

SELECTION, REGRESSION, AND PARENT-PROGENY
CORRELATION IN *APHIS AVENAE* FAB.

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The pure line theory, at one time considered by many as being established upon such a volume of evidence as to be almost unassailable, is passing, like so many of our biological theories, through a period of adverse criticism. Especially have certain workers raised very serious objections to the earlier experiments in pure lines that gave negative results in regard to the effects of selection. These criticisms have recently been summarized by Jennings (1916), but the writer will here call attention to four of them which he intends to consider especially in this paper. These four criticisms are to the effect that:

- a. The characters used in the pure line work have been, for the most part, indefinite, and have not been structural characters that could easily be measured or counted.
- b. The characters used have been such as to be easily affected by environment.
- c. Not enough characters in any one line have been studied.
- d. Selections have not been carried on for a sufficient number of generations in any one case to give a conclusive test of their effect upon somatic change.

In regard to this last point Middleton (1915), who claims his results show positive effects of selection, asks us to compare with his 39 plus selections; "the six made by Johannsen in obtaining his negative results with beans, the three or four made by East with potatoes, the two made by Winslow and Walker with bacteria, and similar small numbers made by most other investigators along these lines, even indeed the selection through fifteen generations made by Agar, in *Cladocera*."

Happily these criticisms so justly raised against the earlier experiments have been better met recently by the work of Middleton, Ackert, Jennings and others, and the writer believes also by his own work with *Aphis avenae* Fab. But subjected to these more rigorous tests what results do we get? They

are just as contradictory as before. Middleton (1915), who made 39.86 (average) plus selection with *Stylonychia*, comes to this conclusion: "Thus in *Stylonychia*, from a single clone of given genotype it is possible to obtain through long continued selection during reproduction by fission, two sets (clones?) of diverse genotype, differing characteristically from each other in rate of fission under identical conditions; and retaining these differences from generation to generation. The selection of small variations, such as appear within the 'pure strain' or clone, is then an effective evolutionary procedure." Jennings (1916), whose work with *Diffflugia corona* was carried on in a very thorough manner, comes to similar conclusions in regard to the effectiveness of long-continued selection. He concludes his work with the following statement: "Thus in general the investigation shows that in *Diffflugia corona* a population consists of many hereditarily diverse stocks; and that a single stock, derived by fission from a single progenitor, gradually differentiates into such hereditarily diverse stocks; so that by selection marked results are produced." Ackert (1916), however, working with *Paramecium* obtains opposite results, and substantiates Jennings' earlier findings with Protozoa, and thus gives further support for the pure line theory. In his summary he states: "In these experiments, in which nearly six thousand animals were measured, the results indicate that selection within the progeny of a single Paramecium is without effect. Even when one of the animals selected was twice as long as the other, diverse groups failed to develop, each of the groups under comparison either having the same mean lengths, or the progeny of the longest Paramecium having the smaller mean length." The writer's results with *Aphis avenae* (Ewing, 1916) are in accord with those of Ackert and the prevailing ideas of the pure line advocates. In my summary they are indicated by the following: "The results of this work with *Aphis avenae* Fab. are, we believe, sufficient to warrant the following generalization: Fluctuating variations in a parthenogenetic pure line of *Aphis avenae* Fab., and presumably in all parthenogenetic pure lines, are in general not dependent upon germinal variations, and for this reason are not capable of increase or summation through the action of continued selection. Or to put it in another way: Fluctuating variability in a partheno-

genetic pure line is devoid of one of its most important causes when exhibited in higher animals that reproduce sexually that is, germinal variability.

When we subject to analysis those experiments that seem to be positive in regard to the effectiveness of selection, and contrary to our accepted ideas in regard to the permanency of a pure line or the genotype, do we find that they were so conducted as to be exempt from the criticisms such as Pearson, Harris, and Castle have raised in regard to the earlier experiments that gave negative results? We find that one of these common objections, that not enough selections were made can hardly apply to the work of Middleton with *Stylonychia*, for he states that in his main experiment on the average 39.86 plus selections were made in the fast-selected lines; 34.36 minus selections in the slow-selected lines. Yet in respect to the other points Middleton's work is open, it appears to me, to the same objections raised in regard to the earlier experiments in pure lines. We find only a single character was studied, that this character, the fission rate, is a physiological one and does not lend itself as accurately to measurement as morphological characters, and is more or less influenced by environment.

Probably the work of Jennings (1916) comes more nearly meeting the various requirements that the critics of the pure line work would impose than those of most others. In his work with *Diffugia corona* six different characters were used. These were all morphological characters, parts easily counted or structures easily measured. Further, they were little affected by environment, and their coefficients of correlation in regard to variation were ascertained. Jennings has applied finer methods of statistical study in regard to variation and correlation in a thorough manner to his work; also controls were run, checks made, and pedigrees kept. Thus it is made possible for other workers to examine his results from different angles, and formulate their own interpretations. The work of Jennings, it appears to me, must be conclusive in most respects for *Diffugia corona*. However, the selections in certain cases were carried on for only a few generations, yet the mass of data given for such selections might cause one, unless making the closest scrutiny, to think that a very large number of generations had been obtained. Again, such strong positive

parent-progeny correlations as were obtained in family 305, were found in a family that appeared abnormal in several respects.

But has the pure line theory been overthrown by these recent experiments? I think far from it. The strongest evidence against the concept is that found in Jennings's work with *Diffugia*. In fact, I believe that this is the one piece of work that shows definite positive results in regard to somatic change through selection (in pure lines), that is not open to the serious objections raised against the earlier work in this field. Jennings himself, apparently does not claim that his results necessarily overthrow his conclusions based on his earlier work with *Paramecium*, or the pure line theory as it applies to higher plants or animals that reproduce by self fertilization or parthenogenesis. In fact, he states that there is a strong probability that selection was effective in *Diffugia* because of a peculiar role the mechanism of inheritance plays in these forms. In his discussion we read: "It would appear therefore that the substances determining the hereditary characters may be distributed with less accuracy than in higher organisms, so that the two products of fission may often receive parts that are not equivalent. As a result, the two products of fission would differ in hereditary characters; and in time diversities of strains would be brought about such as are described in the present paper. The possibility that this is the state of affairs is entirely open, so far as our present knowledge is concerned."

The writer in his work with *Aphis avenae* (Ewing, 1916), attempted, as did Jennings, to meet the objections that had been raised in regard to the earlier experiments in pure lines. My results, I believe, in the main, have met these objections. There is one phase of the work, however, that was not reported in the recent summary of the experiments with *Aphis avenae* in the "Biological Bulletin" for August (1916); that is, the statistical study of selection, regression, and the parent progeny correlation. The data for most of these were collected and in part put in manuscript form at the time the published results were first written. In order to forestall criticisms of the omission of these features in the work with *Aphis avenae*, and in order to help us obtain a more intelligible interpretation of the facts in our pure line work, I submit them in this paper.

Parent-Progeny Correlation in a Subline where Selection was Made in an Attempt to Change the Ratio of the Length of the Third to the Fourth Segments of the Antennae.

The first character which was used in the selection work with *Aphis avenae* Fab. was the ratio existing between the length of the third and fourth segments of the antennae. Eight selections were made in attempting to increase this ratio in the fifteen generations obtained. Already there has been published (Ewing, 1914, b) a statistical study of regression in this subline or isolation, and here I will give the results of working out the parent-progeny correlation and add a few notes on regression. If we group the parents into classes each with a mean difference of 0.10 points in the antennal ratio, the length of the shorter segment (segment four) being taken in each case as unity, we will have the arrangement found in Table I. This has been done and the offspring are grouped into the same classes as the parents, thus making a symmetrical table.

TABLE I.

PARENT-PROGENY CORRELATION TABLE WITH RESPECT TO ANTENNAL FORMULA
(RATIO OF LENGTH OF THIRD TO FOURTH SEGMENT.)

Offspring	Parents	1.20-1.29	1.30-1.39	1.40-1.49	1.50-1.59	1.60-1.69	1.70-1.79	1.80-1.89	1.90-1.99	2.00-2.09	2.10-2.19	2.20-2.29	2.30-2.39	2.40-2.49	2.50-2.59	2.60-2.69	2.70-2.79	2.80-2.89	2.90-2.99	
1.20-1.29																				
1.30-1.39																				
1.40-1.49																				
1.50-1.59										1								1	2	
1.60-1.69					1	3	2	3	1	4										14
1.70-1.79					1	6	5	7	1	2								2		24
1.80-1.89					1	3	7	10	1	1								1		24
1.90-1.99					3	3	7				2							1		16
2.00-2.09						2		5	1		1									9
2.10-2.19					1			1												2
2.20-2.29								1												1
2.30-2.39									1											
2.40-2.49									1											1
2.50-2.59																				
2.60-2.69																				
2.70-2.79																				
2.80-2.89							1													1
2.90-2.99																				
					4	17	18	35	3	7	5							5		94

An examination of this table shows a lack of correlation. The offspring of the three parent classes having the highest

antennal formula have means even below the average. On the other hand the offspring of the 1.80-1.89 class have the highest progeny mean of any parent class.

If we compute the average fraternal mean for all the offspring of the eighteen parents considered in this isolation, we find it to be 1.823 which is only 0.023 above the mean obtained for the line, showing regression to be practically complete. In a previous paper (Ewing, 1914 b), the writer found by computing the regression according to parent-class method that it was more than complete. The correlation table substantiates my earlier conclusions in regard to the negative results of selection in this subline.

An Analysis of the Results of Selection Made in an Attempt to Increase the Length of the Cornicles in Aphis avenae.

In isolation 3, selections were made in an attempt to increase the absolute (not relative) length of the cornicles in *Aphis avenae*. Selections were begun in the 15th generation and were made in each generation up to the 26th. Eleven selections were made in all, and sixty-seven progeny obtained. In Table II there is given a parent-progeny correlation table for the cornicle length for these eleven selected generations as well as for several generations previous during which no selections were made. In these latter generations work was done on the determination of the cornicle length of the genotype.

This table shows a strong correlation between parent and immediate progeny in regard to cornicle length, and the graph which was made in my previous paper (Ewing, 1916, p. 59), showing the results of selection on cornicle length, for the most part appeared to show the same thing. In fact, I was so certain of positive effects after six or seven selections that I presented a seminar paper on my success in creating a new strain of plant lice through selection in a pure line. Continuing the work a few generations farther, however, it was found that there was almost a complete regression in regard to cornicle length, and this in the face of rigid selection. Considering the fact that in these latter generations there was such a strong regression, I am inclined to attribute the earlier gains in cornicle length not to selection, but to environmental

TABLE II.

PARENT PROGENY CORRELATION TABLE WITH RESPECT TO ABSOLUTE CORNICLE LENGTH

Offspring	Parents	2.00-2.09	2.10-2.19	2.20-2.29	2.30-2.39	2.40-2.49	2.50-2.59	2.60-2.69	2.70-2.79	2.80-2.89	2.90-2.99	3.00-3.09	3.10-3.19	3.20-3.29	3.30-3.39	3.40-3.49	3.50-3.59	3.60-3.69	3.70-3.79	3.80-3.89	3.90-3.99	
2.00-2.09									1													1
2.10-2.19					1				1													2
2.20-2.29					1	1			1													3
2.30-2.39									1													1
2.40-2.49								1														1
2.50-2.59					1	1		2														4
2.60-2.69					1				2				1									4
2.70-2.79									2				2	1								5
2.80-2.89								1	1													2
2.90-2.99								1					1				1					3
3.00-3.09				1								1	2	3			2		2			11
3.10-3.19				2								1	2			1						6
3.20-3.29				1								1	3			4		3				12
3.30-3.39												1			1	2	1	2				7
3.40-3.49													1		6	1	2					10
3.50-3.59												1	1		3	7	1					13
3.60-3.69																1						1
3.70-3.79																1						1
3.80-3.89																						
3.90-3.99																						
				4	4	2		5	9			5	6	11		5	24	2	10			87

changes and believe that if the selections had been continued for several generations farther no marked correlation would have been noticed.

Parent-progeny Correlation and Regression in Two Check Sublines, where Selections were Made in One for Increasing the Body Length and in the Other for Decreasing It.

After making selections for several different characters it was decided to select for increasing the body length, and in order to obviate errors through environmental influences on this character, a check subline was run in which minus selections were made. In one subline, No. 5, selections were made for increasing the body length, while in another, No. 6, selections were made for decreasing the body length. Both of these sublines were treated in as nearly the same way as possible. The results obtained for these selections, which were carried on for seven generations, I have already summarized, "Where selections were made in opposite directions (plus and

minus) in two isolations, each being used as a check against the other, it was found that fluctuations were simultaneous in both isolations, and in the same directions, being thus independent of the effects of selection." As additional data on the effects of selection, the parent-progeny correlation table is here given.

TABLE III.

PARENT-PROGENY CORRELATION TABLE WITH RESPECT TO BODY LENGTH IN TWO SUBLINES IN WHICH PLUS AND MINUS SELECTIONS WERE MADE.

Progeny	Parents	1.00-1.19	1.20-1.39	1.40-1.59	1.60-1.79	1.80-1.99	2.00-2.19
1.00-1.19			1		1		2
1.20-1.39			3	3	3	1	10
1.40-1.59			1	6	2	1	10
1.60-1.79	2	1	7	7	6		20
1.80-1.99			5	3	6	5	19
2.00-2.19						2	2
	2	6	21	13	16	5	63

In this table we see a marked correlation between parents and progeny. The highest progeny mode is 1.80-1.99 mm. which was reached by the parent class having the greatest length. The lowest progeny mode 1.20-1.39 mm. is by the parent class having next to the shortest body length. The other progeny modes fall in the 1.60-1.79 group. Thus a considerable correlation is shown.

When we run two check strains, keeping both under as nearly identical conditions as possible, and selecting in one in a plus direction and in the other in a minus direction, we have one of the best tests known for the effectiveness of selection. This was done in the case of the two sublimes in question. It was impossible to separate the two sublimes into strains differing genetically in regard to size. The correlation shown in the table presented, Table III, was equally evident in the plotted curves which were given (Ewing 1916, p. 64) for the results of selection in isolations No. 5 and No. 6; but more evident than this was the fact already mentioned, *i.e.*, that the fluctuations in the two sublimes went together, and that the two could not be separated genetically in regard to body length.

An Analytical Study of Variation and Regression in All Sublines where Selections were Made for Increasing Body Length.

In the work with *Aphis avenae*, a special attempt was made to test the effectiveness of selection on body length, which corresponds to stature in upright animals. The chief reasons for this were that body length was well known to be affected by selection in higher animals that reproduce sexually, and because body length is a character easily and accurately measured. In three different isolations selections were made in an attempt to increase the size or body length in the pure line. This was done by picking out the longest individual of each fraternity as the parent for the succeeding fraternity (next generation) in that isolation or subline. In isolation 5, selection was begun in the 26th generation, and continued for seven generations; in isolation I, selection was begun in the second generation, and continued for five generations; in isolation 11 selections were begun in the 43rd generation and continued for forty-four generations. This last series of selections is, I believe, about as long a series as has been obtained in any pure line work and gives us the rigid test so often suggested by pure line critics. In my previous paper (Ewing, 1916), it was shown that in all three of these selection tests no shifting of the fraternal mean in regard to size had been detected. But critics may insist that if a careful statistical study had been made a shifting might have been detected. In order to find out if such is the case, the following statistical studies are submitted in regard to selection, correlation and regression in the case of these three isolations, or sublines, where selections were made in an attempt to increase the size of the individuals.

In isolations 5, I and 11 we find 55 parent individuals included, which gave 542 measured adult offspring. Let us now place these 55 parent individuals in different classes according to their length. We get the following arrangement:

Lengths in mm.	1.25-1.29	1.30-1.34	1.35-1.39	1.40-1.44	1.45-1.49	1.50-1.54	
No. of parents	1	0	0	2	0	4	
	1.55-1.59	1.60-1.64	1.65-1.69	1.70-1.74	1.75-1.79	1.80-1.84	1.85-1.89
	3	6	4	8	6	12	5
	1.90-1.94	1.95-1.99	2.00-2.04	2.05-2.09	2.10-2.14	2.15-2.19	
	1	2	0	0	0	1	

How do these positions compare with the mean for the line?

If we compute the mean for all the individuals¹ (both parents and offspring) for these three isolations we get 1.544 mm. as the mean for the whole line. Above this mean we find 48 of the 55 parents, and below it only 7 parents. This shows how severe was the test of selection in these experiments. Further, the mean of all the parents selected is found to be 1.728 mm. which is 0.184 mm. greater than the mean for the line, or about 12 per cent greater in length than the average length of all individuals of the three sublimes. In Table IV we find correlations given for the size of these 55 parents and their offspring.

The results observed in Table IV appear to give us a considerable correlation between parents and offspring. But, knowing as I do the conditions of the experiment, I would attach little significance to this table as far as indicating any inherited differences between parent and offspring. We find in the three lowest parental classes containing any individuals, 1.25-1.29, 1.40-1.44, and 1.50-1.54, that the modes for the offspring as well as the means are unusually low, except for the one offspring in the class 1.25-1.29 which can be disregarded. Certainly this shows correlation, our critics say. Yes it does, but not necessarily inheritance. An examination of my notes shows that three of the seven parents included in this class were produced while feeding on older wheat plants than usual, as also did their offspring. It was shown clearly in my experiments that older wheat plants caused a diminution of the size of the individuals. Two of the remaining parents as well as their offspring were produced under exceptionally low temperature, in fact the temperature was many degrees lower than usual. These conditions of course would affect both parent and offspring. The parent going in the highest class, 2.15-2.19, is of special interest. This individual is four classes ahead of the next longest parents which go in the 1.95-1.99 class. Certainly this must be an example of mutation! The mean of its offspring also is far above any other mean. But let us examine the case farther. The parent of this fraternity, measured 2.15 mm., yet this great size was not permanently inherited, for the mean of its grandchildren came down to

1. For the actual measurements of these individuals, of which there were 543, the reader is referred to the previous paper by the writer (Ewing, 1916). The measurements of two individuals were lost, and in a few cases measurements were not made of abnormal ones or those that were seriously distorted.

Probably a more accurate way of detecting inherited effects is by a graphical and statistical study of regression, provided of course that the numbers of individuals obtained are sufficient for such a test, which happily is here the case. The means obtained for the offspring of the parents going in the different classes are as follows:

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TABLE V.

THE MEANS OF ALL THE OFFSPRING OF PARENTS BELONGING TO THE DIFFERENT SIZE CLASSES

Classes (Length indicated in mm.)	Means of Progeny
1.25-1.29	1.600
1.30-1.34	—
1.35-1.39	—
1.40-1.44	1.430
1.45-1.49	—
1.50-1.54	1.357
1.55-1.59	1.486
1.60-1.64	1.497
1.65-1.69	1.538
1.70-1.74	1.556
1.75-1.79	1.508
1.80-1.84	1.554
1.85-1.89	1.614
1.90-1.94	1.742
1.95-1.99	1.585
2.00-2.04	—
2.05-2.09	—
2.10-2.14	—
2.15-2.19	1.890

We can make a plot showing the position of the different parent classes, the means of the offspring of the parents going into these various classes in regard to the mean of the line. This is done in Figure 1.

We find by observing Figure 1 that nearly all of the parents are above the mean of the pure line, which is what we should expect since in each case of selection the longest individual was chosen as the parent for the succeeding generation. Of the thirteen parental groups or classes we find in 12 instances that regression is shown by the offspring. In seven of these the regression is not complete, in five it is more than complete, or beyond the mean of the line. If we compute the mean for all of the parents above the mean of the line, we find it is 1.768 mm., (it is indicated by the heavy circle in figure), and if we compute the mean for all the offspring of these parents we get 1.555 mm., (indicated by heavy arrowhead in figure.)

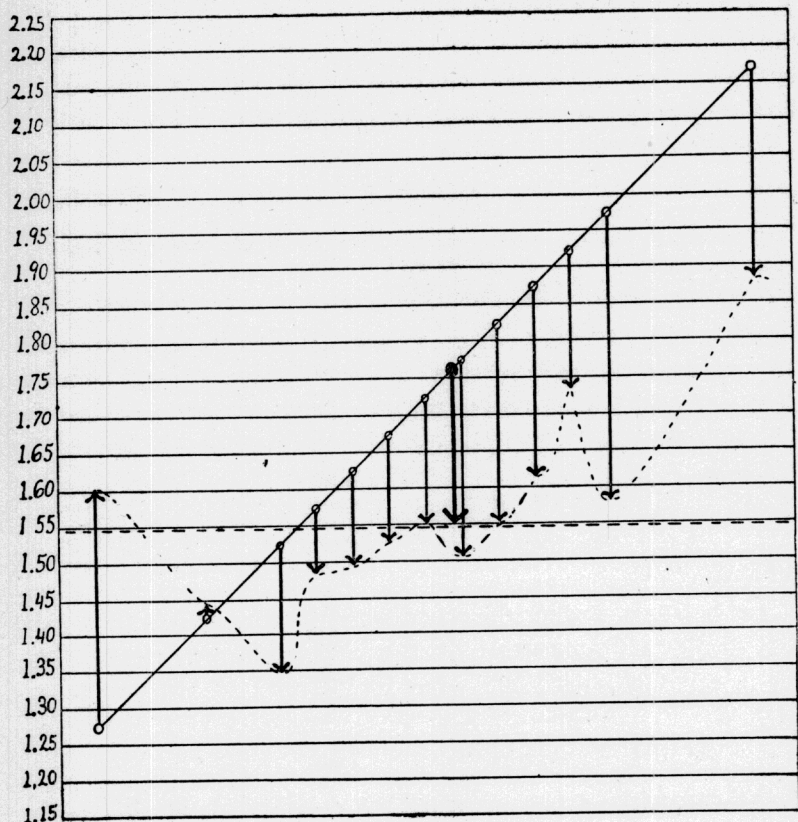


Fig. 1. GRAPH SHOWING REGRESSION IN SUBLINES OF A PURE LINE OF THE PARTHENOGENETIC PLANT LOUSE (*Aphis avenae* Fab.). PARENTS ARE ARRANGED INTO GROUPS REPRESENTING VARIATIONS IN LENGTHS OF 0.05 MM. THESE PARENTAL GROUPS OR CLASSES ARE REPRESENTED IN FIGURE BY CIRCLES SHOWING THEIR RESPECTIVE LENGTHS. THE MEAN LENGTH OF ALL THE OFFSPRING OF PARENTS BELONGING TO EACH GROUP ARE REPRESENTED BY ARROWHEADS. AMOUNT OF REGRESSION IS IN EACH INSTANCE INDICATED BY ARROW. THE BROKEN LINE JUST BELOW 1.55 REPRESENTS THE MEAN OF THE LINE. THE HEAVY CIRCLE IS FOR THE POSITION OF THE MEANS OF ALL THE PARENTS ABOVE THE MEAN OF THE LINE, AND THE HEAVY ARROW FOR THE REGRESSION OF THEIR OFFSPRING.

This mean is only 0.011 mm. above the mean of the line, hence regression, thus measured is found to be practically complete (see heavy arrow in Figure 1). Since so few parent individuals are below the mean, we will have to regard their numbers as being insufficient for a test similar to those above the line.

If the means of the parent groups and the means of the offspring for these groups are reduced to the scale of 100 for the mean of the pure line (by multiplying by 65) we get the following interesting series in which parental lengths are given above, and the means of the offspring below:

Length of parents in mm.; scale, mean of race = 100	82.87	92.62	99.12	102.37	105.62	108.87	112.12
Mean length for offspring; scale, same as for parents.	116.00	92.65	88.20	96.59	97.50	99.97	101.14
	115.37	118.62	121.87	125.12	128.37	141.37	
	98.02	101.01	104.91	113.23	103.25	122.85	

Although we note that two of the low parental groups have low means for offspring, and two of the high parental groups have unusually high means for offspring, yet one of the low parental groups has a high mean for offspring and three of the high parental groups have low means for offspring. The general disagreement of the two sets of figures is evident, hence we see the lack of correlation while the regression is made evident.

Let us study further the regression found in the ten parental classes above the mean of the line. This can be done by the use of common fractions. Let the amount of regression in each case be indicated by a fraction, the numerator being the difference between the mean of the parent class and the mean of the offspring for this class, and the denominator the difference between the mean of the parent class and the mean of the pure line. If the numerator is smaller than the denominator the regression is not complete, if greater it is more than complete, if equal to the denominator it is just complete. If we do this we get the following series for the ten parental groups above the mean:

$$\frac{5.78}{2.37} \frac{8.32}{5.62} \frac{8.90}{8.87} \frac{10.88}{12.12} \frac{17.35}{15.37} \frac{17.61}{18.62} \frac{16.96}{21.87} \frac{11.89}{25.12} \frac{25.12}{28.37} \frac{18.32}{41.37}$$

There being some regression in each case all of the fractions are positive. If we reduce the series to decimals we get:

2.44, 1.48, 1.00, 0.89, 1.13, 0.94, 0.77, 0.47, 0.88, 0.45.

Now then, if we add these fractions together and divide by their number we will get the average amount of regression, which if complete should give 1.00. The actual number which

we obtain is 1.0465, which means that the regression was a little more than complete according to this way of measuring it. We find then that this statistical method of measuring the amount of regression confirms my earlier findings in regard to the effectiveness of long continued selection in a parthenogenetic pure line.

Variation, Selection and Regression under Similar Suboptimum Food and Temperature Conditions.

It has previously been mentioned that environmental conditions in two instances caused such a marked change in the size of both parents and offspring as to give a considerable amount of correlation between the two in size variation. For this reason the correlation noticed in Table I is misleading without the use of the annotated pedigree. During the second score of generations in isolation 11, selections were made under similar suboptimum food and temperature conditions. For this reason we should expect but little influence in size fluctuations coming from variations of these two factors, which were determined as being the two chiefly affecting size. We would expect, therefore, that the common statistical methods in analysis should be more applicable for selections made un-

TABLE VI.

TABLE SHOWING GROUPS TO CONTAIN PARENTS OF SECOND SCORE OF GENERATIONS OF ISOLATION 11, THE NUMBER OF PARENTS TO EACH GROUP, THEIR LENGTHS AND THE MEAN LENGTHS OF PROGENY OF PARENTS BELONGING TO EACH GROUP.

Group (length in mm.)	No. of parents in group	Length of parent	Mean length of offspring
1.50-1.54	1	1.53 mm.	1.518 mm.
1.55-1.59	1	1.59 mm.	1.549 mm.
1.60-1.64	1	1.61 mm.	1.407 mm.
1.65-1.69	2	1.69 mm.	
-		1.69 mm.	1.552 mm.
1.70-1.74	4	1.70 mm.	
-		1.73 mm.	
-		1.74 mm.	
-		1.71 mm.	1.515 mm.
1.75-1.79	3	1.79 mm.	
-		1.76 mm.	
-		1.79 mm.	1.574 mm.
1.80-1.84	5	1.80 mm.	
-		1.81 mm.	
-		1.80 mm.	
-		1.81 mm.	
-		1.84 mm.	1.495 mm.
1.85-1.89	3	1.89 mm.	
-		1.86 mm.	
-		1.86 mm.	1.638 mm.

der more constant conditions. Let us apply them to these 20 generations of isolation 11. We find the 20 parents fall into eight classes or groups which we made before for the parents of the three sublimes. The number of these parents in these different classes, their lengths, and the means of the offspring of the parents belonging to each class are given in the following table:

If we make a plot to show the position of these parent classes and the means of the offspring in relation to the mean of the line, we get the following graph:

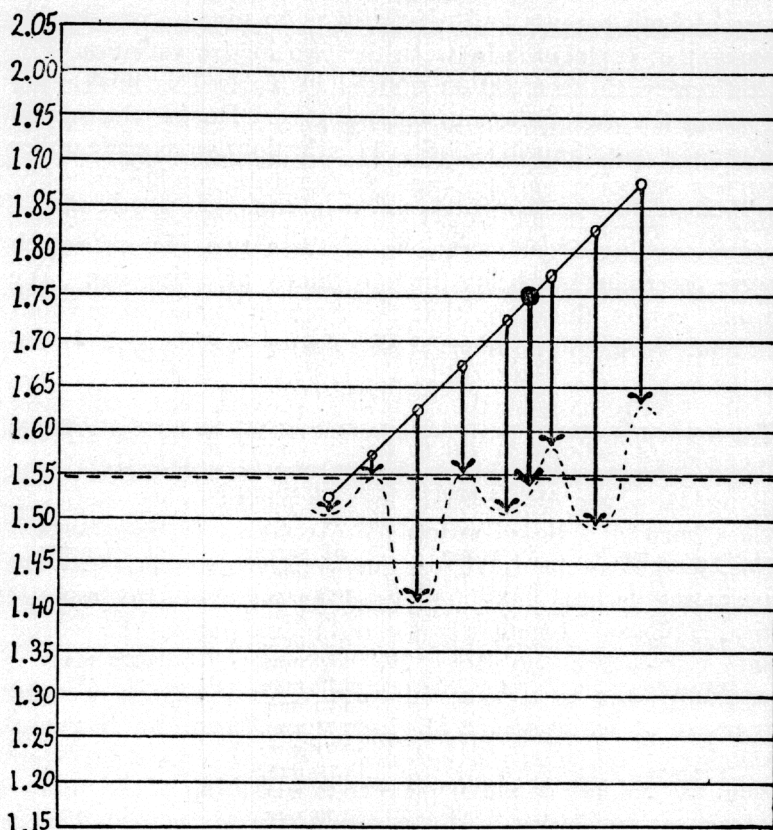


Fig. 2. GRAPH SHOWING REGRESSION IN THE SECOND SCORE OF GENERATIONS OF ISOLATION 11, IN WHICH SELECTIONS WERE MADE FROM THE EXTREME VARIANT OF EACH FRATERNITY IN REGARD TO BODY LENGTH. PLAN OF GRAPH THE SAME AS FOR FIGURE 1.

If we examine this diagram we notice that if the dotted line joining the arrowheads (which we may call the line of

regression) were straightened out it would be almost identical with the mean of the pure line. The mean of the 20 parents represented in this second score of generations is 1.750 mm. The mean for the 221 offspring is 1.538, or 0.006 mm. below the mean for the genotype or pure line. What more could be asked in demonstrating the ineffectiveness of selection!

The mean lengths for the parents in these eight classes are here given reduced to the scale; mean of the line=100, and likewise under these in each case the mean of the offspring reduced to the same scale.

1.50-1.54	1.55-1.59	1.60-1.64	1.65-1.69	1.70-1.74	1.75-1.79	1.80-1.84	1.85-1.89
99.45	103.35	104.65	109.85	111.80	115.70	117.65	119.60
98.80	100.75	91.65	100.75	98.15	102.05	96.85	106.60

If we now express the regression by a series of fractions as was done with all three sublimes we get the following:

$$\frac{-0.65}{0.55} + \frac{2.60}{3.35} + \frac{13.00}{4.65} + \frac{9.10}{9.85} + \frac{12.65}{11.80} + \frac{13.65}{15.70} + \frac{20.80}{17.65} + \frac{13.00}{19.60}$$

These fractions reduced to decimals give the following series:

$$-1.18 + 0.78 + 2.77 + 0.92 + 1.08 + 0.87 + 1.17 + 0.66.$$

In order to measure the regression as usual let us add these fractions and divide by their number. This gives the decimal 0.884, which indicates that the regression is 884/1000 complete. However, if we leave out one parent in the 1.50-1.54 class, the only one selected which was below the mean of the line, we get as the result for the nineteen parents above the mean the decimal 1.031, showing the regression to be more than complete. I think that the method of putting the parents into classes and computing the regression for each class is certainly open to serious objection, as it is not an accurate measure of regression in all cases, even though an enormous number of individuals be included. Of course more important than the number of either parents or offspring is the number of classes considered. If the results are to be plotted, here again we are limited to a relatively small number. Certainly the regression (digression in this case) of the offspring of the single parent in the 1.50-1.54 class should not count for as much as the regression of the five parents in the 1.80-1.84 class. Would it not be better to multiply each fraction by the

number of parents belonging to the class (for which the fraction is supposed to indicate the amount of regression) by the number of parents in this class, then after adding the fractions divide by the total number of parents? This will not be an actual computation of the average for the amount of individual regression between each parent and each of the offspring, yet it will give a more accurate measure of regression according to class grouping method. If we do this we get the decimal 0.943 as a measure of regression, which is only 0.057 from being complete.

What then is the result of these statistical studies? We find that they constitute a further substantiation of my earlier findings in regard to the ineffectiveness of selection in *Aphis avenae* Fab. It is noted, however, if these studies are not carefully applied, especially in the light of a fully annotated pedigree, they may cause us to make very faulty conclusions. A brief summary of this short mathematical study of selection and regression in *Aphis avenae* Fab. is here given:

SUMMARY

1. This statistical study of the selection work done with *Aphis avenae* Fab., in which eighty-seven generations were obtained, substantiates my earlier conclusions in regard to the negative effects of selection. Long continued selection (in one case forty-four) does not produce any positive effect in regard to somatic characters in general, these remaining true to the genotype.

2. By computing the regression through the parent class grouping method and using the mean of the line as standard of reference, it being reduced to 100, such figures as 1.0465 and 0.906 are obtained (according to this method complete regression would be expressed by 1.)

3. Measuring the amount of regression through the parent class grouping method facilitates the plotting (in the form of a graph) of the results, but does not give a very accurate measure of the amount of regression. However, this method is much improved from the standpoint of accuracy, if we multiply the results obtained for each parent class by the number of parents in the class, and divide the sum of such amounts by the total number of parents included.

4. Correlation tables between parents and immediate progeny in regard to any variable characters are deceptive in showing the results of selection in inheritance work. They should only be used in connection with graphic pedigree charts, and complete notes on environmental factors. When correlation tables were so used in regard to my selection work in *Aphis avenae* they substantiated in almost every case, the interpretations previously made.

5. The recent work which has been done in pure lines giving positive results in regard to selection, is to a certain extent open to the criticisms of the earlier work in pure lines which gave chiefly negative results.

6. It is very probable, as Jennings has pointed out, that the mechanism of inheritance in certain lower organisms is quite different from that of higher animals which have a uniparental type of reproduction. This difference may be so great that the principles of the pure line theory will not apply to them, in most respects at least.

7. Recent investigations in pure lines seem to have given us the much desired rigid tests called for by earlier critics, and these results are not in accord.

8. The pure line theory will probably not apply to such large classes of organisms as was at one time supposed, and may be modified in some respects in regard to those classes to which it does apply.

9. In higher organisms with a uniparental type of reproduction we have no strong evidence against the application of the main principles of the pure line theory of inheritance.

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