CHAPTER XVIII

MATERNAL INHERITANCE

THERE is a kind of inheritance shown by eggs and embryos, sometimes called maternal inheritance, that is not the same as plastid inheritance, even although the latter is maternal in another sense. Nor is this so-called maternal inheritance to be confused with cases of inheritance in which all or some of the paternal chromosomes fail to function, leaving the embryo at the mercy of its maternal set alone. Nor should it be confused with sex-linked inheritance where the son gets certain characters only from the mother, because he gets his single sex-chromosome from her.

"True" maternal inheritance relates to peculiarities of the egg or larva that are due to materials already present in the egg-cytoplasm when the egg is laid. For example, if pigment is scattered in the egg, it may collect in certain regions after fertilization, and produce color in them, as does the yellow pigment in the egg of *Cynthia*, studied by Conklin. In this ascidian, much of the yellow pigment is carried at the moment of fertilization to that part of the egg that later goes into the muscle of the tail. If the sperm used to fertilize such an egg should come from a species without pigment in the egg, the inheritance of color of the young embryo would obviously be entirely maternal. In cases like this one, the formed material, or any substance producing such materials, is already present in the cytoplasm, but whether it has always been free from nuclear influence must be shown by other tests. In only one cross, *viz.*, in the silkworm, has a third generation been raised, and until this has been done in others we cannot know whether we are dealing in them with plastid or with deferred nuclear influence ("maternal inheritance").

In certain races of the domesticated silkworm moth, Toyama has shown that pigment develops in the embryonic membrane (serosa) which, seen through the egg-shell, gives a specific color character to the embryo. It is not clear from Toyama's account whether the pigment is present at first, scattered in the cytoplasm, and collects later at the surface, or whether it develops only after the embryo develops. When races are crossed with characteristic but different embryonic membranes, the color of the hybrid is like that of the maternal race only.

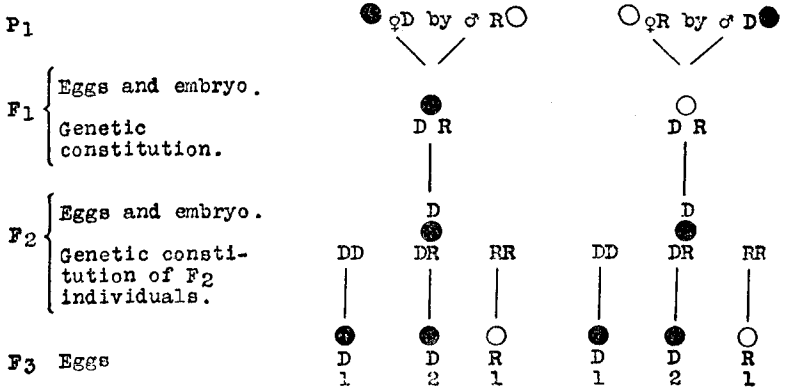

FIG. 105.—Diagram to illustrate maternal inheritance. The black circle stands for a dominant character affecting the serosa coat of the embryo.

If adults (F_1) are raised from these eggs, it is found when they in turn produce embryos, that the color of their embryonic membrane is determined by the dominant character of the preceding generation that had been carried in the chromosomes, irrespective of whether it came in from the father or the mother (Fig. 105). That the result is really chromosomal is shown by still another generation in which some of the females show the dominant character in the membranes of their embryos and others no color in the ratio of 3:1.

It appears therefore in this case, the only one known that furnishes critical evidence, that maternal inheritance

does not differ in any essential respect from ordinary Mendelian heredity.

A peculiar case that in some respects and in certain combinations appears to be maternal inheritance, is shown in the character of the seed of corn (*Zea mais*).

The endosperm of maize is produced, as in some other plants, at the time of fertilization—one pollen nucleus unites with the egg to form the embryo, another pollen nucleus unites with two nuclei in the embryo-sac to produce the endosperm whose cells, therefore, are triploid. Floury corns have an endosperm, that is almost wholly made up of cells containing "soft" starch, while flint corns have only a small amount of soft starch in the centre of the seed which is surrounded by a large amount of hard "corneous" starch. Hayes and East have shown that if a floury corn be used as the mother and a flint corn as the father, the seeds are floury like those of the pure race of floury corn. If a flint corn be used as the mother and a floury corn as the father, the seeds are flinty. In both cases there is apparently maternal inheritance, at least as far as the endosperm is involved, which is not, however, a part of the embryo proper. If the *seeds* from races of the foregoing crosses are sown and the plants allowed to self-fertilize, the following results are obtained: The F_1 derived from floury ♀ by flint ♂ produces both floury and flint in F_2 in the ratio of 1 : 1. The F_1 flinty reciprocal cross gives exactly the same result. The explanation of the F_1 and F_2 results is as follows: If the factor for flinty be F, and that for floury be f, then in the first cross the endosperm is ffF and in the reciprocal cross FFf. Since ffF is floury and FFf flinty it follows that two doses of floury dominate over one dose of flinty, and conversely two doses of flinty dominate over one dose of floury.

The F_1 *embryo*, however, in each of the crosses has only one F and one f factor (Ff). Its gametes are F and f, and so are its endosperm nuclei which, as shown by Weatherwax have the same reduced formula as the ovules

in the embryo sac. Hence half the embryo sacs are *F* and half *f*. The former, *F* (+*F*), fertilized by *F* pollen gives *FFF* endosperm, by *f* pollen give *FFf;* the latter, *f* (+*f*), fertilized by *F* pollen gives *ffF* endosperm, by *f* pollen *fff* endosperm. The four kinds of endosperm fall into two classes, soft and hard, in the ratio of 1:1 in the F_2 seeds.

There are races of maize with yellow dominant endosperm and others with recessive white. If the mother belongs to a yellow race and the father to a white one, the F_1 endosperm is yellow like the mother. In the reciprocal cross it is also yellow. If, however, races with floury seeds are used, the F_1 yellow endosperm in the former cross is somewhat paler than the pure yellow of the yellow race. Races with purple or with red endosperm crossed to white give the same results, except that in these crosses the quantitative effects seen in the floury flint crosses are not observed, for, one dose of the dominant (purple) to two doses of white gives the same color as two doses of purple to one dose of white.

There are two kinds of maize with white endosperm. These when crossed together give F_1 colored endosperm. In these cases one race has one of the factors for color, and the other, another complementary factor—like the two white sweet peas. There is also a race with a dominant white endosperm factor. The occurrence of these kinds of whites led to some confusion in the earlier experiments of Correns on endosperm inheritance. The word Xenia, that had earlier a different meaning, is used to-day for these cases of double fertilization in which the pollen has an influence on the seed (the endosperm) that is not a part of the F_1 plant itself. East and Hayes sum up the results given above (exclusive of the floury-flint cross) as follows:

> When two races differ in a single visible endosperm character in which dominance is complete, Xenia occurs only when the dominant parent is the male; when they differ in a single visible endosperm character in which dominance is incomplete, or in two characters both of which are necessary for the development of the visible difference, Xenia occurs when either is the male.

In cases in which a foreign sperm may start development but take no further part in it, the resulting embryo is like the maternal race. Here we are dealing not so much with maternal inheritance, but rather with a special kind of parthenogenesis. Such eggs, however, rarely go beyond the cleavage stages.

The rate of cleavage of an egg fertilized by foreign sperm usually coincides with that of the species to which the egg belongs. Since the cytoplasm of the egg has, prior to fertilization, always been under the influence of its own nucleus, this relation is what might be expected. It is necessary to study eggs from an F_1 generation in such cases in order to judge how far paternal chromosomes may influence the cleavage. It is thinkable, for example, that a spermatozoön might bring in a factor dominant for rate of cleavage, but because this factor had not had time to influence the cytoplasm its effect would not show in the P_1 cross. In the F_1, on the other hand, the paternal character might prove dominant. Both Driesch and Boveri have shown in the sea urchin that the rate of cleavage, the pigmentation, and the kind of gastrulation are entirely or largely determined by the egg—they differ in opinion only as to how soon the influence of the sperm can be seen.

At the time when the larval skeleton is formed most observers agree that the influence of the foreign sperm makes itself felt. Most of the accounts of the skeleton of hybrid sea urchins describe it as intermediate in structure, but one that varies widely under different external conditions. Tennent has shown, in fact, that the character of the hybrid larval skeleton is so greatly influenced by the alkalinity or acidity of the sea water that it can be artificially thrown towards one or the other side—maternal or paternal. Loeb, King and Moore have attempted to determine whether the larval skeleton has dominant characters in certain parts and recessive ones in other parts. They crossed the sea urchins, *Strongylocentrotus Franciscanus* and *S. purpureus*. Both the straight cross and its

reciprocal showed neither a great predominance of the characters of the paternal race, nor of the maternal race, but rather certain characteristic features of *purpuratus* and others of *Franciscanus*. The larval characters appeared to be dominant or recessive taken singly. Until an F_2 generation can be raised it is obviously hazardous to speak here of Mendelian dominance and recessiveness of characters that are based on F_1 observations alone, especially since it is becoming more and more apparent that many F_1 characters are more or less intermediate, and there are no general grounds for expecting pure dominance or recessiveness.

Many crosses have been made between different species of fish, and in some of these the young, at the time of hatching, are maternal. It has generally been supposed that such cases are due to the absorption of the paternal chromosomes at the first or at later cleavage stages. Loss of chromosomes has in fact been recorded in several of these cases of maternal inheritance. On the other hand, Miss Pinney's observations, summarized in the following table,

Cross	Development Results	Chromosomal Behavior
Ctenolabrus ♀ X Fundulus ♂	Development ceases during gastrulation.	Early mitotic behavior is prevailingly normal.
Ctenolabrus ♀ X Stenotomus ♂	Many hatching embryos of the maternal type.	Early mitoses are normal.
Ctenolabrus ♀ X Menidia ♂	Advanced development.	Early mitoses are normal.
Ctenolabrus ♂ X Fundulus ♀	One hatching embryo reported. Many advanced embryos—maternal type.	Abnormal nuclear behavior occurs.
Ctenolabrus ♂ X Stenotomus ♀	Development ceases during gastrulation.	Abnormal mitosis predominant.
Ctenolabrus ♂ X Menidia ♀	Two hatching embryos reported. Maternal type.	Abnormal mitosis is of frequent occurrence.

show that the maternal type may appear not only when the *early* mitoses are abnormal, but in one case at least when they are normal. It is quite possible, therefore, that while

early loss of the paternal chromosomes may account for some of the cases of maternal embryos, there may also be cases where the chromatin may divide normally but fail to produce any conspicuous effects on the cytoplasm sufficiently soon to become apparent in the young fish. In this connection the tobacco crosses described by Goodspeed and Clausen may be recalled. In these cases it was a particular group of chromosomes, regardless of whether it was of paternal or of maternal origin, whose "reaction system" dominated in the F_1 hybrid.