

## CHAPTER X

### HAPLOIDS

**T**HE genetic evidence indicates that one complete set of chromosomes at least is required for normal development. A cell with one set of chromosomes is said to be haploid, and an individual made up of such cells is sometimes called a haplont or frequently, by extension, a haploid. The embryological evidence also indicates that one set of chromosomes is necessary for development. It does not follow, however, that the diploid set can be replaced directly by a haploid set without serious consequences, so far as the developmental conditions are involved.

Eggs that have been incited to develop by artificial agents may develop into embryos whose cells have only one set of chromosomes. Not infrequently, however, the eggs double the number of the chromosomes (by suppressing a protoplasmic division) before they begin to develop, and these fare better than the haploids.

By cutting off a fragment from a sea urchin egg, and fertilizing it with a single sperm, an embryo can be obtained with only one set of chromosomes, the paternal set. By constricting the egg of triton immediately after fertilization, Spemann and later Baltzer have sometimes been able to separate a piece of the egg that contains only a single sperm-nucleus (Fig. 83), and one such embryo was carried through by Baltzer to the time of metamorphosis.

If frogs' eggs are exposed to X-rays, or to radium for a sufficient time to injure or to destroy the chromosomes,

and if, as Oscar and Gunther Hertwig have shown, these eggs are then fertilized, they may produce embryos whose cells have the half number of chromosomes. Conversely, if the spermatozoa of the frog are radiated they may enter the eggs, but may fail to take further part in the development. Under these circumstances the egg may develop, for a time, with a haploid set derived from the egg nucleus. In some of these eggs, on the other hand,

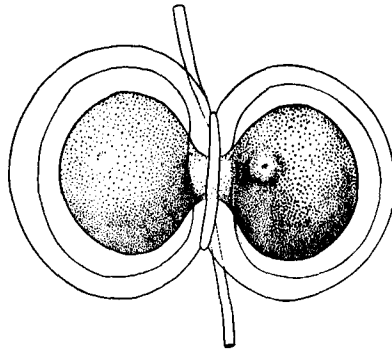


FIG. 83.

Egg of Triton constricted in two, immediately after fertilization.  
In the right half the polar body is shown. (After Spemann.)

the chromosomes of the egg may first divide without the protoplasm dividing, and in this way the full number of chromosomes is restored before development begins. These eggs produce embryos that develop into normal tadpoles.

Most of the artificial haploid forms obtained in these various ways are weak. They die, in most cases, long before the adult stages are reached. It is not evident why this should be true, but there are several possibilities that may be taken into account. If a whole egg with a haploid nucleus is incited by artificial means to parthenogenetic development, and if, before differentiation sets

in, it divides the same number of times as does the normal egg, each of its cells will be in proportion to its chromosome number twice as large as the normal cells in proportion to their chromosome number. In so far as the development of the cell is dependent on its genes there may be an insufficiency of gene material to produce a normal effect on a cytoplasm of double volume.

On the other hand, if such an egg should pass through one more division than does the normal egg before differentiation (organ formation) begins, the number of chromosomes (the nuclear size) would then be proportionate to the cell size—there would be twice as many cells, and twice as many nuclei in the whole embryo as in the normal. The embryo as a whole would then contain the same total number of chromosomes as does the normal embryo. How far the smaller size of the cells in such a case might affect the developmental process we do not know at present. Observation of the cell-size of haplonts seems to show that the cells have the normal size and that the nuclei are only half as large as the normal ones. It appears, then, that the embryo does not rectify its nuclear cytoplasmic relation as just indicated.

It might be possible in another way to determine whether the weakness of the artificial haplonts is due to an insufficiency of genes for cells as large as normal ones. Half of an egg, containing a single sperm nucleus, would, if it passed through the number of divisions characteristic of the normal egg, be made up of cells and nuclei having the normal size-ratio to each other. Sea urchin embryos of this kind have, in fact, long been known. They become plutei that appear to be normal, but none have been carried beyond the pluteus stage because, for one reason, it is difficult to carry even normal embryos further than this stage under artificial conditions. It is not certain, therefore, whether these haplonts are as viable

as normal embryos. Boveri and others have studied extensively fragments of sea urchins' eggs, most of which were probably smaller than half an egg. Boveri concluded that these haplonts die, for the most part, before the gastrulation stages or soon thereafter. It is possible that these "fragments" never entirely recover from the operation, or that they do not contain all the essential constituents of the cytoplasm.

A comparison of these embryos with those obtained by isolating blastomeres of normal diploid eggs has certain points of interest. It is possible by means of calcium-free sea water to isolate the first two, or the first four, or the first eight blastomeres of the segmenting egg of the sea urchin. Here there is no operative injury, and each cell has the double number of chromosomes. Nevertheless, many of the  $\frac{1}{2}$  blastomeres develop abnormally, fewer still of the  $\frac{1}{4}$  blastomeres produce plutei, and probably none of the  $\frac{1}{8}$  blastomeres pass beyond the gastrula stage. This evidence shows that, aside from the number of chromosomes and from the nucleo-plasma ratio, small size in itself has a deleterious influence. What this may mean is not known, but the surface relations to the volume vary with the size and may possibly enter into the result.

These experiments do not hold out much promise of obtaining normal vigorous haplonts by diminishing artificially the amount of the protoplasm of the eggs in species already adjusted to the diploid condition. Nevertheless, under natural conditions there are several cases known where haplonts exist, and there is one case recorded where a haplont of a diploid species has reached maturity.

Blakeslee discovered a plant, in his cultures of *Datura*, that was haploid, Fig. 84. With care it was kept alive and by grafting upon diploid plants it has been maintained

for several years. This plant resembles, in all essential respects, the normal plant, except that it produces a very small number of haploid pollen grains. These pollen



FIG. 84.

A haploid plant of *Datura*. (After Blakeslee, in *Journal of Heredity*.)

grains are the ones that have received one set of chromosomes after a rather devastating attempt to pass through the maturation stages.

Two haploid tobacco plants have been reported by Clausen and Mann (1924) that appeared in a cross between *Nicotiana Tabacum* and *N. sylvestris*. Each had 24

chromosomes, which is the haploid number of the *Tabacum* species. One of these haplonts was "a reduced replica" of the "variety" of the *Tabacum* parent, but the expression of the characters was somewhat exaggerated.

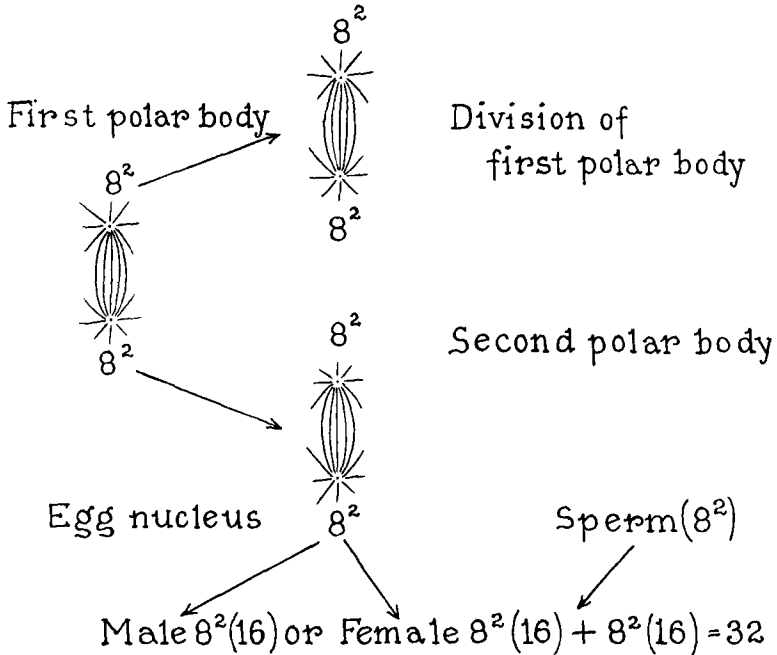


FIG. 85.

Diagram illustrating the two maturation divisions of the egg of the honey bee. The fertilization of the egg by the sperm is indicated in the lower part of the diagram with a subsequent doubling of the chromosomes by breaking into two parts.

It was about three-fourths the height of the parent type; the leaves were smaller, the branches more slender, and the flowers distinctly smaller. It was less vigorous than the parent type; it bloomed profusely but produced no seeds. Its pollen was completely defective. The other haplont showed similar relations to the variety of *Tabacum*

from which it was derived. The first maturation of the pollen mother cells of these haplonts was irregular, few or many of the chromosomes passing to the poles, the rest remaining at the equator of the spindle. The second maturation division was somewhat more regular, but lagging chromosomes failed to reach either pole.

Nature seems to have been successful in producing a few haplonts in species in which one sex is diploid. Male bees, wasps, and ants are haplonts. The eggs of the queen bee contain 16 chromosomes, which become 8 bivalents after conjugation (Fig. 85). Two maturation divisions take place, reducing the number to 8 chromosomes. If an egg is fertilized it produces a female (queen or worker) with the diploid number of chromosomes, but if an egg is not fertilized it develops parthenogenetically with the half number of chromosomes.

An examination of the nuclear and cell-size of the different tissues of the female and male bees (Boveri, Mehling, Nachtsheim) has shown that, in general, there is no constant difference between the diplont and the haplont. There is, however, a peculiar condition in the early embryonic stages both of the female and male bee that has somewhat complicated the situation. In the cells of the embryo of the female, the chromosomes become twice as numerous as at first, apparently by each chromosome *separating* into two parts. In the cells of the embryo of the male, the same process occurs, and is there repeated even a second time, so that there appear to be 32 chromosomes present. The evidence seems to indicate that the chromosomes do not actually increase in number but "fragment." If this is the correct interpretation there is no increase in the number of the genes. The female has still twice the number of those in the male. What relation, if any, this fragmentation may have to nuclear size is not clear at present.

In the germ-track of the male and female the fragmentation does not seem to take place, or if it does the pieces rejoin before the maturation stage.

The best evidence that the male bee is a haplont, or at least that its germ-cells are haploid, is found in the be-

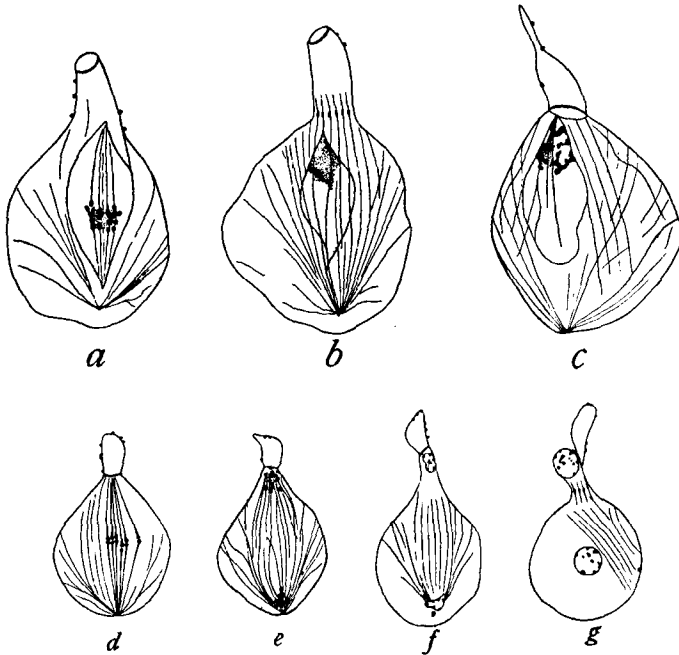


FIG. 86.

The two maturation divisions of the germ-cells of the male of the honey bee. (After Meves.)

havior of the cells at the maturation divisions. The first division is abortive (Fig. 86, a, b). An imperfect spindle forms in connection with 8 chromosomes. A piece of the protoplasm constricts off without chromatin. A second spindle develops and the chromosomes divide (Fig. 86, d-g), presumably by splitting lengthwise, and the daugh-



ter halves pass to the poles. A small cell cuts off from a large one. The latter becomes the functional sperm. It has the haploid number of chromosomes.

The male rotifer, *Hydatina senta*, is said to be haploid (Fig. 87c), and the females diploid. Under unfavor-

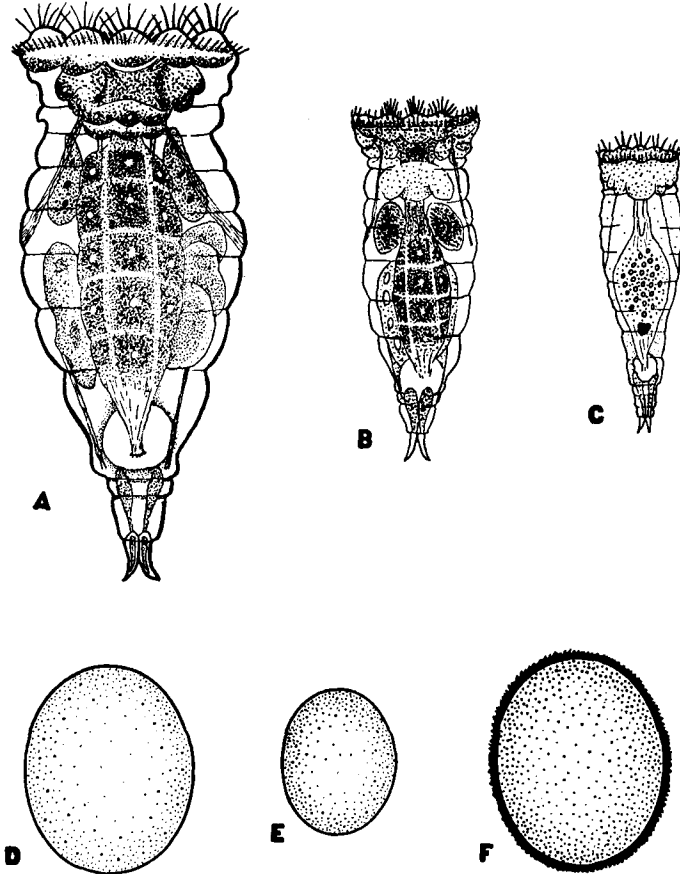


FIG. 87.

A, parthenogenetic female of *Hydatina senta*; B, young female of same; C, male of same; D, parthenogenetic egg; E, male-producing egg; F, winter egg. (After Whitney.)

able conditions of food, or when fed on the protozoön *Polytoma*, only female rotifers occur. Each female is diploid, and her eggs are at first diploid. Each egg gives off only one polar body—each chromosome splitting into like halves. The full number of chromosomes is retained in the egg that develops by parthenogenesis into a female. When fed on other food (*Euglena*, for example), a new type of female appears. If she is fertilized by a male at the moment she emerges from the egg, she produces sexual eggs only, which give off two polar bodies and retain the haploid number of chromosomes. The sperm nucleus, already within the egg, unites with the egg nucleus to form a diploid female that starts once more a parthenogenetic line. If, however, the special type of female, just described, is not fertilized, she produces smaller eggs which give off two polar bodies and probably retain the half number of chromosomes. They develop by parthenogenesis into male haplonts. The male is sexually mature a few hours after birth; he never grows any larger and dies after a few days.

The males of the white "fly," *Trialeurodes vaporariorum*, have been shown by Schrader to be haplonts. It had been discovered by A. W. Morrill that, in America, virgin females of this fly give rise to male offspring only, and Morrill and Back found this in another member of the same family. On the other hand, in England, virgin females of the same white fly give rise to females only, according to Hargreaves and later to Williams. Schrader (1920) studied the chromosomes in the American form. There are 22 chromosomes in the female and 11 in the male. The mature eggs have 11 bivalent chromosomes. Two polar bodies are given off, leaving 11 single chromosomes in the egg. If the egg is fertilized 11 chromosomes are added by the sperm nucleus. If the egg is not fertilized it develops by parthenogenesis with 11 chromosomes

present in all cells of the embryo. In the maturation stages of the germ-cells of the male, there is no evidence of a reduction division (not even a rudimentary process as in the bee) and the equational division does not differ from the spermatogonial divisions.

There is some evidence that the unfertilized eggs of lice develop into males, as suggested by the breeding experiments of Hindle. In one of the mites, *Tetranychus bimaculatus*, the unfertilized eggs produce males, the fertilized eggs, females (according to several observers). It has been shown by Schrader (1923) that the males are haplonts with only three chromosomes, the females are diplonts with six chromosomes. The early ovarian eggs have six chromosomes that conjugate to give three bivalents. Two polar bodies are given off, leaving three chromosomes in the egg. If the egg is fertilized three chromosomes are added, giving six in the female, if the egg is not fertilized it develops directly into a male with three chromosomes in each cell.

Virgin females of one species of thrips, *Anthothrips verbasci*, examined by A. F. Shull, produce only males from unfertilized eggs. These males are probably haplonts.

In mosses and liverworts the protonema and moss plant stage (gametophyte) are haplonts. Wettstein has by artificial means brought about the doubling of the number of chromosomes in cells of the protonema and from these has obtained *diploid protonema and moss plants*. This result proves that the difference between this stage and the sporophyte stage is not due to the number of chromosomes that each contains but is a developmental phenomenon in the sense that in order to reach the sporophyte stage the spore must pass through the gametophyte condition.