CHAPTER VII

CAN MENDELIAN UNIT-CHARACTERS BE MODIFIED BY SELECTION?

IF, as suggested in the last chapter, the potency of a character in crosses may be modified by selection, why may not the character itself be modified by selection, or are not the two things perhaps identical, viz. modification of the potency of a character and modification of the character itself? Darwin firmly believed that the characters of organisms can be modified by selection, and he made this the foundation stone of his theory of evolution. De Vries and Johannsen, however, have taught us a different doctrine, maintaining that selection is able to affect characters in superficial and transitory ways only, that the slight variations in characters which we see everywhere among organisms have no evolutionary significance or permanent value; that they come and go like the wavelets on the ocean beach, but have no more relation to evolution than the waves have to the tides. The brilliancy of the Mutation theory of De Vries, coupled with his great service to biology in rediscovering the Mendelian laws, has somewhat dazzled our eyes and led us, I think, to accept too readily his views concerning the efficacy of selection also. Ten years' continuous work in selection convinces me that much can be accomplished by this means quite apart from the process of mutation. The work of De Vries himself argues strongly in favor of this idea. To be sure, his interpretation of it is adverse to selection, and has seemed to most of us at times overwhelmingly convincing; but from his interpretation we may fairly appeal to the record of the work itself, and with this compare the record of our own work.

One of the most extensive selection experiments conducted by De Vries was made on the common buttercup, *Ranunculus bulbosus,* which occurs as a weed in pastures and meadows in this country as well as in Europe. It has, as is known, regular 5-petaled flowers. An examination of 717 flowers in the field made by De Vries in 1887 showed the rather frequent occurrence of 6 and 7 petaled flowers also, the average number of petals in the entire collection being 5.13. De Vries set himself the task to see if the proportion of many petaled flowers could be increased or the number of petals to a flower be further increased. In both these respects he succeeded surprisingly well. As a result of five successive selections the average number of petals was raised from 5.6 to 8.6, the upper limit of variation from 8 to 31, and the mode (or commonest condition) from 5 to 9. Singularly enough De Vries concludes, in accordance with general ideas which he had adopted, that selection had in this case done practically all that it could accomplish, that further selection, while it might advance the average somewhat farther, would have no permanent effect in modifying the type. This belief seems to have rested on considerations such as these. De Vries had found, as had others, that variations which are heritable have their origin in the germ-cells only. He recognized that the tendency to produce double flowers in the buttercup is a heritable variation and supposed it to be a unit-character, and so to conform with Mendel's law.

Now, if the tendency to produce double flowers were a simple Mendelian character it could exist in only three conditions, — that of a recessive, that of a homozygous dominant, or that of a heterozygous dominant. But recessives and homozygous dominants are pure, that is, they form only one type of gamete, and selection therefore from among their progeny could produce no new type. As regards the heterozygous dominant type, this would itself be unfixable, and selection could accomplish nothing permanent except by isolating a homozygous type. But such types should all be in evidence within two generations; therefore, if a completely and permanently double type had not been discovered within the five generations covered by the experiment, such a type was not to be expected at all from the material in hand, unless either a wholly new unit-character were introduced or an existing one were profoundly modified. De Vries considers changes of both these sorts possible.

He calls them *mutations*, and regards them as the *sole means* of evolutionary progress. But it is a peculiarity of his mutation theory that it regards only *large* changes in unit-characters as having any permanency, namely, such changes as mean a practical making over of the character. To borrow a figure from Bateson, just as the gas carbon monoxide, CO, may change into a very different gas, — carbon dioxide, CO_2, — by taking up a single atom of oxygen, but can make no less extensive change, since oxygen atoms do not split; so, according to De Vries, a unit-character may not change unless it changes profoundly. Various circumstances may modify the degree of its expression, but these are without permanent effect, since the character itself remains unchanged.

But there are both *a priori* and experimental grounds for questioning the correctness of De Vries' conclusions. It is known that the chemical compounds within the germ-cells are not so simple in composition as CO and CO_2. They are very complex substances, made up, it is thought, of very many atoms, often hundreds in a single molecule. If so, it is quite possible that an atom or two might be transposed in position within the molecule without wholly altering its chemical nature, and that thus slight changes in the germ-plasm might result, which, however, would be as permanent as more profound changes.

The argument of De Vries against any permanent effect of selection in modifying unit-characters has been greatly strengthened by the subsequent work of Johannsen and Jennings. Johannsen has found that if one selects from a handful of ordinary beans the largest seeds and the smallest seeds, and plants these separately, the former will produce beans of larger average size than the latter. Selection here has effect.

But if the selection is made, not from a general field crop of beans, but from those beans borne on one and the same homozygous mother plant, then the progeny of the selected large seed will be no larger than that of the selected small seed. Selection here is without effect.

The different result in the two cases may be explained, according to Johannsen, on

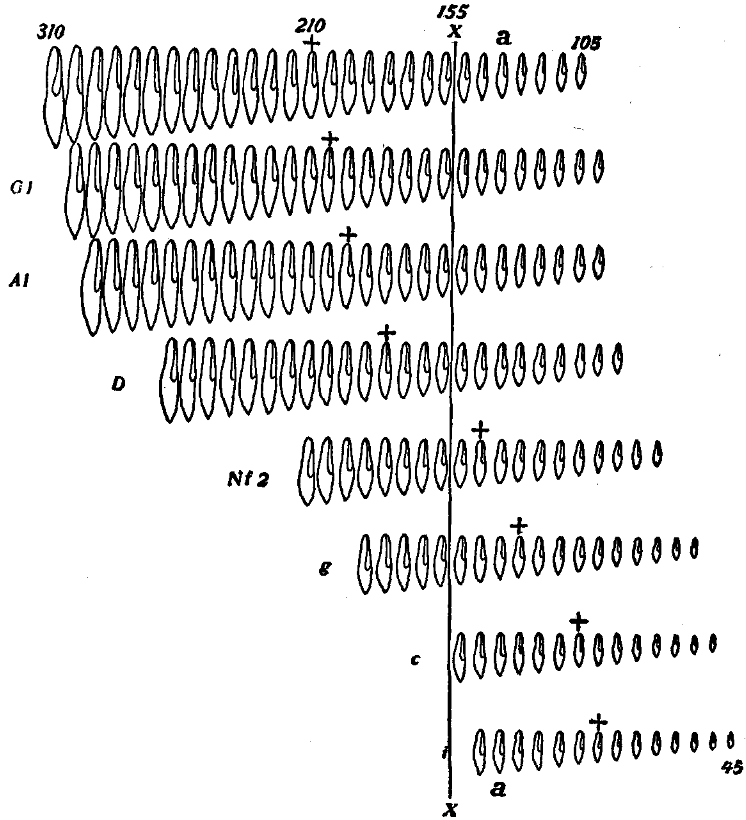

FIG. 40. — Diagram showing the variations in size of eight different races of paramecium. Each horizontal row represents a race derived from a single parent individual. The individual showing the mean size in each race is indicated by a cross placed above it. The mean of the entire lot is shown at X — X. The numbers show the measurements in microns. (After Jennings.)

the principle of the "pure line." The progeny of a single self-fertilized homozygous bean plant constitute a pure line. They are all alike, so far as the hereditary transmission of size is concerned, for they are all derived from like gametes. The differences in size which occur among them are due to differences in nutrition, not to germinal differences, and they are not transmitted. But in a mixed population of beans, such as is represented by a field crop, differences of size occur which are due to heredity as well as those which are due to the environment. In the case of the former, selection naturally has effect; in the case of the latter, it does not.

Jennings has obtained similar results in his studies of paramecium, — a one-celled animal which multiplies asexually by dividing into two similar parts. It lives in stagnant water and may be reared in great numbers in a hay-infusion, for it multiplies with great rapidity, dividing two or three times within twenty-four hours. The variations in size which occur in paramecium are shown in Fig. 40.

When from an ordinary culture of paramecium Jennings selects the largest and the smallest individuals respectively, he finds that the descendants of the one lot will be of larger size than the other. This looks like an effect of selection upon racial size. But if selection is made not within a mixed population but among the descendants of a single individual, it is found that the descendants of large individuals are of no greater average size than those of small individuals.

The explanation of this fact is to be found in the existence of what Johannsen has called pure lines. Jennings has been able to isolate eight distinct pure lines of paramecium differing in average size, as shown in Fig. 40. The range of variation in size within one of these races is great, but if one selects extremely large or extremely small individuals within the same pure line, i. e. among the asexually produced descendants of the same animal, no change in the average size of the race is brought about.

A very different result is obtained, however, if one mixes together several pure lines and then selects from the mixed race on the basis of size.

The larger animals then produce larger average offspring and *vice versa.* An examination of Fig. 40 will show why. Animals of the same absolute size are there placed in the same vertical row. If, now, one selects from the mixed population only the largest individuals, he will naturally secure representatives of only two or three pure lines, viz. of those lines which are characterized by the largest average size, and which, therefore, will produce large average offspring. If on the other hand he selects extremely small individuals, he will secure representatives of only the smallest races, which naturally will produce small offspring, so that selection seems to be effective in modifying racial size, but in reality it does this by sorting out the elementary constituents of the race.

It is impossible to deny the soundness of the reasoning of Johannsen and Jennings. It is perfectly clear that the effects of selection *should* be more immediate and much greater in the case of a mixed race than in that of a pure line, but is it certain, as assumed by them, that selection is *wholly* without effect in the case of a pure line? We know the effects should be *less*, but are they *nil?* Concerning this matter we are perhaps justified in awaiting further evidence. For in the case of beans and of paramecium alike size is subject to very great variation through the influence of nutrition. Variations due to this cause are naturally not inherited, since the germ-cells are not affected by them, but only the body. But is it not possible that along with the striking size differences due to nutrition there may occur also slight size differences due to germinal variation within the pure line, that is owing to variations in the potency of the same unit-character or combination of unit-characters? To be sure, Johannsen and Jennings have not observed these, but this does not prove their non-existence. Others may yet be able to do so; indeed one case is already on record in which such observations have been made in the case of a small crustacean (or water-flea), Daphnia.

Daphnia is a small transparent animal, about the size of a pin-head, which occurs in enormous numbers in fresh-water lakes and pools, forming a large part of the food supply of fresh-water fishes. It multiplies chiefly by the production of unfertilized eggs, — those which undergo no reduction and which develop without fertilization into an individual like the parent. The germinal composition, therefore, of all descendants produced in this way by the same mother should be identical, unless germinal composition can be modified in other ways than by reduction and recombination of unit-characters. Now the German zoölogist, Woltereck, has shown that, among the offspring developed from the unfertilized eggs of the same mother Daphnia, variations do occur which are heritable, so that if one selects extreme variants he obtains a modified race. Systematic zoölogists recognize as a generic distinction between Daphnia and Hyalodaphnia absence from the latter of the rudimentary eye found in Daphnia. Woltereck observed that in a pure line of Hyalodaphnia the rudimentary eye, usually wanting, may occur in individual cases. He found further that it occurred in varying degrees of development, which ranged all the way from a group of pigmented cells outside the brain, through stages in which cells were present without pigment, and others in which pigment was visible within the brain but no cells outside it were developed, and finally to those in which all traces of the eye had vanished, cells and pigment alike. By selection in three successive generations of the mother having the rudimentary eye best developed offspring were obtained, 90 % of which had the pigmented eye, and which would therefore pass for animals of a wholly different genus. The degree of development of the organ in the last generation was also greater than in the previous generations. Here within a pure line produced by parthenogenesis selection served to augment both the degree of development of an organ and the frequency of its occurrence within the race, a result precisely parallel to that which I obtained some years ago by selection in the case of a rudimentary fourth toe in the guinea-pig. The experiment with Daphnia is not open to the objection that may be offered to the guinea-pig experiment, that it is possibly a result of gametic segregation and recombination, for in Daphnia the reproduction was exclusively by unreduced and unfertilized eggs.

The rudimentary eye of Daphnia is an organ the development of which, so far as observed, is wholly independent of environmental influence; but the case is different with another structure of Daphnia, upon which also Woltereck made observations, namely, a projection or spine borne on the head of the animal. This is not a constant structure, but is sometimes present, sometimes wanting altogether, in the same pure line. In extreme cases it forms a great angular extension of the head forward. To a considerable extent its development is subject to control through the temperature of the surrounding water, but independently of such influence the degree of its development varies and is heritable. Although in general, just as in the experiments of Johannsen and Jennings, selection of animals with the best-developed spine did not increase the degree of development of the organ or the frequency of its occurrence, yet in individual cases such increase was observed, so that the structure occurred in over 50 % of the offspring. In such cases, then, it would seem that along with the cases due to environmental influence occurred others due to germinal variation. Although selection of the former would not influence the race permanently, there is every reason to think that the latter would so influence it, and did in the experiment.

Accordingly the results of Johannsen and Jennings on the one hand, and of Woltereck on the other, are *not necessarily in opposition* to each other. Woltereck's conclusions agree with those of Johannsen and Jennings so far as concerns the great bulk of the variations, those caused by external influences. All agree that they are not inherited. Woltereck, however, observes also, what the others have failed to observe, that along with the non-inherited variations occur other similar but less numerous ones which are inherited.

My own observations are entirely in harmony with those of Woltereck. Like him, I find that selection may modify characters. In several cases I have observed characters at first feebly manifested gradually improve under selection until they became established racial traits. Thus the extra toe of polydactylous guinea-pigs made its appearance as a poorly developed fourth toe on the left foot only. Only 6 % of the offspring of this animal by normal unrelated mothers were polydactylous, but among his offspring were some with better developed fourth toes than the father possessed. Such individuals were selected throughout five successive generations, at the end of which time a good four-toed race had been established. It was found in general that those animals which had best-developed fourth toes transmitted the character most strongly in crosses with unrelated normal animals. The percentage of polydactylous individuals produced in such crosses varied all the way from 0 to 100 %. By selection this percentage was increased, as was also the degree of development of the fourth toe in crosses.

Another character which made its appearance among our guinea-pigs, at first feebly expressed, was *a silvering of the colored fur,* due to interspersing of white hairs with the colored ones (see Fig. 37). The first individuals observed to have this character bore white hairs on the under surface of the body only. By inbreeding, a homozygous strain of the silvered animals was soon obtained, one in

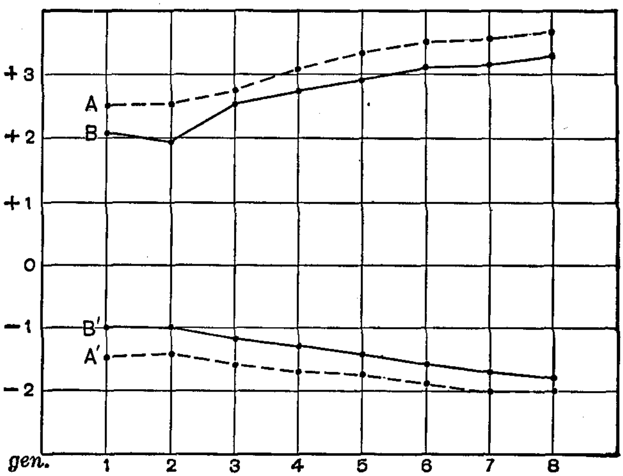

Fig. 41. — Chart showing effects of selection in eight successive generations upon the color-pattern of hooded rats. *A*, average condition of the selected parents in the *plus* series; *B*, average condition of their offspring. *A*[1], average condition of the selected parents in the *minus* series; *B*[1], average condition of their offspring.

which all the offspring were silvered to a greater or less extent. Selection was now directed toward two ends, — (1) to secure animals which were free from spots of red or white, a condition which was present in the original stock, and (2) to secure extensive and uniform silvering on a black background. In both these objects good progress has been made. We have animals which are silvered all over the body except on a part of the head, and the percentage of such well-silvered individuals is relatively high.

But the most extensive selection experiment which I have personally observed is one in which I have been assisted by Dr. John C. Phillips (see Figs. 39 and 41). Selection in this case has been directed toward a modification of the color pattern of hooded rats, — a pattern which is known to behave as a recessive Mendelian character in crosses with either the self (totally pigmented) condition or the so-called Irish (white-bellied) condition found in some other rats. The extreme range of variation among our hooded rats at the outset of this experiment is indicated by the grades — 2 and + 3 of Fig. 39. Selection was now made of the extreme variates in either direction and these were bred separately. Two series of animals were thus established, — one of narrow striped animals, *minus* series; the other of wide striped, *plus* series. In each generation the most extreme individuals were selected as parents; in the narrow series, those with narrowest stripe; in the wide series, those with widest stripe.

TABLE I

Results of Selection for Modification of the Color-pattern of Hooded Rats.

	Generation.	Average Grade, Parents.	Average Grade, Offspring.	Number of Offspring.
Plus series.	1	2.50	2.05	150
	2	2.51	1.92	471
	3	2.73	2.51	341
	4	3.09	2.72	444
	5	3.33	2.90	610
	6	3.51	3.09	834
	7	3.53	3.14	874
	8	3.65	3.30	91
				3,815
Minus series.	1	1.46	1.00	55
	2	1.41	1.07	132
	3	1.56	1.18	195
	4	1.69	1.28	329
	5	1.73	1.41	701
	6	1.86	1.56	1252
	7	2.00	1.70	1544
	8	2.03	1.78	713
				4,921

The result of the selection is shown graphically in Fig. 41 (compare Table I). The offspring in the narrow series became with each generation narrower; those in the wide series became with each generation wider, with a single exception. In generation two the wide stock was enlarged by the addition of a new strain of animals. This caused a temporary falling off in the average grade of the young, the two series overlapping for that generation. No new stock was at any other time introduced in either series, the two remaining distinct at all times except in generation two. It will be observed that a change in the average grade of the parents is attended by a corresponding change in the average grade of the offspring. The amount of variability of the offspring is not materially affected by the selection, but the average about which variation occurs is steadily changed, as are also the limits of the range of variation.

The interesting feature of this experiment is the production, as a result of selection, of wholly new grades; in the narrow series, of animals having less pigment than any known type other than the albino; in the wide series, of animals so extensively pigmented that they would readily pass for the "Irish type," which has white on the belly only, but which is known to be in crosses a Mendelian alternative to the hooded type. By selection we have practically obliterated the gap which originally separated these types, though selected animals still give regression toward the respective types from which they came. But this regression grows less with each successive selection and ultimately should vanish, if the story told by these statistics is to be trusted. As yet there is no indication that a limit to the effects of selection has been reached.

From the evidence in hand we conclude that Darwin was right in assigning great importance to selection in evolution; that progress results not merely from sorting out particular combinations of large and striking unit-characters, but also from the selection of slight differences in the potentiality of gametes representing the same unit-character combinations. It is possible to ascribe such differences to little units additional to the recognized larger ones, but if such little units exist, they are indeed very little as well as numerous, and by adding to the effect of the larger ones they produce what amounts to modification of them.

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