# CHAPTER 19

# MATERNAL EFFECTS

Aristotle wrote at length on the relative effects of the male and female parents on the properties of their offspring—his discussion is now interesting as an example of the Aristotelian method rather than as a real contribution. With the increase in knowledge of development there gradually appeared the idea of preformation, according to which the fertilized egg contains the parts of the developing individual in miniature—development consisting of the unfolding of these parts in a manner similar to the development of a flower from a bud. In its extreme form, this led to the conclusion that each egg also contains miniature representatives of the eggs of all potential future descendants.

With the development of clearer ideas about fertilization, two schools emerged: the "ovists" who thought the preformed parts were contained in the unfertilized egg and were merely activated by the sperm, and the "spermists" who thought of the sperm as a complete animalcule that was merely nourished by the egg.

C. F. Wolff (1759) initiated a reaction from this view. Wolff thought of the fertilized egg as a relatively homogeneous structure, from which the parts of the embryo developed *de novo*. This view, known as epigenesis, was more in accord with the direct observations of embryologists and avoided some of the absurdities to which the preformationists had been led. It came to dominate the thinking of embryologists. It was also more easily reconciled with the cell theory and with the experimental results of the hybridizers.

The older views implied inequalities between the parents in the determination of the properties of their offspring; for example, that the form was determined by the mother, the color by the father. I have, in fact, encountered such views currently held by a few amateur plant breeders.

Kölreuter (1761–1766) seems to have been the first to carry out systematic reciprocal crosses, and to have concluded that the two parents contributed equally to the characteristics of their offspring. This conclusion was confirmed by most of the plant hybridizers who followed him (see Chapter 1), but was long resisted by zoologists.

It may be supposed that the zoologists were at first influenced by the often-discussed differences between the mule and the hinny—the results of reciprocal crosses between the horse and the ass. Hinnies are rare, and I have never been able to find a satisfactory account of them. The only supposed hinny I have ever seen impressed me as being merely a small mule—and the smaller size is the only generally recognized peculiarity. This may be due to their having a smaller mother; it is also probable that they are usually the offspring of small and inferior individuals of both parent species, since they are usually accidental in origin.

In later times zoologists were undoubtedly influenced by the study of hybrid embryos of marine animals, especially species hybrids in sea urchins. Here the effects of foreign sperm are sometimes not at once apparent, and the hybrid embryo begins its development according to the maternal plan. Often the later embryos from reciprocal crosses are not distinguishable (Boveri, 1892, 1903; Driesch, 1896, 1898). These authors concluded that up to a certain point the development is controlled entirely by the cytoplasm of the egg—though Boveri later realized that this cytoplasmic specificity might be under the control of the chromosomes of the mother. Others, however, were led to conclude that the general ground plan of development is not under chromosomal determination. As Loeb (1916, 1919) expressed it, the “embryo in the rough” is determined by the cytoplasm alone, or as Conklin (1918) stated, “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.”

The suggestion that the maternal cytoplasm in such cases may be determined by the chromosomal genes of the mother received experimental support from the work of Toyama (1912) on the color of the embryonic serosa in the silkworm, and more clearly in the case of the snail Limnaea (Boycott and Diver, 1923; Sturtevant, 1923). In this form the shell may be coiled either dextrally or sinistrally, the two types being exact mirror images of each other. It turned out that the difference is due to a single pair of genes, with dextral dominant; but the direction of coiling is determined not by the constitution of the individual but by that of its mother. Thus, for example, a heterozygous individual, mated as a female (the animals are hermaphroditic) to another from a pure sinistral line, will produce only dextral offspring, even though half of these individuals do not carry the gene for dextral coiling. The fate of the egg is thus determined, before polar-body formation and fertilization, by the genes of the mother. The nature of the coiling is visibly determined early in development; the two types can be distinguished by the pattern of cleavage at the second division following fertilization; but the mirror image relation persists throughout the life of the animal.

The somewhat similar case of the color of the sap in pollen grains studied by Correns has already been described in Chapter 5. Many other instances are known; for example, the gene affecting sex in *Drosophila neorepleta,* described in Chapter 13. In a few of them, the maternal nature of the hybrids is due to a failure of some or all of the paternally derived chromosomes to persist in the foreign cytoplasm (Baltzer, 1909; Godlewski, 1911).

There is another group of maternally inherited characteristics that is different in kind, namely, certain chloroplast defects in plants. In many plants there are ordinary chromosomal genes that affect the green pigment, giving regular Mendelian results, with white or pale green seedlings segregating in the usual ratios. One of these, in the snapdragon, has already been described (Chapter 8) as the first clearly demonstrated lethal gene (Baur, 1907, 1908).

In many plants there are strains in which the leaves and stems are variegated with respect to chlorophyll color; some of these behave differently. The first unambiguous case of maternal inheritance in such strains was reported by Correns (1909) in Mirabilis. In one strain of this plant the leaves are irregularly mottled dark green and yellowish white, the difference being in the color of the individual plastids. At the boundaries between the two areas there are some cells that contain both kinds of plastids. The pattern is so irregular that some branches are wholly green and others are wholly white. Correns used flowers on such uniform branches and found that seeds from those on wholly green branches gave green offspring only, regardless of the source of the pollen used; those from wholly white branches gave white seedlings only, again without regard to the source of the pollen used; flowers on variegated branches gave seeds that produced green, variegated, or white seedlings whether selfed or pollinated by wholly green plants. Evidently, then, the plastids act as though they or their precursors were self-reproducing bodies, with their properties unaffected by the chromosomal genes.

Similar results had been obtained by Baur (1908) with a variegated strain of Pelargonium, but this case was complicated by the transmission of some plastids through the pollen. In the earlier literature, the most instructive examples of this sort of inheritance were, perhaps, those described in Oenothera by Renner (1922, 1924). Here it was shown quite conclusively that the color of the chloroplasts is determined by the interaction of the inherent properties of the plastid precursors and of the chromosomal genes present in the individual, with each of these components maintaining and transmitting its potentialities regardless of the other, and therefore of the particular phenotype of the plant in which they occur.

Imai (1928) reviewed the results on barley that were published in Japanese by So in 1921. Here is a recessive gene for chlorophyll variegation, which evidently produces its characteristic phenotype by inducing mutations in occasional chloroplasts, causing them and the plastids descended from them to lose their green color.

A similar situation in maize was studied in detail by Rhoades (1943, 1950, and later). There is a recessive gene known as “iojap,” described by Jenkins in 1924, which causes white striping in the leaves. Rhoades showed that the white plastids in the colorless areas were transmitted as such, even in the absence of the iojap gene. He had previously described a “male-sterile” line, in which the property was transmitted to all offspring of male-sterile plants when these were used as female parents; but when the small quantities of fertile pollen were used on normal plants, there were no male-sterile offspring. In 1950 he showed that this condition was regularly induced in some of the offspring of homozygous iojap plants and was then again inherited maternally even in the absence of the iojap gene.

Here then is a Mendelian recessive gene that induces permanent mutational changes in two different maternally inherited properties (the two mutations are independent, occurring in different cell lines). The male sterility is believed to depend on a mitochondrial defect, and the plastids apparently arise from mitochondria or similar bodies.

There is, then, good evidence that the plastids carry their own genes,[*] and a strong suggestion that at least some elements identified as mitochondria do so. It should be pointed out also that strictly maternal inheritance has been reported in many organisms for characters not obviously related to plastids—notably for flower size and other characters in Epilobium by Michaelis (1943 and later), for numerous characters in mosses by von Wettstein (1925 and later), and for growth rate in yeast (Ephrussi) and in Neurospora (Mitchell). Quite recently it has been found

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[*] The germ of this idea was expressed by de Vries in 1889.

that there is DNA in plastids and in at least some mitochondria (review by Gibor and Granick, 1964, *Science* **145**: 890–897). It may therefore be supposed that these bodies carry genes of the same nature as those in the chromosomes.

A zoologist is sometimes inclined to compare the chloroplasts to the intracellular symbiotic algae found in some animals. As is well known, in *Hydra viridis* these bodies are transmitted through the eggs, and were once thought to be chloroplasts. They were supposedly separated from the host and cultured in vitro by Beijerinck (1890), who identified them as the well-known free-living green alga, *Chlorella vulgaris.* Whitney (1907) removed the algae from Hydra by treatment with glycerin and found that the alga-free individuals could be kept alive and would undergo asexual reproduction; he was, however, unable to reinfect them. Recently Siegel has reported similar results with *Paramecium bursaria* and has been able to infect alga-free lines with free-living Chlorella strains that had no known previous association with Paramecium.

Other intracellular agents have been found to be infective and also to be transmitted maternally. Apparently the first of these to be demonstrated was the organism responsible for Texas Fever in cattle. This organism is transmitted by a tick, which ingests it with the blood of an infected animal and transmits it by biting another animal. It was shown by Theobald Smith and Kilbourne (1893) that an infected female tick transmits the organism to her offspring, who can infect cattle by their first bites. Other disease-producing organisms, such as the Rickettsia of Rocky Mountain Spotted Fever in man, have since been shown to be transmitted through the eggs of ticks, rendering the offspring infective even without their having previously had any contact with an infected host.

Still other types of infective agents that are transmitted to offspring over many generations are known. Examples are: “Kappa” in Paramecium, which is responsible for the production of a substance that is toxic to uninfected animals (Sonneborn, Preer, and others); an agent responsible for $CO_2$ sensitivity in Drosophila (L’Heritier and others); a spirochaete in Drosophila that kills male offspring (Poulson and Malogolowkin); the “milk-substance” in mice that is transmitted from mother to offspring through the milk, and that leads to breast tumors in the adult female (Little and Bittner); and the “temperate” bacteriophages now being actively studied. This last agent forms a transition to the “infective agents” responsible for transformation and transduction in bacteria—which are too recently known for discussion here.