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

PART III.

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The Effect of Temperature upon Variability.

Coefficient of Variability at Different Temperatures.

This study gives some interesting data on the question of individual variability at the various temperatures. The distribution of the counts of Ultra-bar are given in Table XIX. Here the class size is 1 facet. Particular attention is called to the normal distribution in all cases.

An argument for the genetic stability of the Ultra-bar stock is found in 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 departures.

The mean, standard deviation, and coefficient of variability for all three stocks are given in Tables XX to XXII. Two things are apparent: (1) variability increases with the temperature when measured by the coefficient of variability; and (2) the variability of the Ultra-bar stock is much lower than that of the other two stocks. Both these generalizations have their exceptions. Their reliability as compared to statements made by other writers will be discussed later.

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TABLE XIX.

Showing the Distribution of the Facet Counts in the Stock Experiments on Ultra-Bar.

Facet No.	Temperature.																	
	15	16	17.5	20	23	25	27	29	31	15	16	17.5	20	23	25	27	29	31
	Females.									Males.								
5								1	1									1
6									1									1
7									1								1	4
8									2									4
9								2	3									6
10								5	4								6	8
11								8	6								1	15
12							2	14	14								9	20
13							5	19	16							1	10	16
14						1	2	46	21							1	17	26
15						2	11	74	19							1	36	22
16						2	11	63	15							1	40	22
17						1	22	77	11							8	55	16
18						5	38	76	10							20	84	7
19						5	58	72	8						1	26	96	9
20						14	59	52	2						6	34	83	3
21				1	1	26	66	48	2						7	53	82	3
22				2	1	44	61	29	0						14	67	55	2
23				1	5	32	38	17	1					2	23	59	25	1
24				3	8	61	38	12	1					1	27	55	20	1
25				2	9	59	28	10						3	54	55	9	
26				4	8	72	17	3					1	3	51	57	10	
27				2	7	58	15	2					0	3	58	30	2	
28				7	11	50	9						2	5	59	22		
29				6	10	38	8						4	11	59	21		
30				7	10	13							5	8	39	9		
31		1	3	12	7	8	1						6	5	45	8		
32		0	5	13	6	7							7	12	25	6		
33		2	10	8	3	2	1						7	15	12	2		
34		0	8	10	2								9	12	9	1		
35		3	9	6	3								9	5	5	0		
36		4	8	4	2							1	4	3	1			
37		3	12	6	1						2	2	12	3	1			
38		6	10	3			1				1	1	7	2				
39	1	10	11	5							0	2	8	1				
40	0	3	3	1							1	5	4					
41	1	8	7	4							3	9	14					
42	2	11	0	1						1	4	10	8					
43	4	7	5	0						0	3	10	6					
44	3	10	6	3						1	2	7	4					
45	3	5	3	0						1	1	10	0					

TABLE XIX—*Concluded.*

Facet No.	Temperature.																	
	15	16	17.5	20	23	25	27	29	31	15	16	17.5	20	23	25	27	29	31
	Females.									Males.								
46	3	3	0	0						0	0	8	1					
47	3	4	2	1						0	6	9	0					
48	3	4	4							0	10	11						
49	5	2	3							2	7	2						
50	1	2	1							1	5	1						
51	1	3	0							2	9	1						
52	2	2	1							3	9	1	1					
53	2	2	1							3	6	4						
54	5	2								2	4	3	1					
55	2	0								2	7	1				1		
56	1	1								0	4	0						
57	1	1								5	5	1						
58	3	1								4	5	0						
59	0	0								4	2	1						
60	1	0								2	1							
61	1	1								3	3							
62	2									4	1							
63	0									4	1							
64	0									2								
65	1									0								
66	1									1								
67	1									4								
68	0									3								
69	1									1								
70	0									0								
71	0									3								
72	1									1	1							
73	0									0								
74										1								
75										1								
76										1								
77										1								
78																		
79																		
80																		
81																		
82																		
83										1								
84																		
85										1								

TABLE XX.

Coefficient of Variability at the Various Temperatures. Unselected Bar Stock. Females.

Temperature.	Mean facet No.	Standard deviation.	Coefficient of variability.
°C.			
15	213.67 ± 2.12	29.78 ± 1.48	13.94
20	122.20 ± 1.46	23.45 ± 1.02	19.19
25	81.08 ± 1.21	19.19 ± 0.85	23.67
30	39.66 ± 0.87	12.73 ± 0.61	32.10

TABLE XXI.

Coefficient of Variability at Various Temperatures. Low Selected Bar Stock. Females.

Temperature.	Mean facet No.	Standard deviation.	Coefficient of variability.
°C.			
15	189.00 ± 2.26	29.77 ± 1.58	15.75
16	158.20 ± 1.56	23.58 ± 1.10	14.90
17.5	127.27 ± 1.49	22.19 ± 1.04	17.43
20	98.88 ± 1.27	19.23 ± 0.90	19.45
25	74.25 ± 0.87	16.55 ± 0.61	22.29
27	55.13 ± 0.73	13.88 ± 0.52	25.18
29	47.40 ± 0.63	9.31 ± 0.44	19.64
30	36.56 ± 0.79	9.37 ± 0.56	25.63
31	28.85 ± 0.41	6.07 ± 0.29	21.04

TABLE XXII.

Coefficient of Variability at Various Temperatures. Ultra-Bar Stock. Females.

Temperature.	Mean facet No.	Standard deviation.	Coefficient of variability.
°C.			
15	51.51 ± 0.70	7.69 ± 0.49	14.93
16	43.27 ± 0.39	5.83 ± 0.28	13.47
17.5	38.57 ± 0.32	5.03 ± 0.23	13.04
20	32.59 ± 0.32	5.06 ± 0.22	15.53
23	28.30 ± 0.24	3.52 ± 0.17	12.44
25	25.24 ± 0.09	3.12 ± 0.07	12.36
27	21.27 ± 0.10	3.35 ± 0.07	15.75
29	17.23 ± 0.08	3.23 ± 0.06	18.74
31	14.57 ± 0.18	3.16 ± 0.13	21.69

The Sex Coefficient at Different Temperatures.

A marked sexual difference exists in all 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 ratio.

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

Inheritance of Temperature Effects.

Comparison of Offspring Raised at 27°, from Parents Reared at 15, 20, and 27°, Respectively.

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 an inherited effect, Experiment 51 was designed. Flies reared for one generation in the stock experiments at 15, 20, and 27° were used as parents in cultures that were made up under conditions as nearly alike as possible. The offspring from the 15° parents, from the 20° parents, and from the 27° parents were thus allowed to develop simultaneously at 27°.

The distribution of the facet counts of the parents and the offspring is given in Table XXIII. The mean facet values and the standard deviations are given in Table XXIV. The mean facet number, the standard deviation, and the distribution of the F_1 stock reared at 27° are characteristic of the 27° stock counts although those of the parents are markedly different. There is no inherited effect of temperature upon facet number in this case.

TABLE XXIII.

Showing the Inherited Effect of Temperature. Distribution of Facet Number of Parents Reared at 15, 20, and 27°, Respectively, as Compared to Their Offspring All of Which Were Reared Simultaneously at 27°.

Facet No. classes.	Parents reared at.						Offspring reared at 27° from parents at.					
	15°		20°		27°		15°		20°		27°	
	Distribution of individuals.											
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 XXIV.

Mean Facet Number and Standard Deviation of Parents Reared at 15, 20, and 27°, and of Their Offspring Reared at 27°.

Parents reared at.	Mean facet No.	Standard deviation.	Offspring reared at 27° from parents reared at.	Mean facet No.	Standard deviation.
°C.			°C.		
15	50.50 ± 0.96	6.05 ± 0.67	15	23.67 ± 0.35	2.76 ± 0.25
	58.94 ± 1.35	8.28 ± 0.95		24.85 ± 0.28	2.53 ± 0.20
20	35.50 ± 0.54	4.53 ± 0.38	20	20.85 ± 0.24	2.61 ± 0.18
	40.60 ± 0.48	4.29 ± 0.34		23.12 ± 0.24	2.80 ± 0.17
27	20.80 ± 0.34	3.02 ± 0.24	27	20.50 ± 0.29	2.39 ± 0.20
	22.96 ± 0.12	2.43 ± 0.08		22.68 ± 0.31	2.56 ± 0.22

DISCUSSION.

Temperature as a Factor in the Mechanism of Development.

Direct Effect of Temperature upon Growth, Size, Number of Parts, Structure, and Color.

Ordinarily temperature is not a factor capable of modifying structure to any marked extent. Certainly structural variations are in no way comparable with the variations in rate at which they are brought about. The capacity to develop specific color, size, and form is an heritable characteristic; *e.g.*, the present study involves the white-eyed mutant of *Drosophila*, of which all individuals are white-eyed regardless of the temperature at which they develop.

Many organisms, however, exhibit variations in their structural characteristics which may be considered as a direct response to temperature.

Among the earlier investigators of temperature effects on structure were Merrifield, Weismann, Standfuss, Fischer, and Dorfmeister.[1] The chief object of their experiments was the production by environmental manipulation of the various racial and polymorphic forms in the Lepidoptera.

Vernon (1895) found that the size relations between various parts of the echinoderm larvæ could be modified in response to different temperatures at which they developed. Standfuss (1895) found a reduction in the size of the imagos, as a result of rearing lepidopterous larvæ at high temperatures. This he ascribed to the indirect effect of insufficient nourishment.

Tower found that by subjecting larvæ of *Leptinotarsa decemlineata* to various temperatures he could affect the amount of pigmentation in the adult. His results are unique in that an increase from the mean temperature range of the species (22.5°C.) had 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 found a tendency toward melanism with an increase in temperature due to the reduction in 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 relations can be worked out for them.

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[1] For a complete review, see Bachmetjew.

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.

Baur cites a case of *Primula sinensis* which at ordinary temperatures produces red flowers. If a plant is subjected to a temperature of 30–35°C. a few weeks before blooming, the flowers will be white. If the plant is returned to 15–20°C., the buds opening immediately will still be white but those developing later will be red. As Baur points out, white cannot be said to be inherited, red cannot be said to be inherited, but rather the capacity to produce red flowers at 15° and white ones at 30° is the thing inherited.

Hoge found a race of *Drosophila* in which one or more legs showed reduplication. Under ordinary cultural conditions only about 10 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 the character could be raised to practically 100.

Roberts found that a temperature difference of 4–5° C. had a direct effect on the length of the wing in the mutant "vestigial" of *Drosophila,* much greater than twenty-nine generations of selection had produced.

Bar eye is a sex-linked factor that reduces the number of facets in the adult *Drosophila* from 1,000 to 70. Its Mendelian behavior is clear cut and regular. As shown in this paper, however, the number of facets produced, when this factor is present, is dependent upon the specific temperature at which a definite stage in larval development is passed.

In the first three examples only two temperatures are involved. Obviously no quantitative measure can be applied although the results are very definite.

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

In certain cases other environmental factors may be said to determine form. Morgan has shown that a definite amount of moisture is necessary for the development of the abnormal abdomen in *Drosophila.* Metz has several mutants that depend on specific cultural conditions for their recognition.

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

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 affected very little by temperature, while in the bar-eyed mutant there is a very marked effect. It is also evident that the effect is produced only through 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 nearly equal amounts. The rates are increased at the higher temperatures, but at the same time the length of time of the reactions is proportionally shortened, thereby producing a constant number of facets (N) in the full eye.

In the bar eye a new condition has come about. The facet number is reduced to about $\frac{1}{4}$ that of the full eye at 15° and to about $\frac{1}{24}$ at 27° in the Low Selected line. In Ultra-bar the reduction is even greater; $\frac{1}{14}$ at 15° and $\frac{1}{40}$ at 27°.

Hypothesis 1. Reduction in Facet Number $\left(\frac{N}{a}\right)$ *Due to a Reduction in the Facet-Forming Substances* $\left(\frac{n}{a}\right)$.—As in the case of the full eye, increased rates at the higher temperatures with a decrease in the time of the reaction would produce a constant number of facets from a given amount of material at all temperatures.

Hypothesis 2. Surface Tension.—The number of facets in the bar-eyed stocks varies inversely with the temperature. The reaction thus has a negative temperature coefficient suggesting physical phenomena and particularly surface tension. The values of Q_{10} are far too high even to approximate the coefficients of any of the possible physical phenomena. Furthermore, if surface tension were the factor involved, we should expect it active in the full eye also, there producing similar temperature effects as in the bar.

Hypothesis 3. Reduction in the Amount of Facet-Producing Material Plus a Rate of Facet Production Independent of the Temperature.—In this case, the independent rate working through an increased time interval at the low temperatures would produce the greater number of facets as observed in the bar eye. However, when we apply the independent rate to full eye 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 will be proportionally lengthened. At the higher temperatures the rate will increase while the time is proportionally shortened. Its action would therefore be constant and we would have the same number of facets at all temperatures.

Hypothesis 5. Considering the Reduction in Facet Number to Be Due to an Inhibitor, Constant in Amount, but with a Rate Independent of the Temperature.—Under these conditions the inhibitor working through an increased time interval at the lower temperatures would produce a greater reducing effect and we would find more facets at the higher temperatures.

Hypothesis 6. Considering the Amount of Inhibitor to Be a Function of the Temperature, and that More of It Is Produced at High Temperatures than at Low.—Obviously this condition would explain the results obtained in bar, but it is merely restating the question in another form, as we should then have to explain why more inhibitor was produced at one temperature than at another.

Hypothesis 7. Considering the Decrease in Facet Number to Be Due to an Inhibitor the Temperature of Which Coefficient Differs from That of the Normal Facet-Producing Reaction.—Let N be the normal number of facets in the full eye. Let nt be the length of the period at $T_1°$ during which facet rudiments are being produced. t is the length of the period at $T_2°$.

In full eye, at $T_1°$ N facets are formed at a rate of $\frac{N}{n}$ per t for a period of nt; at $T_2°$ N facets are formed at a rate of N per t for a period of t.

In bar eye, N is reduced to Bx at $T_1°$, to By at $T_2°$.

Facets are formed then at the rate of $\frac{Bx}{n}$ per t at $T_1°$.

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

Facets are produced at the rate of By per t at $T_2°$.

Facet number is reduced at the 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 $T_1°$

$$Q_{T_2 - T_1} = n$$

N = rate of production at $T_2°$

		When
$\frac{N - Bx}{n}$ = rate of reduction at $T_1°$	$Q_{T_2 - T_1} = n$	$Bx = By$
$N - By$ = rate of reduction at $T_2°$	$Q_{T_2 - T_1} > n$	$Bx > By$
	$Q_{T_2 - T_1} < n$	$Bx < By$

In all the bar 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.

How can we explain the differences for the various bar-eyed stocks? From the above formulas it is obvious that the greater the difference between Bx and By the greater will be the difference between the Q_{10} for full and for bar. Bar is a changed condition which differs from the full in number of facets and also in the temperature coefficients of some of the reactions concerned in facet production. 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 values of Bx and By, its temperature coefficient is really nearer that of the full than is that of the other bar stock. Ultra-bar is then not an increased condition of both these factors. The reversed change in the temperature coefficient may be a question of the concentration of the inhibitor.

Period during Which the Character of a Certain Structure Is Determined as Shown by the Temperature Effects.

Vernon[2] sums up the work of this nature on Lepidoptera. Dorfmeister concluded that the temperature had its greatest effect during the change from larva to pupa. According to Weismann, temperature acted at the beginning of the pupal period in *Vanessa prosa*. Merrifield concluded that the markings are chiefly affected during the early part of the pupal period, while coloring is affected during the penultimate pupal stage.

Hoge showed that exposure of the eggs to cold produced the greatest percentage of reduplication of legs in the imago of the fruit fly. Evidently the materials which determine the structure of the legs are differentiated in early 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 interest in showing that some of the reactions which are involved in the differentiation of specific adult structures may occur at very early stages of immature life. Environmental stimuli must therefore be applied at definite periods in order to modify the organization of the adult.

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 percentage at 13° and at 31° with a minimum from 22–27°. This curve Plough compares to the curve of Howell for the amount of contraction of the frog muscle at varying temperatures under constant stimulus. It is decidedly not a van't Hoff curve. Plough refers the phenomenon further to Lillie's results on the activation of the 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 change comes at the extreme high and low temperatures, with a minimum between, much as in the above reactions. With Plough, I leave the significance of the similarity of the cases to future research.

Individual Variation as Affected by Temperature.

In his book, Vernon[3] makes the statement that "variability becomes steadily greater as the environment becomes more unfavorable."

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[2] Vernon (1903), p. 241.

[3] Vernon (1903), p. 218.

In an earlier article (1895), he remarks that 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 is made.

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

The present study has value only as a preliminary to the subject of the effect of temperature on individual variation. The two following conclusions are suggested if not proved. (1) When measured in terms of the coefficient of variability, variability increases with temperatures. (2) When measured in terms of standard deviation, variability decreases with increase in temperature.

Considerations of the Straight Line Feature of Physiological Reaction Curves, and of the Exponential Curve for Facet Number.

Variability in Q_{10}.

Variability in the temperature coefficient, Q_{10}, occurs in practically all chemical reactions. The typical variation is a slight decrease as the temperature rises. 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} with increase in temperature.

The variation of Q_{10} for chemical reactions is in no way comparable to those of enzymatic and vital reactions.[4] In nearly every case the latter show a marked optimum. Obviously above the optimum Q_{10} becomes negative. As pointed out in this paper the values of Q_{10} for the rate of immature development vary from 27.31 at the 15–16° interval to − 2.41 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 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, gives the appearance as it increases of checking the primary one when the end-results alone are considered.

Blackman accepts this sort of explanation for vital reactions. In the rate of assimilation by the leaves of the cherry laurel, he has ingeniously demonstrated the probability of the occurrence of increased rates above the optimum although these rates are not directly measurable.

Snyder has attributed the decrease in rate of physiological reactions at the higher temperatures to the differences in viscosity of protoplasm. This physical

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[4] Ernst has shown an optimum in catalytic action of colloidal platinum upon H_2O_2.

phenomenon has a negative temperature coefficient. Experiments demonstrate a decrease in rate of nerve conduction with increase in viscosity at a constant temperature.

Balls maintains that the more rapid accumulation at higher temperatures of the waste products retards the primary reaction. 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 the optimum of growth for the soreshin fungus considerably.

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

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 a linear rather than an exponential function of the temperature.

Loeb's Hypothesis of Secondary Factors.

Loeb has recently explained the straight line character of the rate curves to be due to the flattening out of an exponential curve by secondary factors. 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° demonstrates clearly the presence of secondary factors that would tend to convert a straight line curve into an exponential curve.

A consideration of these various explanations of straight line curves and optima is now in order in light of the present work.

Explanations of the Straight Line Temperature-Rate Relations and Optima, Based on the Data of Facet Number and Developmental Rate in Drosophila.

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

It is quite obvious that for the facet reaction 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 temperature where such destruction would be expected. The secondary factors then are not be to located in the principle of enzyme destruction.

It is likewise as 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.

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

Differential Temperature Coefficients as an Explanation of the Straight Line Feature of Physiological Reaction Curves.

The one idea of Balls that shows greater possibilities of development is that of differential temperature coefficients. Vital reactions are a series of complex processes in which both chemical and physical phenomena are represented. It is inconceivable that all these should have the same temperature coefficients. Vernon (1895) has demonstrated the fact in the gross anatomy of the echinoderm larvæ. Laughlin has recently shown that the various phases of mitosis have markedly different temperature coefficients. Osterhout 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 noticeable. If one stage in development must await another, it is quite obvious that the whole general process would be slackened in speed. At extreme temperatures regulation would become impossible.

As has been shown, the reaction by which the number of facets 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 interdependent 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 development of 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 will be 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 physiological reaction curves, 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, differentiation, and development.

The Inherited Effects of Temperature.

Induction.

Woltereck working on the size of the head in *Daphnia*, Middleton on the fission rate in *Stylonychia*, and Sumner on the length of the feet and tail in mice found that measurable effects could be produced by temperature. Furthermore the effect 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 this 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 high or low temperature, such an effect might be obtained.

Temperature as a Causal Factor in the Production of Mutations.

Tower found among his potato beetles color variations that persisted through subsequent generations. Presumably, since they were reared at high temperatures, the cause of the mutation lay in this fact.

The present study shows marked discontinuous variations at neither high nor low temperature. Temperature in the present study is not a factor in the production of mutations.

SUMMARY.

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

The mean facet number in the bar-eyed mutant varies inversely with the temperature at which the larvæ develop.

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

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

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

The facet curve may be readily superimposed on the development curve between 15 and 27°.

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

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 in the physical state of colloids.

Differential temperature coefficients for the various separate processes involved in development furnish the best basis for an explanation of the straight line feature of the curve representing the effect of temperature on the rate of physiological processes.

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

The mean facet number for fifteen full-eyed females raised at 27° is 859.06.

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

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 0.791.

The average observed difference in mean facet number for a difference of 1°C. in the environment in which the flies developed is 3.09 for the Ultra-bar stock and 14.01 for the Low Selected stock.

The average proportional differences in the mean for a difference of 1°C. are 9.22 per cent for Ultra-bar, and 14.51 for Low Selected.

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

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

The proportional differences in the mean per °C. are greatest at the lower (15–17.5°) and higher (29–31°) temperatures and least at the intermediate temperatures.

Temperature is a factor in determining facet number only during a relatively short period in larval development.

This effective period, at 27°, comes between the end of the 3rd and the end of the 4th day.

At 15°, this period is initiated at the end of 8 days following a 1st day at 27°.

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

The number of facets and the length of the immature stage (egg-larval-pupal) appear related when the whole of development is passed at one temperature.

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 affects the reaction determining the number of facets 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.

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.

Neither inheritance nor induction effects are exhibited by this material.

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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