THE EFFECT OF TEMPERATURE UPON FACET NUMBER IN THE BAR-EYED MUTANT OF DROSOPHILA

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CONTENTS.

I. INTRODUCTION.

Environment plays an important indirect role in the development of every organism. In a few cases it becomes a determinative agent, in that particular structures are developed only under special external stimuli.

The bar-eyed mutant of Drosophila melanogaster (ampelophila) shows such a response to temperature. Primarily this germinal factor produces a reduction in the number of facets in the compound eye. Under a constant environment it produces practically a constant effect. Under varied temperature conditions, the amount of reduction varies inversely with the temperature.

The present study is an attempt to work out these relationships in detail. From the standpoint of the modern physiologist, the results are of particular interest in demonstrating in the same living material, a physiological reaction whose rate is an exponential function of the temperature, while another reaction has a rate which is clearly a linear function of the temperature.

From the standpoint of experimental embryology in its broadest sense, the present study gives an evaluation of some of the external and internal factors involved in the development of a particular structure, the compound eye. Furthermore, the particular stage in development at which the facet determining reaction is initiated, has been ascertained by the use of the temperature differences.

II. MATERIALS AND METHODS.

The bar-eyed mutant of Drosophila was first described by Tice, 1914. Considerable variation was noticed in this character. Zeleny and Mattoon, 1915, and H.G. May, 1917 have shown that part of this variation was due to germinal differences. It was noted, however, that environmental factors were responsible for the greater part of the variation.

A preliminary analysis of temperature effect on facet number was made by E.W. Seyster in this laboratory in 1916.

The present investigation was developed under the direction of Dr. Charles Zeleny. The study was made possible through the excellent equipment for environmental control installed at the Vivarium.

The white bar-eyed mutant of Drosophila was used. Ordinary cultural procedure was followed, except that the banana was sterilized by bringing to the boiling point. After cooling, the banana was inoculated with a pinch of Fleischmann's compressed yeast. Four and eight ounce wide mouth bottles were used. After being fitted with one fourth of a sheet of Scott's Tissue Toweling and a tight cotton stopper, they were subjected to 120° - 150° C in a Sargent's dry air electric oven.

All matings were mass matings. Unselected stock refers to stock #127, in which Dr. Zeleny started selection in 1917. Selected Low F4 is a stock derived from culture #150.3 of the fourth generation of these selections. Ultra-bar is a stock derived from a 19 facet male mutant in the F_2 low generation of

these same selections. These parent stocks were maintained at 27°. The low facet stocks were used more extensively because of the greater ease in counting, and also to eliminate the germinal difference. (See Zeleny's papers on selection and stability of these stocks.)

Temperature Control.

A constant temperature of 15° was maintained in the "cool room" in room 103 A Vivarium Building. The Johnson Heat Regulation System controls the temperature by forcing air over brine coils and redistributing it to the room.

A constant temperature of 23° was maintained in a similar manner in the "warm room."

A battery of aquaria, fitted with Johnson regulators, controlling the flow of hot and cold water, supplied the following temperature:- 16°, 17½°, 20°, 25°, 30°.

Twenty seven degrees was maintained in a Chicago Surgical and Electrical Co. #2 incubator of the type ordinarily used by bacteriologists. At first, very marked differences in temperature were found in various parts of this incubator. (1½° - 3°C). A General Electric nine inch desk fan was installed in the top of the incubator, with the blades inside and motor outside. This fan was run at "high" speed and no further temperature differences were noticed.

Temperature Records.

Temperature records were kept at 27° by a Tycos Recording Thermometer. At 15° and 23°, New Tycos Thermographs were

used. In the aquaria, Friez Soil and Water Thermographs kept the records. Humidity in experiment 60 was controlled by the Johnson system and recorded by Friez Hygrometers.

The experimental material was kept as close to the effective elements of these instruments as was possible. Checks were frequently made on the instruments by standardized thermometers.

The temperature of the banana in which the larvae were developing was tested by inserting a thermometer through the cotton plug into the food. Only very slight differences were found between the food and the surrounding medium.

The temperatures as given in the experimental data vary at most ± 0.5C.°

At the high temperatures, 29° and 31°, additional checks were made on rate of metamorphosis and facet number by using a water thermostat borrowed from Dr. G. Dietrichson. This instrument is of the type used by physical chemists. It is a battery jar supplied with a V-tube mercury regulator closing a secondary heating system by relay. A three inch, motor-driven fan keeps the water stirred up. Variations in temperature do not exceed ± 0.05C°.

Technique.

Counts of the facets were made by methods described by H.G. May, 1917. The flies were etherized and were placed one at a time on a wooden counting block. The upper surface of this block was cut to a slight incline in order to bring the com-

pound eye into the best position for focusing. The facets were counted under a #4 ocular and #3 Leitz objective with direct illumination from a 60 watt tungsten lamp. Adjustments were made with the fine thumbscrew to accomodate the curvature of the head. Facet number was recorded immediately after each individual count. The material was then preserved in alcohol.

Sources of Error.

Errors due to technique have been discussed at length by H.G. May. The chief sources are (1) errors in counting and (2) differences in counts between the right and left eyes. The latter factor is not significant in this study. Counts were made on one eye only but no preference was given either eye in making the counts. The first factor was reduced to a minimum by using the low facet stocks. Ultra-bar at 15° has a mean of only 60.81 facet for the males. In such a stock all the facets are readily counted as no confusion of rows arises. (Figure 15)

There is no direct correlation between the size of the fly and the number of facets. Exceptionally large individuals are produced under the best cultural conditions at 31° and yet show the extreme low facet number of that temperature. The flies are all of practically the same size at all temperatures. Figure 15 shows two females, raised at 27° and at 15° respectively, drawn to exactly the same scale.

Slight variation in the means of individual bottles and between separate experiments may be attributed to slight dif-

ferences in food, acidity, random sampling and other factors.

Some of the variation in the unselected stock may be due to germinal differences in the parents. The Ultra bar and Low Selected bar stocks are practically homogeneous.

The precaution of keeping the parent stocks at a constant temperature was unnecessary as shown by the experiments on the non-inheritance of temperature effects.

Bearing these points in mind we may conclude that temperature is the chief factor involved in the differences obtained in mean facet number in the present studies.

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III. EXPERIMENTAL DATA.

FIRST PART. TEMPERATURE EFFECT ON THE MEAN FACET NUMBER.

1. Temperature Effect on Unselected Bar Stock.

In 1916 E.W. Seyster carried out some experiments on the bar-eyed mutant of Drosophila showing that facet number varies inversely with the temperature.

The preliminary experiments on Unselected bar stock of the present studies confirm these results. The mean facet values for four separate experiments are given in tables 1 and 2. The temperatures used were 15°, 20°, 25° and 30°C. In any one experiment the conditions were as nearly alike as possible, excepting the temperatures. Data on the labels record the parentage, date of mating, food culture number, temperature, date of removal of parents, date of pupation and date of first emergence of imago. While there is some variation in the mean for the same temperature in different experiments, the data for single experiments, and for the average of all experiments show a very decided decrease in facet number with increase in temperature.

A summary of the first four preliminary experiments is given in tables 3 and 4. They include the number of individuals; the mean facet numbers; difference in facet number in the mean per C°. The difference in facet number per C° is found by dividing the difference between the mean values for two observed temperatures by the number of degrees within the interval. The per cent change per C° is found by dividing the difference in facet number per C° by the average of the two means for the ob-

served temperature.

A consistent sexual difference exists in all these experiments which makes the combination of the counts for males and females impossible. They are therefore represented in separate tables. It was found impractical to combine the two into a single table as the sex coefficient is not constant throughout.

The results of these first experiments are shown graphically in figure 1.

2. Temperature Effect on Low Selected Bar Stock.

The preliminary experiments on Unselected bar stock showed the temperature range to be practically limited to 15°-30°C. From this it was decided to interpolate as many intermediate experimental temperatures as the apparatus at hand would permit. For the Low Selected bar stock the temperatures were as follows; 15°, 16°, 17.5°, 20°, 25°, 27°, 29°, 30° and 31°. In tables 5 and 6 are given the results of the individual experiments. Summaries of these experiments are included in tables 7 and 8, while the results are show graphically in figure 2. Temperature has a very marked effect on the mean facet number of the Low Selected bar stock.

3. Temperature Effect on Ultra-bar Stock.

Experiments on this stock involve practically the same temperature as the preceding ones. The results of separate experiments, and separate bottles in a given experiment are shown in tables 9 and 10. As stated before, while there is some varia-

tion between the separate experiments for a given temperature, the differences obtained between different temperatures for a single experiment are consistent throughout. The summaries of the experiments on Ultra-bar stock are given in tables 11 and 12 and shown in figure 3.

4. Temperature Effect On Full-Eyed Wild Stock.

In table 13 are given the counts of the full-eyed wild stock reared at 15° and 27°. Those at 27° are available through the kindness of Dr. Zeleny. They were made on material which was first boiled in caustic potash, cleared and mounted in balsam. The slides were held in a mechanical stage while the facets were counted under a Zeiss #8 objective and a #12 ocular. The ocular field was broken up into rectangles by spider web cross hairs. One rectangle was counted at a time.

The labor involved in the preparation and in counting renders the full-eyed stock unsuitable for a more elaborate study.

The counts at hand show that temperature does not affect facet number in full eye to any appreciable extent. One female of the two at 15° is slightly outside the range of the counts at 27°. The three flies mounted and counted were taken at random from a hatch at 15°. The remainder of the hatch was examined under the binocular. No difference was detected between these flies and the three counted.

5. Temperature Effects on the Three Bar Stocks Compared.

For a direct comparison, the mean facet numbers of the

females of the three bar stocks are shown in figure 4. Here they are all plotted to the same scale. The lower curve is that of the Ultra-bar stock, the middle one is that of the Low Selected stock, while the upper one is that of the Unselected bar stock.

In the Ultra-bar stock, the mean for the females is reduced from 51.51 facets at 15° to 21.27 at 27°. In the Low-Selected, the mean is reduced from 189.00 facets at 15° to 55.13 at 27°. In the Unselected bar stock, the mean is 213.67 at 15° and 81.09 at 25°. There is a very marked reduction in facet number with increase in temperature in each of these three stocks.

The Low Selected bar stock and the Unselected bar stock parallel each other closely in their temperature-facet relations. The Low Selected has a consistently lower mean facet value for all temperatures studied.

The Ultra-bar stock differs from the Low Selected first, in the mean facet value for all temperatures, and second, in the amount of reduction for a degree Centigrade rise in temperature.

We may draw two conclusions from these curves:

1. The mean facet number at any given temperature is not the same for all stocks.

2. The number of facets of difference between the means at any two given temperatures is likewise not the same for all three stocks.

In other words the number of facets is determined by a specific germinal constitution plus a specific environment.

6. The Temperature Coefficients.

a. Change in the mean facet number accompanying a unit temperature change.

In the fifth row of tables 3,4,7,8,11,12 is given the average difference in facet number per C° for the temperature interval indicated. These differences per C° are shown at a glance in figure 5.

The greatest change in facet number for one degree change in temperature is that for the interval 15°- 16° in the Low Selected males. Here one degree change produces a difference of 32.66 facets in the mean value of the facet numbers.

The least change for one degree temperature is for the interval 29°- 31° in the Ultra-bar females. Here one degree change only produces 1.33 facets difference between the two means.

Obviously a change of one degree temperature does not produce a constant difference in facet number. The greater differences are produced at the lower temperature, the lesser at the higher; again, the greater differences are produced in the high mean stocks while the lesser are produced in the low mean stocks.

The average change in facet number accompanying a change of one degree Centigrade is 3.09 for Ultra-bar and 14.01 for Low-Selected Bar.

b. Per cent of change in the mean facet number accompanying a unit temperature change.

In the lower row of tables 3,4,7,8,11,12 the change per C° is expressed in per cent of the mean. It is found by dividing the change in facet number per C° for the interval, by the average of the mean values for the two temperatures.

The per cent of change per C° in Ultra-bar varies from 17.39 to 4.69; in Low Selected from 32.45 to 3.49; in Unselected, from 13.71 to 5.84. Thus the proportional change per degree Centigrade is not (1) constant for all temperatures nor (2) constant for the three stocks.

The average per cent change per C° in the mean of Ultra-bar is 9.22; for Low Selected it is 14.01.

c. Relative change at the different temperatures.

All three stocks show one feature in common. The extreme high (29-31°) and low (15-17.5°) temperatures produce the greatest changes in facet number per C° when the differences are expressed in percentages of the mean. The lowest proportional changes are produced by the intermediate temperatures at or near 23° (Figure 6).

Except for this phenomenon of increased change at the extreme temperatures, the difference in facet number accompanying a change of 1° C is roughly proportional (about 10%) to the mean facet number.

Thus a decrease in the mean, whether produced by germinal or environmental factors, produces a corresponding decrease in the temperature increment.

7. Application of van't Hoff's Law to Temperature Effect on Facet Number.

Many investigators in the past ten years have attempted to obtain an expression for the relationship between temperature and the rates of various biological reactions. The interest in the action has been two fold. First, in an endeavor to reduce all vital processes into terms of dynamics, sorting out the physical from the chemical, the temperature coefficients have been compared to those of various physico-chemical reactions. This has been mostly through the direct application of van't Hoff's law, which for chemical reactions means a doubling or trebling of rate for every rise of $10^{\circ}C$.

The practical application of temperature effects has developed another group of workers. For them van't Hoff's formula was very unsatisfactory. They have given a physiological interpretation and represent the rate of vital processes as a linear function of the temperature.

The formula of van't Hoff and the physiological formula as given by Krogh are as follows :-

$$V_{t+1^{\circ}} = V_t \times Q_1 ; \quad V_{t+10^{\circ}} = V_t \times Q_1^{10} = V_t \times Q_{10}$$

$$V_{t+1^{\circ}} = V_t + K_1 ; \quad V_{t+10^{\circ}} = V_t + 10\ K_1 = V_t + K_{10}$$

Where V is the velocity of the process and Q_1 or Q_{10} are the constants. K is the constant increase in rate in the second formula.

In tables 14 and 16 I have calculated the Q_{10} for the facet number from the formula $Q_{10} = (Q_{T_2-T_1})^{\frac{10}{T_2-T_1}}$ The values of Q_{10} vary from 5.69 to 1.59 The lower values are at the median temperatures while the higher ones occur at the extremes. This is not characteristic of a chemical reaction. Here variation in Q_{10} occurs, but always consistently decreasing with increase in temperature.

The Q_{10} values, however, when calculated directly for ten degree intervals closely approximate the theoretical demands of van't Hoff's law. (Tables 15 and 17).

In Figura 7 the Ultra-bar female facet curve is superimposed on a theoretical van't Hoff curve in which rate at $10^{\circ} = 10$; at $20^{\circ} = 20$; at $30^{\circ} = 40$. Intermediate values are interpolated. The experimental curve is fitted to the other by taking the value of "facets" at 20° as 20 and then applying the $Q_{T_2-T_1}$ as given in table 14. It is plainly evident that the experimental curve for facet number is more than a chance approximation.

8. Temperature Effect On Rate of Metamorphosis.

The time-temperature curves representing the number of days necessary to pass through a given stage in the life history, give an interesting set of data with which to compare the facet curve. Table 18 shows the number of days at the respective temperatures from mating to hatching. Loeb has treated in full the subject of length of particular metamorphic phases in Drosophila as effected by various temperatures. As my results are consistent with his, in so far as the type of curve is concerned, I will say nothing further on this point. My time for the egg-larval-pupal period do not coincide in particular with his, due to differences in technique. My flies were subjected to the experimental temperatures immediately upon mating.

With my cultural methods, I was unable to get the Ultra-bar stock to develop beyond pupation at 33°. The data given in the development curve for this temperature are for wild full-eyed stock. There is some variation in the length of the period as shown by individual bottles. Sets made up at the same time and with the same food, all give the type of curve shown by the averages. (Table 18).

In figure 8 is shown the number of days from mating to hatching. The reciprocal, or rate per day, curve is also shown. This rate curve gives approximately a straight line between 15° and 29°. Beyond 29° it turns down.

This type of curve is found for nearly all physiological

reactions. Krogh has recalculated Loeb's data and shows that they hold for rate of segmentation of the sea urchin eggs. He has shown the same relation to hold for frogs and fishes in egg and larval stages, and for the rate of CO_2 production by Tenebrio larvae. Sanderson, Peairs, Headlee and many others have shown that all the various phases of insect metabolism which they have investigated follow this principle. Lehenbauer, as the most recent worker on the rate of plant growth, has shown the same relation for maize seedlings. An examination of many curves dealing with temperature effect on the rate of growth and the degree of infection of parasite fungi demonstrate the same principle. Simpson and Rasmussen's data for rate of coagulation of blood, give a similar curve.

Snyder (1913) dealing with the rate of heart beat of the cat maintains that this reaction is a logarithmic and not a linear function of the temperature. Groove has applied a similar formula to the length of life of seeds at various temperatures. Loeb has worked out the temperature relations for total length of life of Drosophila and has applied an exponential curve. He compromises on the larval-pupal period however, and admits the straight line relations there.

An important feature of the straight line rate curve is that it holds only between certain temperatures. As already pointed out for the higher temperatures, the rate decreases with increase in temperature above the optimum. Another characteristic of the rate curve is that at the lower temperatures the rate is higher than it theoretically should be. The first feature is

noted in these experiments; the second was not as the lowest experimental temperature was not the minimum for development. In table 19 are shown the Q_{10} values for the rate of metamorphic development as calculated from the $Q_{T_1-T_2}$ experimental values. For the 16°- 15° interval Q_{10} 53.93. There is a steady decrease in the value of Q_{10} throughout the series as we go upward until 0.98 is the value for the 33°- 31° interval.

I wish to point out here that above 29° the values of Q_{10} really become negative.

29°- 30° Q_{10}= -2.240
30°- 31° Q_{10}= -1.293
31°- 33° Q_{10}= -1.098

Obviously Q_{10} has no practical value for these reactions since it varies from 53.93 to -2.240. The negative values are characteristic of physical phenomena. A glance at Lehenbauer's data on rate of growth of maize seedlings show even greater departure for Q_{10}. Here it ranges from 32 at 15°- 13° to -428.2 at 42° to 45°. Exceedingly high temperature coefficients are suggestive of enzymatic reactions and toxicity effects..

9. Relation of temperature effects on the length of developmental periods to those on facet number.

We have seen that the facet curve can be superimposed on the Q_{10} curve with a "closeness of fit" that can hardly be attributed to chance. The next obvious thing is to see how

closely the facet curve and metamorphosis curve agree.

In figure 9 the facet curves for Low Selected bar stock are superimposed on the metamorphic curve. In figure 10 the Ultra bar facet curves are compared with the metamorphic curve. From 15° to 25° the two sets of curves approximate each other closely. Above 25° the metamorphic curve decreases less rapidly. Above 29° it begins to turn up again. The facet curves continue to decrease at their initial rate.

The reciprocal curves are of particular interest. That for rate of development of the immature stages gives approximately a straight line between 15° and 29°. It likewise shows an optimum at 29° with a subsequent decrease in rate with a further increase in temperature. The reciprocal of the facet curve gives an exponential curve, without a decrease in rate at the upper temperatures. The lower part of this curve approximates the straight line feature of the metamorphic rate curve. In other words, the length of the developmental period and the number of facets are correlated up to the point where the time temperature relations for metamorphosis begin to fail.

This leads to the question;

Is the number of facets dependent upon the length of the immature stage?

In the previous experiments it was obvious that there is a certain degree of correlation between the facet number and the length of the egg-larval-pupal period. Are these two phenomena directly dependent or are they separately affected by a third

common factor? Experiment 6 was designed for another purpose but it supplies data here.

In table 25 is shown the distribution of facet numbers in experiment 6 in which the successive bottles, made up by changing the same parents daily, were treated for varying periods at 30° before subsequent development at 15°. The upper row in the table gives the number of days at 30°. Below the class distributions are given the mean facet values for females and males. In the lower row is given the total number of days required to complete the immature stages.

At a glance, it is evident that there is no direct casual relation between the number of days taken to complete the immature stages and the number of facets. Twenty five, twenty four, and twenty three days give practically the same facet counts that are obtained when total development is passed at 15°. In the latter case, thirty one days are required to emerge. Again, those flies hatching at 18 and 20 days are in the same facet classes as those hatching in nine days in the stock experiments at 30°.

Why, then, is there an apparent correlation between the facet count and the number of days of the immature stages when the latter is passed throughout at one temperature? We shall reconsider this question at the end of the succeeding part of this study.

10. Other Environmental Factors Affecting Mean Facet Number.

a. Food.

A preliminary experiment showed that mass cultures could be reared successfully on Fleischmann's compressed yeast and water without the addition of banana. The same was true for Yeast Foam.

Differences in mean facet number from these three foods were noted. Table 21 shows that in all cases Fleischmann's yeast gave the lowest number of facets. At the same time table 22 shows that the length of the immature stages is slightly shortened. Here then we note that an increase in the rate of development is accompanied by a decrease in facet number.

b. Humidity.

Culture bottles were placed in glass breeding cages the humidities of which were 35% and 60% respectively. Very little difference in the mean facet number was observed. (Table 23) This is rather to be expected as the bottles were plugged with cotton as ordinarily. The food surrounding the developing larvae was moist and probably near 100% saturation.

c. Evaporation.

In two cultures reared at the same time as the ones mentioned under "humidity" the 35% or the 60% air was passed directly over the food. The 35% air dried the culture out before larvae appeared. The first pupa to form in the 60% culture was on the same day that the pupae formed in the control bottles. The first hatch, however, did not occur until two days later

than the first hatches in the controls. Fresh food had to be added to this culture several times. (tables 23 and 24)

There is a marked difference in mean facet number between the "humidity" as controls and the "evaporation" bottles. The most striking difference however, is in the occurrence of exceptionally high individuals. The upper range is extended from 35 facets to 49. Evidently all the individuals were not affected alike. Here we note a decrease in developmental rate with an accompanying increase in number of facets.

Food, humidity and evaporation under ordinary cultural procedure are doubtless negligible factors as affecting facet number. Food and evaporation under the widely diverse experimental conditions show perceptible effects, however.

SECOND PART. DETERMINATION OF THE PERIOD DURING WHICH TEMPERATURE IS EFFECTIVE IN MODIFYING THE FACET NUMBER.

1. Preliminary experiments on Unselected bar at 30° and 15°.

A preliminary experiment was designed to determine if temperature had any effect throughout the immature stages, or if it was limited to a specific phase of development. In table 25 are shown the results of subjecting successive cultures for the first day, first two days, first three days, and so on, to 30° before their subsequent development at 15°. Three, two and one day at 30° give the same facet number as those raised throughout at 15°. The early days of larval life may be spent at high temperatures without effect on the facet number.

Six and seven days at 30° followed by transfer to 15° show that the number of facets had been determined prior to the

transfer as all the counts come well within the range of the stock counts at 30°.

Next, if we consider only the counts made on the first day of hatching, the bottles which spent their first four and first five days at 30°, show only the number of facets characteristic of the 30° stock. The counts made on flies hatching on the second and third days of these two bottles are intermediate between the 15° and 30° counts. These intermediates were to be expected. The parents were not removed from the bottles until the end of the first 24 hours. Hence some of the larvae may have been 24 hours older than others. Those four days old had already passed the point (x) in development during which facet number is being determined. They were also the first to hatch. Those hatching later were obviously not so far along in development and hence were affected by the transfer to 15°.

Obviously temperature is not capable of modifying the facet number throughout the immature stages, but is limited to a definite stage in development.

Subsequent experiments on Ultra-bar consider these points more in detail.

2. Effect of temperature during the pupal period.

Experiments of the same type as the preceding were carried out on Ultra-bar at 27° and 15°. We will consider the pupal period first. Subjecting the cultures to 27° for five, six, seven, eight and nine days before subsequent removal to 15°,

gave counts which are characteristic of 27° stock. The first four cultures had pupated before being transferred. The last one had already begun to hatch. From the distribution of counts in table 26 it is obvious that subjecting the immature insect to low temperature after pupation, has no effect on the facet number. (Figure 11)

3. Effect of temperature during the larval period. Initiation and duration of the effective period at 27°.

An examination of table 26 shows that a stay of one or two days at 27° had no effect on the facet number, as only three individuals out of one hundred twenty three are slightly under the lower range of the stock experiments at 15°.

Of those that were three days at 27°, some had passed the point x as shown by the range well within that of the 27° stock experiments. Some were just in the effective period as shown by intermediate counts. Some had not yet reached the period as shown by the counts characteristic of the 15° stock.

Four days at 27° brought nearly all individuals through the effective period. Four individuals out of one hundred four are slightly above the upper range of the 27° stock counts. We may conclude that the stage in development at which the facet number is being determined, is passed prior to the end of four days at 27°. Likewise this stage is not reached by the end of two days at 27°.

To define this period more closely experiment 59 was designed. After many unsuccessful attempts to get a series in

which the eggs were not more than one hour apart in age, the present series was carried through. Here the parents were allowed to lay eggs during a period of twelve hours. This series includes the following number of days at 27° with subsequent removal to 15°; 1 day (24hrs.) 2, 2¾, 3, 3¼, 3½, 3¾ and 4. The results are given in table 27 and figure 12.

This experiment bears out the previous one in that one, two, two and three fourths, and three days at 27° did not bring the larvae up to the point x. This phase of development is initiated between 3 and 3¼ days as shown by the intermediate counts of the latter. These are predominated by the lower temperature.. Three and one half days at 27° gives a preponderance of individuals with the 27° count.. Three and three quarters days at 27° has brought all but one individual through the effective period. After four days all individuals had completed this stage in development.

A second mating, allowed to develop three days at 27° demonstrates individual variation in rate among separate bottles. Here the effective point x had been passed by some individuals and many show an intermediate condition.

A control mating of the same parentage as the foregoing series was reared at 27°. It shows the normal distribution of a 27° stock.

According to this and the previous experiment the reaction, which determines the number of facets and which is subject to temperature modification, is initiated at 27° at or near the end of 3 days' development. This reaction at 27° is practically

over at the end of $3\frac{3}{4}$ days. The duration of the effective period at 27° is not greater than 18 hours.

The actual time during which the fasat determining reaction takes place is doubtless much shorter than this for the individual since under the conditions of the experiment we are dealing with material which may vary twelve hours in age.

4. Initiation and Duration of the Effective Period at 15°.

Experiment 62, of the same type as the preceding ones, was carried out to see when the effective period was initiated at 15° The same parents were used as in Experiment 59. The cultures were made up at 27°, left there for 24 hours, the parents were then removed to the next set, while the bottles containing the eggs and larvae were transferred to 15°. Here they were left for the number of days indicated in table 28 and then returned to 27° to complete development.

It is plainly evident that the effective point x is not reached at the end of seven days at 15° plus the one initial day at 27°. In experiment 62 the change comes on the eighth day at 15°. (Figure 13). Unfortunately this experiment was not planned to cover a longer period; a second experiment was therefore started.

Experiment 72 supplies the data on the length of the period at 15°. (Table 29). As pointed out for experiment 59 there may be a slight difference in the rates of individual bottles. Experiments 62 and 72 show another such variation. In experiment

62 the period was initiated on the eighth day. In experiment 72 only two individuals had passed the point x at 15°. After nine, ten and eleven days an increasing number of individuals show the 15° count and after twelve days only 5 of 94 individuals had not completed the facet determining reaction.

Remembering that among the individuals in a bottle there may be twenty four hours difference in age, the period at 15° is practically limited to the 9th, 10th and 11th days or the length of the period at 15° is about 72 hours.

5. Comparison of the length of the period during which temperature is effective on facet number, with the total length of the immature stage.

It has been shown that the period during which temperature is effective is initiated at very remote time intervals at 15° and 27°. Does the point x represent a definite stage in development?

The total number of days required to complete the immature stage at 15° is 31.87 while at 27° it is 9.21. This gives a daily rate of 3.13% total development at 15° and 10.86% total development at 27°. With these rates we may calculate the point x.

At 27° 3X10.86 = 32.58%.

At 15° 1X10.86 = 10.86
8X3.13 = 25.04
35.90%

In other words the reaction which determines the number of

facets is initiated at the completion of 32-36 per cent of immature development.

Comparing the lengths of the period at 15° and 27° with those of the immature stage we have 18 hours at 27°, 72 hours at 15° as compared to 9.21 days and 31.87. This is a fairly close agreement considering the experimental condition.

Expressing the length of the effective period in per centage of development and adding the result to those of the preceding period, we find that the reaction which determines facet numbers starts at the completion of about 32 per cent of the immature development and is completed with the completion of 45 per cent.

Thus the length of a particular phase of development is proportional to that of any other phase. Reciprocally, the rate of a given reaction such as that which determines facet number, is proportional to the rate of general metabolism.

In the first part of this study we note a correlation between facet number and length of immature stage when the latter was completed at one temperature. Subsequently it appeared that facet number and total length of immature stage may be independent. Why do we have the apparent correlation?

The facet determining reaction has been shown to be of relatively short duration. It is obvious that a change in temperature following its completion could affect the total immature period without subsequently effecting the facet numbers.

We may conclude that the number of facets and the length of the immature period are not directly dependent but rather

that the former is determined by a specific reaction whose rate is correlated with that of the general metabolic activities extant while this particular phase of development is going on.

THIRD PART. THE EFFECT OF TEMPERATURE UPON VARIABILITY.

1. Coefficient of variability at different temperatures.

This study gives some interesting data on the question of individual variability at different temperatures. The distributions of the females and males of the Unselected bar stock are given in tables 30 and 31. The class size is here arbitrarily taken as ten per cent of the mean. Low Selected females and males are shown in tables 32 and 33. The distribution of Ultra-bar is given in table 34. Here the class size is one facet. Particular attention is called to the normal distribution in all cases.

An argument in favor of the genetic stability of the Ultra-bar stock is shown by the relatively infrequent occurrence of individuals outside the bounds of normal distribution. At 27° a single 55 facet male, and at 16° a 72 facet male, are the only two extremely wide departuras. (For further data see Zeleny's papers on Ultra bar.)

The mean, standard deviation and coefficient of variability for all three stocks are given in tables 35-40. Two things are apparent; One, variability increases with the temperature when measured by coefficient of variability; and two, the variability of the Ultra bar stock is much lower than that of the other two stocks. Both these generalizations are subject to exceptions.

Their reliability as compared to statements made by other writers will be discussed later.

2. The Sex coefficient at different temperatures.

The chief interest in table 41 lies in the marked sexual difference existing throughout these experiments. The average value for the ratio between the mean facet number of the females and that of the males is 0.791. Temperature has no consistent effect in altering this coefficient.

In the Ultra-bar stock there seems to be a tendency to reduce this sexual difference. At 31° the mean facet value of the females is slightly in excess of that of the males. This however, is doubtless accidental, as some of the individual bottles showed normal ratios.

An explanation of the sexual difference is to be sought in the fact that we are dealing with a sex linked factor. On the chromosomal hypothesis, a double dose of the restricting factor is present in the female while only a single dose is present in the male.

FOURTH PART. INHERITANCE OF TEMPERATURE EFFECTS.

1. Comparison of offspring raised at 27° from parents reared at 15°, 20° and 27°.

The interest in this phase of the work is both practical and theoretical. To preclude any inherited effect in the stock experiments care was taken to keep the parent stocks at 27°. To determine whether or not there was any inherited effect, experi-

ment 51 was designed. Flies reared for one generation in the stock experiments at 15°, 20° and 27° were used as parents in cultures which were made up under conditions as nearly alike as possible and which were allowed to develop at 27°.

The distribution of parents and offspring is given in table 42. The mean facet numbers and standard deviations are given in table 43. The mean, standard deviation, and distribution of the F_1's reared at 27° are characteristic of the stock 27° counts although those of the parents are very markedly different. <u>There is no inherited effect of temperature upon facet number in this case.</u>

IV. DISCUSSION.

A. TEMPERATURE AS A FACTOR IN THE MECHANISM OF DEVELOPMENT.

1. Direct effect of temperature upon growth, size, number of parts, structure and color.

Ordinarily the temperature is not a factor capable of modifying structure to any marked extent. Certainly structural variations at different temperatures are in no way comparable to the variations in rate at which they may be brought about. The capacity to develop specific color, size and form is a heritable characteristic, e.g. the present study involves the sex linked mutant white eye and all individuals are white eyed ragardless of the environment in which they develop.

Many organisms however, exhibit variations in these structural characteristics which may be considered as direct responses to temperature.

Among the earlier investigators of temperature effects on structure were Merrifield, Weismann, Standfuss, Fischer and Dorfmeister.* The chief object of their experiments was the production, by environmental manipulation, of the various racial and polymorphic forms in Lepidoptera.

Vernon (1895) found that the size relationships between various parts of echinoderm larvae could be modified in response to different temperatures.

* For a complete review see Bachmetjew 1901 .

Standfuss (1895) found a reduction in the size of the imagoes, as a result of rearing larvae of Lepidoptera at high temperatures. This he ascribed to the indirect effect of insufficient nourishment.

Tower (1906) found that by subjecting larvae of Leptinotarsa decemlineata to various temperatures he could affect the amount of pigmentation of the adult. His results are unique in that an increase from the mean temperature range, (22.5°C) of the species had practically the same result as a decrease. He obtained an increase in melanism down to 16° and up to 28° followed by a decrease to albinism beyond these temperatures.

Shelford (1917) found a tendency toward melanism with an increase in temperature due to reduction in the size of the unpigmented areas on the elytra of the tiger beetles.

All these reactions are complex and the materials do not lend themselves to close quantitative study. It is obvious that no simple temperature relation can be worked out for them.

2. Examples in which a specific structure depends upon a definite environmental stimulus.

In three well marked cases, specific temperatures determine the character of the organism.

Bauer (1911) cites a case of Primula sinensis which at ordinary conditions produces red flowers. If a plant be subjected to 30°- 35°C a few weeks before blooming the flowers will be white. If the plant be returned to 15°-20°C, the buds opening immediately will still be white but those developing later will again be red. As Bauer points out white can not be said to be inherited, red

cannot be said to be inherited: but rather the capacity to produce white flowers at 30° and red flowers at 15° is the thing inherited.

Miss Hoge (1915) found a strain of Drosophila in which one or more legs were reduplicated. Under ordinary cultural conditions only about ten per cent of the individuals from a pure reduplicated mating showed the condition. It was later discovered that by subjecting the eggs to 9°- 10°C, the percentage of offspring showing this character could be raised to practically 100.

Bar eye is a sex-linked factor which reduces the number of facets. The Mendelian behavior is clear cut and regular. As shown in this paper, however, the amount of reduction in facet number is dependent upon the specific temperature at which the larvae develop.

In the first two examples only two temperatures are involved.. The results were very definite, but obviously no quantitative measure can be applied.

In bar-eye, observations have been made at close intervals over a range of 15°-31°. The temperature relations have been shown to closely approximate those of many physiological reactions.

In certain cases, other environmental factors may be said to determine form.. Morgan (1915) has shown that a definite amount of moisture is necessary to the development of the character abnormal abdomen.. Metz (1916) has several mutants

which depend on specific cultural conditions for their recognition.

As shown by the constant results under given external conditions, the hereditary mechanism remains constant. The reactions involved in transforming the hereditary materials into somatic tissues have been shown to be modifiable through various external factors, chief of which is temperature.

3. Consideration of the means by which temperature can produce an effect on facet number.

We have seen in the foregoing pages that facet number in the full eyed wild fly is very little affected by temperature, while in the bar eyed mutant there is a very marked effect. It is also evident that the effect is produced only during a relatively short period in larval life. What hypothesis can explain these facts?

Assuming a normal mechanism for facet production (A B C D E) we may say that temperature affects the rate of all the various processes involved in a nearly equal amount. The rates are increased at the higher temperatures, but at the same time the length of the time of the reaction is shortened proportionately thereby producing a constant number (N) of facets in the full eye.

In the bar eye a new condition has come about. The facet number is reduced to about one fourth that of the full eye at 15° and to about one twenty-fourth at 27° in the Low Selected line.

In Ultra-bar the reduction is even greater; one fourteenth at 15° and one fortieth at 27°.

HYPOTHESIS 1. Reduction in facet number($\frac{N}{a}$) due to a reduction in the facet forming substances($\frac{n'}{a}$). As in the case of the full eye, increased rates at the higher temperatures with proportional decreases in the time of the reactions, would produce a constant number of facets from a given amount of material.

HYPOTHESIS 2. Surface Tension. The number of facets in the bar-eyed stocks varies inversely with the temperature. The reaction has then a negative temperature coefficient suggesting surface tension. The values of q_{10} are too high,however, for this phenomenon. Furthermore, if surface tension were the factor involved, we should expect to find marked temperature differences in the full-eyed stock.

HYPOTHESIS 3. A reduction in the amount of facet producing material and a rate of facet production independent of the temperature. In this case,the independent rate working through an increased time period at the low temperatures would produce the greater number of facets as observed in bar. Applying the independent rate to full eye again, we should obtain a proportional difference at high and low temperatures, a condition shown not to exist.

HYPOTHESIS 4. Considering the reduction in facet number to be due to an inhibitor. Assuming the inhibitor to be constant

in amount for all temperatures, then if it follows the time temperature laws of the other metabolic reactions, its rate will be decreased at the low temperatures while the time during which it acts is proportionately lengthened . At the higher temperatures the rate will increase while the time is shortened. Its action would thus be constant and we would have the same number of facets produced at all temperatures.

HYPOTHESIS 5. Considering the reduction in facet number to be due to an inhibitor, constant in amount, but whose rate is independent of the temperature. Under this condition the inhibitor working through a lengthened time interval at the lower temperatures would produce a greater effect and we should have more facets at the high temperatures.

HYPOTHESIS 6. Considering the amount of inhibitor to be a function of the temperature, and that we have more produced at high than at low temperatures. Obviously this condition would explain the results obtained in bar, but it is merely restating the observed results in another form, that is, that the facet number is a function of the temperature.

HYPOTHESIS 7. Considering the decrease in facet number to be due to an inhibiting factor whose temperature coefficient differs from that of the normal facet producing reaction

Let N be the normal facet number of full eye

nt is the length of the period at T,° during which facet rudiments are being produced.

t is the length of the period at T_2°

In full eye N facets are produced at rate of $\frac{N}{n}$ per t for nt at T_1°

at rate of N per t, for t at T_2°

In bar eye N is reduced to Bx at T_1°

By at T_2°

facets are produced at rate of $\frac{Bx}{n}$ per t at T_1°

facet number is reduced at rate of $\frac{N}{n} - \frac{Bx}{n}$ per t at T_1°

facets are produced at rate of By per t at T_2°

facet number is reduced at rate of N-By per t at T_2°

Then the rates of production and reduction have the following temperature coefficients.

$\frac{N}{n}$ rate of production at T_1°

N rate of production at T_2°

$\frac{N-Bx}{n}$ rate of reduction at T_1°

N-By rate of reduction at T_2°

$Q_{t_1 - t_2} = n$

	When
$Q_{t_1 - t_2} = n$	Bx = By
$Q_{t_1 - t_2} < n$	Bx < By
$Q_{t_1 - t_2} > n$	Bx > By

In all the bar eyed stocks, Bx is greater than By, where T_1° is the lower temperature. Hence the temperature coefficient for the reduction reaction in bar is greater than that of the production reaction. We can thus explain the difference in temperature relations between the full-eyed stocks and the bar eyed stocks.

What can be said about the differences obtained for the various bar eyed stocks? From the above formula it is obvious that the greater the difference between Bx and By, the greater will be the difference between the Q_{10} for the full and the Q_{10}

for the bar. Bar is a changed condition which differs from full in number of facets and in the temperature coefficient. Is Ultra bar a change in the same direction?

Ultra-bar effects a further decrease in the number of facets, but as seen by the value of Bx and By, its temperature coefficient is really nearer that of full than is that of bar. Ultra bar is then, not an increased condition of both these factors. The reversed change in the temperature coefficient may be a question of concentration of a single substance, however.

4. Period during which the character of certain structures is determined as shown by the temperature effects.

Vernon (1903 P.241) sums up the work on Lepidoptera: "Dorfmeister concluded that the temperature had its greatest effect during the change from larva to pupa. According to Weismann on V. prosa, temperature acted at the beginning of the pupal period. Merrifield 1891 concluded that markings are chiefly affected by temperature during the early part of the pupal period, while colouring was affected during the penultimate pupal stage."

Miss Hoge showed that exposures of the eggs to cold produced the greatest percentage of reduplication of legs in the imago. Evidently the materials which determine the structure of the legs are differentiated in embryonic development.

The bar eye factor comes into play after about three fourths of the larval period is finished.

These last two cases are of extreme interest in showing that some of the reactions which are involved in the differentiation of adult structure may occur at very early stages of immature life. Environmental stimuli must therefore be applied at specific periods in order to modify the organization of the adult.

5. The Direct Effect of Temperature upon the Mechanism of Inheritance.

Plough has shown that temperature has a definite effect on the percentage of crossing over between the hereditary materials of the second chromosome in Drosophila. He gets a maximum per centage at 13° and at 31° with a minimum from 22°-27°. This curve Plough compares to Howell's curves on the amount of contraction of frog muscle at varying temperature under constant stimulus. It is decidedly not a van't Hoff curve. Plough refers the phenomenon further to Lillie's results on activation of starfish eggs at various temperatures and concludes that temperature "probably causes some alteration in the physical basis of the egg."

The temperature effect on actual facet number seems to have nothing in common with the above results. If, however, we consider the per cent of increase or decrease per C° some very interesting relations appear. Here too, we find that the maximum changes come at the extreme high and low temperatures with a minimum between, much as in the above reactions. With Plough, I refer the significance of the similarity of the cases

to future workers.

6. Individual variation as affected by temperature.

In his book on Variation in Animals and Plants, Vernon (1903 p. 218) makes the statement that variability becomes steadily greater as the environment becomes more unfavorable.

In his paper in 1895 he remarks that the variability reaches a maximum at 18°- 20°,. the temperature most favorable for development.

The temperature experiments on bar-eye offer data on this subject. As was pointed out previously, the data are not altogether consistent when any attempt to draw striking conclusions are made..

An examination of the data published by Vernon is even less satisfactory and warrants neither of the statements above ascribed to him.

The present study has value only as a preliminary experiment on the subject of individual variation. The two following conclusions are suggested, if not proven..

1. When measured in terms of the coefficient of variability, variability increases with the temperature.

2. When measured in terms of standard deviation, variability decreases with increase in temperature.

B. CONSIDERATIONS OF THE STRAIGHT LINE FEATURE OF PHYSIOLOGICAL REACTION CURVES, AND OF THE EXPONENTIAL CURVE FOR FACET NUMBER.

1. Variability in Q_{10}

Variability of the temperature coefficient, Q_{10} occurs in

practically all chemical reactions. The typical variation is a slight decrease as the temperature increases. Trautz and Volkmann give some interesting values for saponification reactions in which there is first a slight increase and then a steady decrease in Q_{10} as the temperature rises.

The variability of Q_{10} for chemical reactions is in no way comparable to that shown by enzymatic and vital reactions.* In nearly every case the two latter processes show a marked optimum. Obviously above the optimum temperature, Q_{10} becomes negative. As pointed out in this paper the values of Q_{10} for rate of metamorphosis vary from 53 at the 15° to 16° interval to − 2.24 at the 29° - 30° interval. These values are out of all proportion to the 2 to 3 requirements of van't Hoff's law.

This change in the value and sign of Q_{10} has been explained by Arrhenius 1915 and others as due to secondary factors. Two processes are involved; (1), the increase of activity of the enzyme and (2) the destruction of the enzyme itself at the higher temperatures. The temperature having a combative effect on the two processes, as it increases gives the appearance of checking the primary one when the end results alone are considered.

Blackman (1905) accepts this sort of an explanation for vital reactions. In the rate of assimilation by leaves of the cherry laurel he has ingeniously demonstrated the probability of the occurrence of increased rates above the optimum although

* Ernst has shown an optimum in catalytic action of colloidal platinum upon H_2 O_2

these rates are not directly measurable.

Snyder (1911) has attributed the decrease in rate of physiological reactions at higher temperature to the difference in viscosity of protoplasm. This physical phenomenon has a negative temperature coefficient. Experiments demonstrate a decrease in rate of nerve conduction with increase in viscosity at a constant temperature.

Balls (1905) maintains that the more rapid accumulation at higher temperatures of waste products, retards the primary reactions. While these products are formed at the lower temperatures, they are disposed of at a rate sufficient to prevent the checking of the primary reaction. At high temperatures they are formed more rapidly than they can be carried away. Their experimental removal, by dilution of the surrounding medium, raised decidedly the optimum of growth for the sore-shin fungus.

Coagulation of proteins, which has been advanced as an explanation of death at the higher temperatures, might be suspected of producing the retardation in rate at the sub-maximal temperatures.

2. Straight line physiological reaction curves.

Most physiologists have given up van't Hoff's formula as too inaccurate to have any practical value. They have abundantly demonstrated the metabolic rate relations to be linear rather than exponential functions of the temperature.

3. Loebs hypothesis of secondary factors.

Loeb has recently explained the straight line character of the rate curve as due to the flattening out of an exponential curve by secondary causes. He shows that the "rate of life" of the imago of Drosophila may be plotted as an exponential curve, and that there is no falling off at the higher temperatures.

The criticism can be made, however that an examination of his rates above 31° demonstrate clearly the presence of secondary factors which would tend to convert a straight line curve into an exponential curve.

A consideration of these various hypotheses developed to explain optima, and straight line curves, is now in order in the light of the present work.

4. Explanations of the straight line features and optima considered from the data on facet number and developmental rate in Drosophila.

In the bar-eyed mutant of Drosophila, two distinct reactions have been examined in regard to their temperature relations. One gives a typical straight line curve with an optimum at 29°. The other gives an exponential curve without decrease in rate at the upper temperatures. From 15° to 27° these two curves approximate each other, suggesting a close similarity in the primary nature of the two reactions throughout. Above 27° the two reaction rates diverge. Secondary factors have entered to retard the rate in the one, and to transform an exponential

curve into a straight line.

It is quite obvious that for the facet curve there is no 'enzyme' destruction, as there is no falling off in rate at the higher temperatures. The optimum in the metamorphic curve shows that we are in the range of temperatures where such destruction of emzyme would be expected. The secondary factors which modify the metamorphic curve are as a result not to be located in the principle of 'enzyme destruction'.

It is likewise evident that changes in viscosity of the protoplasm cannot explain the differences observed in the two reactions since both occur simultaneously in the same material.

We may extend the same objections to such explanations as coagulation of proteins, physical state of protoplasm and allied phenomena.

Ball's explanation of optima consisted in the more rapid accumulation of waste products at high temperatures. The by-products retard the rate of the primary vital reactions. Their experimental removal raised the optimum decidedly, but did not carry it up to the maximum temperature of growth as would be the case were his the only explanation.

5. Differential temperature coefficients as an explanation of the straight line feature of physiological reaction curves.

The one idea of Ball's that shows greater possibilities of development is that of differential temperature coefficients.

Vital reactions are a series of complex processes. Both chemical and physical phenomena are represented. It is incon-

ceivable that all these should have the same temperature coefficients. Vernon (1895) has demonstrated this fact in the gross anatomy of echinoderm larvae. Laughlin, (1919) has recently shown that the various phases of mitosis have very markedly different temperature coefficients. Osterhout (1917) has pointed out the complications arising from complex systems, in which the various reactions have different Q_{10} values.

Differentiation and growth are of a necessity synchronized processes. It is at the higher temperatures that the effects of diverse temperature coefficients would be most noticable. If one stage in development must await another it is quite obvious that the whole process would be slackened in speed. At extreme temperatures regulation would become impossible.

As has been shown, the reaction by which facet number is determined is of relatively short duration. It is not complicated by the processes of growth. It shows a true chemical temperature coefficient throughout.

Metamorphosis involves many long and complicated processes. The separate reactions do not have the same temperature coefficients. This is evident from Hertwig's curves for a close sequence of stages in the frog tadpole. A rapid reaction must await with its end products the slower one, before further development can proceed. The higher the temperature the more erratic the separate temperature effects, and the slower becomes the total rate of development.

It seems reasonable to conclude with Loeb that the straight

line feature of the physiological rate curve, together with the special feature of optima, is due to the flattening out of an exponential curve by secondary factors. These factors are not specific, such as enzyme destruction, viscosity changes, protein coagulation, or accumulation of waste products, but are the normal results of a differential temperature effect on the separate phases of growth and development.

C. THE INHERITED EFFECTS OF TEMPERATURE.

1. Induction.

Wolterack (1911) working on the size of the head in Daphnia; Middleton (1918) on fission rate in Stylonychia, and Sumner (1915) on the length of the feet and the tail in mice, found that measurable effects could be produced by temperature.

Furthermore, the effect produced, showed itself in a less degree, in subsequent generations although the causal factor, extreme temperature, had been removed. To this phenomenon Woltereck gave the name of "induction" or "pre-induction" according to the number of generations involved.

No such effect as these was noted in connection with facet number as investigated in experiment 51. It is possible however, that by continued existence, generation after generation, at a low or high temperature, such an inherited effect could be produced.

2. Temperature as a causal factor in the production of mutations.

Tower (1906) found among his potato beetles, color variations that presisted through subsequent generations. Presumably, since

they were reared at high temperatures, the cause of the mutations lay in this fact.

The present study shows no marked discontinuous variations at the high temperatures. Temperature here is not a factor in the production of mutations.

V. SUMMARY.

1. Three strains of the bar-eyed mutant of Drosophila melanogaster have been reared at constant temperatures over a range of 15°-31° C

2. The mean facet number in the bar-eyed mutant varies inversely with the temperature.

3. The temperature coefficient (Q_{10}) is of the same order as that of chemical reactions.

4. The facet-temperature relations may be plotted as an exponential curve for temperatures from 15° to 31°.

5. The rate metamorphosis of the immature stages give a straight line temperature curve between 15° and 29°. Beyond 29° the rate decreases again with a further rise in temperature.

6. The facet curve may be readily superimposed upon the metamorphosis curve between 15° and 27°.

7. The straight line feature of the metamorphosis curve is probably due then to the flattening out of an exponential curve by secondary factors.

8. Since both the straight line and the exponential curve appear simultaneously in the same living material, it is impractical to locate the secondary factors in enzyme destruction, differences in viscosity, or physical state of colloids.

9. Differential temperature coefficients for the various separate processes involved in development furnish the best basis for an explanation of the straight line feature of physiological reactions.

10. Facet number in the full-eyed wild stock is not effected by temperature to a marked degree.

11. The mean facet number for 15 full eyed females raised at 27° is 859.06.

12. The mean facet number for the Low Selected bar stock females at 27° is 55.13; for the Ultra-bar stock females at 27° is 21.27.

13. A consistent sexual difference appears in all the bar stocks, the females having fewer facets. This relation may be expressed by the sex coefficient, the average value of which is .791.

14. The average change in facet number in the mean per C° is 3.09 facets for Ultra-bar, and 14.01 for Low Selected.

15. The average percent of change in the mean per C° is 9.22 for Ultra-bar, and 14.51 for Low Selected stock.

16. The differences in the number of facets per C° are greatest at the low temperatures and least at the high temperatures.

17. The difference in the number of facets per C° varies with the mean.

18. The per cent of change in the mean facet number is greatest at the lower (15°-17.5°) and higher (29°-31°) temperatures and is least at the intermediate temperatures.

19. Temperature is a factor in determining facet number only during a relatively short period in <u>larval</u> development.

20. This effective period, at 27°, comes between the end of the third and the end of the fourth day.

21. At 15°, this period is initiated at the end of 8 days following a first day at 27°.

22. At 27° the period is approximately 18 hours long. At 15° it is approximately 72 hours long.

23. The number of facets and the length of the immature stage (egg, larva, pupa) appear related when the totaldevelopment is passed at a single temperature.

24. That the number of facets is not dependent upon the length of the immature stage is shown by experiments in which only a part of development was passed at one temperature and the remainder at another temperature.

25. Temperature affects the reaction determining facet number in approximately the same way that it affects the other developmental reactions, hence the apparent correlation between facet number and the length of the immature stage.

26. Variability as expressed by the coefficient of variability has a tendency to increase with temperature. Standard deviation on the other hand appears to decrease with rise in temperature.

27. Neither inheritance nor induction effects are exhibited by this material.

28. This study shows that environment may markedly affect the somatic expression of one Mendelian factor (bar-eye), while it has no visible influence on another (white eye).

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TABLE 1.

MEAN FACET NUMBER FOR THE SEPARATE EXPERIMENTS ON UNSELECTED BAR STOCK ♀♀

	15°	20°	25°	30°
			(27°)	
Exp. 1	206.34±3.73		(30.85±1.87)	25.20±2.08
4	209.75±3.01	115.96±4.34	73.14±1.32	38.87±1.35
7	210.80±2.30	122.43±1.60	91.47±1.76	34.02±0.94
16	257.00±6.83	130.04±3.21	86.86±2.88	47.38±1.63

TABLE 2.

MEAN FACET NUMBER FOR THE SEPARATE EXPERIMENTS ON UNSELECTED BAR STOCK ♂♂

	15°	20°	25°	30°
			(27°)	
Exp. 1	259.50±7.01		(88.51±3.32)	46.25±5.69
4	265.00±5.70	143.23±6.07	98.43±2.19	70.42±2.80
7	285.10±6.61	160.99±2.26	122.73±2.36	60.00±2.09
16	no hatch	175.32±4.77	172.42±3.70	87.70±4.03

TABLE 3. UNSELECTED BAR STOCK SUMMARY, EXP. 1,4,7,16 ♀♀

	15°	20°	25°	30°	
Number of individuals.	90	117	114	97	
Mean Facet Number.	213.67	122.20	81.09	39.66	
Difference in facet Number for the interval	91.47	41.11	41.43		average
Difference in facet number per C°	18.29	8.22	8.28		11.59
Mean facet number for interval.	167.93	101.64	60.37		average
% change per C°	10.89	8.08	13.71		10.89

TABLE 4. UNSELECTED BAR STOCK SUMMARY EXP. 1,4,7,16 ♂♂

	15°	20°	25°	30°	
Number of individuals	92	109	109	92	
Mean Facet Number	269.76	161.76	120.52	73.54	
Difference in facet number for the interval	108.00	41.24	46.98		average
Difference in facet number per C°	21.60	8.25	9.39		13.08
Mean facet number for the interval	215.76	141.14	97.03		average
% change per C°	10.01	5.84	9.67		8.50

TABLE 5.

MEAN FACET NUMBERS IN SEPARATE EXPERIMENTS ON LOW SELECTED BAR STOCK ♀♀

	15°	16°	17.5°	20°	25°	27°	29°	30°	31°
Exp. 12	195.47±3.49	161.12±2.53	142.14±9.80	112.51±2.52	87.29±2.04	57.78±2.46		40.57±1.10	
" 22	184.40±9.11	155.74±1.96	118.29±1.44	93.68±1.81	79.32±1.32	54.15±1.10		32.35±0.84	
" 27					68.28±1.14	55.00±0.99	47.40±0.63		28.85±0.41

TABLE 6. MEAN FACET NUMBER IN SEPARATE EXPERIMENTS ON LOW SELECTED BAR STOCK ♂♂

	15°	16°	17.5°	20°	25°	27°	29°	30°	31°
Exp. 12	255.35±4.50	211.73±8.46	169.00±2.65	142.72±3.58	126.52±3.12	91.64±4.75		82.26±3.31	
Exp. 22	220.50±2.26	205.46±2.33	161.54±6.67	117.53±1.38	114.56±2.90	71.83±1.59		44.80±1.49	
" 27					94.36±1.52	78.55±1.29	65.58±0.90		41.70±0.69

TABLE 7 LOW SELECTED BAR STOCK SUMMARY. EXP. 12, 22 & 27 ♀♀

	15°	16°	17.5°	20°	25°	27°	29°	30°	31°	
Number Individuals	79	104	94	105	165	164	100	64	100	
Mean facet number	189.00	158.18	127.27	98.88	74.25	55.13	47.40	36.56	28.85	
Diff. infacets for interval	30.82	30.91	28.39	24.64	19.12	7.73	10.87	7.71		average
Diff. in facets per C°	30.82	20.61	11.36	4.93	9.56	3.86	10.87	7.71		12.46
Mean for interval	173.59	142.72	113.07	86.56	64.69	51.26	41.98	32.70		average
% increase per C°	17.75	14.44	10.04	5.69	14.78	7.53	25.82	23.57		14.95

TABLE 8. LOW SELECTED BAR STOCK SUMMARY EXP. 12, 22 & 27 ♂♂

	15°	16°	17.5°	20°	25°	27°	29°	30°	31°	
Number individuals	74	107	95	104	164	167	100	61	100	
Mean facet number	240.21	207.55	164.66	122.88	103.12	79.46	65.58	57.85	41.70	
Diff. in facets for interval	32.66	42.89	41.78	19.76	23.66	13.88	7.73	16.15		average
Diff. in facets per C°	32.66	28.59	16.71	3.95	11.83	6.94	7.73	16.15		15.57
Mean for interval	223.88	186.10	143.77	113.00	91.29	72.52	61.71	49.77		average
% increase per C°	14.58	15.31	11.62	3.49	12.95	9.57	12.52	32.45		14.06

TABLE 9. ULTRA BAR SHOWING VARIATION IN MEAN FACET NUMBER FOR THE SEPARATE BOTTLES. ♀♀

Exp.	15°	16°	17.5°	20°	23°	25°	27°	29°	31°
23	45.70	40.58	36.88	28.81		24.65	23.33		17.44
		41.81	37.63	33.08		21.69	17.78		15.12
							19.81		
35							21.09	18.10	12.90
							23.06	17.36	
							19.75	17.22	
36							22.87		
37								17.28	
(40.4)			(45.24					16.30	
			35.73					16.05	
(42.1)		(43.75	38.28)	(34.81				20.11	
(50.1)	(53.16)	44.25		36.82)				18.87	
		46.33)						18.84	
38						24.26			
						25.90			
						24.25			
40						24.71	21.12	17.31	
41						25.93			
						25.16			
						25.69			
						25.80			
						26.16			
						24.00			
						25.08			
46B					27.26				
48								15.69	15.00
									13.33
									14.21
									14.13
55					26.29				
61					29.94				
					29.22				

( ) Not simultaneous with 37.

TABLE 10.

ULTRA BAR SHOWING VARIATION IN MEAN FACET NUMBER FOR SEPARATE BOTTLES. ♂♂

Exp.	15°	16°	17.5°	20°	23°	25°	27°	29°	31°
23	56.84	46.77	44.66	32.69		26.59	25.71		16.61
		52.61	42.40	37.32		25.26	22.03		15.00
							22.61		
							25.47	20.09	13.26
							22.39	18.11	17.52
							22.91	20.52	
36							25.58		
							23.84		
37								18.75	
(40.4)			(45.15					17.65	
			45.31					17.25	
(42.1)		(54.57	46.45)	(40.28				19.72	
		52.06		41.00)				20.05	
(50.1)	(62.61)	53.72)						20.23	
38						25.20			
						25.84			
						27.78			
40						26.94	24.36	19.15	
41						28.72			
						27.19			
						28.93			
						28.89			
						28.17			
						28.33			
						27.77			
46B					28.76				
48								18.33	12.88
									13.53
									13.59
									12.85
55					32.20				
61					32.11				
					33.73				

( ) not simultaneous with 37.

TABLE 11. SUMMARY. ULTRA BAR ♀♀

Temperature	15°	16°	17.5°	20°	23°	25°	27°	29°	31°	
Number indiv.	55	101	112	112	94	500	490	629	138	
Mean Facet Number	51.51	43.27	38.57	32.59	28.30	25.24	21.27	17.23	14.56	
Diff. in facets for interval		8.24	4.70	5.98	4.29	3.06	3.97	4.04	2.67	average
Diff. in facets per C°		8.24	3.13	2.40	1.43	1.53	1.98	2.02	1.33	2.76
Mean for Interval		47.39	40.92	35.58	30.49	26.77	23.75	19.25	15.88	average
% Change per C°		17.39	7.64	6.47	4.69	5.72	8.33	10.49	8.37	8.63

TABLE 12. SUMMARY ULTRA BAR ♂♂

Temperature	15°	16°	17.5°	20°	23°	25°	27°	29°	31°	
Number indiv.	65	103	100	130	94	496	538	641	187	
Mean Facet Number	60.81	51.10	45.18	37.20	31.43	27.60	23.70	19.02	14.16	
Diff. in facets for interval		9.71	5.92	7.98	5.77	3.83	3.90	4.68	4.86	average
Diff. in facets per C°		9.71	3.95	3.19	1.92	1.91	1.95	2.34	2.43	3.42
Mean for Interval		55.95	48.14	41.19	34.31	29.51	25.65	21.36	16.59	average
% Change per C°		17.35	8.20	7.74	5.59	6.47	7.60	10.95	14.64	9.82

Temperature	27°	27°	15°	
Exp. number	398	345	513	
No. of individuals ♀	5	10	2	
Average Facet Number	956	810.6	1084	
Range in facet number	886-1082	632-924	912-1256	
No. of individuals ♂		10	1	
Average facet number		849.8	1016	
Range		700-980		

TABLE 13. SHOWING EFFECT OF TEMPERATURE UPON FACET NUMBER IN THE FULL-EYED WILD STOCK.

TAble 14. Q_{10} (Calculated from $Q_{T_1-T_2}$) FOR MEAN FACET NUMBER. ULTRA BAR ♀

Temp.	15°	16°	17.5°	20°	23°	25°	27°	29°	31°
Mean facet number	51.51	43.27	38.57	32.59	28.30	25.24	21.27	17.23	14.56
$Q_{T_1-T_2}$	1.19	1.122	1.184	1.151	1.117	1.189	1.234	1.184	
Q_{10}	5.695	2.1525	1.967	1.1597	1.736	2.375	2.867	2.321	

TABLE 15. Q_{10} Calculated directly for facet number. Ultra bar ♀

Temperature Interval	Q_{10}
15–25°	2.04
17–27°	1.88
20–30°	2.11

TABLE 16. Q_{10} (calculated from $Q_{T_1-T_2}$) FOR MEAN FACET NUMBER. LOW SELECTED

Temp	15°	16°	17.5°	20°	25°	27°	29°	30°	31°
Mean Facet Number	189.00	158.18	127.27	98.88	74.25	55.13	47.40	36.56	28.85
$Q_{T_1-T_2}$	1.195	1.243	1.287	1.331	1.346	1.163	1.296	1.267	
Q_{10}	5.938	4.264	2.744	1.771	4.418	2.128	13.36	10.66	

TABLE 17. Q_{10} Calculated directly for facet number Low selected. ♀

Temperature Interval	Q_{10}
15–25°	2.54
20–30°	2.70

TABLE 18. EFFECT OF TEMPERATURE ON DEVELOPMENT. PERIOD IN DAYS FROM MATING TO HATCHING.

Exp. No. Stock	15°	16°	17.5°	20°	23°	25°	27°	29°	30°	31°	33°
7UnB	34			14		10			9		
16UnB	38	24	19	15		10	10	10			
22 LB	28	20	17	11		10½	9		9½		
		21	17	13		11					
23 UB		21	20	13		10	9½		8 2/3		
			18							11	
		20	18	14		10	8			10	
26 LB							8 1/2	7 3/4		9¼	
27 LB						10 7/8	9 5/8	8 5/8		8 5/8	
29 Wild						8 2/3	7 5/8	8 2/3		8 2/3	
29 UB							10	7		-	-
							12	9		8?	-
29 Wild								8½			12
" "							7¾	7½		7¾	8 2/3
" "							9½	8		9	-
" UB							10	7		-	--
" LB							8 5/8	8½		-	8 2/3
" UB							11	10¾		-	--
" Wild								7			10
35 UB							8	8		10	--
							12	9		12	
							9	7			
36UB							8 1/2	7 3/4			
							8½	8 1/2			
38 UB						11		8 1/2			
						11		8 3/4			
								8 1/2			
								8 3/4			
40 UB						11	9	8			
41 UB						10					
						11					
						11					
						10					
						10					
						10					
						11					
44 UB							9	8½		8½	
Wild								8½		10½	
UB								8½		11	
LB								9		8½	
LB								8½		10	
UB								9		8½	
UB								8½		8½	
UB								8½		8½	
47 Wild							7¾	6¾		6¾	7 11/12
								6¾		6¾	
63 UB								8		9	
										10	

TABLE 18. Continued.

	15	16	17.5	20	23	25	27	29	30	31	33
64 UB										8	
										11	
										9	
										11	
40.4 UB			20								
42		23	21	16							
		23	21	15							
		25	21								
50.1	31	25									
	30	21									
	32	25									
	32	23									
	30	25									
		25									
61 UB					11						
					13						
55 UB					13						
46 UB					10						
Temp.	15	16	17.5	20	23	25	27	29	30	31	33
Average number days immature stage	31.87	22.93	19.20	13.62	11.75	10.37	9.21	8.31	9.02	9.26	9.44
Reciprocal	.0313	.0431	.0521	.0724	.0851	.0964	.1086	.1203	.1109	.1080	.1059

TABLE 19. Q_{10} (Calculated from $Q_{T_2-T_1}$) FOR VELOCITY OF DEVELOPMENT OF THE IMMATURE STAGES.

Temperature	15	16	17.5	20	25	27	29	30	31	33
Velocity	.0300	.0448	.0542	.0769	.0964	.1086	.1203	.1109	.1080	.1059
$Q_{T_2-T_1} = \frac{V_2}{V_1}$	1.49	1.209	1.41	1.25	1.12	1.107	.921	.973	.980	
Q_{10}	53.93	3.50	3.95	1.56	1.76	1.46	0.44	0.76	0.82	

$V_{(T+1)^\circ} = V_{T^\circ} \times Q_1$

$V_{(T+10)^\circ} = V_{T^\circ} \times (Q_1)^{10} = V_{T^\circ} \times Q_{10}$

$\frac{V_1}{V_2}$	-1.084	-1.026	-1.019
Q_{10}	-2.24	-1.29	- 1.10

TABLE 20. SHOWING RATE OF DEVELOPMENT AND RECIPROCALS OF FACET NUMBERS.

	15°	16°	17.5°	20°	23°	25°	27°	29°	30°	31°	33°
Average days in immature period	31.87	22.93	19.20	13.62	11.75	10.37	9.21	8.31	9.02	9.26	9.44
Rate of reciprocal	.0313	.0431	.0521	.0724	.0851	.0964	10.86	12.03	11.09	10.80	10.59
ULTRA-MAK Mean Facets	5.151	43.27	38.77	32.59	28.30	25.24	21.27	17.23		14.56	
Reciprocal	.0194	.0235	.0259	.0307	.0349	.0393	.0479	.0579		.0685	
Low Selected Mean Facets	189.00	158.18	127.27	98.88		74.25	55.13	47.40	36.56	28.85	
Reciprocal	.0053	.0063	.0078	.0091		.0134	.0181	.0216	.0273	.0346	

TABLE 21. SHOWING EFFECTS OF FOOD ON MEAN FACET NUMBER ULTRA-BAR STOCK.

23°		Fleischmann's Compressed Yeast.	Yeast Foam.	Banana.
Exp. 46	♀		27.72±.38	27.33±.36
	♂		28.81±.38	28.77±.38
Exp. 55	♀	23.72±.34	27.53±.73	26.69±.62
	♂	27.37±.27	28.80±.82	32.20±.48
Exp. 61	♀	22.40±.19	24.04±.26	29.54±.34
	♂	25.01±.18	26.92±.32	32.50±.28
27°				
Exp. 71	♀	18.28±.24		20.80±.34
	♂	19.85±.74		22.96±.12

TABLE 22. SHOWING EFFECT OF FOOD ON RATE OF DEVELOPMENT.

	Fleischmann's	Yeast Foam	Banana
Exp. 46		10	10
55	13 10	13 10	14 11
61	10	11	13
71	8		9

Days from mating to emergence of imago.

TABLE 23. EFFECT OF HUMIDITY AND EVAPORATION ON MEAN FACETNUMBER - ULTRA-BAR. EXP. 60

	35% Humidity		60% Humidity		Direct evaporation 35% humid air	Direct evaporation 60% humid air	
Mean ♀ stand dev.	26.59±.32	2.78±.23	28.32±.34	2.96±.28	No larvae. Dried out	32.21±.71	6.05±.50
♂	28.86±.37	3.25±.28	30.14±.33	2.90±.23	No larvae . Dried out	34.48±.90	5.55±.49
Range	21 - 32 23-38		22 -35 24 -35			16-47 26-49	

Temp. 23° - 25°

TABLE 24. EFFECT OF HUMIDITY AND EVAPORATION ON DEVELOPMENTAL RATE. Exp. 60.

	35% Humidity	60% Humidity	Direct evaporation 35% humid air	Direct evaporation 60% humid air
Days mating to emergence of adult	12	12	---	14

TABLE 25. EXP. 6. UNSELECTED BAR. LARVAE SUBJECTED TO 30° FOR PART OF DEVELOPMENT. REMAINDER AT 15°.

Days at 30°	1 ♀	1 ♂	2 ♀	2 ♂	3 ♀	3 ♂	4 ♀	4 ♂	5 ♀	5 ♂	6 ♀	6 ♂	7 ♀	7 ♂	Stock at 15°		Stock at 30°	
Facets 15-44							4	1	7	3	4	2	10	3				
45-74							4	7		10			2	7				
75-104							6	2	4	2	1							
105-134							5	1	3	2								
135-164					2		1	1	2	1								
165-194					3	4	5	1	3	5								
195-224	3	1	7	1	10	4	6	3										
225-254	6	3		2	11	6		2										
255-284	1	1	1	3	2	6	2	1										
285-314		4			1	4		4										
315-344		1				2												
Mean Facet Number	230	279	216	251	221	246	152	224	93	95	44	59	36	48	213	269	39	73
Total days of immature stages	25		24		23		22		22		20		18		31.87		9.02	

TABLE 26. EXP. 45 SHOWING DISTRIBUTION LARVAE WERE ALLOWED TO COMPLETE PART OF DEVELOPMENT AT 27° AND THEN CHANGED TO 15°

No. of days at 27° before transfer to 15°		1		2		3		4		5		6		7		8		9	
		♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Mean facet number	7-10							4	1		1								
	11-14							4	2	7	2	2							
	15-18						1	8	6	15	8	4	1	7		4	1	6	3
	19-22							23	11	19	17	9	5	21	9	14	9	14	6
	23-26					2		8	12	7	7	9	15	17	18	21	28	16	17
	27-30					7	3	2	6		3		2	2	8	5	12	2	7
	31-34					3	3	6	7	Upper range of 27 stock counts							1		1
	35-38					6	3	2	2										
	39-42		1	2		8	4	Lower range of 15° stock counts											
	43-46	5	0	16	2	8	7												
	47-50	3	1	12	7	3	4												
	51-54	1	2	11	10	3	8												
	55-58	1	2	8	16	1	7												
	59-62	1	4	1	5		2												
	63-66	1	0		6		1												
	67-70		1		2		1												
	71-74				2		1												
No. of individuals		12	11	50	60	48	45	57	47	48	38	24	23	47	35	44	51	38	34
		← Larval period. →								← Pupal period →								← Adult period →	

TABLE 27. EXP. 59 SHOWING DISTRIBUTION - LARVAE ALLOWED TO COMPLETE PART OF DEVELOPMENT AT 27°

Days at 27° before transfer to 15°	1		2		2⅜		3I		3II		3¼		3½		3⅝		4			Control 27°	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂		♀	♂
Mean facet No.																					
15-18													5		2		3			6	3
19-22									2				5	1	8	4	8	5		36	23
23-26									3				7	3	11	11	11	14		37	38
27-30									4		1		4	10	3	7	3	11		19	32
31-34 upper range of 27° stock counts									2	2	4	1	8	5		1				4	3
35-38									4	7	3	1	12	4		1					
39-42					1		1		9	5	3	2	12	9	Lower range of 15° stock counts.						
43-46	1		1	2	1	1			7	3	7	7	3	5							
47-50	4		6	2	4	1	9		9	4	4	2	2	6							
51-54	17	2	11	3	9	11	9	3	13	7	2	6	2	5							
55-58	12	7	4	4	8	9	5	1	1	3	3	2	2	2							
59-62	6	7	6	6	6	5	2	4	2	4	1	3	4	1							
63-66	4	7	2	3	3	6	2	11	2	3		2	1	2							
67-70	3	10	2	5		2	1	7		3	1										
71-74	3	5		1				4		2		1									
75-78		2																			
79-82								1													

TABLE 28. EXP. 62- SHOWING DISTRIBUTION IN MEAN FACET NUMBER LARVAE WERE ALLOWED TO COMPLETE PART OF DEVELOPMENT AT 15°

Days at 15° before transfer to 27°	1		2		3		4		5		6		7		8	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
11-14			4						2		1		1			
15-18	5	1	8		5	1	7	2	15	5	13	7	3	1		
19-22	15	16	35	16	25	25	23	15	18	21	17	22	4	6		
23-26	23	26	50	63	15	18	26	32	6	18	8	7	3	1		
27-30	2	12	7	21	3	9	4	12		2	1	1		1		
31-34						2		1							1	
35-38																
39-42															1	
43-46															1	
47-50															1	
51-54															1	
55-58																
59-62																1
63-66																
67-70																1
71-74																
75-78																
79-82																

The bottles were at 27° the first 24 hours.' Then removed to 15° for the number of days indicated before return to 27°

Parents the same as in Exp. 59.

TABLE 29. EXP. 72 DISTRIBUTION OF MEAN FACET NUMBER. ULTRA BAR LARVAE SUBJECTED TO 15° FOR PARTIAL DEVELOPMENT.

Days at 15° before return to 27°		6		7		8		9		10		11		12	
		♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Mean	11-14			1				2							
facet	15-18	1		2	3	2	1	1		1		1			
number	19-22	6	6	4	4	5	3			3	1	1	1		
	23-26	1	2		2	5	1	2		3	4	3	2		
	27-30						2	4	4	2	3	4	3		
	31-34	1	1				2	3	2	1	3	2		1	
	35-38							1	3	1	1	3		1	
	39-42						1	2		2	1	2	1	3	
	43-46							1	1	1		2	3	7	
	47-50										2	1		8	3
	51-54									2	1	2	2	16	7
	55-58							1			2		1	6	8
	59-62									1			2	3	14
	63-66													1	6
	67-70						1						1		8
	71-74												1		1
	75-78														1

The bottles were at 27° the first 24 hours.

Then removed to 15° for the number of days indicated, before subsequent return to 27°.

TABLE 30. SHOWING DISTRIBUTION OF UNSELECTED BAR STOCK.♀♀
EXP. 1,4, 7 & 16.

30°		25°		20°		15°	
Class=4		Class = 8.		Class=12		Class = 21	
18-21	4						
22-25	5						
26-29	11						
30-33	16						
34-37	14						
38-41	5						
42-45	15						
46-49	10						
50-53	6						
54-57	4						
58-61	1	39-46	1				
62-65	2	47.54	8				
66-69	1	55-62	5				
70-73	0	63-70	20	33-44	1		
74-77	2	71-78	22	45-56	0		
78-81	0	79-86	14	57-68	1		
82-85	0	87-94	14	68-80	3		
86-89	1	95-102	14	81-92	4		
		103-110	4	93-104	17		
		111-118	8	105-116	18		
		119-126	2	117-128	27		
		127-134	2	129-140	23		
				141-152	11		
				153-164	8	143-163	3
				165-186	4	164-185	12
						185-205	20
						206-226	28
						227-247	15
						248-268	10
						269-289	0
						290-310	2

TABLE 31. SHOWING DISTRIBUTION OF UNSELECTED BAR STOCK ♂♂
EXP. 1,4,7 & 16.

30°		25°		20°		15°	
Class=7		Class=12		Class=16		Class=27	
29-35	5						
36-42	4						
43-49	6						
50-56	12						
57-63	9						
64-70	13						
71-79	14						
78-84	6						
85-91	3	46-67	5				
92-98	6	68-79	9				
99-105	2	80-91	9	58-73	1		
106-112	2	92-103	16	74-89	1		
113-119	3	104-115	13	90-105	5		
120-126	0	116-127	15	106-121	5		
127-133	2	128-139	14	122-137	14		
134-140	2	140-151	7	138-153	14		
141-147	1	152-163	9	154-169	26		
148-154	1	164-175	2	170-185	24		
155-161	0	176-187	3	186-201	8		
162-168	0	188-199	4	202-217	6	175-201	2
169-175	1	200-211	2	218-233	1	202-228	10
		212-223	1	234-249	3	229-255	12
				25P-265	1	256-282	24
						283-309	10
						310-336	11
						337-363	1
						364-390	0
						391-417	1

TABLE 32. SHOWING DISTRIBUTION OF LOW SELECTED BAR STOCK ♀♀
EXP. 12,22,27.

30°		27°		25°		20°		17.5°		16°		15°	
Class=4		Class=6		Class=7		Class=10		Class=13		Class=16		Class=9	
15-18	0												
19-22	1												
23-26	6												
27-30	10												
31-34	14												
35-38	11	23-28	2										
39-42	9	29-34	4										
43-46	4	35-40	17	29-35	1								
47-50	4	41-46	18	36-42	0								
51-54	1	47-52	36	43-49	5								
55-58	2	53-58	30	50-56	20								
59-62	1	59-64	23	57-63	19								
63-66	0	65-70	13	64-70	26								
67-70	1	71-76	10	71-77	29	54-63	2						
		77-82	2	78-84	23	64-73	9						
		83-88	4	85-91	16	74-83	12						
		89-94	3	92-98	16	84-93	20						
		95-100	2	99-105	3	94-103	18	82-94	4				
				106-112	3	104-113	21	95-107	16				
				113-119	2	114-123	11	108-120	17	103-118	4		
				120-126	2	124-133	10	121-133	21	119-134	13	104-122	1
						134-143	1	134-146	22	135-150	23	123-141	4
						144-153	0	147-159	5	151-166	28	142-160	10
						154-163	1	160-172	7	167-182	17	161-179	12
								173-185	1	183-198	16	180-198	21
								186-198	0	199-214	2	199-217	18
								199-211	1	215-230	1	218-236	9
												237-255	4

TABLE 33. SHOWING DISTRIBUTION OF LOW SELECTED BAR STOCK ♂♂
EXP. 12, 22, 27.

30°		27°		25°		20°		17.5°		16°		15°	
Class=6		Class=8		Class=10		Class=13		Class=16		Class=21		Class=24	
19-24													
25-30	4												
31-36	10	17-24	1										
37-42	7	25-32	0										
	8	33-40	0										
49-54	6	41-48	2										
55-60	4	49-56	17										
61-66	3	57-64	21	39-48	1								
67-72	1	65-72	33	49-58	3								
73-98	3	73-80	29	59-68	10								
79-84	4	81-88	18	69-78	19	52-64							
85-90	3	89-96	12	79-88	19	65-77	2						
91-96	3	97-104	11	89-98	20	78-90	2						
97-102	2	105-112	9	99-108	29	91-103	12						
103-108	1	113-120	6	109-118	21	104-116	29	108					
109-114	1	121-128	2	119-128	14	117-129	21	109-124	3				
115-120	0	129-136	3	129-138	9	130-142	23	125-140	11				
121-126	0	137-144	0	139-148	10	143-155	6	141-156	24				
127-132	1	145-152	2	149-158	3	156-168	6	157-172	24	133-153	1		
		153-160	0	159-68	5	169-181	2	173-188	17	154-174	10		
		161-168	1	169-178	0	182-194	1	189-204	12	175-195	27	156-179	1
				179-188	1			205-220	2	196-216	36	180-203	3
								221-236	1	217-237	13	204-227	27
								237-252	1	238-258	16	228-251	23
										259-279	3	252-275	12
										280-300	1	276-299	4
												300-323	1
												324-347	2
												348-371	0
												372-395	0
												396-419	1

TABLE 34. SHOWING DISTRIBUTION OF INDIVIDUALS IN ULTRA BAR.

Facet numbers	15°	16°	17°.5	20°	23°	25°	27°	29°	31°	15°	16°	17°.5	20°	23°	25°	27°	29°	31°
0																		1
1																		1
2																		2
3																		3
4																		4
5									1									6
6									1									14
7									4									16
8									6								1	21
9								2	8								6	19
10								5	15								1	15
11								8	20								9	11
12								14	26								17	10
13							2	19	16							1	10	2
14							2	46	22							1	16	2
15							11	74	22							1	36	1
16							11	63	22							1	40	1
17							22	77	16							8	55	
18							38	76	7							20	84	
19							55	72	3						1	26	96	
20							59	52	2						6	34	83	
21				1	1	1	50	48	1						7	53	82	
22				2	1	2	66	29						2	14	67	55	
23				1	5	11	61	17						1	23	59	85	
24				3	8	38	38	12						3	27	55	20	
25				2	9	59	28	10						3	54	55	9	
26				4	8	72	15	3						3	51	57	10	
27				2	7	58	9							3	58	30	2	
28				7	6	50	6							5	59	22		
29				6	10	32							1	11	59	21		
30				7	10	13							0	8	59	9		
31		1	3	12	7	2	1						4	5	49	6		
32		0	5	13	6	7							5	12	24	8		
33		2	10	8	3	2	1						6	15	12	2		
34		0	3	10	2								7	2	9	1		
35		4	6	6	1							1	9	5	2	0		
36		3	12	6								1	4	3	1			
37		6	10	3								2	5	3				
38		11	11	2								5	9	2				
39	1	3	7	1								9	4	1				
40	2	11	5	1								12	7					
41	1	7	6	1								7	8					
42	4	10	5	3								9	4					
43	3	5	3									14	8					
44	3	3	4									8	6					
45	3	5	4									6	4					
46	3	3	4									4	1					
47	3	5	4	1								1						
48	3		4															
49	5	2	3							2	7	2	1					
50	1	2	1							1	5	1	1					
51	1	3	0							2	9	1	1					
52	2	2	1							3	9	4	1					
53	2	2	1							3	6	1						
54	2	2								2	7	3						
55	2									0	4	1						
56	1	1								5	5	0						
57	1	1	1							4	2	1						
58	3		1							3	3	1						
59										4	4	1						
60	1									2	0	1						
61	1	1								1	4	1						
62	2									3	3	1						
63										4	1							
64										4	0							
65	1									2	1							
66	1									1	4							
67	1									3	3							
68										1	0							
69	1									3	1							
70										0	3							
71										1	0	1						
72	1									1	1							
73										1	1							
74										1	1							
75										1	1							
76																		
77																		
78																		
79																		
80																		
81																		
82																		
83										1								
84																		
85										1								

Females | Males

TABLE 35. COEFFICIENT OF VARIABILITY AT VARIOUS TEMPERATURES UNSELECTED BAR STOCK ♀♀

	15°	20°	25°	30°
Mean facets	213.67±2.12	122.20±1.46	81.09±1.21	39.66±0.87
Stand. dev.	29.77±1.48	23.45±1.02	19.19±0.85	12.73 0.61
Coef.of var.	13.93	19.19	23.66	32.09

TABLE 36. COEFFICIENT OF VARIABILITY AT VARIOUS TEMPERATURES LOW SELECTED BAR ♀♀

	15°	16°	17.5°	20°	25°	27°	29°	30°	31°
Mean facets	189.00±2.23	158.18±1.56	127.27±1.49	98.38±1.27	74.25±.87	55.13±.73	47.40±.63	36.56±.79	28.85±.41
Standard deviation	29.43±1.57	23.58±1.10	22.19±1.04	19.23± .90	16.55±.61	13.88±.52	9.31±.44	9.37±.56	6.07±.29
Coefficient of variability.	15.57	14.90	17.43	19.44	22.28	25.17	19.64	25.63	21.04

TABLE 37 COEFFICIENT OF VARIABILITY AT VARIOUS TEMPERATURES- ULTRA BAR ♀♀

	15°	16°	17.5°	20°	23°	25°	27°	29°	31°
Mean facet number	51.51±.70	43.27±.59	38.37±.32	32.59±.32	28.30±.24	23.24±.09	21.27±.10	17.23±.10	14.56±.18
Standard deviation	7.69±.49	5.75±.41	5.03±.23	5.06±.22	3.52±.17	3.10±.07	3.32±.07	3.23±.07	3.16±.13
Coefficient of variability	14.93	13.28	13.04	13.18	12.44	12.28	15.61	18.74	21.70

TABLE 38. COEFFICIENT OF VARIABILITY AT VARIOUS TEMPERATURES UNSELECTED BAR STOCK. ♂♂

	15°	20°	25°	30°
Mean facet	269.76±3.22	161.76±2.20	120.52±2.31	73.54±1.99
Stand. dev.	40.24±2.25	34.02±1.54	35.65±1.62	28.28±1.39
Coef. of var.	14.91	21.03	29.69	38.54

TABLE 39. COEFFICIENT OF VARIABILITY AT VARIOUS TEMPERATURES LOW SELECTED BAR ♂♂

	15°	16°	17.5°	20°	25°	27°	29°	30°	31°
Mean facet	240.81±2.82	207.55±1.90	164.66±1.68	122.88±1.42	103.12±1.41	79.46±1.18	65.58±.90	57.85±2.13	41.70±.69
Stand. dev.	36.00±1.99	29.18±1.34	24.29±1.19	21.52±1.00	26.76±1.00	22.62±.83	13.35±.63	24.64±1.51	10.29±.48
Coef. of var.	14.98	14.06	14.75	17.51	25.95	28.46	20.35	42.59	24.67

TABLE 40. COEFFICIENT OF VARIABILITY AT VARIOUS TEMPERATURES ULTRA BAR ♂♂

	15°	16°	17.5°	20°	23°	25°	27°	29°	31°
Mean facet	60.81±.74	51.10±.40	45.18±.30	37.20±.30	31.43±.24	27.60±.09	23.70±.11	19.02±.08	14.16±.17
Stand dev.	8.85±.52	6.05±.28	4.43±.21	4.93±.21	3.54±.17	3.29±.07	3.79±.08	3.04±.06	3.39±.12
Coef. of var.	14.55	11.84	9.81	13.25	11.26	11.92	15.99	15.98	23.94

TABLE 41. SHOWING THE SEX COEFFICIENT FOR THE STOCKS AT VARIOUS TEMPERATURES.

	15°	16°	17.5°	20°	23°	25°	27°	29°	30°	31°
UNSELECTED BAR STOCK										
Mean facet number ♀	213.67			122.20		81.09			39.66	
Mean facet number ♂	269.76			161.76		120.52			73.54	
Sex Coefficient	.7'2			.755		.673			.539	
LOW SELECTED BAR STOCK.										
Mean facet number ♀	189.00	158.18	127.27	98.88		74.25	55.13	47.40	36.56	28.85
Mean facet number ♂	340.21	207.55	164.66	122.88		103.12	79.46	65.58	57.85	41.70
Sex Coefficient	.786	.762	.772	.804		.720	.693	.723	.631	.692
ULTRA BAR STOCK										
Mean facet number ♀	51.51	43.27	38.57	32.59	28.30	25.24	21.27	17.23		14.56
Mean facet number ♂	60.81	51.10	45.18	37.20	31.43	27.60	23.70	19.02		14.16
Sex Coefficient	.847	.846	.853	.876	.900	.914	.897	.905		1.028

	P'						F'at 27°					
	15°		20°		27°		P₁at 15°		P₁at 20°		P₁at 27°	
12-15					1				1		1	
16-18					7	2	1		4	2	3	2
19-21					13	6	4	3	26	11	15	7
22-24					10	11	11	15	12	28	10	14
25-27					4	9	10	14	5	15	1	8
28-30			4				2	5		1		
31-33			9					1				
34-36			6	6								
37-39	1		8	8								
40-42	1	1	2	12								
43-45	2		2	9								
46-48	2	3	1									
49-51	2											
52-54	7			2								
55-57	1	4										
58-60	1	1										
61-63	1	2										
64-66		3										
67-69		1										
70-72		1										
73-75		1										

TABLE 42. SHOWING DISTRIBUTION OF PARENTS AND OFFSPRING. PARENTS REARED AT 15°- 20°- 27°. OFFSPRING AT 27°

Parents reared at	15° ♀	15° ♂	20° ♀	20° ♂	27° ♀	27° ♂	
Mean of parents	50.50±.96	58.04±1.35	35.50±.54	40.60±.48	20.80±.34	22.96±.12	
Standard deviation	6.05±.67	8.28±.95	4.53±.38	4.29±.34	3.02±.24	2.43±.08	
Mean of offspring	23.67±.35	24.85±.28	20.85±.24	23.12±.24	20.50±.29	22.68±.31	Offspring reared at 27°
Standard deviation	2.76±.25	2.53±.20	2.61±.18	2.80±.17	2.39±.20	2.56±.22	

TABLE 43. SHOWING MEAN FACET NUMBER & STANDARD DEVIATION OF PARENTS AND OFFSPRING.

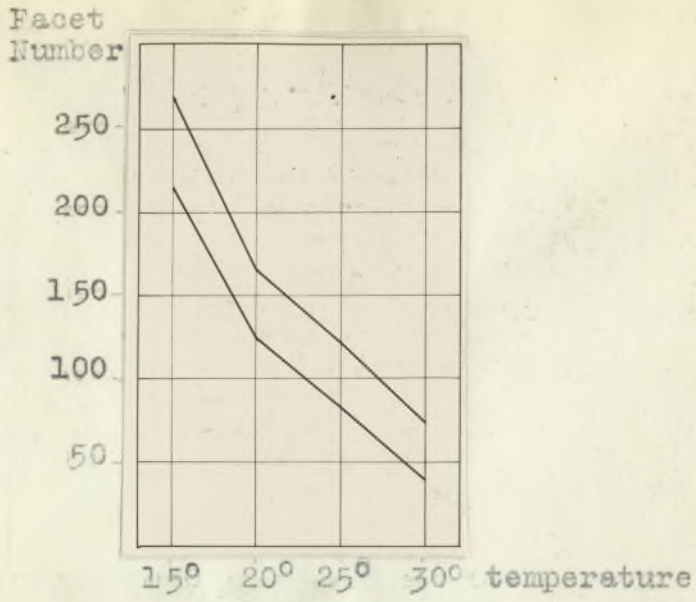

Figure 1. Temperature effect on mean facet number in Unselected bar stock. The upper curve is that of the males, the lower one is that of the females.

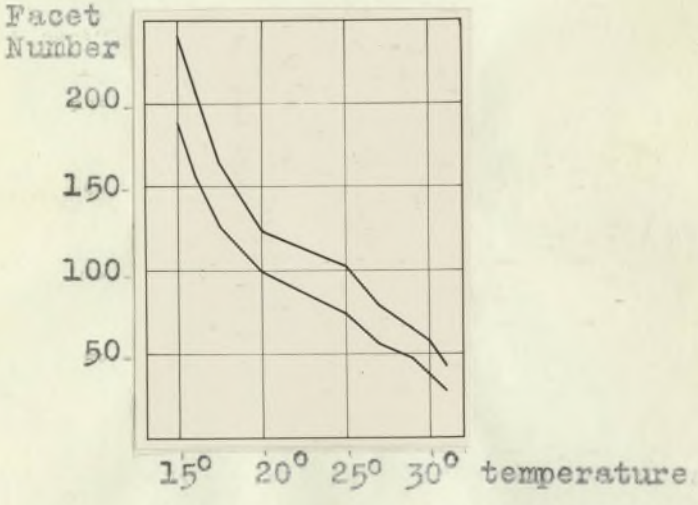

Figure 2. Temperature effect on facet number in Low Selected bar stock. The upper curve is that of the males and the lower is that of the females.

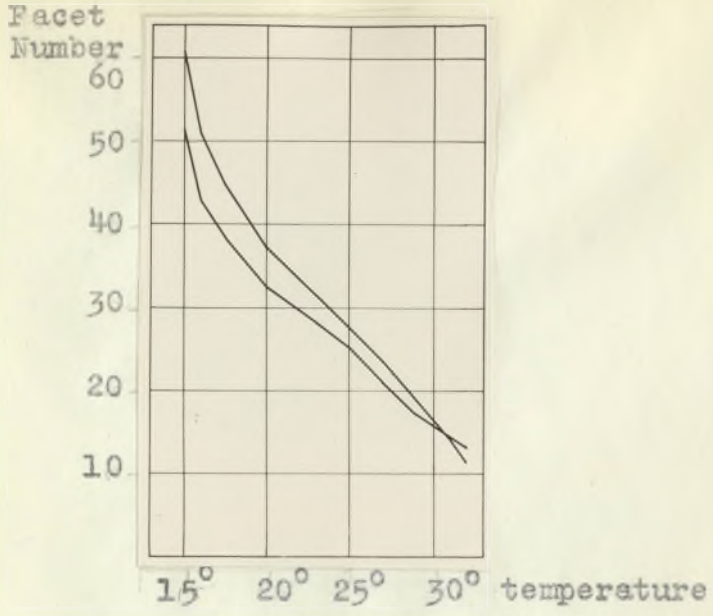

Figure 3. Temperature effect on mean facet number in Ultra bar stock. The upper curve is that of the males, the lower one is that of the females.

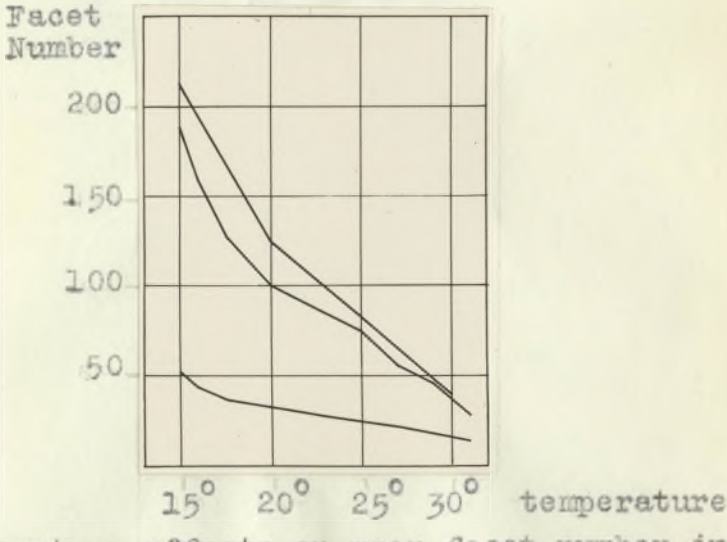

Figure 4. Temperature effects on mean facet number in the three bar stocks compared. These curves are for the females only. The lower one is that of the Ultra-bar stock; the middle one is that of the Low Selected bar stock; and the upper one is that of the Unselected bar stock.

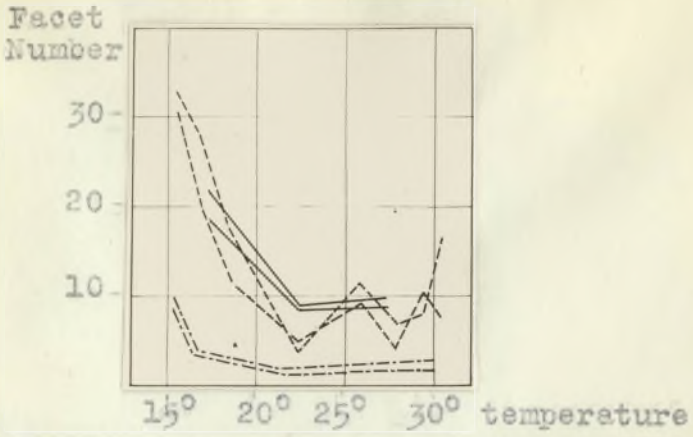

Figure 5.

Number of facets change in the mean accompanying one degree change in temperature. The solid line represents the Unselected bar stock. the broken line represents the Low Selected bar stock; the dot and dash represents the Ultra bar stock. The upper one of a pair represents the males in each case.

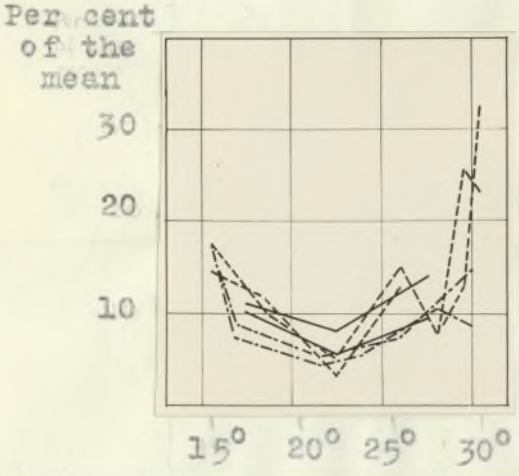

Figure 6. Percentage change in the mean facetnumber accompanying a change of one degree in temperature. The solid line represents the Unselected bar stock; the broken line represents the Low Selected bar stock, and the dot and dash represents the Ultra bar stock. The upper one of a pair represents the males in each case.

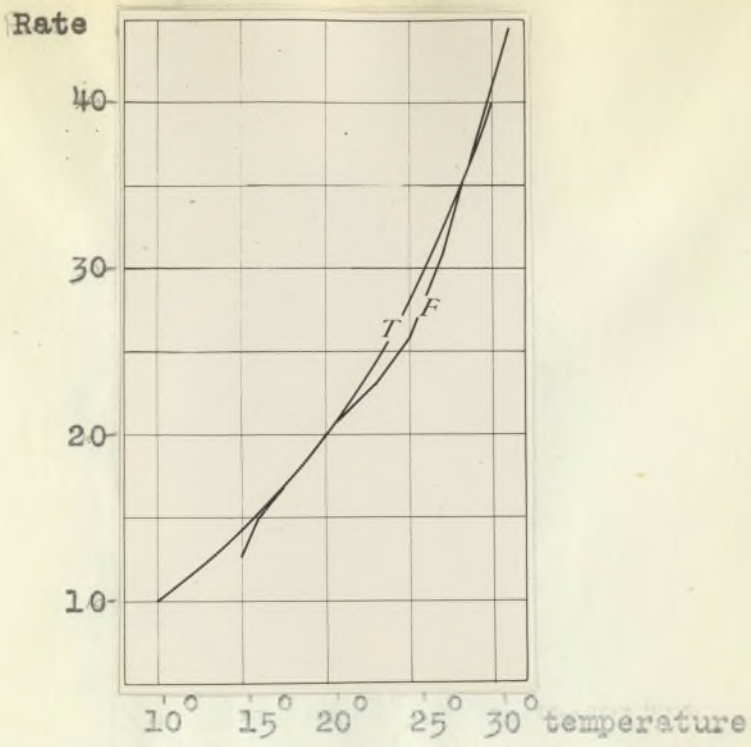

Figure 7. A theoretical van't Hoff curve (T) rate at 10°=10, rate at 20° = 20 rate at 30°= 40. The reciprocal of the Ultra bar female facet curve (F) is shown superimposed. The curves were thrown into juxtaposition by taking the value 20 for facets at 20° and then calculating the remaining values by applying $Q_{(T_1 - T_2)}$ as given in table.14.

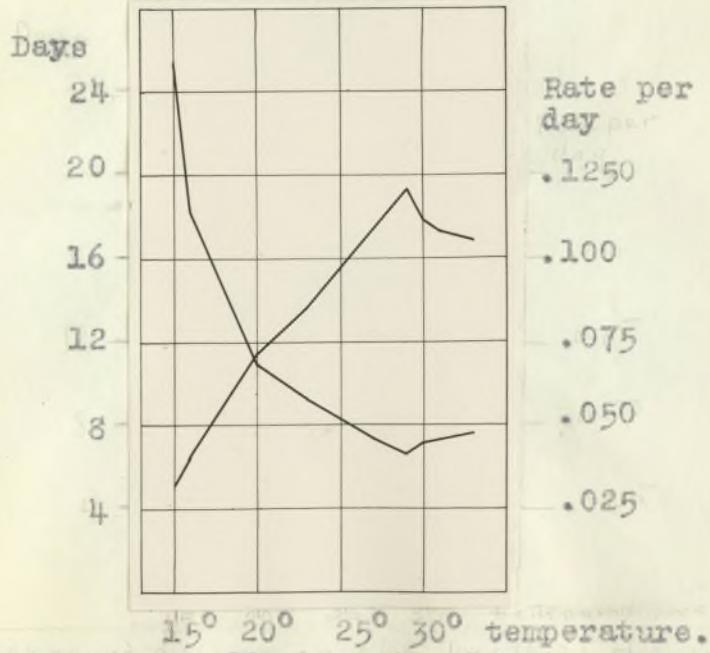

Figure 8. Temperature effect on the length of the immature stages and on the rate of development. The curve that starts at the top to the left in the figure represents the number of days from mating of the parents to the emergence of the mature offspring. The reciprocal curve represents the percentage of the total period completed in one day.

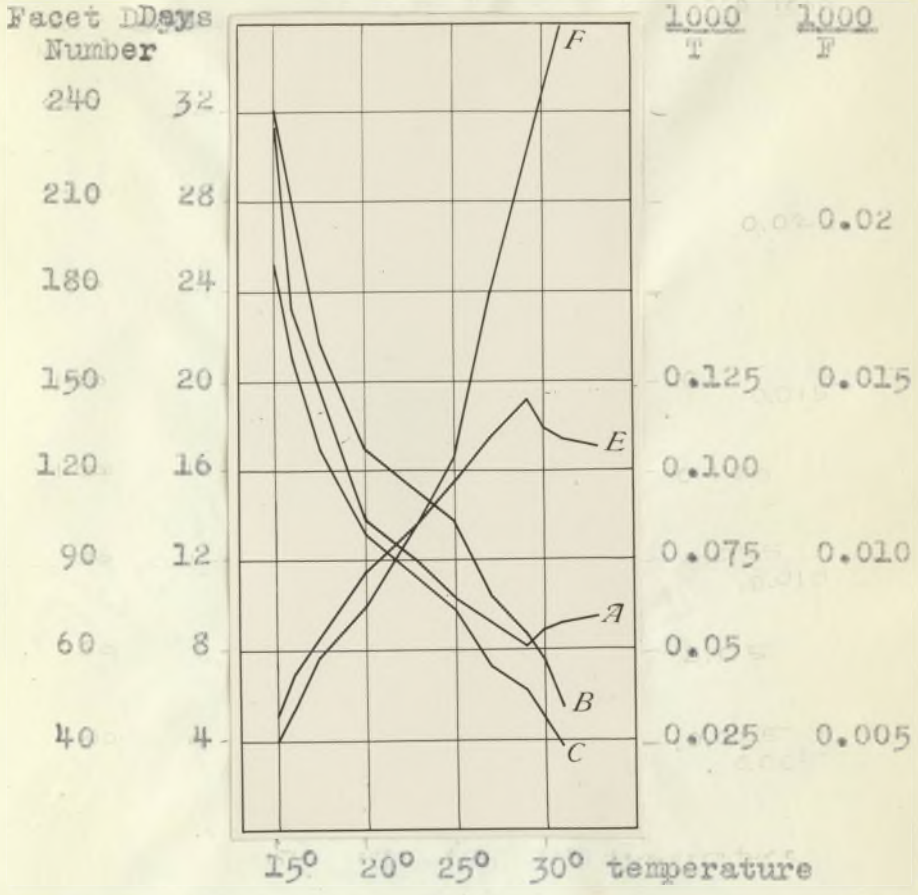

Figure 9. The Low Selected bar stock facet curves, superimposed on the curve for the length of development of the immature period. These curves are thrown into juxtaposition by arranging the scale so that the development curve A lies about half way between the male facet curve B and the female facet curve C. The reciprocal curve E for the rate of development and the reciprocal of facet number of the female F are likewise brought into comparison by arranging the scale of values.

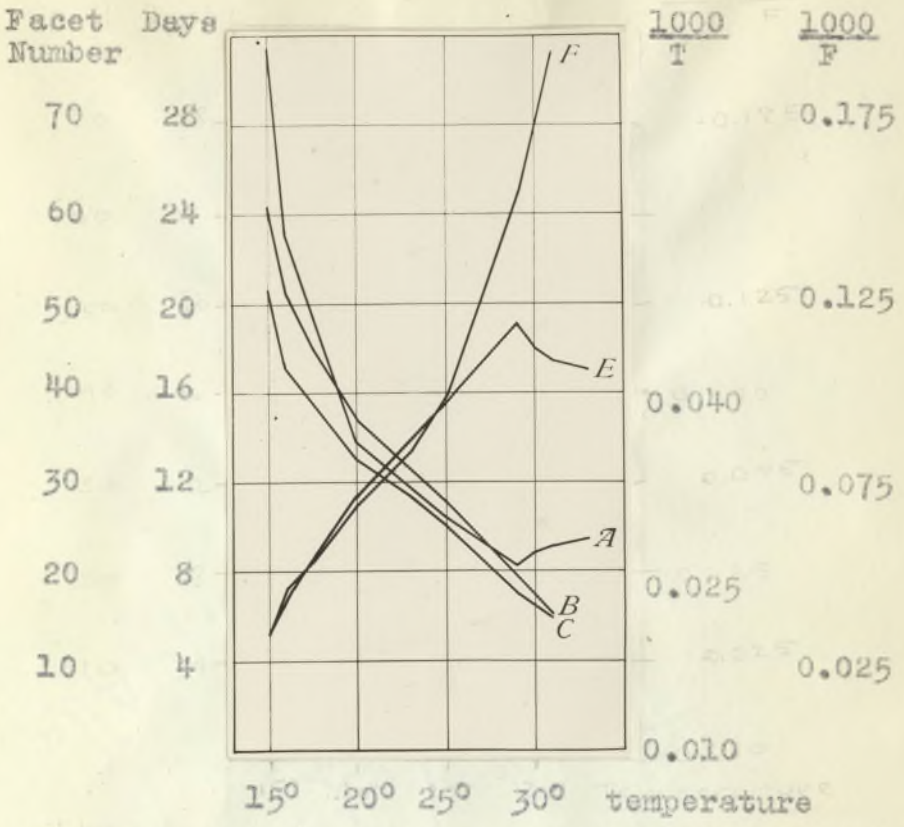

Figure 10. The Ultra bar stock facet curves superimposed on the curve for the length of development of the immature period. The curve A represents the number of days from the mating of the parents to the emergence of the mature offspring. The curve B is for the facet numbers in the male, while C represents those of the female. E is the reciprocal or rate of development per day curve, while F represents the reciprocals of the female facet numbers.

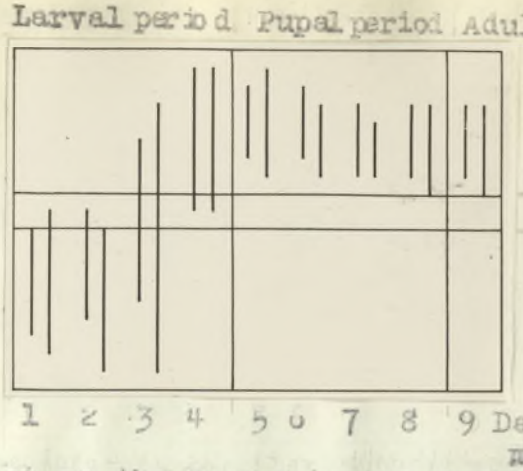

Figure 11. The effect on the range in the facet number in Ultra bar as a result of subjecting successive bottles from the same parentage to varying periods of time at 27° before subsequent development at 15°. After mating, the first bottle was left 24 hours at 27° and then removed to 15°; the second bottle was at 27° for the first two days or 48 hours; the third was at 27° for the first three days, etc. The first vertical line of a pair represents the range of the female counts, the second that of the males in a single bottle. Those cultures to the left of the first full vertical line were in the larval stage when the transfer from 27° to 15° was made. Those between the two full vertical lines were in the pupal stage at the time of transfer.

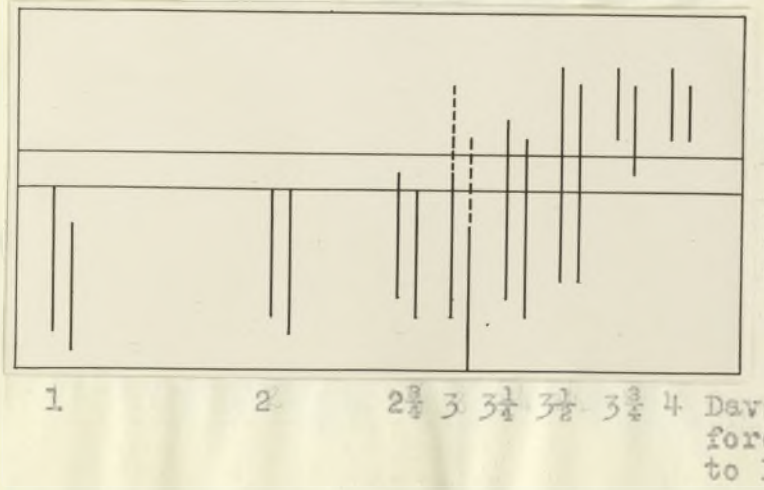

Figure 12. The effect on the range in the facet number in Ultra bar as a result of subjecting successive bottles to 27° for 1, 2, 2¾, 3, 3¼, 3½, 3¾ and 4 days respectively.

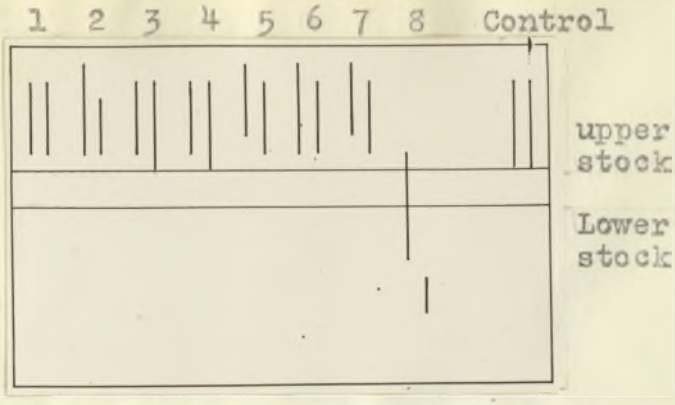

Figure 13. Effect on range of facet number in Ultra bar as a result of subjecting successive bottles to varying periods at 15° before subsequent development at 27°.

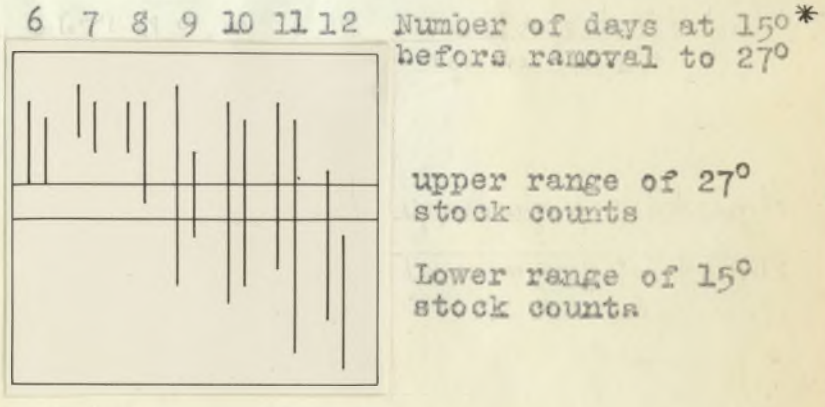

Figure 14. Duration of the effective period at 15°. Results on range of subjecting successive bottles to varying length of time at 15° before subsequent development at 27°.

* Following an initial day at 27°

Figura 15. Camera lucida drawings of the heads of two Ultra bar females. The one on the left has 21 facets and was raised at 27°. The one on the right has 48 facets. She was raised at 15°. The magnification is the same in both drawings.

VITA.

Joseph Krafka Jr. was born August 14, 1890 at Ottumwa, Iowa. He received the degree of Bachelor of Arts from Lake Forest College in 1914 and the degree of Master of Arts in 1915. During the last two years he acted as assistant in Biology. The summers of 1914 and 1915 were spent at the Marine Biological Laboratory at Cold Spring Harbor, Long Island, New York. During the year from September 1915 to September 1916 he was employed as research assistant at the Station for Experimental Evolution, Carnegie Institution of Washington, Cold Spring Harbor, Long Island, New York. In September 1916 he came to the University of Illinois as research assistant and as a graduate student in zoology.

PUBLICATIONS.

1915. A Key to the Families of Trichopterous Larvae. Canadian entomologist, 47; 217-226; 2 plates.