CHAPTER XVII

CYTOPLASMIC INHERITANCE

In the preceding pages so much emphasis has been laid on the chromosomes as bearers of the hereditary material that it may appear that no very important rôle is left to the rest of the cell. Such an impression would be quite misleading; for the evidence from embryology appears to show that the reactions by means of which the embryo develops, and many physiological processes themselves, reside at the time in the cytoplasm. Furthermore, there is also genetic evidence to show that certain forms of inheritance are the outcome of self-perpetuating bodies in the cytoplasm, most of which go under the name of plastids. Recognition of plastid inheritance carries with it the idea that if there are such materials in the cytoplasm that are self-perpetuating they will have to be taken into account in any complete theory of heredity.

In the case of certain chlorophyll characters there is excellent genetic evidence to show that a peculiar kind of inheritance is due to the mode of transmission of plastids in the cytoplasm. There is a race of four-o'clocks known as *Mirabilis Jalapa albomaculata,* whose leaves are made up of patches of green and white. Such leaves are said to be checkered (Fig. 102, *b*). The amount of green, or of white, varies on different leaves, and on such plants there frequently appear leaves and entire branches that are green and others that are white. The white is due to the absence of green in the chlorophyll grains. Some cells have only green chlorophyll bodies, and others only white, still others may have the two mixed in various amounts.

Correns has shown that if the flowers on a green branch are self-fertilized they produce only green plants, and these again only green plants. Flowers on white branches give only white offspring. Flowers on the checkered branches give some checkered plants, some white plants and some green plants. The proportions in which these different types arise varies according to the amount of green in the branch from which the selfed seed came.

When the ovary of a flower on a green branch is fertilized by pollen from a white branch, the plant produced is green like the maternal branch. If the ovary of a flower on a white branch is fertilized by pollen from a

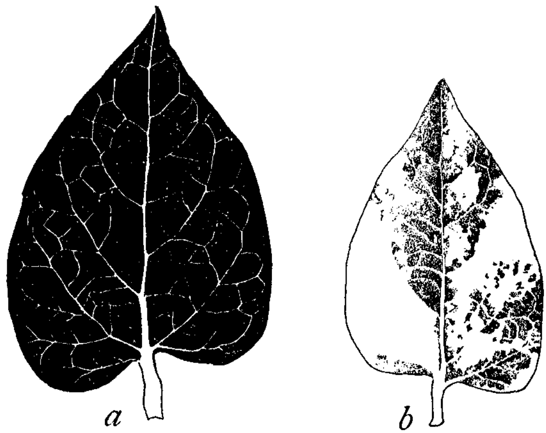

FIG. 102.—Green leaf and checkered leaf of four-o'clock. (After Baur.)

green branch the offspring is white like the maternal branch. These and other combinations show that this color inheritance is only through the mother. The results are explicable on the assumption that there are normal (green) chlorophyll bodies and abnormal chlorophylless bodies, both kinds propagating in the cytoplasm by division, and that these two kinds are transmitted only through the egg-cell. The green or white color of the leaves of a given branch is an index of the kind of chlorophyll body that the ovaries will probably contain. At each division of the body-cells the chlorophyll grains present in it are sorted out more or less at random—hence from a cell that contains both kinds, more white granules than green ones may at times get into a cell, and at other times only white granules will get into one daughter cell, so that a white branch arises.

In other species of plants that have white leaves and branches and green leaves and branches, the cross may give a different result. Thus in *Melandrium* and *Antirrhinum,* green by white gives green F_1 (whichever way the cross is made), in F_2 there are 3 green to 1 white plant. In this case the results can be explained as due to the action of genes in the chromosome on the production of chlorophyll in the cytoplasm—an action of such a kind that

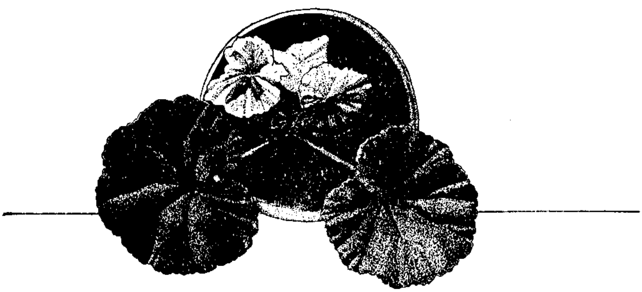

FIG. 103.—Pelargonium that gave rise to a white branch. (After Baur.)

the granules do not develop green color unless the (normal) gene is present, in single dose at least. In this case, even if the eggs only transmit plastids, the F_1 individual from a white-leaved mother by a green-leaved father is green, because the paternal nucleus introduces a gene that causes the green color to develop in the plastids. It is the segregation of the genes in the germ-cells of the F_1 individual that leads to the 3:1 ratio in F_2, and not the distribution of the plastids as in the preceding case.

The most peculiar case is that of *Pelargonium* described by Baur. White leaves and branches, and green leaves and branches occur on the same plant (Fig. 103). Self-fertilized seeds from each breed true to color of branch. White to green gives a different result, *viz.,* mosaic seedlings with patches of green and white on stems and leaves (Fig. 104). When these seedlings grow into plants, the color of the leaves will depend on the color of that part of the stem from which the terminal bud, and lateral buds grow out. If a bud lies in a green part of the stem the new part will be green (Fig. 104, *a*): if the new bud lies in a white part of the stem the new part will be white (Fig. 104, *c*): and if it lies in a partly green, partly white region the new part will have some white, some

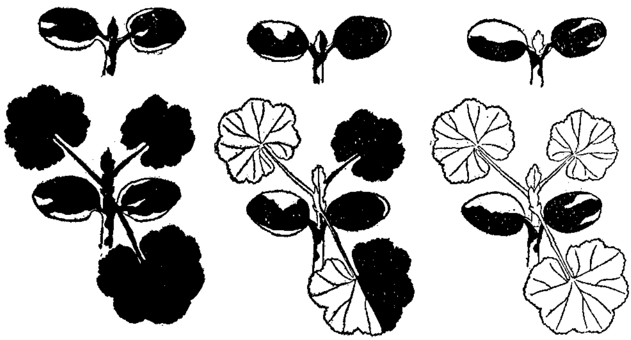

FIG. 104.—Diagram to show how a sectorial chimera may be produced. If the terminal bud has come from a region of the seedling entirely green, all of the future leaves will be green, *a;* if from a region without chlorophyll, all the future leaves will be white, *c;* but if the terminal bud lies partly in one, partly in the other region, some white and some green leaves will arise, *b*. (After Baur.)

green parts (Fig. 104, *b*). The only explanation that is suggested by Baur is that in this plant the plastids are transmitted both by the egg and by the pollen. The white plant with defective plastids contributes part of the plastids in the fertilized egg, the green plant with normal plastids the other part. The fertilized egg contains therefore both kinds of plastids. During division of the egg and embryo, the granules become irregularly distributed in the cells. Whenever a cell gets only defective granules, it and its descendants are white, producing white parts: when a cell gets mostly or only green granules, it and its descendants are green, producing green parts. Hence arise the checkered seedlings from which white or green branches grow out.

The preceding facts and theories relating to plastid inheritance show that if any element outside the nucleus has the power to propagate itself it may be transmitted through the egg, and even possibly through the sperm (pollen) also. There is no contradiction here in any sense to Mendelian inheritance but only an additional type of inheritance that can be studied by as exact methods as those used in Mendelian work. The chief difference between chromosomal and plastid inheritance lies in the orderly sequence of the distribution of the genes in all divisions by means of the mitotic figure, whereas the plastids are supposed to be shuffled about at random to the daughter cells (partly because their division period does not correspond with that of the cell). This haphazard distribution of the plastids at any and all divisions is in striking contrast to the sorting out of the genes that occurs only at one specific cell-division when the germ-cells pass through the maturation stage. Hence the orderliness of Mendelian inheritance as contrasted with the more irregular procedure in plastid inheritance.

To embryologists familiar with the fact that differentiation of the egg is closely associated with the cleavage pattern, it was a natural inference that in the cytoplasm lay the *inherited characteristics that gave form to the* embryo, and even to all of its essential features. Little room would seem to be left for the action of the chromosomes except to fill in the details of the characters already outlined by cytoplasmic activity. This view might be laconically referred to as the theory of the "Embryo in the Rough," or more generally as the "Theory of the Organism as a Whole." Boveri discussed some such view (1903), and at first considered it favorably. It has since been seriously discussed by others. Boveri pointed out that when a horse is crossed to an ass it makes no difference which way the cross is made, for both egg and sperm bring in the characteristics that make the organism first a bilateral one, then a vertebrate, then a mammal, and, lastly, a perissodactyl. In all these aspects, both parents agree, and beyond these limits hybridizing is impossible. Whatever the germ develops into must contain these common characters. The important point to determine, Boveri thought, is whether the *species* characteristics are or are not in the nucleus. He concluded, after discussing the pros and cons, that it is doubtful if these preformed qualities of the egg-protoplasm extend beyond the larval periods, but that in general all characteristics that distinguish the individual from all others of its species and from the characteristics of related species are inherited through the chromosomes. Later he restated his conclusion as follows: "All essential characteristics of the *individual* and of the *species* are epigenetic, and the determination is brought about through the nucleus." Conklin at one time expressed even more sharply the idea that group characteristics may be inherited in a different way from specific characters in the following paragraph:

> We are vertebrates because our mothers were vertebrates and produced eggs of the vertebrate pattern; but the color of our skin and hair and eyes, our sex, stature, and mental peculiarities were determined by the sperm as well as by the egg from which we came. There is evidence that the chromosomes of the egg and sperm are the seat of the differential factors or determiners for Mendelian characters, while the general polarity, symmetry and pattern of the embryo are determined by the cytoplasm of the egg.

In another statement, however, Conklin takes what seems to me to be more nearly a correct view in regard to the question, *viz.*, that "There is no doubt that most of the differentiations of the egg cytoplasm have arisen during the ovarian history of the egg, and as a result of the interaction of nucleus and cytoplasm; but the fact remains that at the time of fertilization the hereditary potencies of the two germ-cells are not equal, all the early stages of development, including the polarity, symmetry, type of cleavage, and the pattern, or relative positions and proportions of future organs, being foreshadowed in the cytoplasm of the egg-cell, while only the differentiations of later development are influenced by the sperm. In short, the egg cytoplasm fixes the general type of development, and the sperm and egg nuclei supply *only the details.*" If, as implied, the egg nucleus at first has already produced its effect on the cytoplasm, it has done something more than supply the details; and as to the sperm nucleus I should substitute nearly all the stages of development later than the gastrula. Moreover, sex is *certainly one* of the fundamental characters of the organism, yet it appears to be determined at fertilization by the chromosomal combination formed at that time. Conklin later abandoned his earlier interpretation.

Quite recently, in his book on "The Organism as a Whole," Loeb has discussed the question as to whether the protoplasm of the egg is "the future embryo in the rough," the sperm furnishing only the "individual characters." Loeb suggests that the "specificity of the species" must be due to their proteins, and that the "heredity of the genus is determined by proteins of a definite constitution differing from the proteins of other genera. This constitution of the proteins would therefore be *responsible for* the genus heredity. The different species of a genus have all the same genus proteins, but the proteins of the species of the same genus are apparently different again in chemical constitution and hence may give rise to the specific biological or immunity reactions." The possible *relations of* these considerations to heredity are summed up in the following paragraph:

It is thus doubtful whether or not any of the constituents of the nucleus contribute to the determination of the species. This in its ultimate consequences might lead to the idea that the Mendelian characters which are equally transmitted by egg and spermatozoön determine the individual or variety heredity, but not the genus or species heredity. It is, in our present state of knowledge, impossible to cause a spermatozoön to develop into an embryo, while we can induce the egg to develop into an embryo without a spermatozoön. This may mean that the protoplasm of the egg is the future embryo, while the chromosomes of both egg and sperm nuclei furnish only the individual characters.

The evidence from Mendelian heredity is adverse to any such distinctions as those made by the three authors referred to above. We find in them, I think, an echo of an old and somewhat mystical conception of fundamental distinctions between order, family and generic characters of animals and plants—distinctions that even most systematic writers recognize to-day as little more than conventions that change from group to group. In the second place, since the cytoplasm of the egg has been under the influence of its own nucleus with a paternal and a maternal group of chromosomes there is no direct means of determining whether its characteristics are due to such an influence or have always been free from it. The fact that sperm of a foreign species does not change the cytoplasm of the egg at once is to be expected even from a chemical viewpoint. Mendelian workers can find no distinction in heredity between characteristics that might be called ordinal or specific, or fundamental, and those called "individual." This failure can scarcely be attributable to a desire to magnify the importance of Mendelian heredity, but rather to experience with hereditary characters. That there may be substances in the cytoplasm that propagate themselves there and that are outside the influence of the nucleus, must, of course, be at once conceded as possible despite the fact that, aside from certain plastids, all the Mendelian evidence fails to show that there are such characters. In a word, the distinction set up between generic versus *specific* characters or even "specificity" seems at present to lack any support in fact.