CHAPTER XV

PARTHENOGENESIS AND PURE LINES

In so far as parthenogenetic reproduction takes place without reduction in number of the chromosomes, the expectation for any character is that it will have the same *frequency distribution in successive generations*, because the chromosome group is identical in each generation. There are a few cases where parthenogenetic inheritance has been studied. The results conform to expectation.

The only difference between a species reproducing by diploid parthenogenesis and one propagating vegetatively is that in the latter a group of cells starts the new generation and in the former only one cell, *viz.*, an egg, that no longer undergoes reduction, or needs to be fertilized. In both, the chromosome complex remains the same as in the parent. Strictly analogous to the two foregoing methods of propagation are the cases of sexual reproduction in a homozygous group of individuals, composed of males and females or in a group of hermaphroditic forms that are homozygous. Successive generations are here also expected to have the same frequency distribution, whether selected or not, because they have the same germ-plasm. Johannsen's pure lines furnish an example of the last case, for, in principle, pure lines, parthenogenetic reproduction, and vegetative propagation, are concerned with nearly the same situation.

Johannsen worked with one of the garden beans (*Phaseolus vulgaris*) taking the weight of the seeds, in some cases, and *measuring their sizes in other cases*. It is known that this bean regularly fertilizes itself. As a consequence of self-fertilization there is a tendency for the descendants of any form to become in time homozygous, even when heterozygous forms were present at first.

In fact, in a few generations perpetuated by self-fertilization with chance elimination of individuals, a homozygous race will result. This comes about as follows: Starting with a heterozygous hermaphroditic individual, some of its offspring will, through recombination of factors, become homozygous, and if self-fertilization prevails they will continue homozygous; other offspring will be heterozygous. From the latter both homo- and hetero-zygous offspring will again be produced, the former remaining such in later generations, the latter continuing the process of splitting. Since only a part of each generation survives, there is in the long run a better chance that the homozygous individuals will be the survivors, because those that have become such in each generation are fixed, and those that are not will continue to produce some homozygotes. There will be in consequence a steady process of recurrence of homozygotes which, on chance alone, will sooner or later win out.

The beans that Johannsen worked with had apparently reached a homozygous condition, and at the start there must have been several such lines. He studied nineteen of them. The offspring of any one plant produced beans that gave the same frequency distribution as the beans of the last generation. This condition continued through all successive generations. It is to be noted that the beans on any one plant differ in size, but any one will give the same frequency distribution as the beans of the preceding generation. It made no difference whether the larger or the smaller beans were chosen for planting—they gave the same group in the next generation.

It is interesting to compare this result with what would have happened had the beans been propagating by cross-fertilization at the time when Johannsen began his work with them. If this had been their normal method of reproduction they would probably have been heterozygous at the start, and would have given different genetic types for several generations, even if self-fertilized. Pure lines would have appeared only after the beans had become homozygous through repeated inbreeding. But Johannsen, starting with homozygous beans, was able to obtain his extremely important results, because if selection could bring about any change it would have to be due to a change in the genes themselves. Here, by means of a crucial experiment, he exposed an error that had been accepted by selectionists from 1859 to 1903. It would have been difficult, almost impossible, to give this demonstration on any plant or animal in which self-fertilization or asexual reproduction was not the rule; for, if the material had been heterozygous either for the main factors for a character, or for modifying factors for that character, selection in one or another direction would be expected through recombination of factors to change the original frequency distribution. It is true that any stock, even such as reproduces by males and females, may be made homozygous by inbreeding brother and sister for ten or more generations, but even such stock would have to be constantly watched for mutation.

Johannsen defined a pure line as a race or family of individuals descended through an unbroken series of self-fertilizations from an ancestor homozygous in all its genes. By making this definition precise he made clear the essential point of his demonstration. Now that his point is made, it seems no longer necessary or even desirable, I think, to narrow the definition of a pure line to races that self-fertilize, since this is only one form of inbreeding, resulting in the production of homozygous individuals. By extending the definition of a pure line to all forms whose genes are the same in all individuals (whether the pairs are homozygous or not), the definition covers all cases of parthenogenesis that do not undergo reduction, and all cases propagating by non-sexual means, for, in these cases the same complex of genes is present in successive generations.

Many plants are propagated by offshoots, stolons, tubers, cuttings, etc. East has studied the effect of selection of tubers of certain races of the common potato. A race was first grown from a single tuber. By boring holes into the tubers enough material could be obtained for a chemical test of the amount of nitrogen in them. The rest of each tuber could, if desired, be cut into pieces of standard size and planted. Ten tubers, high in nitrogen, and ten, low in nitrogen, were selected. The tubers of the next generation showed that there was no relation found between the amount of nitrogen in the original tuber and in those that came from it. A repetition of the experi-

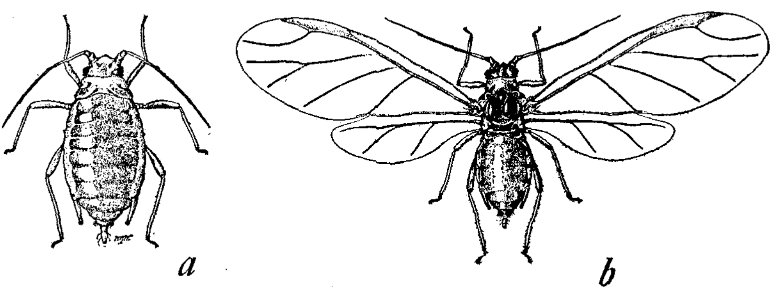

FIG. 95.—A wingless aphid to the left and a winged to the right, both belonging to the same species. (After Webster and Phillips.)

ment in another generation gave only meagre results owing to drought. As far as the facts went, this generation, too, showed no effect of selection.

Most of the protozoa propagate by dividing into equal or nearly equal parts—*i.e.,* by a process of cell-division. Jennings has studied the effect of selection in a culture of paramecium, all members of which had descended from a single individual. No change was induced. Later, however, working on another protozoön, *Difflugia corona,* Jennings found that selection brought about changes in the direction of selection. In this case, the method of division may possibly include irregular distribution of the chromatin material, and the recent work of Hegner indicates that such an interpretation is not improbable. Possibly, too, the irregular distribution of chromatin particles (chromidia) in the cytoplasm—aside from the nuclear phenomena, or in connection with them—may make the results similar in certain aspects to the distribution of plastids in certain plant cells.

Many species of plant lice—aphids—(Fig. 95, *a*) propagate throughout the summer by parthenogenesis. There is no chromosomal reduction during the development of the egg. Each egg gives off only one polar body,

FIG. 96.—Curve showing the non-effect of selection for the first twelve generations for increase in body length, the heavy solid lines represent the fluctuations of the fraternal means; the light solid line the fluctuations of the longest variant; the broken line the fluctuation of the shortest variant. (After Ewing.)

each chromosome splitting into two daughter chromosomes, so that the egg retains the whole number of chromosomes. Ewing has carried out an extensive experiment with *Aphis avenæ,* selecting individuals through a number of generations for the length of the cornicles (honey-dew tubes), for the length of the antennæ, and for body length. Considering here only the last, individuals were selected for forty-four generations in a plus and in a minus direction. The graph for the fourty-fourth to the sixty-third generation is shown in Fig. 96. The heavy solid line represents the fluctuations of the longest variants, the broken line the fluctuations of the shortest variants. *It was found that much of the fluctuation* observed was connected with temperature. The temperature was therefore kept constant at about 65° F. for the next twenty generations, and as shown in Fig. 97, the fluctuation in the fraternal line was cut down. No influence of the selection is observable in the chart. This evidence, in conjunction with that for other characters, shows that no change takes place in the characters of

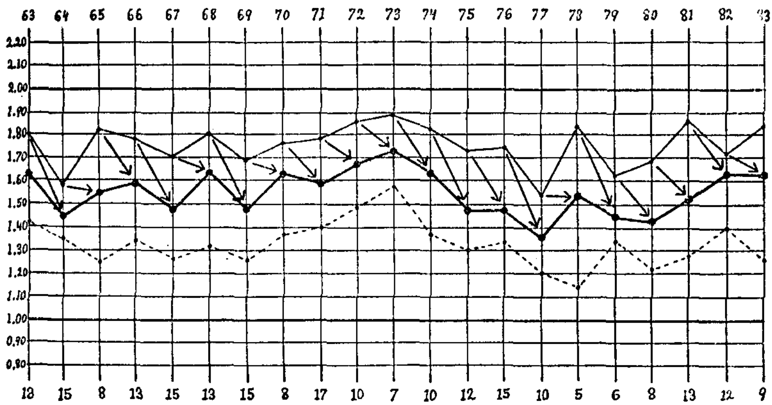

FIG. 97.—Curve showing the effect of selection for the second score of generations. (See Fig. 96.)

the insect so long as the same group of chromosomes remains. It would be difficult to find a better example than these parthenogenetic insects to test the claim that selection can change the germ-plasm, for here the conditions are even simpler than in unisexual forms unless they have first been made homozygous.

The aphids also furnish favorable material to illustrate how the environment may cause very great changes, even when the genetic complex remains the same. The parthenogenetic aphids appear often as winged individuals (Fig. 95, *b*). There is an entire change in structure involving practically every part of the body. The winged and wingless individuals may differ more strikingly than do species of the same genus. The winged forms arising *from the wingless produce wingless forms again in the* next generation that may be identical with those from which they came. It has long been believed that environmental influences bring about these transitions in aphids, but only recently has critical evidence been obtained. The clearest evidence is that of Shinji, with the rose aphid. By sticking twigs of the rose in sand and flooding the sand with water containing substances in solution—a method first suggested by W. T. Clarke—the fluid being drawn up into the leaves is sucked out by the aphids on the leaves. As the following table shows, young aphids reared on the

	Winged Individuals.	*Apterous* Individuals
$AgNO_3$	51	0
$CuSo_4$	34	1
$HgCl_2$	31	6
$NiSO_4$	955	5
$SbCl_3$	41	5
$PbCl_2$	12	2
$SnCl_4$	579	8
$ZnCl_2$	49	2
Mg salts	840	9
Sugar	365	160
Alcohol	2	288
Alum	3	34
Acetic acid	0	67
Na salts	2	1029
Ca salts	1	433
K salts	3	324
Sr Salts	1	220
Tannin	1	14
Urea	5	153
Water, distilled	0	394
Water, tap and creek	17	461
Peptone		15

salts of the heavy metals as well as on magnesium salts and sugar became winged, while those reared on the other substances in this list remain apterous. Here we have an excellent example of how in one environment a given germ-plasm produces one result, and in another environment a different result without any intermediate forms.

The change from wingless to winged aphids is far greater than most mutational changes that we know, yet must involve a different kind of change because the result is reversible, while a mutation, having once taken place, is relatively irreversible.

Summing up, it may be said that the evidence shows that whenever the same chromosomal complex containing the same genes is found, the measurements of any character in successive generations show the same frequency distributions of the measurements, and the form may be said in a general sense to belong to a *pure line*. The evidence shows that whether the chromosomal complex is heterozygous or homozygous, the results are the same, so far as the pure line is concerned; but it is also obvious that in most animals and plants, where redistribution (reduction) of the chromosomes takes place in each generation, only forms already homozygous will give pure lines. This was the special feature of the material that Johannsen worked with, but aside from its practical value in studying the selection problem, the limitation of the definition of pure lines to such an exceptional situation leaves out of sight the wider bearing of the evidence.