CHAPTER V

ALTERNATION OF GENERATIONS IN ITS RELATION TO THE IDIOPLASM

STARTING from the germs specially adapted for amphimixis (sexual intermingling), we have designated as *germ-plasm* the definitely arranged group of determinants which must be contained in the sexual cells. By this term is meant an idioplasm which contains all the determinants of the species. At the same time a large number of species exist in which the sexual cells are not the only ones which contain all the determinants, and in which the *development takes place, for the second time during the course of the life-cycle, from a single cell;* the idioplasm of this cell must therefore also be composed of all the determinants of the species. This is the case in most of the lower plants, such as mosses, horse-tails, and ferns, — in all of which sexual reproduction alternates with the formation of asexual 'spores,' — as well as in those groups of animals in which that form of alternation of generations which is known as *heterogeny* occurs. But even in the case of alternation of generations in the more restricted sense, — *i.e.*, the alternation of sexual reproduction and gemmation, — the development of an individual may take place twice successively from a *single* cell, as was mentioned above with regard to the stocks or colonies of plants and of Hydroid-polypes. In all these a cell, the idioplasm of which contains all the specific determinants, occurs twice in the course of the life-cycle from one fertilised ovum to the next one. The question therefore arises as to whether the idioplasm in each case is to be considered identical, and may merely be described as germ-plasm.

This question has already been discussed in the section on the process of gemmation in plants; and it was there concluded that the idioplasm of the apical cell and that of the fertilised ovum cannot be assumed to be perfectly identical, owing to the fact that the course taken by embryogeny — in which process the first shoot and roots are formed — is different from that followed by the cell-divisions which result in the apical cell producing a new shoot. The same is true as regards the formation of a new polype from a blastogenic cell and from an ovum. In both cases the final result is the same, or at any rate very similar, though the method by which it is attained is different. Although a precisely similar organism might be produced by either of the two methods of development, and the primary cells would therefore contain the same determinants in both cases, the grouping of the latter in the two idioplasms at any rate must be different, for they must pass through different groups during ontogeny before their ultimate disintegration into single determinants. Even in this very simple case it is necessary to distinguish the 'germ-plasm proper' of the egg- and sperm-cells from the 'apical-plasm' or 'blastogenic germ-plasm.' It is convenient, however, to speak of every kind of idioplasm which contains all the determinants of the species as *germ-plasm in the wider sense*, and to distinguish its various subdivisions as 'blastogenic' and 'sporogenic' germ-plasm, and so on; these latter may all be included under the term *accessory germ-plasms* or *para-germ-plasms*, in contrast to the *primary* or *ancestral germ-plasm*.

Wherever two kinds of germ-plasm occur in the life-cycle of a species, we might be inclined to assume that they change into one another in the course of life. But this view is untenable, as has been shown above, and we are on the contrary forced to assume that *both kinds of germ-plasm continually pass simultaneously along the germ-tracks, and that each of them becomes active in turn*.

This assumption is unavoidable, for the phyletic development of the species shows that *the individual generations in cases of alternation of generations can vary independently and hereditarily*. It, however, presupposes that *special* determinants are present in the germ-plasm in each generation, for otherwise both generations would be affected at the same time by a variation in the germ. A similar assumption must be made in the case of metamorphosis. The wings of a butterfly must be represented in the germ-plasm by a group of determinants. If the wings were formed by the transformation of some of the determinants of the caterpillar, they could never vary without at the same time producing a variation in some parts of the caterpillar, and *vice versâ*.

It will not be uninteresting to give some examples by way of illustration.

We will first take a case of *heterogeny*, or alternation of generations in which the two generations do not differ at all from one another in the full-grown condition. As a rule, the difference between the two successive generations in the *Daphnidæ* or water-fleas, for example, consists in the fact that one generation is developed from summer-eggs, which contain a small amount of yolk, while the other arises from winter-eggs, in which the yolk is very abundant. From both of these two kinds of eggs similar females are developed: — the complication arising from the periodic appearance of the male may be neglected for the present. The summer-eggs are nourished by the blood of the mother, while the winter-eggs are not; for the amount of yolk in the latter necessitates a different kind of

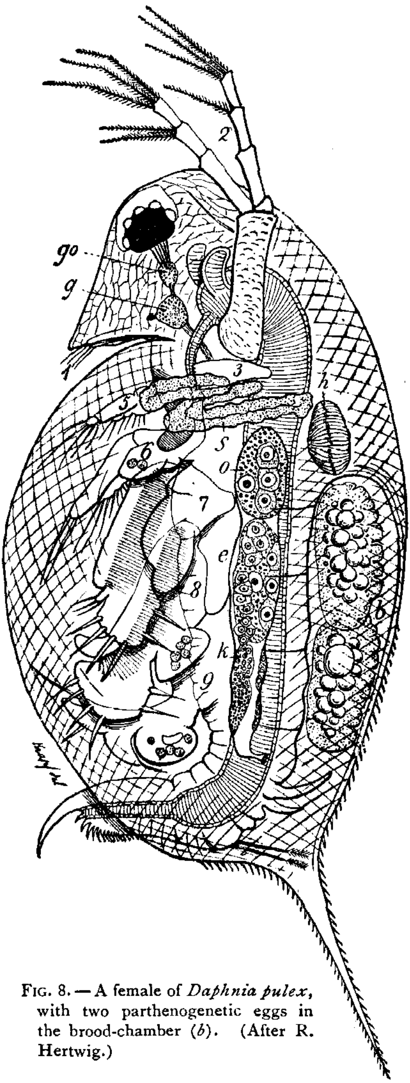

FIG. 8. — A female of *Daphnia pulex*, with two parthenogenetic eggs in the brood-chamber (*b*). (After R. Hertwig.)

ontogeny, and this presupposes not only a difference in the arrangement of the determinants in the germ-plasm as compared with the meta-germ-plasm ('Nach-Keimplasma'), but also the presence of *different determinants for some of the embryonic stages*. The case becomes still clearer if we take one particular species of Daphnid (*Leptodora hyalina*) into consideration. In this animal the embryogeny of the winter-eggs only extends as far as to the formation of the primitive crustacean larva, or nauplius, which possesses three pairs of limbs: the summer-eggs, on the other hand, develop at once into the adult form of the animal, in which all the limbs are present. The summer-eggs certainly also pass through the stages from the ripe ovum to the nauplius, but these are abbreviated, and

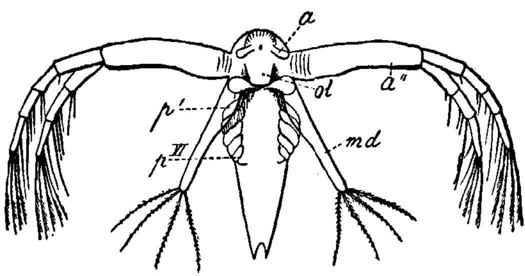

FIG. 9.—Nauplius larva of *Leptodora hyalina*. (After Sars, from Korschelt and Heider's 'Lehrbuch der vergleichenden Entwicklungsgeschichte.')

though this nauplius also possesses three pairs of limbs, these are only rudimentary, and are useless as swimming organs. There must therefore be two kinds of germ-plasm in *Leptodora*, one of which still contains all the determinants of the nauplius, while the other only contains a portion of them, and even these have probably undergone some change. The two kinds of germ-plasm must be passed separately along the germ-tracks from one generation to another, so that each must always contain the other, which is, so to speak, stored away in it in an inactive condition. It seems to me impossible to explain the facts in any other way, for it is inconceivable that the germ-plasm of the summer-eggs, which has undergone reduction, and possesses comparatively few determinants, *should be able to develop the lost determinants out of its own substance*.

The *phyletic development* of these two kinds of germ-plasm would be very enigmatical if we were compelled to assume that only a single unit of the germ-plasm is present in the nucleus of the germ-cell. We have, however, made the reverse assumption from the first, and it will be shown later on that a consideration of sexual reproduction, or amphimixis, leads us to *assume that several, and in fact probably a large number of* units or ids must be contained in the germ-plasm of every species which multiplies sexually. If now a reduction of the determinants for the nauplius in the summer generation of *Leptodora* were advantageous, it would have appeared, increased, and become fixed in the course of generations by selection, and an abbreviation of embryogeny would thus have resulted. This would only have occurred gradually, so that at first the summer-eggs would contain more reduced than unreduced ids only in the case of a few individuals; and if the original unabbreviated form of embryogeny were of greater advantage to the winter generation, the determinants for the nauplius would not become lost or modified in all the ids, but only in certain of them. A balance of the two kinds of ids would finally take place from the struggle between the modified ids, which were more advantageous in summer, and the unmodified ones, which were of greater advantage in winter, and this would result in the germ-plasm of the species being composed of an equal number of modified and unmodified ids; these would *alternately* control the cell, so that each would remain inactive and unalterable during a certain number of generations, and become active during certain others.

This regular alternation between definite periods of activity and inactivity in the two kinds of germ-plasm can be directly observed, for we can determine how many generations occur which give rise to summer-eggs before one again appears in which winter-eggs are produced. As I was able to prove a considerable time ago, this regularity varies very much in different species of Daphnidæ, and stands in close relation to the mode of life of the species. In those species which live in very small bodies of water which are liable to become rapidly dried up, the formation of the two kinds of eggs alternates very frequently; this is due to the fact that the extermination of the animals by the sudden drying up of the pond is only prevented by the thick shells by which the winter-eggs are surrounded. On the other hand, all the species which live in large bodies of water, such as pools and lakes which never become dried up, produce summer-eggs alone for a large number of generations, and only give rise to eggs of the other kind on the approach of winter; and these, on the death of the animals which produced them, ensure the continuance of the species in the following spring.

The occurrence of changes in the *final stages* of ontogeny must be accounted for in a similar way.

In plant-lice belonging to the genus *Aphis*, the fertilised egg gives rise to females, which are, however, incapable of being fertilised, for the receptaculum seminis is wanting, and this is essential in the process. Their eggs are, however, capable of undergoing development in the ovary parthenogenetically. The resulting offspring give rise to similar females possessing no arrangements for fertilisation, and these again produce others of the same kind. Ultimately, however, one of these gives rise parthenogenetically to females which are capable of fertilisation, as well as to males. The two sexes as a rule differ as regards the shape and colour of the body, apart from the structure of the reproductive organs and sexual products, but the embryogeny of these sexual animals is similar to that of the others.

In this case, therefore, the determinants of the mature animal become modified in the parthenogenetic generations, for sexual reproduction is the more primitive of the two forms of the process. If therefore we make the assumption, which, however, is not a strictly correct one, that the sexual generations have remained quite unaltered since the introduction of alternation of generations in these animals, we should have to represent the phyletic change in the germ-plasm as being of such a nature as to cause the degeneration of the determinants of the seminal vesicle in one half of the ids, and to produce a change in other determinants, such as those which control the colour of the integument, for instance. The modified, as well as the unmodified ids, must be contained within the same germ-plasm, but they control the egg *alternately*, and never become active at the same time.

In this instance the generations which have been interpolated have only suffered a slight change as regards the structure of the whole body. But in many cases of alternation of generations very important differences of structure occur, so that not infrequently one might easily believe that the different generations belong to two entirely different groups of animals.

This is the case in the *alternation of generations in medusæ.* The polype is the original form, and even at the present day the fertilised ovum of the medusa gives rise to a polype in most species. By the budding of this polype, or at any rate of the offspring which have been produced by gemmation, medusæ are again developed. If, for the sake of simplicity, we neglect the slight differences which may exist between the germ-plasm of

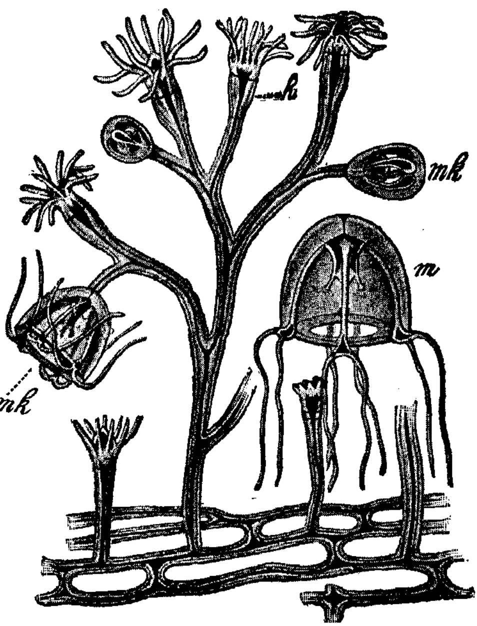

FIG. 10.—*Bougainvillea ramosa.* (After Allman.) Polype stock with gastrozooids (*h*) and medusoid buds (*mk*); *m*, young Medusa (*Margelis ramosa*), which has become free. (From A. Lang's 'Lehrbuch der vergleichenden *Anatomie.*')

the egg and that of the bud, it is evident that two germ-plasms take part in the cycle of development of the species, and these must differ as regards very many, if not almost all, of their determinants, for the medusa is provided with a number of parts and organs which the simple polype does not possess. Thus we must assume that there are two different kinds of ids of which the germ-plasm is composed in equal numbers, the periods of activity of which alternate with one another. The ids of the accessory germ-plasm, which arose subsequently, must be larger than those of the ancestral germ-plasm, because they contain more numerous determinants. If at some future time it should be definitely ascertained that those granules or microsomes, which are arranged like beads in a necklace in the nuclear rods, really correspond to ids, we may possibly, perhaps, be able to prove by the aid of the microscope that such differences in size actually exist. A knowledge of the entire number of nuclear rods or idants may also possibly help to confirm the theory, for it is probable that in species in which alternation of generations occurs, the ids, and therefore the idants also, have been doubled during the development of the species. For if my view is correct that a definite amount of germ-plasm is necessary for the normal development of a certain kind of egg, the periodical inactivity of half the ids must have been accompanied by a corresponding doubling of these structures.

The mechanism of the idioplasm in alternation of generations becomes somewhat different, and rather more complicated, as soon as the second generation arises, not from a single cell, but from several cells at the same time, derived from different layers of the body. This is the case as regards *the strobilation of the higher medusæ and that of tape-worms*, and an intermediate stage is seen in the *gemmation of the Salpæ*.

In the last-named animals, two generations differing as regards the form of the body and mode of reproduction follow one another. A number of individuals are united into a 'chain' in the first generation, in which sexual multiplication occurs; and in the second generation the individuals are separate, and multiply by budding. It has already been pointed out in the chapter on gemmation that this budding is produced by a co-operation of the ectoderm and mesoderm cells. We must imagine that in this case, again, the germ-plasm of the egg- and sperm-cells is composed of two kinds of ids, which alternately become active, one of which contains the determinants for gemmation, and the other those for embryogeny. In the case of the Hydroid-polypes and medusæ, the determinants of the 'blastogenic' ids remain together in *one* cell, but in the single form of Salpa they must be separated into groups during embryogeny, and these groups would be supplied — in part to the ectoderm, and in part to the mesoderm and endoderm—as inactive and 'unalterable' accessory idioplasm. These only become active, and cause budding, when they have reached some definite part, such as the ovary or *proliferating stolon*.

The development of the higher medusæ or *Acalephæ* by strobilation can easily be traced from the above processes. In these animals the sexual forms arise asexually: the polype becomes divided into disc-shaped portions, and so comes to resemble a pile of saucers, each disc eventually being trans-

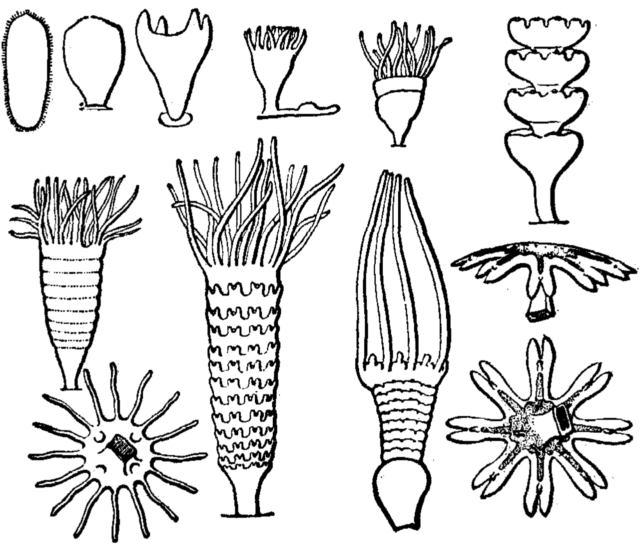

FIG. 11.—*Development of Medusæ by strobilation*—1, the young larva; 2–5, its development into a polype; 7, a polype viewed from the oral pole; 6, 8, and 9, transverse division of a polype into disc-shaped portions; 10, the constriction of these portions into young *Medusæ*; *11 and 12, a young Medusa.* (From Hatschek's 'Lehrbuch der Zoologie.')

formed into a medusa. If the medusa underwent division, the process would be one of simple regeneration: the differentiation of one of these discs into a medusa depends on a mechanism in the idioplasm exactly similar to that which gives rise to the process of regeneration in a worm the anterior end of which has been cut off, or which has undergone spontaneous division. The various cells in the body of the polype must be provided with different groups of determinants of the medusæ in the form of inactive accessory idioplasm, and these must become active in the process of strobilation, and cause the development of highly complex medusæ with eight or more radii, and provided with eyes, auditory organs, and olfactory pits. The difference between this process and that of simple division followed by regeneration, consists in the fact that in the latter the supplementary determinants of the cells of the body are of the same kind as those from which the body was constructed: in strobilation, on the other hand, the germ-plasm of the egg- and sperm-cells, which gives rise to the sexual generation or medusa, must contain not one, but two kinds of ids, viz., those of the polype and those of medusa; the latter, although they remain inactive during the ontogeny of the polype, and take no part in the control of the cell, are nevertheless not absolutely unalterable, for they break up during ontogeny into many different groups of determinants, and at the same time become distributed among *different* cells in a regular and perfectly definite manner. It is very probable, however, that *all* the cells of the polype — those of the ectoderm as well as of the endoderm — are provided with accessory determinants, so that each cell of the polype contains in addition the primary constituents of some cell of the medusa. We have, however, no positive knowledge on this point, for no investigations have as yet been made with regard to the succession of the cells which lead to the formation of the medusa from the polype.

The basis of the alternation of generations as regards the idioplasm must therefore in all cases consist of a germ-plasm composed of ids of at least two different kinds, which ultimately take over the control of the organism to which they give rise.