

On the Phenomena of Reproduction in Animals and Plants.

Reducing Division in Metazoan Reproduction.

BY

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A REDUCING division in itself, apart from the previous history of the cell in which it occurs, or of the ancestors of that cell, is of course unintelligible. It is needful to enquire in both animal and plant how from this past history the reduction was rendered imperative. It is, as Strasburger has insisted, 'a return to the original generation from which, after it had attained sexual differentiation, offspring was developed having a double number of chromosomes'¹. Theoretically it is the undoing of the displacement of balance among the 'organs' of a cell due to duplication at a previous conjugation².

In the researches of recent years on the mode in which the reduction takes place in oogenesis and spermatogenesis the burning question has been whether it was by a longitudinal, or by a transverse, fission of chromosomes. A longitudinal division is proved to be incapable of effecting this, because it is the mode in which any ordinary cell-division is brought to pass. And the failure of the chromosomes to

¹ Loc. cit., p. 289.

² The term 'conjugation' is used to represent generally the union of two nuclei whether in Protozoan or Metazoan. The final act of union is fundamentally the same in both cases, as will appear subsequently.

unite after the conjugation, until the first division of the zygote shall have happened, is again an indication that a longitudinal splitting does not bring about a reduction. When actual union of chromosomes after conjugation is effected, this is obtained by the union of the chromosomes from an individual A with a corresponding number of chromosomes of an individual B; the chromosomes must, as others have often enough insisted, retain their identity and they only become disunited for the purposes of a cell-division.

Ultimately it becomes necessary to finally undo the linking, in order to prevent a duplication of the number which would increase it to fourfold what it originally was. This can only be effected by a transverse splitting. In other words, chromosomes may be considered as possessing two axes, along one of which (the longitudinal) they may divide, along the other (the transverse) they may unite with other chromosomes. It is along the latter—that along which union takes place—that the reduction must be effected. A reduction is nothing more than an undoing of the union effected at a previous conjugation, but by this it must not be concluded that there is any intention of supposing it to be a separation of all the male-parental chromosomes from all the female-parental ones. The facts of heredity, as Weismann has proved, go to show that the process is more complicated, and an excellent discussion and explanation of it have been furnished by Haecker in his reply to Strasburger and elsewhere. The theoretical mode of the undoing has quite recently been proved by an able investigator in the case of the Copepoda¹.

Rückert has shown that in this group the reduced number is brought about by a transverse division of what seemed to be half the normal number of chromosomes, and that in the ripening of the egg this takes place in the formation of the second polar body. He states² that the reduction in the number of chromosomes before fertilization is attained by the

¹ Rückert, J., *Die Chromatinreduction bei der Reifung der Sexualzellen. Ergebnisse der Anat. und Entwicklungsgesch.*, Bd. III, 1893, pp. 517-583.

² Summary on p. 582.

united action of two processes. (1) It is initiated before the maturation, perhaps at a very early period, by the suppression of a transverse division of the chromatin loop, in consequence of which the chromosomes remain attached in pairs or couples. (2) It is accomplished in the second division of the ripening by the passage of the chromosomes of each pair to opposite poles¹. He goes on to say that the first process alone leads only to a pseudo-reduction, the true number of chromosomes persisting, being only masked, and therefore capable of reappearing. The process, however, appears necessary in order that the subsequent reduction should be effected. A theoretical explanation of this has been attempted above.

It may at this juncture be useful to consider what must have been the general result of the initiation of conjugation between unicellular organisms in past ages. When conjugation between pairs of similar cells arose among the primeval Protozoa (or Protophyta) the original form of this process was bound to result in the 'creation' of two different generations. These were characterized primarily by a difference in the number of chromosomes. The one generation with double chromosomes was itself never capable of conjugation, it could only give rise to new forms by fission, and it, or its progeny so produced, could only bring about a new conjugation by first producing (spore-formation) a generation in which the number of chromosomes was reduced in each individual product to the original one, which obtained antecedent to a conjugation.

¹ It is worthy of notice that Farmer has recently stated the following facts concerning the reduction in plants:—Two features characterise the karyokinesis of the spore mother-cell in Hepaticae. The first of these is that the number of chromosomes is reduced to one half as compared with antecedent mitoses in the sporophyte, and this reduced number is apparently retained in the gametophyte. The second point is that the spore-forming mitoses are what Fleming has termed 'heterotypic' in character. (J. B. Farmer, Spore-formation and Karyokinesis in Hepaticae. *Annals of Botany*, Vol. ix, June, 1895, pp. 363-364.) These facts appear to agree absolutely with what Rückert found in Copepods, but of course in the one case (animals) the reduction occurs at the 'ripening' of the sex-products, in the other (plants) at the spore-formation.

Notwithstanding all those facts of Protozoan modes¹ of reproduction which may appear to tell against this, notwithstanding all the botanists believe about the secondary nature of alternation of generations, it must be insisted that a simple antithetic alternation of generations was obligatory from the very nature of the original conjugation.

All subsequent higher developments must be considered as effected by further specializations on the original 'plan.'

The Protozoan stage might be improved upon by the one generation or the other, or by both. The conjugating generation may have become Metazoan, or the spore-producing one, or both together may have undergone the higher evolution². It is probable that there were originally variations here, and some of these still persist. In plants the amplification of the zygote stage has given rise to the sporophyte, which is sharply separated from the sexual generation or gametophyte by a one-celled stage (the spore) and a reducing division. The whole of the cells of the gametophyte must be looked upon as morphologically aequivalent, some becoming differentiated as vegetative organs by sterility, others retaining the primitive character of becoming conjugating gametes. Bower³ has attempted with some success to derive the members of the sporophyte by a similar sterilization of sporogenous tissue. The standpoint here taken up is, in fact, an application of his method to the other generation. Indeed, it may be regarded as certain that what Weismann terms somatic cells in both kingdoms owe their origin in all cases to sterilization.

When one seeks in the higher animals for an equivalent of the alternation of generations in plants in the light of recent work on the reducing division of spore-formation, such a mor-

¹ In the sequel an attempt will be made to show, by concrete instances which have been thoroughly investigated by other observers, that many of these are secondary in nature.

² This must be held as true for the plant kingdom also.

³ Bower, F. O., *Studies in the Morphology of Spore-producing Members*. Phil. Trans. 1894, B.

phological mark would only be found in the maturation of the egg and in spermatogenesis. If the process were here a spore-formation, the whole Metazoan body, in which it took place, would represent the asexual generation, and any apparent alternation of generations in the life-cycle would be homologous¹ in character, not antithetic. But the total lack of homology between the organs of certain larvae and those of the adults which arise upon them,—as well as other facts and factors in course of publication elsewhere—leads to a suspicion that here we have a real antithetic alternation of generations masked by omission of the spore (apospory), and a consequent delay of the reducing division. Such a delay might easily arise as a result of the close association of the two generations observable in the development by substitution so characteristic of animals. In fact the frequency of substitution is one of the most striking differences between animal and plant development.

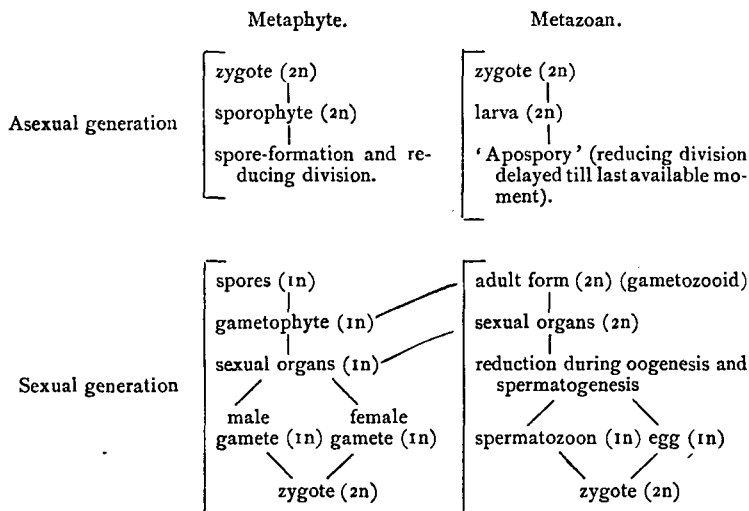
As before stated, it is not intended in this place to attempt any proof that Metazoan development is a form of antithetic alternation of generations with apospory. That must be assumed, and the consideration of the evidences in favour of it be reserved for another place.

On this supposition a comparison of Metaphytic and Metazoan modes of reproduction would be as shown in the table on the next page.

It is thus apparent that the life-cycles of a higher Metaphyte and of a Metazoan exhibit close correspondence, if animal development be a form of antithetic alternation of generations masked by aposporous formation of the sexual generation or gametozoid. The omission of a spore-formation has, as one of its results, the delaying of that reduction of the chromosome-number which must take place before the next conjugation. It thus happens that the cells of both generations contain a similar, i. e. duplicated, number

¹ As a matter of fact such a homologous alternation may become intercalated, and there is no intention of denying its existence alongside an antithetic one in many instances, such as *Trematoda*, *Ascidia*, &c.

of chromosomes, and the reduction itself is necessarily deferred until the last possible moment, i. e. to the period of ripening of the sexual elements. 'Necessarily deferred' is undoubtedly the term to describe the fact, and the explanation of the why and wherefore of this affords an opportunity of considering a very obvious objection to the view here adopted.



In the above table n equals the number of chromosomes prior to the duplication ($2n$) at conjugation.

It may be urged that, if the fact of the occurrence of an antithetic alternation in animal development were admitted, the reason for an aposporous formation of the gametozooid would not be at all obvious. Spore-formation with the necessary reduction might none the less occur at the proper juncture, and the gametozooid might, directly or indirectly, arise from one of these spores; whilst the remainder, whatever number of them there were, might be abortive. As a matter of fact, as will be presently demonstrated, something of this sort is the course of events in the conjugation of the Infusoria. It does not hold for Metazoa for the following reasons:—(1) Generally speaking, only one gametozooid makes its appearance on the larva, there are no traces of

abortive spores, and the formation of one true spore alone appears to be out of the question ; for, in order that cells with the reduced number of chromosomes, i. e. spores, should arise, four of them at least must be formed. (2) That there is no spore-formation is, of course, also proved by the circumstance that there is no reduction before the origin of the gametozoid, and as previously shown, the primary object of spore-formation is to effect a reduction.

The modifications in development which this aposporous alternation brings about are far too numerous and too varied to admit of treatment here. It would be necessary, even with the facts already available, to write a treatise on animal development from this standpoint, in order to display them.

But it may be of interest to indicate one or two developmental facts, which clearly have their natural interpretation in an aposporous formation of the sexual generation in the Metazoa.

The marine Annelida with an obvious larval development admit readily of inclusion in such a scheme as that suggested. Kleinenberg¹, in his brilliant *Lopadorhynchus* memoir, has amply demonstrated such an alternation as that here recognised, while just failing to draw the manifest conclusion. By way of parenthesis it may be remarked how marvellously close on a recognition of this 'law of development' Kleinenberg's meditations, along with those of Johannes Müller and Von Baer, really verge.

A Chaetopod origin of the group of *Hirudinea* is commonly admitted, and in them R. S. Bergh has demonstrated facts in his memoirs furnishing as valuable confirmation of the views here advocated as could be wished.

Passing next to the group of the *Oligochaeta*, we are apparently brought to a standstill in our further search for confirmation. But not really so. When we take up the researches of E. B. Wilson², these at first sight seem hope-

¹ Zeitschrift f. Wiss. Zool., Bd. XLIV, 1886.

² Wilson, E. B., The Germ-bands of *Lumbricus*. Journ. of Morphology, Vol. i, 1887.

lessly at variance with any such idea as that of alternation of generations with apospory. It was long ago foreseen that here obstacles seemed to block the way. However, when looked at in the light of spore-formation, Wilson's lines of cells, mesoblasts, neuroblasts, &c. readily admit of interpretation, not as due to an actual spore-formation, but as an early modification of this, which has already led some distance along the path of apospory; really as a step in advance from the former formation of the sexual generation, or gametozoid, from a spore-mother-cell, in the direction of its origin from a few cells. Carry the process still further, and we obtain the counterpart of the primitive streak of the Vertebrata. It is very interesting to note that, altogether apart from theoretical considerations, Assheton points out how in the embryology of the frog and rabbit the first attempts at development result in products formed in a totally different direction from that subsequently adopted.

Assheton¹ has really proved that the embryo (i.e. the sexual generation) is not formed by the segmentation of the egg, but by a proliferation in a totally different direction, i.e. in a zone which gradually grows backwards whilst proliferating in front. In other words, his researches may be explained as showing how the gametozoid arises from an aposporous tissue within a larval or asexual generation resulting from the segmentation of the egg—from the so-called 'primitive streak.'

The pole-mesoderm-cells of Hatschek may also be mentioned, and it may be suggested that a possible interpretation of them would be that they might represent spore-mother-cells, which had of course undergone no reduction.

¹ Assheton, R., The Growth in length of the Frog Embryo. *Quart. Journ. of Microsc. Sci.*, Vol. xxxvii, N.S. pp. 223-243.