CHAPTER VIII

MODIFICATIONS OF THE GERM-PLASM CAUSED BY AMPHIMIXIS

1. The Necessity of a Halving of the Germ-Plasm

By the process of amphimixis the hereditary substances of two individuals become united into one substance in the offspring. If the process is repeated in every generation, a doubling of these individually different hereditary substances must take place each time, and the mass of germ-plasm and the number of idants must likewise be doubled. As a matter of fact this cannot and does not occur, for in every species the number of idants remains the same throughout all generations. The unlimited increase of the germ-plasm must therefore be prevented in some way or other.

The mass of germ-plasm might possibly remain constant if its growth stopped in the young germ-cells when only half the normal quantity had been formed. It is quite conceivable that a continual increase in mass might in this way be prevented, if, contrary to the theory of the germ-plasm here propounded, we were to imagine that the idioplasm merely consists of ultimate vital particles — 'pangenes,' 'primary constituents,' or whatever else we choose to call them — which are not combined into units of a higher order.

If, however, we assume the existence of a germ-plasm in the sense in which I use the word, — *i.e.*, an idioplasm in which the ultimate bearers of vitality (biophors) are combined to form units of a higher order, the determinants and ids, having a definite structure and size, — it is evident that the amount of germ-plasm would not remain constant, or at most it would only remain so for a few generations, as long, that is, as each kind of germ-plasm is represented by several ids. As soon as this stage was reached, a decrease in growth could no longer prevent a doubling of the mass; this could, in fact, only be prevented by the *removal of half of the number of ids present in the cell.*

This actually occurs before the germ-cells unite in the process of 'reducing division' of the nuclear matter of the germ-cells. This fact may probably be taken as indicating the correctness at any rate of the fundamental idea on which the theory of the germ-plasm is based, viz., that the hereditary substance is composed of ids. These parts of this substance, the existence of which I formerly concluded from purely theoretical considerations, and which I have called 'ancestral germ-plasms,' must exist in reality. I venture to make this assertion with all the more assurance, owing to the fact that at the time when I postulated the 'reducing division' merely on theoretical grounds, the existence of such a process could not be gleaned from recorded observations even in the case of the female germ-cells of animals, in which it can be observed comparatively easily, quite apart from that of the male cells of animals, or of the germ-cells of both sexes in plants.

We now know that this reduction of the number of ids by one half is of general occurrence, and is effected by means of the nuclear divisions which accompany cell-division. The divisions which result in the formation of the polar bodies perform the function of the 'reducing divisions' as regards the ovum, and the final divisions of the sperm mother-cells have this function in the case of the spermatozoa. In both cases the reducing division does not consist in the idants becoming split longitudinally, and in their resulting halves being distributed equally amongst the two daughter-nuclei as in ordinary nuclear division, but in one half of the entire number of rods passing into one daughter-nucleus, and the other half into the other. The process is somewhat more complicated than would appear from this statement, and it will be discussed more fully later on; but the final result is the same.

The following considerations may perhaps help to explain why the constant doubling of the germ-plasm could only be prevented by this method of removing entire nuclear rods, and will at the same time indicate what are the primary causes of the changes in the structure of the germ-plasm caused by amphimixis.

As already remarked, the nuclear rods must, before the introduction of the process of amphimixis into the organic world, have consisted of a number of *identical* ids, each corresponding exactly to the individuality of the organism in question. These ids must have been united into idants, which were all equal in value, their number, as well as that of the ids, remaining the same in subsequent generations. When sexual reproduction first arose, the same number of idants from both parents became enclosed in one nucleus, the total number of idants and mass of germ-plasm of which were thereby doubled. This may have been of no disadvantage if it occurred once only, but as the process was repeated, an arrangement for preventing the germ-plasm from increasing to an unlimited extent became necessary each time amphimixis took place.

Were the germ-plasm an unorganised, or even a perfectly homogeneous substance with no internal differentiation, — *i.e.*, were it not composed of units of different orders, — its doubling every time amphimixis occurred might have been prevented simply by a limitation of its growth in each germ-cell, so that the latter would contain only half the mass of germ-plasm formerly present. But as soon as the germ-plasm came to consist of a definite number of units, a diminution of the latter could not result from a mere limitation as regards growth, for their number would nevertheless remain the same. This result could only be attained by the appearance of a process by means of which the *number of units was reduced to half*, and we have seen that such a process occurs in the form of the remarkable 'reducing divisions' already described.

It is not difficult to ascertain what changes must result in the composition of the germ-plasm by the combination of this process with continued amphimixis.

Let us suppose that before the introduction of the latter process the germ-plasm of a species consisted of sixteen idants. When amphimixis, accompanied by the 'reducing division,' occurred for the first time, eight paternal idants A would unite with eight maternal idants B in the fertilised egg-cell to form the segmentation nucleus. In consequence of the reducing division, each of the germ-cells of the next generation would contain a combination of the idants A and B, — *e.g.*, 4 A + 4 B. These would again unite in the next amphimixis with eight idants — *e.g.*, 4 C + 4 D — in the germ-cell of another individual with different hereditary tendencies; and the ontogeny of the third sexual generation would therefore be controlled by a germ-plasm composed of the idants 4 A + 4 B + 4 C + 4 D. Let us assume, for the sake of simplicity, that the reduction always affected every kind of idant to the same extent; the germ-plasm of the fourth generation would then consist of the idants 2 A + 2 B + 2 C + 2 D + 2 E + 2 F + 2 G + 2 H, and that of the fifth, of a number of individually different idants, — provided, of course, that interbreeding had not occurred. The germ-plasm of this fifth generation would therefore consist of the idants A — Q.

This naturally does not imply that the process would really take place in such an even and systematic manner; it must, on the contrary, be a very irregular one. But although it may not in five generations have resulted in the germ-plasm being composed of a number of different ids, this result must certainly follow in the course of a greater number of generations.

The modification of the germ-plasm will not, however, then have reached its limit. If my view of the composition of idants out of ids is a correct one, and the id is really a unit which contains all the primary constituents of the species, — that is to say, if it contains all the determinants required for the construction of a single individual, — it follows that the *composition of the individual idants must gradually have become changed, so that each idant, instead of being made up of similar ids, comes to be constituted by dissimilar and individually different ids.*

The idants are not, in my opinion, perfectly invariable quantities; certain phenomena of heredity have led me to conclude that they are in any case only *relatively* constant, and that their composition becomes modified from time to time, so that the ids which previously belonged to the idant A may later take part in the composition of the idant B or C. Our present knowledge of the processes of the division of the nuclear substance does not enable us to say how frequently and regularly this occurs; but even if it only takes place at irregular intervals, during long periods of time, it must nevertheless have resulted in a very varied composition of the idants in the course of the enormous number of generations which have ensued since the introduction of the process of amphimixis into the organic world. As new idants are always added to those already present in one of the parents each time amphimixis occurs, a continual interpolation of new ids can take place in the idants; and as this process is repeated an indefinite number of times, a single idant must ultimately — if we neglect the repetition of similar ids which results from interbreeding — come to consist of a number of *individually* different ids.

The process of mingling the ids would proceed most rapidly if the paternal and maternal ids regularly combined each time amphimixis took place, so as to bring together the half of the different kinds of ids in the idants of both parents. If, for in-

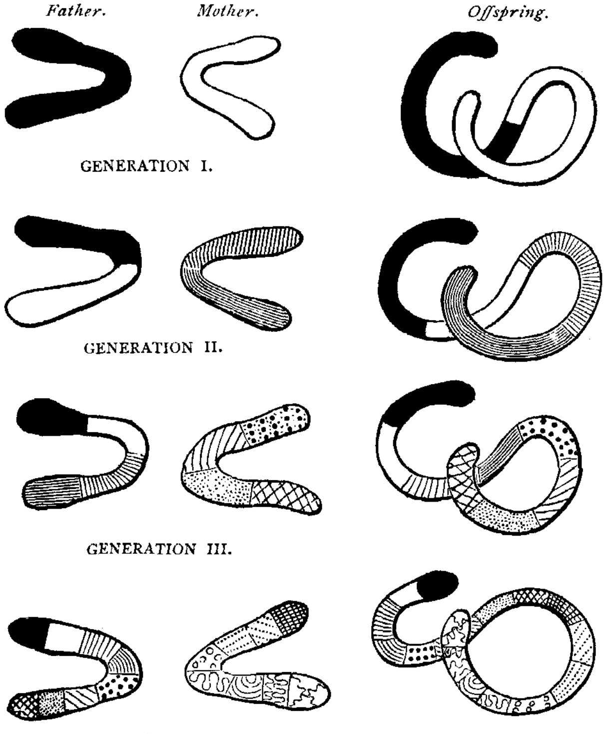

FIG. 19. — Diagram illustrating the composition of the idants out of individually different ids. (From Weismann's 'Essays,' Vol. I., p. 369.)

stance, each idant in an individual consisted of sixteen ids which were all similar to one another on the first appearance of sexual reproduction, the first occurrence of amphimixis would result in idants consisting of eight paternal and eight maternal ids, which are represented respectively by the black and white parts in the accompanying diagram (Fig. 19). (The boundaries between the single ids are only indicated in generation IV. in the figure.) In the second generation four groups, each consisting of four similar ids, would be combined; in the third, eight groups of two ids; and in the fourth, sixteen groups, each consisting of only one id. The accompanying diagram illustrates this process: the two parental idants are shown on the left, and their fusion to one idant in the offspring on the right. The different kinds of shading and dotting indicate the individual differences between the ids.

The mingling of the ids in the individual idants, just as in the case of the mingling of the idants themselves, will not have occurred so quickly and regularly as is indicated in the diagram; but the final result is the same, whether the process takes place more quickly or more slowly.

The introduction of sexual reproduction will thus have gradually resulted in a greater degree of complication of the germ-plasm, so that it is no longer composed of *similar* ids, but is mainly made up of ids which are individually different from one another. *All those phenomena of heredity which are spoken of as the intermingling of the characters of ancestors, such as degeneration or atavism of all kinds and degrees, depend, I believe, on this complicated structure of the germ-plasm.*

In the following chapter an attempt will be made to explain these phenomena theoretically. It will, however, first be necessary to glance for a moment at the process of the reduction of the ids, as far as we are acquainted with it.

2. Proof that the Essential Part in the Process of 'Reducing Division' consists in the Extrusion of Ids

In the chapter on the architecture of the germ-plasm, it was pointed out that the ids are probably identical with the 'microsomes' which are known to exist in many cases in the nuclear rods, and not with the *entire* rods, or idants. This conjecture was based on the fact that the rod-like chromosomes, the structure of which we are best acquainted with, consist of a series of granules, or microsomes, which are separate and independent structures. The composition of these rods evidently excludes the possibility of considering each of them to be equivalent to a *single id*. For an id is a vital unit, with a definite structure, and cannot be composed of a row of loosely-connected spherical bodies, each containing only a portion of its determinants. Moreover, the fact that the number of idants is on the whole a small one, speaks against their being regarded as ids: the phenomena of reversion alone, it seems to me, require the assumption of a larger number of ids.

The chromosomes are not, it is true, in all cases rod-like, and may have a more spheroidal form; the existence of microsomes has, moreover, not been definitely proved in all cases. We might therefore be inclined to look upon the chromosomes as structures which are not always and absolutely equivalent, and to regard some of them as single ids, and others as rows of ids. This conception receives support from the fact that a considerable variation as regards the number of chromosomes is seen in nearly allied species, in which we might expect the processes of heredity to occur in almost the same way. Thus, for instance, the usual number of nuclear rods in *Ascaris lumbricoides* is twelve, and in *Ascaris megalocephala* two or four; in other worms belonging to the same order the normal number of rods may be eight, twelve, or sixteen. I should not, however, consider these differences sufficiently great to warrant the assumption that these rods have a different value in different cases; and this view receives support from the observations of Boveri and Oscar Hertwig, which prove that in the same species (*Ascaris megalocephala*) two varieties occur, in one of which two, and in the other four, nuclear rods are present in the cells. In this case, then, the one variety likewise possesses twice as many microsomes as the other; and although it is not always easy to determine the number of microsomes in the case of other Nematodes, we may infer their existence from the form of the idants. For these reasons I am inclined *to regard the microsomes as corresponding individually to ids, and the nuclear rods as representing groups of ids*; for this reason I have called them *idants*.

The number of idants, and even that of the ids contained in each of them, is a definite one for each individual species, but it varies considerably in different species. Each id of any particular germ-plasm could direct the entire ontogeny if it were present in sufficient numbers; that is to say, every id contains all the determinants required for one individual: but, as has already been remarked, the ids contained in the idants of a species which multiplies sexually do not contain precisely identical determinants, but these differ more or less from one another, at any rate to such an extent that they correspond to the individual differences existing in the species at the present day. It results from the mechanism for nuclear division that *all the different kinds of ids pass into all the cells throughout ontogeny, and therefore the character of every individual cell occurring in ontogeny must be determined by an aggregate of ids; so that all, or at any rate the greater portion of the ids of which the idants are made up, determine the constitution of the cell in question, this determination resulting from the forces within the cell.* These preliminary remarks will serve as a general basis for the following considerations on the effects of sexual reproduction.

We can now consider the process of the 'reducing divisions' somewhat more closely. We require to know *what influence the reducing division exerts on the composition of the germ-plasm, and of what kind are the ids which are consequently respectively removed from, and retained in, the germ-plasm.*

Direct observation of the process is not *alone* sufficient to explain it; for not only do the ids and idants appear alike to our eyes, but we cannot even determine whether the idants of the young germ-cells of a new individual are the same as those of the fertilised egg-cell from which this organism arose; that is to say, whether an idant is a *permanent* structure, and whether a *particular* idant remains the same from one generation to another.

We know that during the process of amphimixis the paternal and maternal idants are situated close together, and are enclosed within a common nuclear membrane. There is often a small, though distinct space between the two groups of rods; and did this remain distinct during the whole period of ontogeny until new germ-cells were formed and underwent reducing divisions, we might be able to determine directly whether the paternal and maternal groups became separated, or whether half the number of the paternal rods remained in connection with the maternal ones, or also whether different combinations of rods are removed by the reduction.

The matter is, however, not so simple as this: the idants of the fertilised ovum only retain this form during the first division of the egg-cell, and then become broken up into a number of minute granules, which are distributed throughout the nuclear substance, and only recombine to form nuclear rods when the second division begins to take place. This process of disintegration and subsequent recombination of the idants is repeated every time a cell is formed by division during ontogeny, and thus it is impossible to decide whether a certain idant of any particular cell is derived from the father or from the mother. And further, we cannot even ascertain with any degree of certainty by mere observation, whether the idants of the subsequent cells are the same as those of the fertilised egg-cell, — that is to say, whether they contain the same kinds of ids in the same order. It is very possible that the ids may become entirely separated from each other whenever the idants undergo disintegration, and then become arranged in some other order subsequently. The number and nature of the ids contained in the entire idioplasm would then certainly remain the same as before, but the individual idants would differ, because the combination of ids would be different. It would then be immaterial whether the idants on the right were separated from those on the left in the reducing division, or whether the halving of the number of idants were effected in some other way; all the idants would consist of new combinations of ids already present, and their combination would necessarily differ completely from that of the idants of the fertilised egg-cell, which is almost always separated by a number of cell-generations from the new germ-cells, in each of which a rearrangement of the ids must have taken place. The removal of *entire* idants in the reducing division would obviously therefore be unnecessary, for the mere qualitative division of the whole of the idioplasm into two halves would be sufficient for the purpose.

As, however, the reducing division actually consists in the removal of half the number of idants, and as, moreover, this division is, as we shall see, a double one, I conclude that the *disintegration* of the idants after every nuclear division is *only an apparent one*, and that the separate ids of the idant, on the contrary, remain connected together by fine threads of the cementing substance, or 'linin'; and at the approach of nuclear division, they become rearranged in the same order as before.

That this is the case may be concluded from certain phenomena of heredity; a child, for instance, not unfrequently takes after one parent, *e.g.*, the father only, or at any rate to such an extent that the resemblance to the mother is unnoticeable. We must therefore suppose that the fertilised ovum from which the child arose contained a very similar combination of ids and idants to that which controlled the ontogeny of the father. It must therefore be possible, and cannot be altogether a matter of chance, that the germ-cell of the father contains these paternal or maternal idants, — or, in other words, almost precisely the same ids as those which directed the development of the father or mother, arranged in almost the same order. This is only conceivable, it seems to me, if the combination of ids into idants usually, at any rate, persists even during the disintegration of the latter in the nucleus.

Many recent observations support this conclusion, inasmuch as they show that fine threads of 'linin' connect the individual microsomata (ids), even when the idant has apparently undergone disintegration. In fact, Dr. Otto vom Rath * has just shown that such connecting threads even extend between the idants. It is therefore probably not too bold an hypothesis to assume the existence of such an arrangement for connecting the ids together.

I am therefore of the opinion that the idants only apparently undergo disintegration into granules during the 'resting-stage' of the nucleus, and I agree with van Beneden and Boveri in considering the idants to be *essentially permanent* structures. I do not, however, as already mentioned, wish this statement to be taken too literally: it must not be supposed that the structure of an idant must always remain the same throughout all generations, or that the reconstruction of an idant after its disintegration must *in all cases result in the ids being rearranged in the same order*. I imagine, on the contrary, that deviations from the original serial arrangement frequently occur in the ids. The fact of the constant change of individuality and non-recurrence of the same individual which can actually be observed in the human race in the course of generations, indicates, in my opinion, that an occasional change of the ids within the idants can take place in the course of generations, although this does not occur every time the idants are reconstructed.

If this is the case, and essentially the same idants persist during ontogeny from the fertilised ovum to the germ-cells of

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* 'Zur Kentniss des Spermatogenese von Grylloptalpa vulgaris. — Arch. f. Mikr. Anat., Bd. 40, p. 120.

the new organism,* we may conclude from certain phenomena of heredity that the reduction of the number of ids to one half does not result in the separation of groups of ids which are *always the same, and are definitely determined* beforehand, but in the removal of *different groups on different occasions. The germ-cells of one and the same organism must consequently contain very different combinations of ids, and consequently also of primary constituents, than those which were present in the parents of this organism.* The reduction affects the paternal and maternal idants in a precisely similar and equal way; it takes place in such a manner that any combinations may result from the halving of the number of idants. Let us take, for instance, four idants a + b and c + d; not only may the paternal group a + b and the maternal group c + d, as well as combinations of a + b and c + d, be present in the fully-formed germ-cell, but also the combinations a + c and b + d, or a + d and b + c, — that is to say, combinations each of which consist of one paternal and one maternal element.

A moderate amount of difference between the germ-cells of an organism as regards their contained primary hereditary constituents will thus result. In the case of the four idants taken above as an example, only six combinations would be possible, and consequently there could only be six kinds of germ-cells differing from one another in respect of their primary constituents. The number of possible combinations, however, increases very considerably with the increase in the number of idants; for example, 70 combinations are possible with eight idants, 12,870 combinations with sixteen idants.

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* Appearances certainly seem to contradict this assumption, and I am fully aware of the fact that Oscar Hertwig, and more recently Guignard, have stated their opinion to the contrary. In many conditions of the nucleus it is, in fact, impossible to recognise the idants, and they certainly do not exist *as such*, — that is, in the form of compact rods. But it is quite conceivable that the connection of the ids in an idant may nevertheless persist, and that the individual ids are connected together by fine threads of 'linin.' An observation made by my assistant, Dr. Häcker, supports this view. He noticed that the microsomes of the rod-like idants of the growing egg in Copepods become separated from one another, but always remain connected by a delicate thread of linin, which in this instance can be stained: the linear arrangement of the microsomes certainly persists in this case. (*Cf.* Häcker, 'Die Eibildung bei Cyclops und Canthocamptus, Zool. Jahrbücher, Abth. f. Anat. und Ontog., Bd. v., p. 237.)

In *Ascaris megalocephala* the number of idants is only two or four; but as far as we know, a greater number is present in the case of all other animals, and also in that of plants: thus there may be eight, sixteen, thirty-two, and even a hundred or more.* A simple and single reduction, such as we have hitherto assumed, will therefore in general secure a very considerable amount of variety as regards the combinations of primary constituents caused by the reducing division. Nature seems, however, to have aimed at a far greater degree of variety, at any rate in the case of animals, in which a *double instead of a single reduction of the number of idants to one half* always occurs; and this, as I have recently attempted to show, must have the effect of increasing the number of possible combinations of idants very considerably.†

The facts as they concern the Metazoa may be briefly summarised as follows. In all those species which have been investigated for this purpose, the germ-cells are formed by the mother-cell undergoing two consecutive divisions, each of which results in a halving of the number of idants, one half passing into the one daughter-cell, and the other half into the other. In the second division this would lead to the presence of only a quarter of the original number of idants, if the number in the mother-cell were not *doubled by each idant becoming split into two before the first division takes place.* Thus there is first a doubling, and then a halving, of the number of idants. It is a matter of secondary consideration in the question of heredity that in the formation of the female germ-cell or ovum three of the cells produced by the division of the mother-cell give rise to the evanescent 'polar-bodies,' one cell alone becoming an ovum capable of development, while all four of the male germ-cells become functional. The chief point which now concerns us is the process of doubling, and the two subsequent halvings of the number of idants: this is known to occur in all classes of the Metazoa from the lowest to the highest forms, and, as far as we know, is only wanting in those eggs which are adapted for parthenogenesis. Even in these cases the doubling also occurs, but it is followed by only a *single halving* of the number of idants, in

* Dr. vom Rath informs me that in the crayfish (*Astacus fluviatilis*) the number of idants reaches 108–125.

† *Cf.* 'Amphimixis,' Jena, 1891 (Essay xii. in the English Translation, Vol. ii., p. 105).

correspondence with the absence of amphimixis. For the full number of idants only appears a second time in an ovum adapted for fertilisation, by the union of the nucleus of the sperm-cell with that of the ovum.

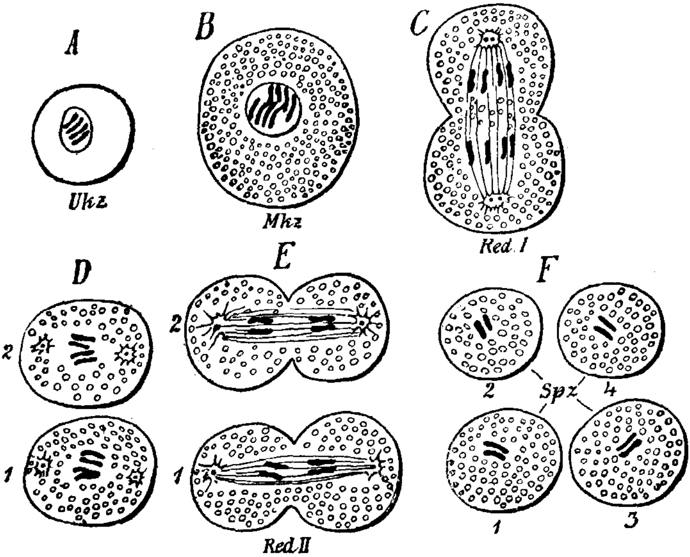

FIG. 20. — Diagram of the formation of spermatozoa in *Ascaris megalocephala*, var. *bivalens*. (Modified from O. Hertwig.) — A, primitive sperm-cells; B, sperm-mother-cells; C, first 'reducing division'; D, the two daughter-cells; E, second 'reducing divisions'; F, the four granddaughter-cells (the sperm-cells).

I consider this remarkable and apparently useless * process of the doubling and two subsequent halvings of the idants *as a method of still further increasing the number of possible combinations of idants in the germ-cell of one and the same individual*, and have given reasons for this opinion in the above-named

* It might be supposed from the observations of Rückert on the ovum of the dog-fish, which were described in Chapters I. and II., that this doubling is simply concerned with a doubling as regards mass, and consequently with the *activity* of the idants: their activity must be very considerable in this case, for the egg of the dog-fish is very large, and requires a considerable amount of multiplication of the 'oogenetic' determinants. But a doubling of the idants occurs also in all other animal eggs, even in the

essay. As already stated, a single halving of four idants can only result in six combinations. But if, as actually occurs, each

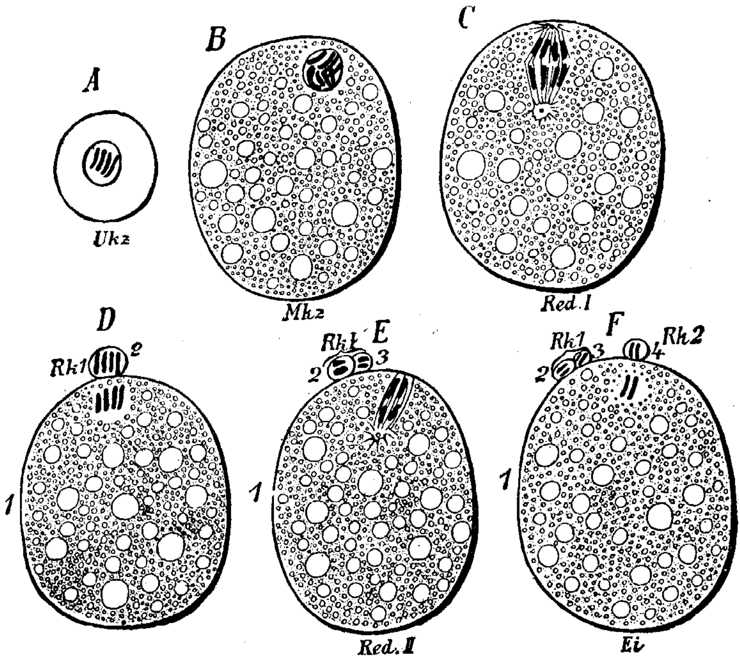

FIG. 21. — Formation of ova in *Ascaris megalocephala*, var. *bivalens*. — A, primitive germ-cell; B, fully-developed egg-cell, the number of the idants in which have increased from four to eight; C, first 'reducing division'; D, the egg with the first polar-body, immediately succeeding the stage represented in C; E, the first polar-body has divided into two daughter-cells (2 and 3), the four idants which remain in the egg giving rise to the second 'reducing spindle'; F, stage immediately succeeding the second 'reducing division' — 1, the ripe egg-cell; 2, 3, and 4, the three polar-cells; each of the four cells only containing two idants.

smallest — in which a very small amount of yolk is contained — as well as in the sperm-mother-cells, which never attain to such a size or structural differentiation as do the ova. The process cannot be concerned with an increase of the germ-plasm contained in the idants, for in the formation of the ova three-quarters of the mass of germ-plasm passes into the polar bodies and is again lost. The explanation of the process here given seems therefore to be the only possible one.

idant were doubled before the division, ten combinations would be possible. This means that one individual of any species possessing four idants in each of its cells can produce ten kinds of ova and spermatozoa differing from one another as regards individual hereditary tendencies. Two new idants are added to such an ovum when one of them is fertilised by the spermatozoon of another individual; and since each parent produces ten different kinds of germ-cells, as many offspring differing in character from one another may arise from these two parents as there are possible combinations of the ten kinds of spermatozoa of the father with the ten kinds of egg-cells of the mother, *i.e.*, $10 \times 10 = 100$.

With eight idants, 70 combinations are possible without, and 266 with, doubling; and following this up, twelve idants will thus give 924, or 8,074 combinations; sixteen, 12,870, or 258,570; twenty idants, 184,756, or 8,533,660; and with thirty-two idants, about five hundred times as many combinations would be obtained with doubling as without it.

Since the same number of idants from each of the conjugating cells come together in the process of fertilisation, and each of the parental germ-cells only contains one of the many possible combinations of idants, the number of variations in the germ-plasm which it is possible for two parents to produce must be an enormous one. It can be calculated by multiplying the number of possible combinations in the two conjugating cells together: thus in the case of twelve idants only, it would amount to $8{,}074 \times 8{,}074$. Unfortunately we are unacquainted with the number of idants in the human subject, in which we are best able to recognise individual differences in most minute detail. We may, however, suppose that this number is more than four. If, for instance, it were as high as twelve, we need not wonder that two children born consecutively are never identical, as must be the case if they had originated from the same combination of ids of the germ-plasm. Approximately identical children only occur in the case of twins, and we have every reason to believe that these originate from one sperm-cell and one ovum.

We cannot as yet judge with certainty as to how far the entire idants pass unchanged as regards their constituent ids from the germ-cells of one generation into those of the next. The phenomena of the reduction in the germ-cells which have recently been made known to us in the case of various Arthropods by the researches of Henking, vom Rath, and Häcker, indicate that even the idants *may* become changed during the process. If we suppose that in the mother germ-cell, when it is preparing for the first reducing division, the ids become arranged in their original order so as to form a long thread which doubles back on itself, and thus gives rise to a ring, the latter would become transversely divided in certain places. If the transverse divisions could take place at different points, it would be possible either for the old idants to be accurately restored, or for the new ones to differ from them to a greater or lesser extent.

This assumption is not, however, essential for a theory of amphigonic heredity, and we may here disregard it, although it will doubtless be found to apply to some extent, as was indicated above with regard to such a slow and slight change of the idants due to the disarrangement in the combinations of ids contained in them. It must be left to future researches to follow out this process in detail, and to show whether the differences in the combination of ids is merely due to the halving and rearrangement of the idants, or whether regular, or at any rate frequent, changes in the composition of the idants out of ids also occur. For the present we must be content with knowing that the *germ-cells of an individual contain very many different combinations of idants, and that a frequent repetition of amphimixis never indeed results in the germ-cells of the same parents containing the same combinations.* It therefore follows that the combination of parental and ancestral characters continually varies, and this variation is characteristic of amphigonic heredity.

This statement also holds good for plants, in which we know that a reduction to half the number of idants takes place in the germ-cells. According to the researches of Guignard,* the

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* L. Guignard, Compt. rend. May 11, 1891, and 'Nouv. études sur la fécondation,' Ann. scienc. nat. Bot. Vol. xiv., 1891, p. 163.

Particulars regarding Guignard's valuable researches cannot be entered into here. They have not only proved that in plants the mature germ-cells likewise contain only half as many ids as do the somatic cells, and that the normal number is again produced by the union of the nuclei of the male and female cells, but have also shown that the centrosome passes on from one generation to the next. In spite of the fact that these observations are obviously perfectly accurate, I cannot help doubting whether the reduction in the number of idants actually occurs *without a nuclear division*, as Guignard states is the case. I have arrived at this conclusion not somatic cells, as well as the mother-cells of both kinds of germ-cells in *Lilium martagon*, contain twenty-four idants, while the mature germ-cells contain twelve only. We do not as yet know whether this reduction is effected by a single reducing division, or by two such divisions preceded by a doubling, as in the case of animals. For evident theoretical reasons I consider it extremely unlikely that the reduction occurs in the mother-cell while it is preparing for division, as Guignard thinks is the case. It is very possible, however, that only one reducing division takes place in this instance.

The details of these processes in the lower plants are quite unknown, probably owing to the minute size of the idants, which till now has rendered the difficulties of such investigations insurmountable. It has, however, at any rate been ascertained that in many marine algæ (*Fucoideа*) the development of the egg-cells is accompanied by the formation of 'polar bodies,' which certainly correspond to stunted and phyletically degenerated ova: this was first shown to be the case by Bütschli and Giard, and the fact has long been recognised by other zoologists besides myself. In the genus *Fucus* these polar bodies do not occur, and eight eggs are formed from the primary ovum,— if I may venture to apply this term to the original cell of the so-called oogonium or ovary; in an allied species of wrack, *Ascophyllum nodosum*, only four eggs are formed from the primary ovum, but four polar bodies are also produced; in *Pelvetia canaliculata* the primary ovum gives rise to two eggs and six polar bodies;

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merely from a comparison of the analogous process in animals, but also because I cannot help thinking that it is possible, and even probable, that in this respect these otherwise admirable observations are not quite complete. In the formation of the male germ-cells, a reducing division may perhaps take place between the 'cellules mères primordiales' and the 'cellules mères définitives;' and as regards the female germ-cell, it will occur in the division which gives rise to the 'cellule mère du sac embryonnaire.' In both cases even the most acute observer might fail to notice the reducing division if his attention were not specially directed to this point. Why should an arrangement for a 'reducing division' have been made in the case of animals if the reduction could take place without nuclear division, and could produce the same result? Of all the other numerous observations which have been made on the process of karyokinesis, *not a single one supports the view that the single (?) chromatin band* of the 'skein' stage can become disintegrated into half as many idants as were previously present in the nucleus.

and in *Himanthalia lorea* only a single egg and seven polar bodies are formed.*

We have here, however, no information as regards the reducing divisions, which, as I pointed out long ago, need not by any means be connected with the degeneration of several germ-cells. We can only state that the three successive divisions of the primary ovum, which occur in all the above-mentioned cases, affords more than sufficient opportunity for one or even two reducing divisions, and that it is extremely probable that one, at least, actually occurs.

We may therefore assume that in plants very varied combinations of the germ-plasm derived from each parent usually take place in the germ-cells of the offspring, and that perfectly '*identical*' germ-cells can very rarely occur either in plants or in animals.

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* *Cf.* Oltman's 'Beiträge zur Kentniss der Fucaceen,' Cassel, 1889.