MATTOON

The Effect of Selection on the Number of Facets in the Eye of the "Barred-Eye" Mutant of Drosophila Ampelophila

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THE EFFECT OF SELECTION ON THE NUMBER OF FACETS IN THE EYE OF THE "BARRED-EYE" MUTANT OF DROSOPHILA AMPELOPHILA

BY

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THIS IS TO CERTIFY THAT THE THESIS PREPARED UNDER MY SUPERVISION BY

EDWIN WHITAKER MATTOON

ENTITLED The effect of selection on the number of facets in the eye of the "barred-eye" mutant of Drosophila ampelophila.

IS APPROVED BY ME AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE

DEGREE OF BACHELOR OF ARTS.

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THE EFFECT OF SELECTION ON THE NUMBER OF FACETS IN THE EYE OF THE "BARRED-EYE" MUTANT OF DROSOPHILA AMPELOPHILA.

I. Statement of the Problem.

The problem involved in this experiment has been to determine what effect, if any, could be produced by selection in plus and minus directions with regard to the number of facets in the eye of the "barred-eye" mutant of Drosophila ampelophila.

The theoretical problem involved is that of the stability of the germ plasm. If selection on the basis of somatic variation is productive of any effect, there must be a change in the germinal constitution, since the common conception of heredity is based on the organic relation between parent and offspring through the medium of the germ cell.

II. Material and Methods.

The material used in this experiment consisted of a strain of Drosophila known as the "barred-eye" mutant (so-called because the eye is confined to an oblong, bar-like area), which arose in one of Professor Morgan's cultures of wild stock late in 1913. In this strain a considerable variation has been

observed in the number of facets in the eye. The curve of variability for this character in the general population is shown in Figure I.

As the Figure indicates, the number of facets in the eye of the "barred-eye" mutant constitutes a good and feasible basis for selection in that (1) there is a wide range of variation which offers ample room for selection to be made, and (2) the values are definite and may be taken with ease and accuracy.

The method of breeding was to place the individuals selected in 1 ounce salt-mouthed, glass bottles, sterilized before using. The bottles were stopped with cotton to provide for ventilation. The food used consisted of bananas. These were purchased while green, allowed to ripen in a tightly sealed jar, and cooked to the boiling point for ten minutes to avoid contamination by the presence of eggs of the wild species. A small amount of yeast was added to aid fermentation and to prevent the attack of the food by molds.

In making the first selection, food containing eggs and larvae was removed from the culture of the "barred-eye" stock and placed in glass vials. Every twelve hours the individuals which had emerged from the pupal cases were slightly etherized and examined as to the number of facets in the eye under the low power of the microscope. Males and females with high and low numbers of facets were selected out, high being mated with high and low with low. Each pair was placed in one of the small bottles with sufficient food to last until the offspring were all produced.

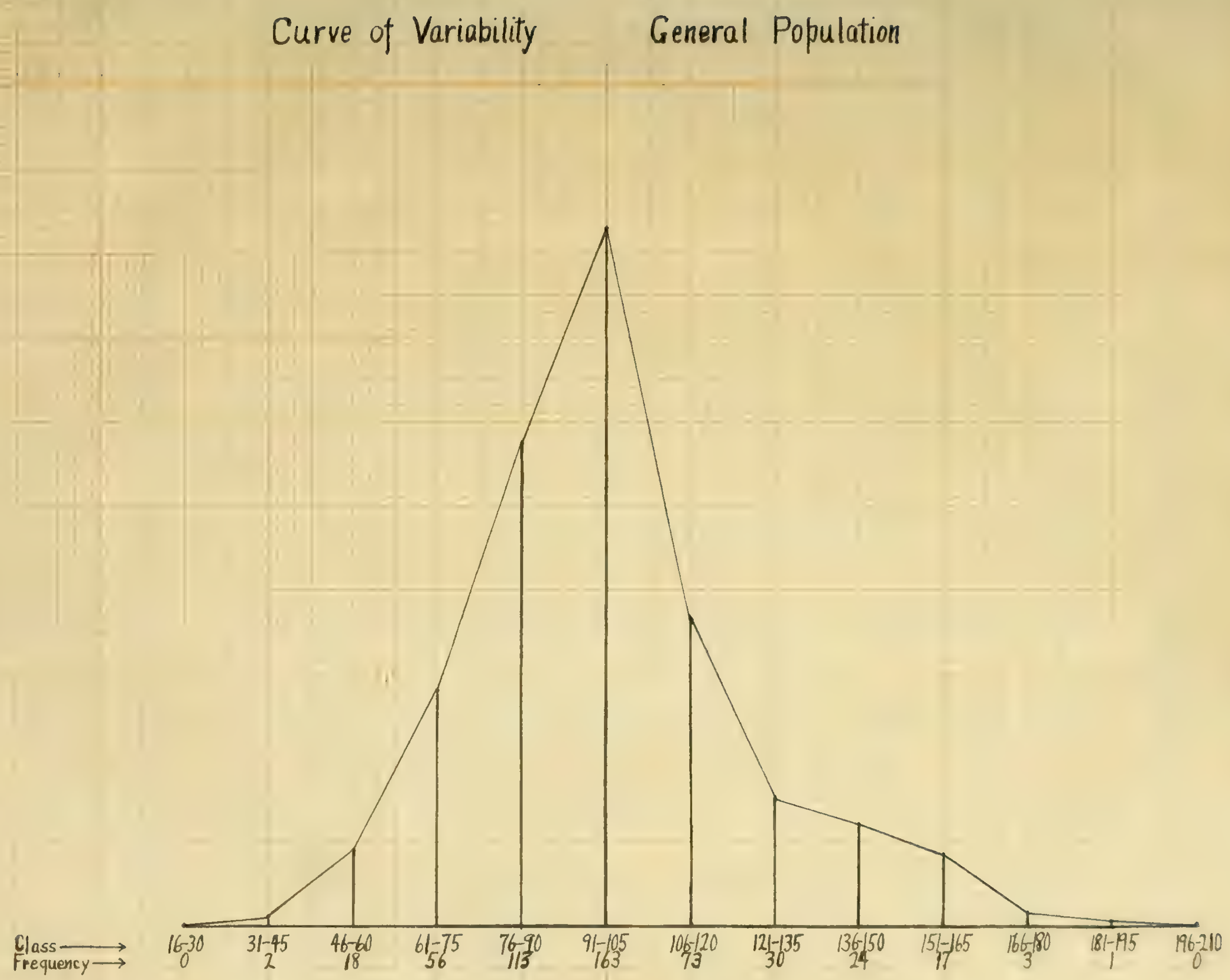
Curve of Variability General Population
Class →
Frequency →
16-30
0
31-45
2
46-60
18
61-75
56
76-90
113
91-105
163
106-120
73
121-135
30
136-150
24
151-165
17
166-180
3
181-195
1
196-210
0

FIG 1.

When larvae began to appear in one of the bottles, the parents were etherized and the number of facets recorded in each case. They were then preserved in pasteboard boxes bearing proper labels.

As the offspring hatched out they were examined and the highest or lowest individuals, as the case might be, were used to continue the selected stock. At least two pairs from the offspring of each of the original pairs were selected out in this way to continue that particular line. The remainder of the brood were etheriaed and preserved in pasteboard boxes, as were their parents. In this way the parents and offspring of each generation were kept for later reference.

When the first generation of selected stock had been produced it appeared from general observation that as the hatching period progressed the number of facets in the eye increased. Counts were made, therefore, of the number of facets in five broods from the beginning to the end of the hatching period, and it was found that the totals for the individuals produced during the first and second halves of the hatching period were approximately equal.

Late in December (1914), before the third generation of selected stock was completed, the entire stock was killed owing to sudden changes in temperature in the laboratory and also to the food being badly infected by molds. This necessitated starting the experiment all over again. To avoid repetition of the accident the work was practically doubled and two sets of

selected stock were run in different rooms, until the coming of warm weather.

Owing to the fact that an average of twenty-eight days were required for the production of a single generation, only enough time remained after the hatching of the third generation to complete the counts on this and the previous generations for comparison with each other and with the count on the general or unselected population.

When the counting was begun the number of facets in both the right and left eyes was taken on account of there being a slight variation in some cases between the two. For 100 individuals, however, the sums of the facets in right and left eyes respectively, were practically the same, there being a difference of only 0.245 per cent in favor of the left. In subsequent counting the number of facets in the right eye only was recorded.

At the beginning of the experiment eight lines both high and low, sixteen in all, were started from as many pairs of original ancestors. Of these only about 60 per cent were fertile or succeeded in producing any offspring, and by the time the third generation was produced, only four each of these high and low lines remained.

The counting was completed in each generation for three "high" lines called A, B, and C, and for three "low" lines called D, E, and F. Fifty individuals were measured for each generation in each of the lines, with the exception of the third

generation in line B, where only forty-six individuals were available.

In order to determine the range of variability in the general population a count was made of the number of facets in the eyes of 500 individuals. Of these 250 were taken from the cultures of the general population in November 1914, and 250 in April 1915. The mean number of facets for those removed in November was 98.04, and for those removed in April 98.03, with a difference of 0.01. It is evident from this that there is no noticeable tendency for the general population to shift toward a higher or lower number of facets.

The sexual dimorphism in the number of facets does not appear in the data, since the female values were reduced to the respective male values. This was accomplished by dividing the mean male value, 98.035 by the mean female value, 65.06 and multiplying each of the female values by the quotient, 1.51. This reduction made possible the use of mid-parental values in showing the effect of selection in Figures 2, 3, and 4.

III. Data.

In the following Tables the data are given for the counts made in the general population and in lines A, B, C, D, E, and F of the selected population.

Table I. - General Population

Male	Reduced Male	Male	Reduced Male	Male	Reduced Male	Male	Reduced Male	Male	Reduced Male
88	94	109	91	104	157	79	97	157	109
132	152	98	62	78	100	104	62	80	89
87	92	126	107	72	101	107	98	105	182
45	148	91	89	137	145	67	51	119	91
60	107	46	98	93	100	69	118	68	80
142	92	64	83	75	140	98	88	83	165
139	103	150	74	143	115	136	94	92	79
94	112	135	156	59	85	151	65	141	162
77	75	97	72	50	110	65	166	100	94
73	77	69	94	81	104	49	60	76	106
140	86	66	89	131	83	90	104	128	89
81	138	135	68	86	78	128	69	91	125
110	77	77	92	138	75	98	97	50	60
123	98	108	83	80	128	137	82	82	92
68	100	115	128	108	85	77	94	143	74
115	95	62	91	121	91	110	118	85	148
89	106	122	72	66	107	115	95	105	65
105	71	95	83	114	88	63	62	118	113
78	149	97	103	87	113	123	98	71	82
72	74	81	95	104	63	96	91	112	109
116	82	70	98	76	154	98	106	93	92
154	95	118	104	71	69	82	86	101	57
80	103	157	137	114	89	71	116	81	162
106	71	117	97	153	88	120	127	76	110
111	66	100	88	84	57	101	104	109	77

Table I. - General Population (Cont.)

Male	Reduced Male	Male	Reduced Male	Male	Reduced Male	Male	Reduced Male	Male	Reduced Male
89	95	111	154	94	45	81	162	95	91
84	72	90	101	101	98	79	79	99	92
109	92	88	88	158	80	80	68	96	127
74	121	86	91	70	112	89	125	113	115
104	98	101	68	96	139	72	69	134	100
89	107	98	109	82	101	129	103	67	82
91	127	95	57	81	85	78	107	106	133
130	79	93	75	148	89	96	98	97	128
58	116	103	97	97	115	88	83	98	95
93	185	96	86	69	83	90	62	108	100
102	94	99	89	127	103	91	97	64	101
85	113	114	94	92	106	135	100	97	94
89	91	82	80	100	77	94	85	106	110
105	77	128	98	85	95	65	95	86	97
94	104	97	95	102	91	76	104	142	92
100	100	75	115	98	103	60	94	98	106
99	88	89	82	79	95	69	80	83	74
79	92	107	60	120	107	103	91	100	92
112	116	91	97	84	89	85	65	96	88
84	103	93	88	104	94	89	94	77	100
83	106	54	83	95	107	100	119	92	94
90	94	81	133	62	91	98	101	126	106
106	56	118	104	144	75	111	104	169	101
87	104	87	122	77	74	96	109	98	83
175	83	125	113	156	72	137	106	94	115

Table II. - Plus Selection

LINE A.

	Generation 1		Generation 2		Generation 3	
	Males	Reduced Males	Males	Reduced Males	Males	Reduced Males
Parents	127	133	179	169	177	195
Offspring	103	69	125	112	117	137
	116	116	133	153	140	186
	86	148	124	89	107	97
	94	91	118	142	204	163
	102	128	99	94	98	119
	109	101	180	110	126	103
	134	89	125	133	180	136
	107	110	102	156	142	124
	118	94	95	137	92	153
	92	107	148	103	108	174
	140	106	97	119	135	115
	79	74	130	91	141	127
	101	151	176	187	192	134
	105	88	99	110	117	109
	107	133	88	113	93	95
	122	71	147	139	118	131
	99	115	90	100	167	160
	92	149	189	134	109	143
	112	106	142	115	103	137
	91	118	98	122	126	127
	118	149	84	148	159	171
	96	76	210	125	98	142
	127	100	103	163	187	131
	67	83	95	97	154	151
	179	169	177	210	139	157
Mean of Offspring	108.74		127.52		135.48	

Table III. - Plus Selection

LINE B.

	Generation 1		Generation 2		Generation 3	
	Males	Reduced Males	Males	Reduced Males	Males	Reduced Males
Parents	139	121	184	165	182	222
Offspring	89	95	166	148	154	116
	108	124	122	137	123	159
	145	76	144	127	118	165
	102	100	90	201	99	137
	80	80	101	113	156	175
	131	148	95	79	169	124
	74	131	132	101	100	148
	112	106	140	145	145	154
	156	118	93	76	207	166
	105	125	160	143	147	104
	95	145	118	107	172	207
	90	91	86	163	141	122
	147	128	171	95	128	156
	115	57	92	119	197	118
	98	137	125	157	102	169
	133	97	144	131	130	136
	79	108	183	111	139	95
	104	95	137	134	175	89
	82	89	108	139	158	189
	167	133	126	175	96	131
	100	85	99	103	124	163
	75	91	97	110	160	137
	98	149	127	149	121	124
	68	85	172	137		
	184	165	182	222		
Mean of Offspring	110.10		128.64		141.93	

Table IV. - Plus Selection

LINE C.

	Generation 1		Generation 2		Generation 3	
	Males	Reduced Males	Males	Reduced Males	Males	Reduced Males
Parents	178	157	208	159	194	198
Offspring	82	106	140	137	166	137
	117	142	67	91	108	180
	86	151	105	130	163	106
	99	131	99	88	119	181
	96	113	140	177	142	137
	101	152	133	124	139	162
	85	121	169	98	100	97
	112	128	102	186	187	131
	146	85	100	122	151	143
	122	130	118	165	120	163
	131	103	94	121	121	100
	93	101	177	79	118	139
	123	134	101	153	213	172
	118	136	105	118	127	130
	176	63	93	180	162	205
	126	106	113	174	158	157
	147	124	189	115	143	127
	121	133	168	153	98	146
	103	107	97	110	120	165
	97	89	141	149	182	130
	100	163	160	174	177	149
	124	71	193	127	165	127
	126	112	154	101	109	107
	90	121	135	118	95	140
	208	159	194	198	134	116
Mean of Offspring	116.92		133.46		140.97	

Table V. - Minus Selection

LINE D.

	Generation 1		Generation 2		Generation 3	
	Males	Reduced Males	Males	Reduced Males	Males	Reduced Males
Parents	52	60	69	71	63	58
Offspring	102	74	104	86	104	116
	87	109	78	94	79	60
	79	65	49	104	68	68
	116	103	75	69	100	62
	97	116	102	75	87	104
	65	85	88	133	74	65
	70	127	121	92	69	71
	108	83	75	56	77	72
	69	74	110	91	58	36
	92	103	84	103	103	107
	95	75	89	79	97	74
	78	78	66	59	74	68
	90	62	99	100	75	98
	110	98	54	85	89	71
	98	110	92	92	100	88
	74	103	77	88	88	60
	100	82	95	97	66	91
	96	94	78	60	115	104
	67	101	105	82	56	115
	115	66	69	63	137	50
	93	56	76	86	48	95
	97	91	91	77	51	60
	44	82	92	103	92	115
	89	106	100	91	64	127
	69	71	63	58	83	53
Mean of Offspring	88.28		85.46		81.66	

Table VI. - Minus Selection

LINE E.

	Generation 1		Generation 2		Generation 3	
	Males	Reduced Males	Males	Reduced Males	Males	Reduced Males
Parents	82	80	64	74	60	62
Offspring	92	97	114	76	62	97
	53	121	83	94	106	100
	101	89	73	124	89	88
	84	121	91	95	111	60
	107	91	122	74	99	68
	85	50	65	51	58	109
	69	122	87	98	103	57
	118	107	58	107	80	82
	93	74	82	59	46	63
	109	118	93	80	75	106
	74	68	76	116	88	77
	108	77	98	97	94	100
	86	91	103	69	123	80
	141	86	50	113	61	71
	99	154	79	83	70	92
	94	72	95	89	67	72
	88	104	134	101	78	136
	123	77	68	85	91	77
	75	88	97	109	101	91
	87	97	99	66	59	72
	91	106	103	104	84	83
	117	101	86	76	98	63
	99	83	100	92	80	113
	71	101	94	98	106	60
	64	74	60	62	97	92
Mean of Offspring	93.94		89.56		84.78	

Table VII. - Minus Selection

LINE F.

	Generation 1		Generation 2		Generation 3	
	Males	Reduced Males	Males	Reduced Males	Males	Reduced Males
Parents	89	78	76	71	61	64
Offspring	78	100	91	95	114	100
	92	88	143	63	79	56
	63	128	89	112	60	89
	110	109	71	104	92	62
	98	151	108	69	104	79
	71	68	95	92	95	48
	103	92	92	80	65	72
	87	115	67	116	90	91
	96	104	48	59	61	137
	104	57	110	82	89	74
	70	65	97	122	99	88
	73	118	99	100	58	92
	119	121	54	75	80	130
	84	95	59	103	89	74
	102	72	91	71	111	116
	159	107	89	89	98	80
	75	85	106	80	74	66
	79	86	112	60	67	53
	96	125	95	104	110	47
	63	118	83	109	89	95
	88	83	107	97	88	91
	100	51	102	80	101	83
	107	63	90	91	94	94
	75	94	86	98	82	107
	76	71	61	64	78	60
Mean of Offspring	94.63		89.64		84.68	

Table VIII. Summary of Tables II. to VII.

	Mean Number Of Facets	Mean Number of Facets	Extreme Variates Offspring	
	Parents	Offspring	High	Low
General Population	---	98.035	182	45
LINE A.				
Gen. I	130	108.74	179	69
" 2	174	127.52	210	24
" 3	186	135.48	204	32
LINE B.				
Gen. 1	130	110.10	184	75
" 2	174.5	128.64	222	79
" 3	202	141.93 *	207	89
LINE C.				
Gen. 1	167.5	116.92	208	63
" 2	183.5	133.46	198	67
" 3	196	140.97	213	95
LINE D.				
Gen. 1	56	88.28	127	44
" 2	70	85.46	133	49
" 3	60.5	81.66	127	36
LINE E.				
Gen. 1	81	93.94	141	50
" 2	69	89.56	134	50
" 3	61	84.78	123	46
LINE F.				
Gen. 1	83.5	94.63	159	51
" 2	73.5	89.80	143	48
" 3	62.5	84.68	137	47

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* This mean is calculated from the values of 46 individuals instead of 50.

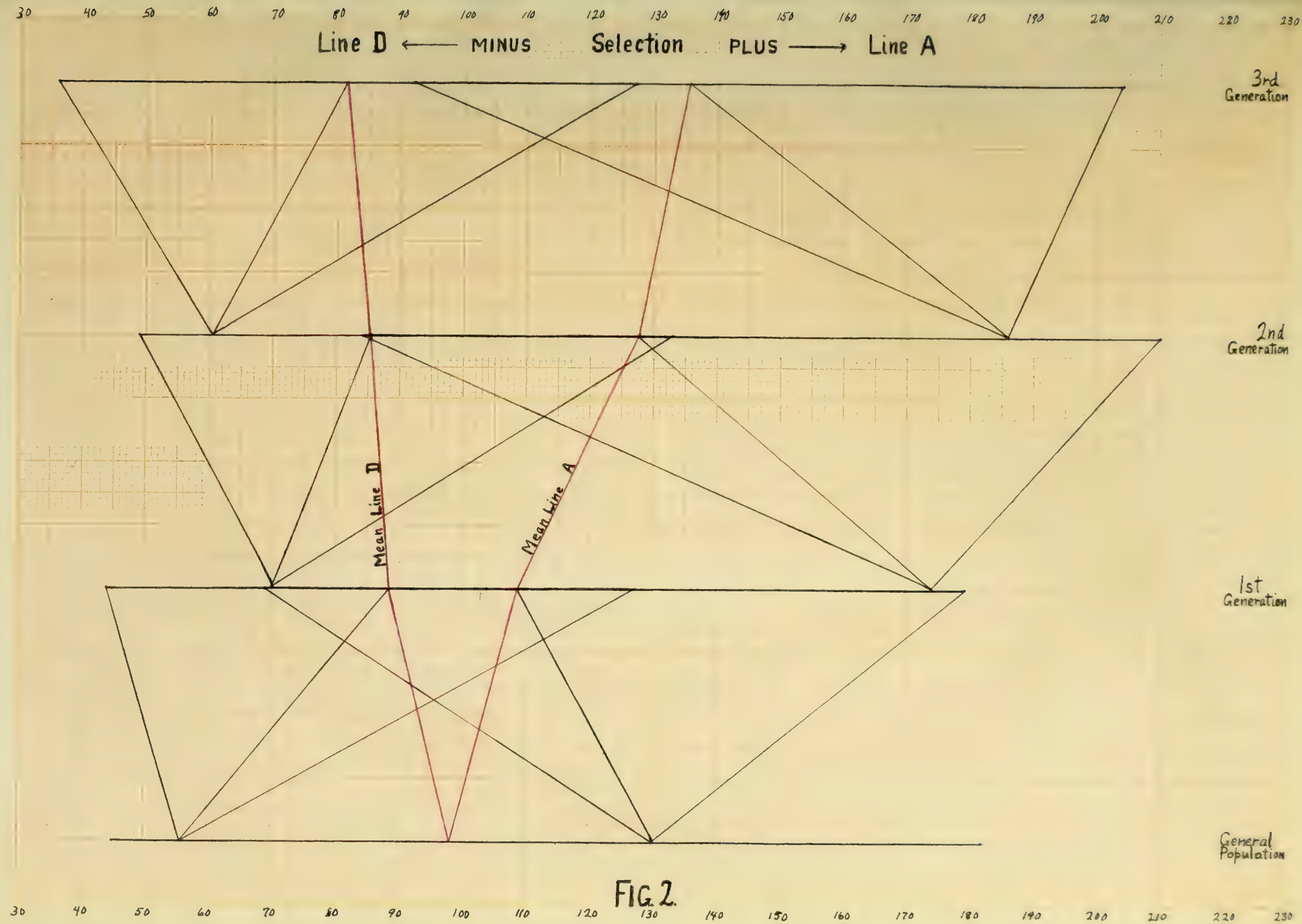
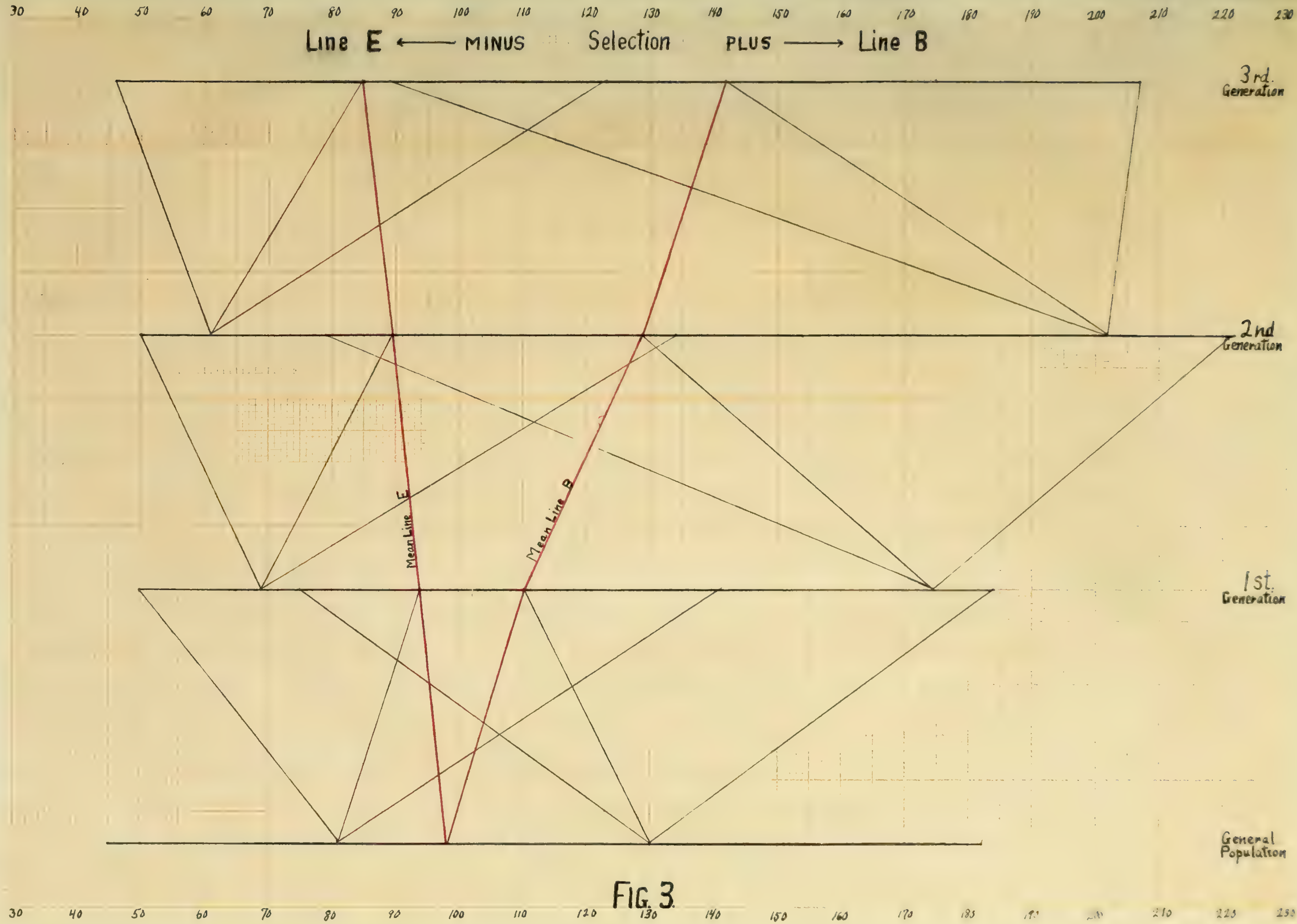

30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200 210 220 230
Line D ⟵ MINUS Selection PLUS ⟶ Line A
3rd Generation
2nd Generation
1st Generation
General Population
Mean Line D
Mean Line A
30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200 210 220 230

FIG. 2.



30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200 210 220 230
Line E ⟵ MINUS Selection PLUS ⟶ Line B
3rd. Generation
2nd Generation
1st. Generation
General Population
Mean Line E
Mean Line B

FIG. 3.

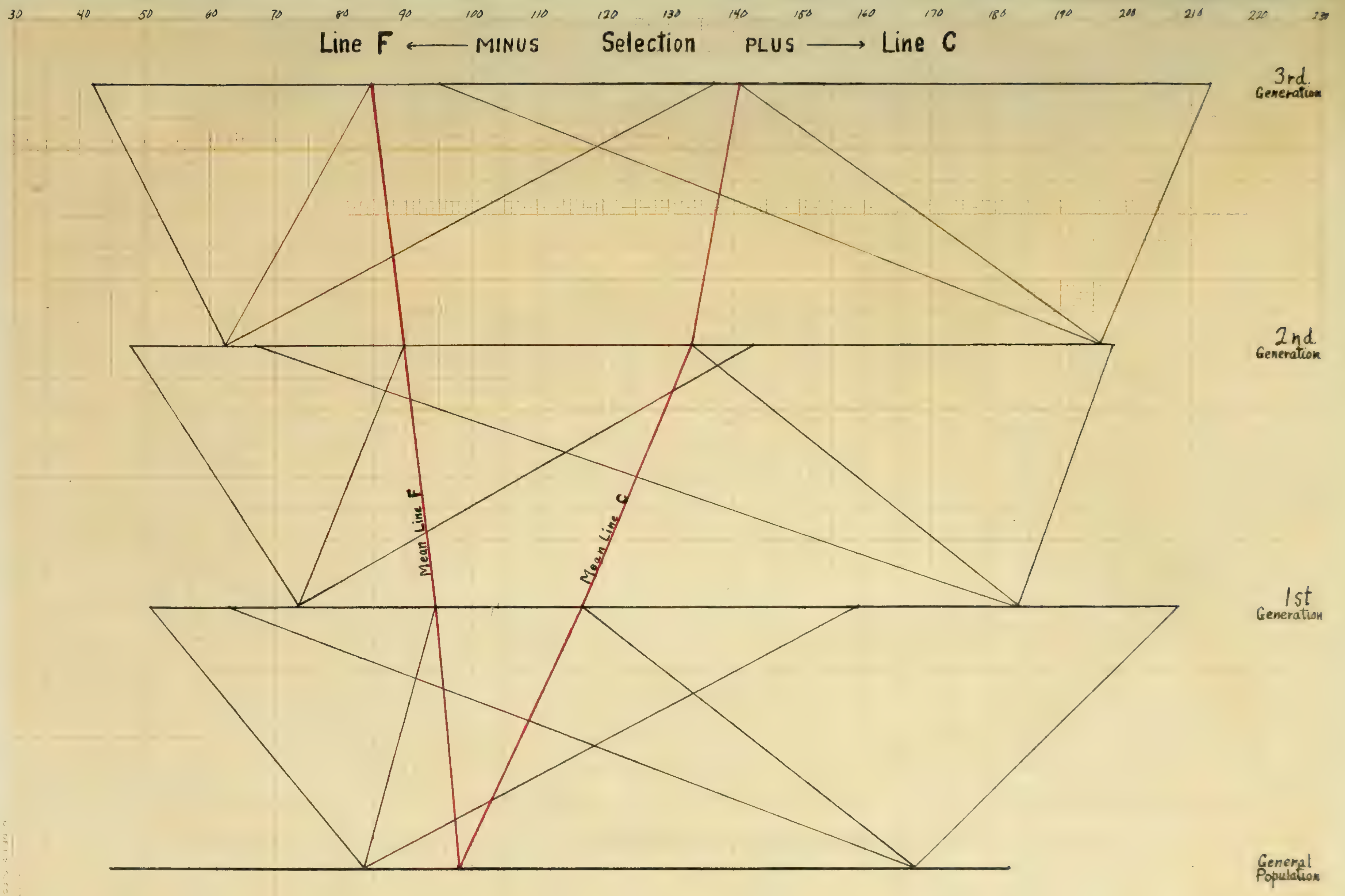

Line F ← MINUS Selection PLUS → Line C
3rd. Generation
2nd Generation
1st Generation
General Population
Mean Line F
Mean Line C
30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200 210 220 230

FIG. 4.

IV. Discussion.

Figures 2, 3, and 4 show graphically the effect of selection for three generations as summarized in Table VIII. A study of these figures indicates (1) that the means of the lines in which selection was carried on have been considerably displaced from the mean of the general population, the displacement toward a high number of facets being two to three times as great as that in the opposite direction; (2) that there is in each case, however, a marked regression toward the mean of the general population; (3) that as a result of selection the extremes of variation in the general population have been exceeded in both directions. This is common and of rather surprising magnitude in the case of high selection, but it occurs only once (in the third generation of line D), in the case of the low; (4) that there still exists in the third generation a very considerable overlapping between the populations of the high and low lines. In this generation, however, the means of the high lines, with the exception of line A, are higher than the extreme high variaties in the low lines, and the means of the low lines are appreciably lower in each case than the extreme low variates of the high lines.

Selection, therefore, has proved effective first, in tending to separate two opposite races, and second, in producing new degrees of variation beyond those that exist in the unselected population.

It remains for continued selection to demonstrate to what extent these new degrees of variation produced are heritable. It also remains to test out the pure line hypothesis in determining the extent to which selection is able to isolate lines which breed true and which no amount of subsequent selection can modify. That there are a number of these lines or races differing only slightly from each other in the general population of the "barred-eye" stock, and that many generations of selection will probably be required to isolate these races is indicated by the persistent overlapping already referred to between the populations of the gross divisions of high and low. That these lines are incapable of modification is not evident, however, from the fact that new extremes of variation have been produced within a very few generations of selection.

On the basis of results obtained thus far no definite conclusions can be drawn as to whether selection has or has not effected the stability of the germ plasm. As to the possibility of changing the germinal constitution by selection, different investigators have arrived at opposite conclusions.

Johannsen (1903) working with the common garden bean found that when he selected heavy and light individuals from a general population and sowed them, the resulting crops could be grouped according to their weights in normal curves around the characteristic weights of the parent individuals, rather than around the mode representing the weight of greatest frequency in the general population. Therefore, selection was effective. When,

however, the heavier and lighter individuals were selected from a family raised from a single self-fertilized seed, no further effect of selection could be obtained. Johannsen explains this variation within a pure line as being due to environmental or external rather than internal interferences, which, because they are external, cannot indicate that variations in the offspring of a pure plant are caused by variations in the germ cells from which they were produced.

Jennings (1908), who carried on extensive experiments with Paramecium, arrived at practically the same conclusion as did Johannsen. He found that by progressively selecting in opposite directions with regard to size from a wild culture of Paramecium, it was possible to obtain two lots of very marked difference in size, the difference being hereditary. But when the progeny of a single individual (forming a pure line) were tested, it was found that not the least effect was produced by methodical and long continued selection. Although there were large differences among the individuals in a pure line, these differences were not inherited. Jennings concluded that the effect of his selection consisted "solely in the isolation of races that already existed."

Castle (1914) is one of the investigators who holds an opposite viewpoint. He has experimented with a variety of hooded rat in which selection has been made for increase and decrease in the pigmented area of the coat. The result has been that the average pigmentation in one series steadily increased, while

in the other it steadily decreased. At present the selection has progressed to the extent that the increase and decrease in pigmented area have far transgressed the original limits of variation. Castle's conclusions are that in this case the character acted on by selection has been modified steadily and permanently, and that since the variations of which advantage is taken in selection are inherited, they must have a germinal basis.

Similar results were obtained by DeVries (1903) in an experiment with buttercups in which he succeeded by means of selection in raising the extreme number of petals from eleven to thirty-two.

In general, those who take the positive side of the issue, that the germinal constitution may be modified by selection, base their conclusions upon the results of experimentation with forms which reproduce bisexually. Those who hold the negative view have usually worked with forms reproducing asexually or by means of self-fertilization. Obviously, in the former case there is a greater chance for variations to occur which have a germinal basis and of which advantage may be taken in selection.

V. Summary.

1-As a result of three generations of plus and minus selection the mean number of facets in the "barred-eye" mutant of Drosophila ampelophila was raised from 98.03 to 141.93 and lowered from 98.03 to 81.66. 2- This change was progressive from generation to generation.

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