

STUDIES ON MODIFIER OF BAR. A MUTANT WHICH AFFECTS THE EXPRESSION OF THE BAR MUTATION OF *DROSOPHILA MELANOGASTER*

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INTRODUCTION

TEMPERATURE experiments on Bar (a semi-dominant sex-linked mutant in *Drosophila melanogaster*) have shown that the facet number of Bar varies inversely with temperature and that temperature is effective during only a limited period of the larval stage. A facet inhibiting reaction with a Q_{10} higher than that of the rest of the developmental processes was postulated to explain these data (see GOLDSCHMIDT 1938 and BEADLE 1939 for review and literature). The temperature effective period was considered to be the period during which the reduction in facet number by virtue of the facet inhibiting reaction occurred.

By a study of the growth curves of the eye discs of Bar, modified Bar (see below) and wild type and of the effect of different temperatures on the size of the eye discs, it has been found (STEINBERG 1941) that the temperature effective period is not primarily responsible for the reduction of facet number in Bar. On the basis of the data there presented, it was postulated that the range of facet number over which an eye is able to vary is determined at the time of origin of the cephalic complex (that is, in the egg stage) and that the exact facet number is not determined until pupation. It was pointed out that several extrinsic factors, temperature being one, are capable of affecting the final facet number in Bar. It was postulated that these factors are able to do this because a group of cells is labilely determined to form either facets or head chitin and that the factors affecting facet number simply shift the path of development of this labilely determined tissue.

The mutant to be reported in this paper (modifier of Bar, $m(B)$) has an effect on facet number only in the presence of some one of the Bar mutants. Inasmuch as the modifier was found to have no effect on either optic disc size or cell size, it was assumed that it has no effect on the number of cells which are labilely determined—that is, the number of labilely determined cells in Bar and modified Bar are assumed to be the same. The modifier is considered to be an intrinsic factor which affects the path of development of the labilely determined cells in such a way that more of them form facets than do so in its absence.

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Although the evidence presented in the previous paper (STEINBERG, 1941) strongly indicated that the modifier affected facet number by shifting the path of development of labilely determined cells, it by no means proved this, and experiments testing this point are therefore desirable.

This paper is a presentation of data concerning the mode of inheritance of $m(B)$ and the nature of its interaction with various mutants affecting eye size.

Modifier of Bar (STEINBERG 1937a, b; STEINBERG and ABRAMOWITZ 1938) was found during the course of some unpublished experiments in which Bar was used as a marker and crossing over was measured in the "all" complex of the second chromosome. The cross was XXY; "all" / + ♀ ♀ by B ; "all" / dp^2Cy ♂ ♂ ("all" = al (aristaless), dp (dumpy), b (black), pr (purple), c (curved), px (plexus), and sp (speck); Cy = Curly).

Crossing over was followed in the non- Cy "exceptional" offspring. Those males showing Bar were of course "exceptional," having their X chromosome from their fathers. The experiment was discontinued shortly after its inception because SCHULTZ (MORGAN, BRIDGES, and SCHULTZ 1935) at that time reported the results of a similar type of experiment and the data of the present author were simply confirming his. In three different cultures exceptional males with large Bar eyes appeared.

Culture No. 211 yielded only one exceptional male. It was phenotypically B ; $px sp$. It had exceptionally large Bar eyes.

Culture No. 215 yielded three exceptional males. One was B ; ++ and had the usual type of Bar eyes; another was B ; $px sp$, its eyes were similar to those of the male from culture No. 211; the third was B ; $al dp b px sp$ and it also had large eyes.

Culture No. 232 yielded one exceptional male; it was B ; $px sp$ and had large eyes.

Other exceptional males (with "normal" Bar eyes) were as follows:

Culture No.	Phenotype
205	B ; +
212	B ; $al dp b pr$
214	B ; sp
220	B ; +
224	B ; $al dp b$
	B ; $c px sp$
227	B ; $px sp$
228	B ; al
230	B ; b

From the nature of the cross, all the males must have had the "all" complex in one second chromosome. Only those males homozygous for

px and *sp* showed the large eye (see cultures 211, 215, 232); however, the presence of *px* and *sp* did not necessarily lead to a large eye, as evidenced by cultures No. 224 and 227.

It seems likely from these data that the "all" chromosome in some cases carried a modifier of Bar which is close to *px* and *sp*. Direct tests for the location of *m(B)* reported below confirm this.

The *B*; *px sp* males from cultures 211 and 215 were mated to Oregon-R (Or-R) wild type females. In the F₁, heterozygous Bar females were mated to sib males. From this mating *B*; *px sp* males and *B/+*; *px sp* females were selected and a stock started.

LINKAGE GROUP

To determine the linkage group to which *m(B)* belongs females homozygous for Bar, modifier of Bar, plexus and speck were crossed with *Cy/pm*; *H/In(3R)Mo*, *Sb sr* males (*Cy*=Curly wings, a mutant associated with inversions in both arms of chromosome II; *H*=Hairless, *In(3R)Mo*=inversion in 3R, *Sb*=stubble bristle, *sr*=stripe). F₁ *B*; *Cy*; *Sb* males were backcrossed to females like their mothers. To avoid facet counts, an arbitrary grading system was adopted in which the largest modified Bar eye was graded as 4 and "normal" Bar eye as 1.

Two such experiments were performed. In the first the F₁ flies were not graded for eye size. However, their eyes were observed to be small (like "normal" Bar). In the second experiment the F₁ males were classified as to eye size, *Cy*, *Pm*, *H*, and *Sb*. In both experiments the backcross male offspring were classified as to eye size, *Cy* and *Sb*. All males were, of course, genotypically *B*. Table 1 shows the results of these crosses, all of which were made at 25 ± 1°C. The eyes of F₁ males of all four classes appear to be somewhat larger than the "normal" Bar, having an average eye size rang-

TABLE 1

Summary of the data for the location of the linkage group to which *m(B)* belongs. See text for further explanation.

Cross: <i>B/B</i> ; <i>m(B) px sp/m(B) px sp</i> ♀ × +; <i>Cy/Pm</i> ; <i>H/C Mo Sb</i> ♂					
F ₁ ♂ phenotype	<i>B</i>				N
	<i>Cy</i> ; <i>H</i>	<i>Pm</i> ; <i>Sb</i>	<i>Cy</i> ; <i>Sb</i>	<i>Pm</i> ; <i>H</i>	
Average grade (Exp. 2)	1.9	1.5	2.0	1.4	80
Cross: F ₁ <i>B</i> ; <i>m(B) px sp/Cy</i> ; +/ <i>C Mo Sb</i> ♂ × <i>B/B</i> ; <i>m(B) px sp/m(B) px sp</i> ♀					
Phenotype	<i>B</i>				N
	<i>Cy</i> ; +	+; <i>Sb</i>	<i>Cy</i> ; <i>Sb</i>	+; +	
Average grade (Exp. 1)	1.5	4.0	1.9	3.7	34
(Exp. 2)	1.9	3.9	1.9	3.7	592

ing from 1.4 for *Pm*; *H* to 2.0 for *Cy*; *Sb*. There can be no doubt, however, that they are smaller than modified Bar. The modifier therefore is not dominant, although it may be semidominant. The backcross data for both experiments clearly show that the modifier is located in the second chromosome, since in the absence of *Cy* (that is, when both second chromosomes are derived from the modified Bar stock) the average eye size ranges from 3.7 to 4.0, in good agreement with the eye size of the modified Bar stock. In the presence of *Cy*, however, the average eye size varies from 1.5 to 1.9, well within the range of the F_1 .

Since both plexus and speck are in the second chromosome and are present in the modified Bar stock, the question arises as to whether either or both of these are the cause of the increased facet number shown by modified Bar. To test this possibility, modified Bar, plexus, speck females (B/B ; $m(B)$ *px sp*/ $m(B)$ *px sp*) were crossed to Curly/plexus, brown, morula, speck males (Cy/px *bw mr sp*). The F_1 males were all *B* and either *Cy* or *px sp* (phenotypically). Twenty-five of each type were graded with regard to eye size. The *Cy* males had an average grade of 1.5; the *px sp* males 1.7. These values compare favorably with those found for the F_1 males and the *Cy* males of the backcross reported in table 1. Therefore *px* and *sp* are not the cause of the increased facet number, and hence their presence may be ignored in the experiments to be reported below.

Unpublished data of MR. CHARLES HENDLEY indicate that $m(B)$ is located between 6 and 7 units to the left of *px*.

FACET COUNTS OF BAR AND MODIFIED BAR AT 25° AND 29°C

The Bar stock used in the following experiments had been rendered isogenic with an inbred Florida wild type stock and then maintained for more than 100 generations by brother sister matings before these experiments were begun. This stock was the source of the Bar mutant in the B/B ; $m(B)$ *px sp*/ $m(B)$ *px sp* stock. The latter stock had been inbred for about ten generations before the facet counts were made. No attempt was made to render it isogenic with the Bar stock. Facet counts were made of Bar and modified Bar at $25 \pm 1^\circ\text{C}$ and $29.2 \pm 0.1^\circ\text{C}$. Eggs were collected from six to ten females in large shell vials over a 24 hour period at $25 \pm 1^\circ\text{C}$. The females were then removed and the vials transferred to the desired temperature, where they were left for the remainder of the experiment. The food consisted of the standard cornmeal-agar-molasses medium to which 1.5 percent of dried brewers yeast had been added. Facet counts were made by dissecting off the cornea of the eye, mounting it on a slide in a drop of water, and then projecting the image. The data are presented in tables 2, 3, and 4.

The facet counts confirm the earlier observations that the modifier has

TABLE 2

Facet numbers of Bar and modified Bar males and females at 25 ± 1°C.

GENOTYPE	MEAN ± σ_M	RANGE	V ± σ_v	N
		Males		
<i>B</i>	74.2 ± 2.7	41-129	25.1 ± 2.78	46
<i>B; m(B) px sp</i>	220.9 ± 4.8	143-315	15.2 ± 1.55	50
		Females		
<i>B</i>	75.2 ± 2.5	44-104	23.1 ± 2.43	50
<i>B; m(B) px sp</i>	141.1 ± 2.3	115-211	11.7 ± 1.19	50

TABLE 3

Facet numbers of Bar and modified Bar males and females at 29.2 ± 0.1°C.

GENOTYPE	MEAN ± σ_M	RANGE	V ± σ_v	N
		Males		
<i>B</i>	38.0 ± 0.8	33-50	10.0 ± 1.43	25
<i>B; m(B) px sp</i>	169.7 ± 4.6	117-234	19.2 ± 1.99	50
		Females		
<i>B</i>	35.7 ± 0.6	30-44	9.5 ± 1.15	34
<i>B; m(B) px sp</i>	114.5 ± 2.4	82-174	14.6 ± 1.49	50

TABLE 4

*Facet numbers of Bar males and females heterozygous for the modifier.
Temperature = 29.2 ± 0.1°C.*

GENOTYPE	MEAN ± σ_M	RANGE	V ± σ_v	N
		Males		
<i>B; m(B) px sp/+</i>	75.0 ± 0.8	62-87	7.9 ± 0.79	50
		Females		
<i>B/B; m(B) px sp/+</i>	56.7 ± 0.8	42-68	9.5 ± 0.95	50

a marked effect on Bar males and a much slighter effect on Bar females. In both sexes, however, the increase over "normal" Bar is considerable and significant. Furthermore, there is no overlap at either 25 or 29°C (tables 2, 3).

At neither temperature is there a certainly significant difference between the facet number of "normal" Bar males and females. (D/σ_D at 25°C = 0.27; D/σ_D at 29°C = 2.3.)

The situation, however, is quite different in the case of the modified Bar males and females. At 25°C modified Bar males have 79.8 more facets

than the females ($D/\sigma_D = 15.1$), while at 29°C the modified Bar males have 55.2 more facets than the females ($D/\sigma_D = 10.8$).

Comparison of the facet number of the Bar males at 25° and 29°C and of the Bar females at the same two temperatures shows that at the higher temperature as compared with the lower there has been a reduction of approximately 50 percent in facet number in both sexes. This is in agreement with the observations of earlier workers. However, when a similar comparison is made for the modified bar males and females, it is found that the reduction in the case of the former is 23 percent and in that of the latter 19 percent. These values, while not significantly different from each other ($D/\sigma_D = 1.16$), are each different from those for Bar (D/σ_D for males = $6+$ and for female = $9+$). Thus, while in both Bar and modified Bar an increase in temperature leads to a decrease in facet number, a change in temperature from 25° to 29° has only about half as great an effect on modified Bar as on Bar.

The facet counts on Bar males and females heterozygous for the modifier establish that the modifier is a semi-dominant (table 4). Its effect in the heterozygous state is slightly less than one third of that in the homozygous condition (at 29°C); here again the effect is greater in the males. It is worth noting that the degree of dominance is the same in both sexes; 28.1 percent in the males and 26.6 percent in the females ($D/\sigma_D = 0.8$). (The percentage dominance was determined by dividing the increase of facet number caused by the modifier in the heterozygous state by that caused by it when homozygous and multiplying by 100.)

THE EFFECT OF THE MODIFIER ON THE BAR "ALLELES," EYELESS² AND WILD TYPE

The effect of $m(B)$ on the Bar "alleles" (double Bar (BB), infra-Bar (B^i), and double infra-Bar (B^iB^i)), eyeless² (ey^2), and wild-type was determined from facet counts in stocks rendered homozygous for the modifier and the mutant in question (px and sp were also present, but in view of the data presented above, they may be ignored).

These counts were made somewhat later than those on Bar, and the method of egg collection was modified. In these experiments 40 newly hatched larvae were placed in a $1'' \times 4''$ vial where they completed their development. The food was the same as in the Bar experiment. None of the stocks was isogenic. The temperature for all counts was $25 \pm 1^\circ\text{C}$. In all but one case the stocks with and without $m(B)$ were reared simultaneously. The sole exception was the second run of the $fB^iB^im(B)$ for which no special controls were counted. The data are presented in table 5.

With regard to the presence or absence of an effect of the modifier on facet number in BB ; B^i ; B^iB^i , and ey^2 , the data are clear. The modifier

increases the mean facet number expressed by each of the alleles of Bar and has no effect on the mean of eyeless². In the case of wild type—that is, absence of any mutant other than $m(B)$ which affects facet number—there is an effect when the Florida (+fla) stock is used as control and none at all when Oregon-R is used. (Both these wild type stocks were inbred.)

TABLE 5

Facet numbers in the B "alleles," ey^2 and + with and without $m(B)$. Temperature = $25 \pm 1^\circ C$.

GENOTYPE	♀ ♀				♂ ♂			
	$M \pm \sigma_M$	$V \pm \sigma_V$	RANGE	N	$M \pm \sigma_M$	$V \pm \sigma_V$	RANGE	N
<i>BB</i>	27.2 ± 0.70	15.8 ± 1.86	18-34	37	28.9 ± 0.8	15.6 ± 1.97	17-36	33
<i>BB; m(B)</i>	40.5 ± 1.05	16.0 ± 1.86	33-62	38	46.8 ± 0.9	11.9 ± 1.40	37-62	37
<i>fBⁱBⁱ</i>	65.4 ± 1.5	16.4 ± 1.64	48-99	53	66.8 ± 2.3	14.8 ± 1.65	50-98	42
(a) <i>fBⁱBⁱ; m(B)</i>	166.1 ± 9.0	34.3 ± 4.26	81-344	40	140.6 ± 6.2	29.1 ± 3.39	80-263	43
(b) <i>fBⁱBⁱ; m(B)</i>	143.4 ± 5.9	29.5 ± 3.13	80-283	52	131.4 ± 3.7	21.0 ± 2.05	84-204	57
Average of a and b	153.3 ± 5.1	32.2 ± 2.61	80-344	92	135.4 ± 3.4	25.1 ± 1.88	80-263	100
<i>fBⁱ</i>	342.1 ± 14.5	21.6 ± 3.13	223-530	26	345.3 ± 8.6	12.7 ± 1.79	226-460	26
<i>fBⁱ; m(B)</i>	679.6 ± 9.1	9.3 ± 0.95	529-850	48	691.4 ± 7.3	6.7 ± 0.74	558-821	41
+ <i>Fla</i>	746.4 ± 3.6	2.5 ± 0.34	717-798	27	680.6 ± 2.7	2.0 ± 0.28	658-707	25
+ <i>Or-R</i>	833.4 ± 5.0	3.0 ± 0.42	767-872	25	765.2 ± 4.2	2.7 ± 0.38	703-790	25
+; <i>m(B)</i>	826.0 ± 4.6	3.2 ± 0.39	729-882	34	766.1 ± 3.1	2.3 ± 0.29	734-801	31
<i>ey²</i>	377.4 ± 12.3	20.8 ± 2.46	199-519	41	363.6 ± 10.7	19.7 ± 2.16	186-486	45
<i>m(B); ey²</i>	347.3 ± 22.5	39.5 ± 5.33	146-619	36	380.8 ± 23.0	38.0 ± 4.82	103-616	40

In view of the fact that the original modified Bar males were crossed to Or-R females and in view of the fact that the +; $m(B)$ $px\ sp$ stock was derived by crosses with Or-R, it seems to the author that the comparison with Or-R is the more valid one, and therefore it is concluded that $m(B)$ has no effect on mean facet number in the absence of some one of the Bar "alleles."

DISCUSSION

So far as the present author is aware, there is only one other major modifier of Bar known, namely minusbar reported by NORDENSKIÖLD (1934). It, however, is located in the third chromosome and appears to have a similar effect on males and females and therefore cannot be the same as the one reported in this paper.

Modifier of Bar ($m(B)$) is probably a point mutation for the following reasons: (1) It has little or no effect on viability or fertility when homozygous and is viable when opposite a deficiency for its locus (unpublished data of P. N. BRIDGES); therefore it is probably not a deficiency. (2) Although it is close to px , it has no effect on recombination between px and sp ; thus it is not likely to be an inversion. (3) It does not affect random

assortment between the X, II and III chromosomes (see table 1); therefore, if it were a translocation, it could be only a II-IV translocation. This, however, is unlikely because of its viability and fertility when homozygous and because of (2) above. The possibility of its being a short duplication such as Hairy wing or Bar is of course not eliminated.

EFFECT OF $m(B)$ ON FACET NUMBER IN BAR AND DOUBLE BAR

There is at present no satisfactory explanation of the vastly greater effect of the modifier in Bar males than in Bar females (tables 2, 3, 5, 6). It may be pointed out, however, that a nitrogenous extract of *Calliphora*

TABLE 6
Ratios of facet numbers of the Bar "alleles" with and without the modifier.
Temperature = $25 \pm 1^\circ\text{C}$.

GENOTYPE	♀ ♀ RATIO $\pm \sigma_R$	♂ ♂ RATIO $\pm \sigma_R$
$B; m(B)$ $B; +$	1.88 ± 0.069	2.98 ± 0.125
$BB; m(B)$ $BB; +$	1.49 ± 0.055	1.62 ± 0.055
$fB^iB^i; m(B)$ $fB^iB^i; +$	2.34 ± 0.093	2.03 ± 0.085
$fB^i; m(B)$ $fB^i; +$	1.99 ± 0.087	2.00 ± 0.054

larvae which when fed to Bar larvae causes an increase in facet number also has a greater effect on males than on females (EPHRUSSI, KHOUVINE, and CHEVAIS 1938; CHEVAIS and STEINBERG 1938) as does also pure oxygen atmosphere (MARGOILIS 1939).

† The data of tables 2 and 3 indicate that temperature has much less effect on the facet number of modified Bar than on that of "normal" Bar. If, as postulated above, facet number within a given genotype is shifted by changing the path of development of a group of labilely determined cells, both the modifier and temperature are acting on the same cell-group and in opposite directions. It is to be expected therefore that some compromise would be reached—that is, an intermediate number of facets would result.

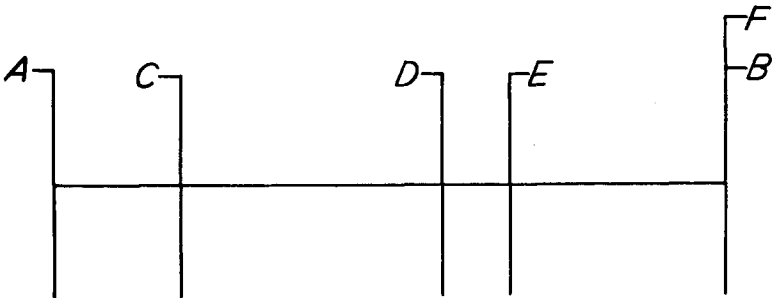
With regard to double-Bar it seems necessary merely to indicate that the effect of the modifier is not so great on it as on Bar (tables 2, 5, 6) and that there does not appear to be any difference between the effect of the modifier on the two sexes (table 6). (Facet number counts were made at only one temperature. But it has been shown by other workers that double Bar responds to temperature in the same manner that Bar does, and therefore

it may be predicted that the response of modified double Bar to temperature will be similar to that of Bar—that is, an intermediate number of facets.)

EFFECT OF $m(B)$ ON FACET NUMBER IN INFRA-BAR
AND DOUBLE INFRA-BAR

The data of table 5 show that in the presence of $m(B)$ the facet number of infra-Bar flies is increased (to the same extent in both sexes, compare table 6) and that the coefficient of variation is significantly reduced.

If the postulate that the changes in facet number expressed by a given mutant are the result of shifts in the path of development of labilely determined cells is correct it follows that the range of variation of which the phenotype is capable is fixed by the number of such labilely determined cells present in the eye disc. Naturally there must be both a lower and an upper limit to the potential range of variation. At 25°C in the absence of the modifier a portion of the potential range of the infra-Bar eye is realized (226 to 460, compare table 5). In the presence of the modifier another portion of the potential range is realized (558 to 821, table 5). The decreased variability exhibited by infra-Bar in the presence of the modifier may be explained by assuming that the range of variation is shifted so as to include the maximum facet number of which the eye is capable and that therefore the upper portion of its range is cut off. This may be illustrated by the following diagram. The limits of the line AB represent the complete range



of facet number which a given genotype may express (in the present discussion infra-Bar). The interval CD represents the range realized at 25°C in the absence of the modifier (compare B^i , table 5). The interval EF (F coincides with or is very close to B) represents the range realized at 25°C in the presence of the modifier (compare $B^i; m(B)$, table 5).

Facet number in both infra-Bar and double infra-Bar increases with an increase in temperature. Hence unlike the situation in Bar and double-Bar, an increase in temperature acts in the same direction as does the modifier. No facet counts were made at temperatures other than 25°C, but it is

possible to predict from the data at hand what would be the combined effect of increased temperature and the modifier. Consider infra-Bar first. (Since the situation is the same in both sexes, only the males will be discussed.) In the absence of the modifier the mean facet number was 345.3 the coefficient of variation was 12.7 ± 1.79 , and the range of facet number extended from 226 to 460; in the presence of the modifier the mean facet number was increased to 691.4, the coefficient of variation was reduced to 6.7 ± 0.74 , and the range changed to 558-821 (see table 5). The reduction in the coefficient of variation is significant ($D = 6.0 \pm 1.9$). (The modifier does not characteristically tend to lower the coefficient of variation but has different effects in different cases (see table 5); this will be discussed more extensively below.) Obviously a facet number greater than that at B (see diagram) cannot be realized in the case of infra-Bar (or any other mutant, since B by definition is the upper limit of variation of facet number). This upper limit has already been realized in modified infra-Bar but not in infra-Bar at 25°C. Therefore an increase in temperature would be expected to have less effect on facet number in the presence of the modifier than in its absence. However, other things being equal, it would be expected to decrease the coefficient of variation in the presence of the modifier.

In the case of double infra-Bar the presence of the modifier increases rather than decreases the coefficient of variation (table 5). It would appear therefore that an increase in temperature should cause a relatively greater increase in modified double infra-Bar than in modified infra-Bar, since in the former the upper limit of the potential range of facet number which the double-infra-Bar eye may have has not been realized. In other words, it seems likely on the above hypothesis that a B^iB^i female having more than 344 facets (table 5) may be derived.

It is of interest to consider the data on Bar derived at the two different temperatures in the light of the above discussion. At 25°C the modifier causes a significant decrease in the coefficient of variation (table 2), although both stocks are inbred (but not isogenic with each other) and both were raised under identical conditions. It would appear therefore that the upper limit of facet number which the Bar genotype may express is approximately 315 in the males and 211 in the females (table 2). At 29°C the presence of the modifier increases the coefficient of variation relative to that of unmodified Bar at the same temperature. The decrease in the coefficient of variation in Bar at 29°C as compared with that at 25°C is due largely if not entirely to the much more accurate control of temperature at the higher level though possibly also because the lower limit of facet number in Bar has been reached. But note that despite the more accurate temperature control at 29°C the coefficient of variation of modified Bar has increased relative to that at 25°C. Consequently the change in relationship

between the values of the coefficients of variation of Bar and modified Bar at the two temperatures cannot be accredited to the great reduction in the variability of unmodified Bar at 29°C as compared with 25°C. The increased variability of modified Bar at 29°C may be explained (1) by the fact that its entire range of variation at this temperature (117-234, compare males in table 3) falls well within the potential range of Bar, which must extend at least from 33 to 315 for the males, and (2) by the interaction of the antagonistic effects of temperature and $m(B)$.

As stated above, the modifier does not affect the mean facet number of either wild type or ey^2 . It is perhaps worth noting that in wild type the upper limit of the range is increased in both sexes (table 5). The change is minute, but in view of the low range of variation of wild type even under extremes of temperature (MARGOLIS and ROBERTSON 1937 report average values for wild type of 770.4 at 18°C and 694.6 at 28°C for males and 847.6 at 18°C and 749.0 at 28°C for females), it is perhaps significant. In $eyeless^2$ not only is the upper limit of the range of variation greatly raised (table 5) but also the coefficient of variation. In view of these considerations, the statement that the modifier affects facet number only in the presence of the Bar "alleles" should perhaps be qualified to read "mean facet" number, for it seems very likely that it does affect the development of the eye in wild type and $eyeless^2$ although not in such a way as to modify the mean facet number.

SUMMARY

It was found that modifier of Bar ($m(B)$) is a semi-dominant mutant located in the second chromosome about seven crossover units to the left of plexus.

Evidence is offered which indicates that $m(B)$ is a point mutation.

Facet counts of Bar, double-Bar, infra-Bar, double-infra-Bar, $eyeless^2$ and wild-type with and without the modifier were made. The data indicate that $m(B)$ increases the mean facet number of each of the Bar "alleles" but does not affect that of $eyeless^2$ or wild type.

The data are discussed in the light of a hypothesis on the mode of development of the eye. The hypothesis appears to be consistent with the data.

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