>S_x</i>	0.262	0.212	0.185	
51	20.01	<u>6.52</u>	<u>7.16</u>	4.00	<i>N</i> = 13				
54	20.32	6.46	<u>8.38</u>	4.10					
59	20.42	6.44	8.42	3.98					
T52	20.57	7.52	8.02	4.06					
3/3	20.99	6.30	8.18	3.98					
<i>S_x</i>	0.259	0.330	0.226						
<i>N</i> = 20									

TABLE 14

Recombinants from the fifth section

<i>e⁺ ca</i>			<i>C 2 + 5</i>	<i>e ca⁺</i>		
<i>n</i>	50	7		<i>n</i>	50	10
Line.....	St	Sp		Line.....	St	Sp
2/2	24.57	9.46		2/2	24.57	9.46
A29	23.40	6.71		B1	23.71	6.75
30	24.27	5.93		7	24.29	6.70
6	<u>24.51</u>	7.33		12	24.65	7.80
7	25.12	6.71		8	24.87	9.15
9	25.46	7.35		21	<u>24.97</u>	7.80
19	25.62	8.50		15	25.21	7.90
36	26.25	8.15		3	25.35	<u>7.60</u>
15	26.33	6.79		17	25.64	9.75
25	<u>26.42</u>	8.57		20	25.67	8.00
5	26.59	8.86		4	<u>25.93</u>	9.55
10	26.78	8.43		27	<u>26.85</u>	7.95
11	26.86	9.29		18	<u>27.89</u>	10.45
28	26.97	8.15		19	28.57	11.20
22	<u>27.69</u>	8.28		22	<u>29.23</u>	9.55
8	28.10	7.50		36	29.63	9.00
16	28.11	9.07		5	29.81	10.25
2	28.16	7.07		29	29.90	8.90
13	28.23	<u>9.00</u>		30	30.59	9.25
24	28.29	11.07		11	30.93	8.90
26	28.70	10.86		B40	30.94	9.60
20	<u>29.09</u>	10.29		2 + 5/2 + 5	29.84	
12	29.62	8.72		<i>S_x</i>	0.320	0.596
21	<u>29.75</u>	9.50		<i>N</i> = 20		
4	29.89	9.14				
34	29.99	11.50				
33	30.09	9.58				
23	30.31	8.93				
3	30.44	9.21				
18	30.71	9.14				
A32	31.30	9.71				
2 + 5/2 + 5	29.84					
<i>S_x</i>	0.338	0.664				
<i>N</i> = 30						