PHENOGENETIC STUDIES ON SCUTE-1 OF DROSOPHILA MELANOGASTER.

I. THE ASSOCIATIONS BETWEEN THE BRISTLES AND THE EFFECTS OF GENETIC MODIFIERS AND TEMPERATURE

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INTRODUCTION

This paper deals with the quantitative variations, under different environmental conditions, of the bristle numbers of the mutant scute-1 in *Drosophila melanogaster*. The genetic factor "scute" was discovered by BRIDGES in 1916 (unpublished). Since 1929, when other alleles of scute were found at the same locus, the original scute has been designated as scute-1. Figure 1 shows the position and nomenclature of the bristles

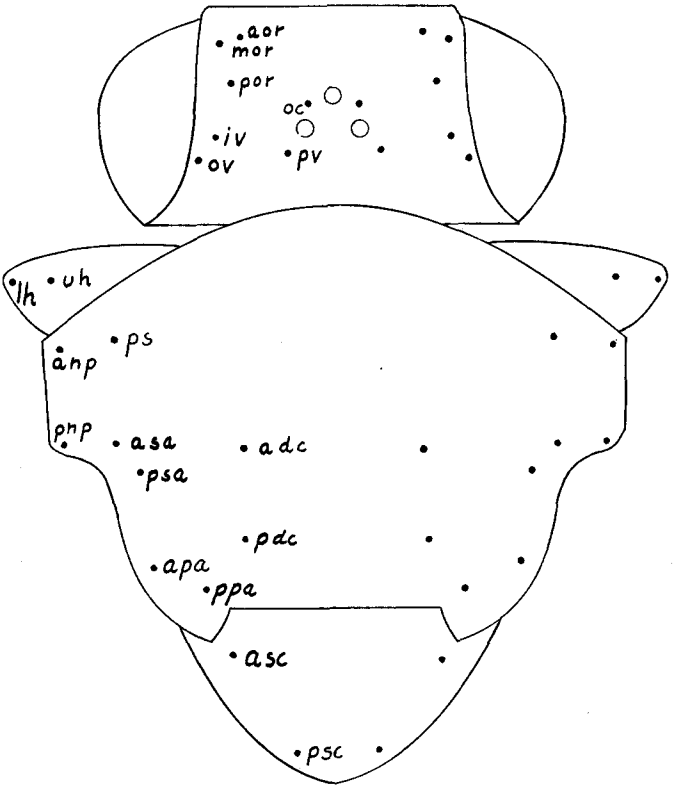

FIGURE 1.—(After PLUNKETT 1926) Location and names of bristles of *D. melanogaster* (wild-type): aor, mor, por, anterior, middle, and posterior orbitals; oc, ocellar; pv, postvertical; iv, ov-inner and outer verticals; u h, l h, upper and lower humerals; anp, pnp, anterior and posterior notopleurals; ps, presutural; asa, psa, anterior and posterior supra-alars; a pa, p pa, anterior and posterior postalars; adc, pdc, anterior and posterior dorsocentrals; a sc, p sc, anterior and posterior scutellars.

of the wild-type fly, and the abbreviations used throughout this paper. Scute-1 flies differ from wild in the absence of certain of the bristles in a certain proportion of the flies. The proportion of flies in which these bristles are missing is affected by genetic and environmental factors. The mean number (in a particular group of flies) of each bristle is susceptible to exact quantitative determination. These means have been determined under various definite environmental conditions in stocks homozygous for genetic modifiers, to obtain evidence on the effects of certain environmental and genetic modifying factors in conjunction with effect of the "main" genetic factor scute-1.

The present paper is concerned with the following questions:

1. Does scute affect the same bristle under different conditions, specifically at different temperatures?

2. Are all the bristles affected in the same way by modifying factors, specifically (a) genetic modifiers, (b) temperature?

3. Do the several bristles vary independently of each other, or are there definite associations between them?

ACKNOWLEDGMENTS

I wish to express my deepest gratitude to Dr. C. R. PLUNKETT for his aid and guidance and to my colleagues for their sympathetic help during the elaboration of this work.

EXPERIMENTAL

Materials and methods

Culture methods

The usual Drosophila culture methods were employed with additional precautions for insuring uniform conditions (PLUNKETT 1926). The food medium in each half pint milk bottle consisted of 30 gm water to 30 gm ripe banana with two percent of agar-agar to gel the mixture. The bananas were never boiled and the food never used until twenty-four hours after being made up. Where only fifty offspring were expected per bottle, two drops of a thick yeast suspension, (one cake to 100 cc water) were added after the gel had set. It was found during the course of the experiments that no effects of crowding were obtained when as many as 300 flies were raised in a bottle to which solid crumbled yeast was added from time to time as the larvae required it. The temperature was regulated in incubators held constant to within 0.1°.

Flies four to seven days old, raised under favorable conditions, were used for egg laying. Twenty pairs were used in each bottle for laying periods of one-half to three hours depending on the number of offspring desired.

Selection

Before starting the experiments the scute-1 flies were inbred for 22 generations (brother-sister matings) and selected for low bristle numbers in order to make them uniform for all genetic factors affecting bristle numbers.

Table 1 shows the parent-offspring and left-right correlation coefficients for the bristles counted.

TABLE 1

Correlation coefficients.

BRISTLE	TEMP.	r♀♀	r♂♂
A. PARENT-OFFSPRING			
aor+mor	28°	+0.12 ±0.070	−0.02 ±0.060
oc	28°	−0.13 ±0.070	−0.092±0.61
anp	28°	+0.06 ±0.073	−0.02 ±0.060
asc	15°	+0.10 ±0.13	+0.14 ±0.12
psc	15°	+0.19 ±0.12	
B. LEFT-RIGHT			
aor	28°	+0.05 ±0.037	−0.02 ±0.038
mor	28°	+0.04 ±0.036	+0.02 ±0.038
oc	28°	+0.09 ±0.036	+0.04 ±0.038
anp	28°	+0.02 ±0.036	−0.004±0.038
asc	15°	+0.02 ±0.041	+0.04 ±0.041
psc	15°	+0.002±0.041	+0.06 ±0.041
pv	15°	+0.04 ±0.041	−0.04 ±0.041
apa	15°	+0.18 ±0.079	+0.35 ±0.088
adc	28°	+0.22 ±0.069	+0.12 ±0.060
iv	14°		+0.54 ±0.11

The parent-offspring correlations are not statistically significant, and of themselves would indicate the success of the inbreeding in making the stock uniform for modifiers affecting the bristles being selected. The use of the left-right correlation coefficients as a measure of genetic and environmental uniformity has been described by PLUNKETT (1926). The frequency of occurrence of a bristle on either side of any fly depends upon the genetic factors present in the fly and the environmental factors acting upon it. In an isogenic stock raised in a uniform environment, the bristles should be distributed at random among the flies. If such is the case the frequency of flies with two, one and zero bristles should be p^2, $2p(1-p)$ and $(1-p)^2$ respectively, p being the mean number of any particular bristle per half fly (PLUNKETT 1926). In other words there should be no correlation between the two sides of a fly. The absence of any left-right correlation (table 1) for most of the bristles shows that this condition has been realized in this test. The stock is therefore suitable for quantitative phenogenetic studies. This also justifies using the "half fly" rather than the whole fly

as the unit. The statistically significant positive left-right correlations obtained for the adc, apa and iv bristles indicate that the stock has not been made fully isogenic for genetic modifiers of these bristles.

The result shows that some genetic modifiers, at least, do not affect all the bristles similarly. This will be discussed more fully later (p. 119).

The associations between bristles

To ascertain whether or not the several bristles affected by scute vary independently of each other, the degrees of association between the bristles on the same side, as measured by the association coefficients (YULE 1911) were determined. Let A indicate the frequency of presence, that is, number of half flies having the bristle, and a the frequency of absence of a particular bristle and let B and b indicate the frequency of presence and absence, respectively, of another particular bristle. The association between these bristles is measured by

$$\frac{(AB)\ (ab)-(Ab)\ (aB)}{(AB)\ (ab)+(Ab)\ (aB)}$$

where AB is the number of half flies having both bristles, ab the number having neither bristle, et cetera. There is complete positive association (association coefficient $=+1$) between the bristles when either

$$(AB)=A \ \therefore\ (Ab)=0 \text{ and } (ab)=b$$
$$\text{or } (ab)=a \ \therefore\ (aB)=0 \text{ and } (AB)=B.$$

There is complete negative association between the bristles (association coefficient $=-1$) when either

$$(AB)=0$$
$$\text{or } (ab)=0.$$

There is no association between the bristles (association coefficient $=0$) when

$$\frac{(AB)}{B}=\frac{(Ab)}{b}$$

and therefore

$$(AB)\ (ab)=(Ab)\ (aB).$$

The statistical significance of the association coefficient can be obtained by the following method. If there is no association

$$\frac{(AB)}{B}=\frac{(Ab)}{b}=\frac{A}{N}$$

where N is the total number of half flies in the population. The proportion

of A in the population is therefore the theoretical value that $\frac{(AB)}{B}$ and $\frac{(Ab)}{b}$ should each have if the bristles were unassociated. The standard error of the difference between $\frac{(AB)}{B}$ and $\frac{(Ab)}{b}$ is therefore

$$\sqrt{\frac{A}{N}\left(1-\frac{A}{N}\right)\left(\frac{1}{B}+\frac{1}{b}\right)}.$$

If there is an association between the bristles the difference between $\frac{(AB)}{B}$ and $\frac{(Ab)}{b}$ should be greater than twice its standard error.

In table 2 the association coefficients are listed, with the differences between $\frac{(AB)}{B}$ and $\frac{(Ab)}{b}$ and the standard errors of these differences.

TABLE 2

Associations between bristles.

TEMP.	BRISTLES	♀♀ ASSOC. COEF.	♀♀ $\frac{(AB)-(Ab)}{B \quad b}$ S.E.	♂♂ ASSOC. COEF.	♂♂ $\frac{(AB)-(Ab)}{B \quad b}$ S.E.
28°	aor–mor	−1.0	$\frac{0.195}{0.026}$	−1.0	$\frac{0.17}{0.024}$
28°	oc–anp	+0.047	$\frac{0.025}{0.025}$	−0.057	$\frac{0.011}{0.024}$
28°	mor–oc	+0.014	$\frac{0.013}{0.025}$	+0.053	$\frac{0.019}{0.035}$
28°	mor–anp	+0.049	$\frac{0.025}{0.045}$	+0.030	$\frac{0.005}{0.030}$
28°	anp–asc	+0.014	$\frac{0.004}{0.029}$	+0.040	$\frac{.011}{0.014}$
28°	mor–asc	−0.038	$\frac{0.008}{0.029}$	−0.12	$\frac{0.002}{0.030}$
28°	oc–asc	+0.057	$\frac{0.012}{0.029}$	−0.12	$\frac{0.005}{0.030}$
14°	apa–asc	−0.14	$\frac{0.07}{0.015}$	−0.19	$\frac{0.021}{0.047}$
14°	iv–mor			−0.33	$\frac{0.13}{0.15}$
15°	asc–psc	−0.25	$\frac{0.09}{0.057}$	+0.42	$\frac{0.024}{0.038}$

A clearly significant association is found only between the aor and mor bristles. This complete negative association suggests that these two bristles, which I had been considering as different, are possibly the same bristle shifted in position. The aor in the wild fly is much longer and closer to the median line than the mor, and directed anteriorly, whereas the mor is directed posteriorly. In the scute-1 flies the aor is small, seldom in the same position as in the wild-type and pointing in various directions in different flies. A comparable shifting of the pdc bristles in Dichaete has been observed by PLUNKETT (1926). In scute-3, which removes aor and mor bristles in definite proportions of the flies, these two bristles have been found on the same side and in the same relation to one another as in the wild-type. What I have called the "aor" in scute-1 may, then, in all probability be a shifted mor. Because of the difficulty in distinguishing between these two bristles, they were recorded jointly in many of the experiments.

The absence of association between any of the other bristles is evidence that they vary independently of each other. In a later section the absence of association will be discussed with reference to the concept of a pattern of bristle removal which has been postulated for scute by a number of investigators.

Effects of temperature

Effect on mean bristle numbers

Flies were reared at various temperatures from 14° to 31° for their total period of development, to determine the mean bristle numbers at each temperature. Most of the means are based on counts of at least 500 flies of each sex; more than 1,000 flies of each sex were measured at the control temperature, 28°. There is a pronounced difference between the males and females in bristle numbers, the former having a lower mean for all bristles at all temperatures. The sexes are therefore treated separately. These results are shown graphically in figures 2 to 6. The curves drawn through the points are merely to aid the eye in following the slopes; they are of no theoretical significance.

The effect of temperature is not the same on all the bristles of the scute-1 flies. With increasing temperature there is an increase in mean numbers of the aor, oc, anp, apa, iv, and por; a decrease in the psc, and adc; the asc, and pv reach maxima at 20.0° and 24.5° respectively; the mor and the sum of the aor and mor reach minima at 28.0°. The coxal-1 bristles, on the coxae of the first pair of legs, were never found at any temperature studied. The humeral and sternopleural bristles seemed to be affected by temperature but they were not counted extensively.

PAYNE (1920) reported that in his high selected "reduced" (undoubtedly from his description, some scute allele) there was a decrease in scutellar bristles with increasing temperature. If the present results on the scutellar bristles are extrapolated to the temperature at which PAYNE observed an

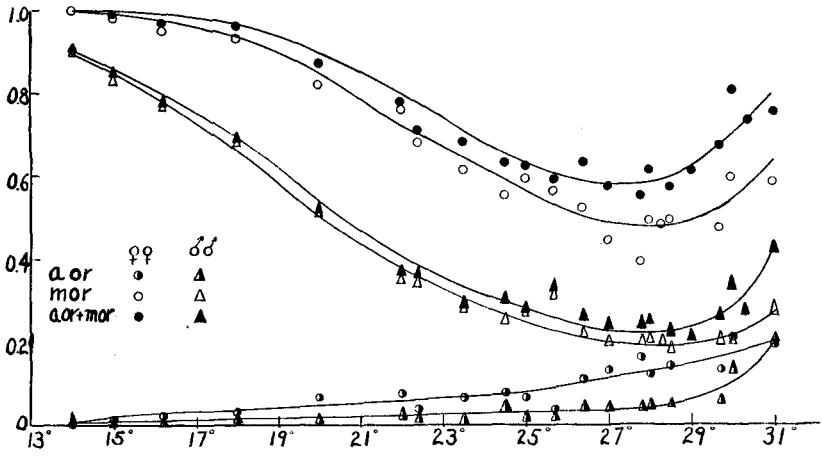

FIGURE 2.—Effect of temperature on mean bristle number of scute-1. Ordinates, mean bristle number per half fly; abscissae, temperature in °C.

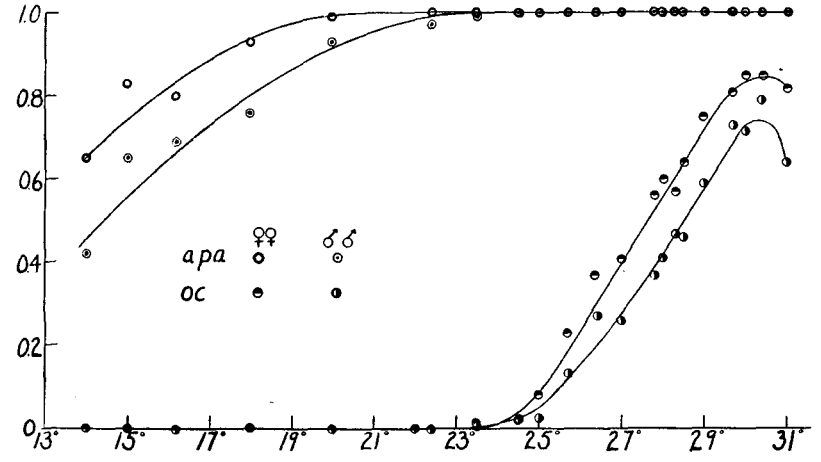

FIGURE 3.—Effect of temperature on mean bristle number of scute-1. Ordinates, mean bristle number per half fly; abscissae, temperature in °C.

increase in scutellar bristles (10°–13°), the sum of the asc and pac is greater than their sum at the higher temperature (23°–26°) studied by PAYNE. METZ (1920) in analyzing the effect of temperature on bent in *D. virilis* and *D. melanogaster* found that at low temperatures there was a decrease in the scutellar bristles of the former species but an increase in the latter.

PLUNKETT (1926) reported that in Dichaete there was a decrease in asc at high temperatures.

The effect on the adc bristles is the same as reported by PLUNKETT (1926), a decrease with increasing temperature. For these few bristles it appears

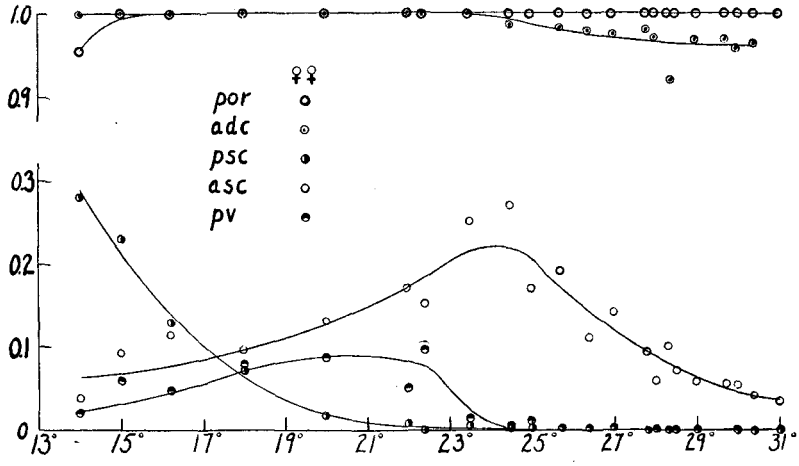

FIGURE 4.—Effect of temperature on mean bristle number of scute-1. Ordinates, mean bristle number per half fly; abscissae, temperature in °C.

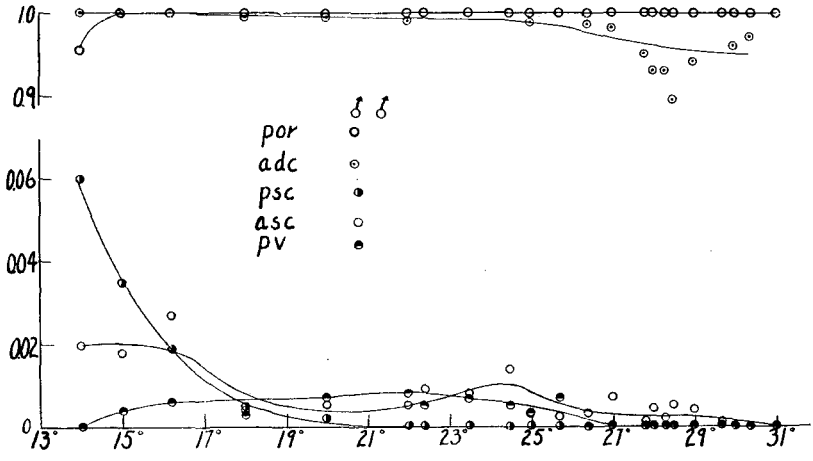

FIGURE 5.—Effect of temperature on mean bristle number of scute-1. Ordinates, mean bristle number per half fly; abscissae, temperature in °C.

that each particular bristle is affected in the same direction by temperature, even in different mutants. This is not considered necessarily significant since the data on other mutants are too few to make an extensive comparison.

The great changes in slope found, for example, in the oc (figure 3) and anp (figure 6) are not uncommon in temperature studies on Drosophila. HARNLY (1929) and STANLEY (1930) in their studies on wing length of vestigial flies reported that between 29° and 32° there was a great increase in wing length; at lower temperatures between 15° and 29° the increase in size of the wing is very slight. HERSH (1925), studying the effects of temperature on Bar heterozygotes, reported a marked change in facet number between 27° and 28°.

The effect of temperature on the bristles of scute-1 as shown by the data here presented is evidently quite complex, each bristle behaving differently from the others. No generalization as to this effect seems possi-

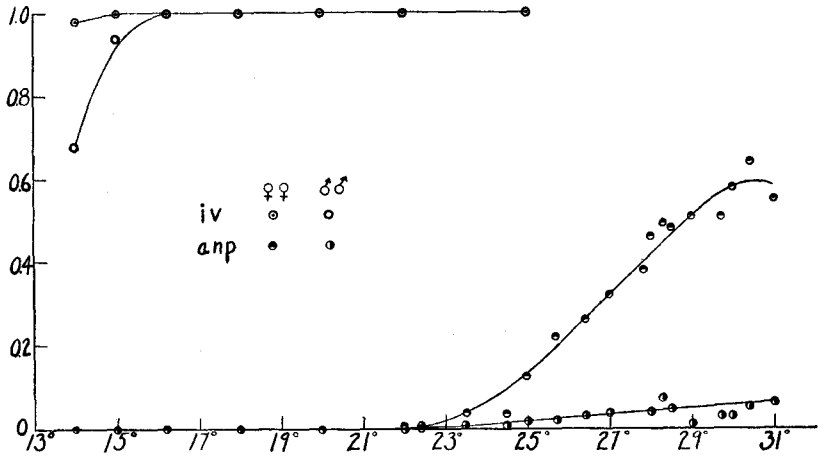

FIGURE 6.—Effect of temperature on mean bristle number of scute-1. Ordinates, mean bristle number per half fly; abscissae, temperature in °C.

ble except that every bristle which is at all variable is affected by temperature, at least in some part of the temperature range.

It is also obvious from these data that certain bristles (mor, oc, por, iv, apa, adc) are apparently not affected at all by the scute-1 gene (that is, do not differ phenotypically from the wild-type) at some temperatures, but are markedly affected at other temperatures.

DISCUSSION

The sub-gene hypothesis

These results may be used as a test of certain theories which have been advanced to explain the effect of scute on the bristles of *Drosophila melanogaster*.

In a series of papers DUBININ (1929, 1932), SEREBROVSKY (1930), LEWIT (1930), AGOL (1930, 1931) and their colleagues have described sixteen

other acute alleles, each differing from the others by removing certain definite bristles and not affecting other bristles. As a result of their careful studies they have elaborated an interpretation of the nature of the scute locus. According to their hypothesis the normal allele of the scute gene, the "basigene," is not a single unit but it is divided into a number of elementary units called "sub-genes" or centers, arranged in a linear order in the scute locus. Each center is concerned with the development of a certain one or few bristles of the fly. Each scute allele, according to their interpretation, represents a mutation in some one or more of these centers, and only one kind of mutation is possible in any one center.

The bristles of the fly have been arranged in a linear series which corresponds to the postulated linear order of the sub-genes. STURTEVANT and SCHULTZ (1931), in presenting evidence against the sub-gene hypothesis,

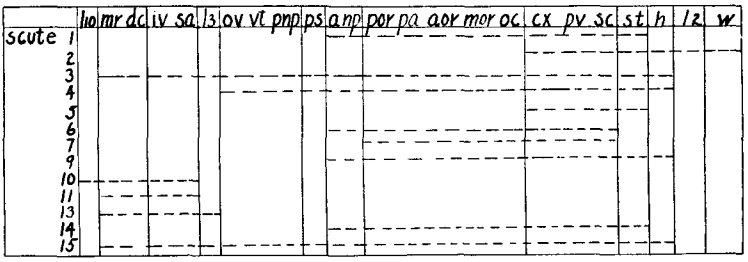

FIGURE 7.—(After DUBININ and FRIESEN 1931) The scute step-alleles 1_{10}, 1_3, 1_2=lethals associated with scutes-10, -3, and -2 respectively.
mr=microchaetes on the thorax
vt=ventral bristles between the first pairs of legs
cx=coxal bristles
w=crumpled wings
The other abbreviations are the same as those used previously (figure 1).

have constructed a slightly different seriation based on their own data. Using this series as a base line they have drawn a curve for each allele, plotting as ordinates the mean bristle number for each bristle. That most of the curves are smooth and unimodal is taken as evidence that the seriation is of some significance.

Figure 7 (DUBININ and FRIESEN 1932) illustrates the seriation as postulated by the proponents of the sub-gene hypothesis. As can be seen from this chart, scute-1 is interpreted as being a mutation involving four centers therefore affecting the bristles determined by these four.

In figure 8 the means of each bristle from my data have been plotted against this seriation of the bristles. The limits of the centers are shown by the black solid lines. At 22.0° which is probably approximately the temperature at which the Russian workers raised their flies, the

bristles affected in my experiments are the same as found by them with one exception, the por, which is affected at lower temperatures. At 14° the iv center affected by scutes-3, -10, -11, and -15 is affected by scute-1, and the mor, which according to their hypothesis is affected by scute-1, is not affected in the females. At higher temperatures there is a decrease in M adc and therefore the postulated dc center which they find affected by scutes-3, -10, -11, -13, and -15, is now being affected by scute-1; whereas the apa in one of the postulated affected centers is unaffected in both males and females. These facts show that bristles outside the centers postulated for scute-1 may be affected by merely changing the temperature, and that bristles in the mutated centers postulated for scute-1 may be unaffected at some tem-

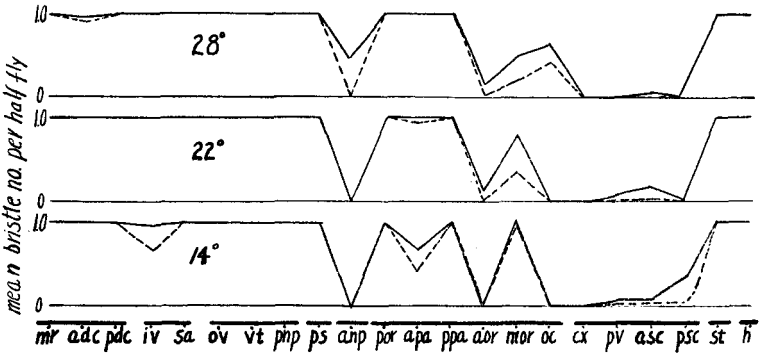

FIGURE 8.—Mean bristle numbers *vs.* seriation of DUBININ et al.
— = ♀ ♀ · · · = ♂ ♂ when differing from ♀ ♀.

peratures. A few preliminary experiments on other scute alleles show similar exceptions. These results seem to remove the essential basis of the sub-gene hypothesis.

STURTEVANT and SCHULTZ (1931), studying various scute alleles in the presence of duplicated fragments of the X chromosome, found that in these instances the effect of scute on the bristles is a function of the genetic system as a whole, including modifiers in other loci as well as the scute locus itself. Evidence bearing on the validity of their conclusion was obtained during the course of selection of the scute stock used in my experiments. It was found that it was possible to select for certain bristles without affecting others. In fact I found that after the stock was made isogenic for modifiers affecting the oc and mor bristles, the anp still showed significant positive left-right and parent-offspring correlations. The anp bristle was then selected for and the stock was made isogenic for modifiers affecting it without changing the means of the other bristles. There was no selection for the iv, adc, and apa and table 1 shows that the stock is

not uniform for factors modifying these characters. The conclusion reached by STURTEVANT and SCHULTZ, that the effect of scute on bristles is a function of the genetic system as a whole rather than merely the single scute locus, is supported by these results.

Experiments of another nature also support the validity of this conclusion. PLUNKETT (1926) found that two genes neither of which separately removes certain bristles may do so when combined. It appears therefore that the action of these genes is less specific than might at first appear. It seems as though each gene has a tendency to remove more bristles than it ordinarily does but the effect is not strong enough to remove the bristles

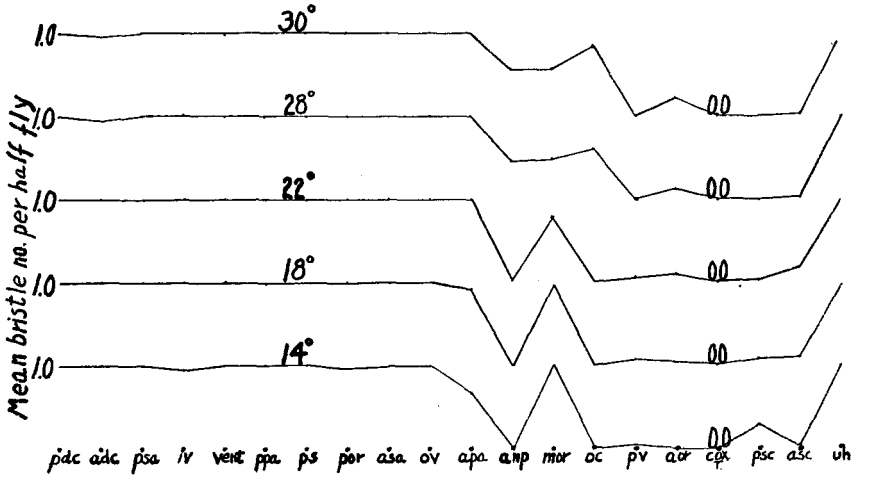

FIGURE 9.—Mean bristle numbers of scute-1 ♀ ♀ *vs.* seriation of STURTEVANT and SCHULTZ (1931).

unless intensified by the action of another bristle-reducing gene. STURTEVANT and SCHULTZ (1931), using this method of intensifying the action of one gene by another, showed that scute-1 in combination with Hairless removed many more bristles than either would when acting separately. One of the bristles removed was the iv which is not affected by scute-1 at ordinary temperatures but is affected at very low temperatures (figure 6).

These results of STURTEVANT and SCHULTZ and my own observations show quite clearly that the sub-gene hypothesis is inadequate in that it does not meet these experimental tests. Despite their conclusion with respect to the sub-gene hypothesis, STURTEVANT and SCHULTZ still thought that their seriation of the bristles was of some significance. They based their belief in the fact that they obtained smooth unimodal curves when the bristle numbers were plotted against this seriation. In figure 9 the means for each particular bristle have been plotted in this way (using the seriation of STURTEVANT and SCHULTZ) at several temperatures. It

can be seen from this figure that it would be necessary to change the seriation for almost every change in temperature in order to obtain smooth unimodal curves in all cases. These facts seem to raise a serious doubt that the seriation is of any significance.

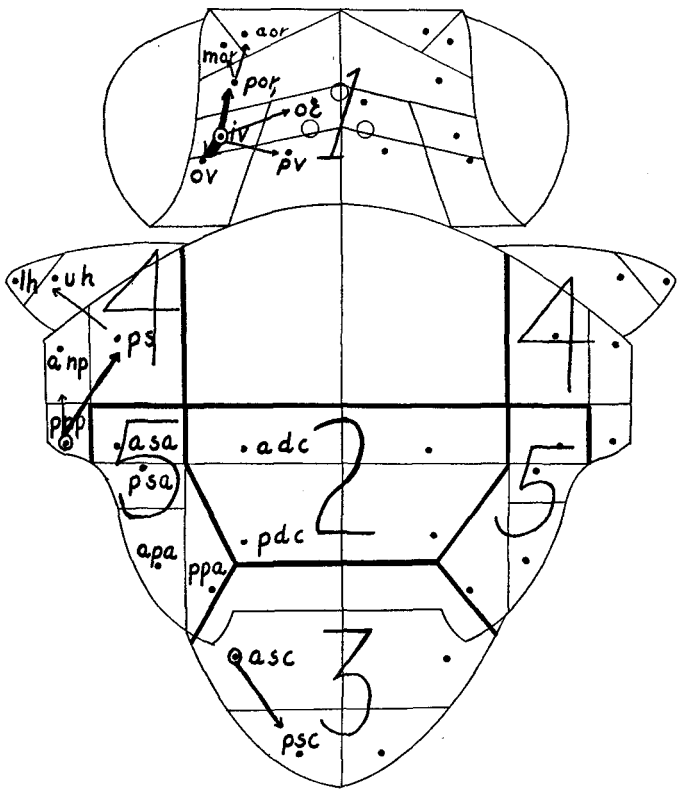

FIGURE 10.—(Modified from GOLDSCHMIDT 1931) The fields are delineated by the heavy lines. The arrows indicate the direction diffusion of the bristle-determining substance from the centers in these fields; the diffusion occurring first along the path of the heavier arrows before it takes place along the path of the lighter arrows.

The diffusion hypothesis

GOLDSCHMIDT (1931) has advanced an hypothesis to explain the behaviour of the scute series of alleles. The essential points of his theory are as follows:

1. There are present on the fly five fields within each of which a bristle-determining substance diffuses in definite patterns from centers in these fields (figure 10).

2. The period in development when the diffusion of this bristle-determining substance can be initiated differs for the different centers of the fly.

3. The diffusion from a center is initiated by the presence of a minimal

amount of a second substance. This minimal amount must be present at a time in development which falls within the part of the period during which the diffusion from that center can be initiated "Die Zeitspanne der Öffnung der Austrittstellen des Stroms" (GOLDSCHMIDT 1931, p. 530). If it is present before the diffusion can take place it will not remain to initiate the diffusion process at a later period.

4. The rate of formation of this initiating substance is determined by the scute allele or alleles present in the fly.

Figure 10 shows the location of these fields and centers as postulated by GOLDSCHMIDT. Following the suggestion by PLUNKETT (1926), STURTEVANT and SCHULTZ (1931) had also considered a diffusion hypothesis for scute. They thought that a single center in the median line near the pdc was sufficient to explain the pattern of bristle determination on the whole fly.

In describing the diffusion of bristle-forming substance on the head of the fly, GOLDSCHMIDT (1931, p. 513) states, "In der Kopfregion liegt diese Austrittstelle offenseitlich jederseits in der Region der vordern Verticalborsten," (the iv in figure 10). "Von hier dringt der Strom zuerst nach hintern zu den hintern Verticalborsten (ov in figure 10) und dann zu den dritten Orbitalborsten" (por in figure 10) . . . "Vom 3 Orbitalfeld aus geht der Strom nach vorn, und vom Verticalfeld nach der Mittelinie . . . ." This is shown by means of the arrows in figure 10 as explained by the legend. The bristle-determining substance is therefore postulated to be at its greatest concentration around the iv, from which center the other regions on the head receive their bristle-determining substance. As a logical deduction from this postulate it follows that if the M iv is low, the mean numbers of the other bristles on the head must be correspondingly reduced. At 14°, however, in the females the M iv = 0.96 and the M mor = 1, in the males the M iv = 0.68, and the M mor = 0.90. This seems to be a direct contradiction of the result to be expected if the iv were the center with the greatest concentration of bristle-determining substance from which the mor received this substance by diffusion. Another contradiction is found at low temperatures. The M psc being greater than the M asc, the asc being the location of the postulated center of the scutellar field. DUBININ and FRIESEN (1932) point out similar contradictions with respect to other scute alleles. From the fact that he does not locate the centers in the fields 2 and 5 (figure 10), it appears that GOLDSCHMIDT himself thought that this part of his theory was weak.

The data on scute-1 in the present paper show in another way the inapplicability of any diffusion hypothesis. If this process affected the distribution of bristle-forming substances, it should be expected that the bristles in a field would show some degree of association with each other.

Table 2 showed that there was no association between any of the bristles in scute-1 (except for the special case of the aor-mor which has been discussed previously).

These results indicate that in scute-1 the distribution of bristles on the fly is not governed by the diffusion of bristle-forming substances from a few centers, but that each bristle varies independently of the others. Each bristle has its own separate center, if we chose to express the facts in such terms, where processes go on that determine whether the bristle shall be present or absent. (This does not necessarily imply that the primary action of the scute gene itself is strictly localized for each bristle.)

This conclusion, which rejects the entire concept of pattern as applied to scute, may appear somewhat radical to those who have observed these flies. It is not difficult to see how the concept arose that in scute there is a certain pattern of bristle distribution. If the mean bristle numbers and not the individual flies are considered, the impression one obtains is that certain bristles are affected more than others, in a definite pattern. When the individuals are considered separately, however, it is seen that there is no consistent pattern. The distribution of bristles on one fly may differ in any way from that of another fly. This has been shown by the fact that there is no association between the bristles. When the flies raised at different temperatures are compared with each other the concept of a general pattern in scute becomes even more inapplicable. Flies raised at 14° show variations in some bristles which are constant at higher temperatures, and *vice versa*. These flies appear as different from each other as do two different scute alleles raised at the same temperature.

These data show that the concept of pattern of distribution in scute is based on nothing more than differences in the mean numbers, in a group of flies, of different bristles and does not correspond to any developmental processes in the individual fly.

These results are in striking contrast to those found by PLUNKETT (1926) in Dichaete flies. In Dichaete it was found that a diffusion hypothesis could be included as part of the developmental theory explaining the phenotypic effect of this mutant gene as compared with its wild-type allele. A definite pattern of bristle distribution was found with association coefficients of 1 between bristles very close to one another, adc–pdc, and lh–uh. The associations between pairs of bristles further away from one another than the examples cited were less than one, but still significantly greater than 0. This is quite logically explained by PLUNKETT (p. 234) as due to "diffusion from a center but with considerable random local variation in its course. Such irregularities in diffusion are by no means inconceivable when it is realized that we are dealing with a substance of probably high molecular weight, colloidal dimensions, and present in a

very small quantity, diffusing through the physically heterogeneous medium of a highly differentiated egg or a multicellular embryo."

Although quite unessential to this theory, GOLDSCHMIDT thought that the period during which the diffusion can be initiated is the same as the period during which temperature is effective in changing the phenotypic expression of the gene. The fact that in my experiments, as will be reported in a later communication, it is found that the effects of temperature on all bristles (with certain few exceptions) occur during the same time does not detract from the theory. It may very well be that temperature is effective in changing the bristle number by affecting some processes earlier in development, which process occurs at the same time for all bristles.

The present data on scute-1 have no bearing, one way or another, on the remaining postulates of GOLDSCHMIDT'S theory. These have been discussed by DUBININ and FRIESEN (1932), whose results seem to cast serious doubts on the validity of this entire theory.

The general "rate" theory of gene action

GOLDSCHMIDT (1927), from his work on intersexuality in Lepidoptera, and PLUNKETT (1926), from his analysis of Dichaete in *Drosophila melanogaster*, have elaborated the general theory that genes act by affecting the rates of developmental processes in the organism. The effects of temperature on the bristle number of the wild-type are very slight and found only near the extremes of the temperature range in which the flies will develop to maturity at all (these were not extensively studied, and are therefore not included in the data). The bristles of the scute fly, however, are markedly affected by temperature, every bristle which is at all variable being affected in at least some part of the temperature range.

The difference in effects of temperature, and also of other environmental factors, on the bristles of scute and those of the wild-type, is ascribed, on the basis of the general theory, to the differences in the effects of these environmental factors on the rates of developmental processes leading to bristle formation in scute and the wild-type. Thus in scute flies, either the rates of the processes or the periods during which these processes go on, or both, must differ at different temperatures to produce different bristle numbers. In view of the nature of the experimental material there is no means of determining the rate independently of the duration, whereas the duration of the processes differentially affected by temperature may be independently determined. The duration of these processes have been determined for scute-1 and a discussion of the bearing of these results on the general theory of GOLDSCHMIDT and PLUNKETT must await the presentation of these data in a subsequent paper.

SUMMARY

1. A scute-1 stock inbred and selected for 22 generations was made isogenic for genetic modifiers of the bristles selected but not for the other bristles.

2. With but one exception no association was found among the bristles on the same side of the fly.

3. The exception, aor-mor was found to have an association coefficient of -1, and the possibility is discussed that the bristle recorded as aor was the mor shifted in position.

4. The bristle numbers of the males were lower than those of the females under all conditions.

5. With an increase in temperature the mean numbers of some bristles increase, some decrease, some reach maxima, and others minima.

6. These results on scute-1 seem to remove the essential basis of the sub-gene hypothesis and to cast grave doubts on the significance of any seriation of bristles.

7. The concept of a pattern of bristle distribution, whether determined by diffusion or by any other mechanism, seems to be inapplicable to scute-1.

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