was taken, that then the second step consisted in the formation of stationary spores arising by a tetrad division. With such assumptions, the transition to the simple Liverworts—e.g. *Riccia*, does not appear very great, and, starting from this form, the different series included in the Bryophyta may be derived. Though we have thus gained certain connecting points for the phylogeny of the Mosses, the question as regards the Ferns, in which the fertilized ovum develops into the leafy plant, is in quite another position. It has been recognized on many sides how great a contrast there is between Mosses and Ferns. The common peculiarity in the structure of the archegonium might be a purely parallel development without its necessarily indicating any phylogenetic connexion. It is not my purpose to enter now upon these difficult questions, the less so since they will be dealt with here from an official quarter. They deal with the most interesting, but also the most obscure, points in the phylogeny of the vegetable kingdom. For the spot where the first indication of a Fern-sporophyte appeared was the birthplace of the vastly-developed series of the Phanerogams. The Thallophytes hitherto known do not give the least clue to the discovery of that spot.

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ALTERNATION OF GENERATIONS IN THE ARCHEGONIATAE.—One of the most important facts in the morphology of all plants higher than Thallophytes is the occurrence in their life-history of two alternating stages, which differ widely from each other both in structure and reproduction. Of recent years advances in our knowledge in several distinct departments of botanical investigation have raised anew the question of the nature of this Alternation of Generations. The subject has been discussed from two very different standpoints in the Presidential Addresses to this Section of the British Association this year and at the Liverpool Meeting[1]. These expressions of opinion by Dr. Scott and Professor Bower render an introductory paper to this discussion in one sense superfluous. While, however, repetition of much that has been already said is unavoidable, the existence of such diverse views suggests a slightly different treatment of the question, which may be useful for the

[1] The existence of these recent statements of the problem renders references to the literature of the subject unnecessary.

purposes of the discussion. Instead of advocating either the theory of antithetic or of homologous alternation, I shall try to present a dissection of the subject; with this object the main facts known as to alternation of generations will be briefly discussed, and the possible interpretations of them considered. The facts will as far as possible be kept apart from the theoretical views to which they have given rise, and the points on which our knowledge is deficient will be emphasized rather than minimized.

The general facts regarding alternation of generations in archegoniate plants can be dismissed very briefly. In all the main groups a definite alternation of a sexual with an asexual generation is found. The latter is normally developed from the fertilized ovum, the former from the spore. The Bryophyta and Pteridophyta are, however, opposed to one another in the relative complexity attained by the two generations. The sporophyte in the Bryophyta remains dependent on the Moss or Liverwort plant, and has as its main function the production of the spores. It may, however, attain very considerable complexity of structure and possess a well developed assimilation tissue. In both Hepaticae and Muscineae very simple sporogonia lead on to complex ones in which the sterile tissue of the wall, foot, seta, &c., forms a considerable proportion of the whole structure. The gametophyte, on the other hand, is always independent and often shows a complicated external form with clearly differentiated stem and leaves. In the Vascular Cryptogams also the gametophyte is always independent, but is of relatively simple form and structure. The sporophyte, which develops from the fertilized ovum, very soon produces roots, and attains independence by the death of the prothallus. It shows a distinction of stem and leaf, is highly organized, and does not develop spores until after a period of vegetative growth. While these points of difference which indicate the great gap between the Bryophyta and Pteridophyta are borne in mind, due weight must be given to the points of agreement. Of these, the similar structure of the sexual organs, the fact that in both the sporophyte is at first dependent on the gametophyte, the presence of stomata and intercellular spaces in the sporophyte, and the similarity in the spore-production may be mentioned. A consideration of these facts by themselves indicates no view as to the mode of origin of the two generations. At no stage do the two generations in any Archegoniate closely resemble one another, except in the case of the young plant

and the prothallus of *Lycopodium cernuum*. The deviations from the normal life-history, which will be considered later, may somewhat modify this statement.

We are justified in assuming that the Bryophyta and Pteridophyta arose from ancient Thallophytes; the study of the life-histories of the Algae and Fungi, which exist at present, may accordingly be expected to aid in arriving at probable conclusions as to the origin of the alternation in archegoniate plants. It is naturally among the Green Algae that indications of this sort might be expected, nor are they wanting, though the precise weight to be attached to them is a matter of uncertainty. The higher Fungi and the Red and Brown Algae may for the sake of simplicity be left on one side with the remark that in Ascomycetes and Florideae we see a development which presents analogies with the alternation in Archegoniates. Confining ourselves to the Green Algae and the simpler Fungi we find among them two sorts of phenomena which have been termed alternation of generations. Most of these organisms reproduce both sexually and asexually, and sexual and asexual individuals, resembling one another in their vegetative structure, are often found. The same individual may, however, bear both kinds of reproductive organs, and Professor Klebs has shown in a number of cases that the mode of reproduction is largely determined by the external conditions and can be brought under experimental control. There is thus no doubt that these sexual and asexual individuals are homologous in the full sense of the term. But there are a number of Thallophytes in which another stage in the life-history is found, which, by its regular recurrence and the position it occupies in the life-cycle, suggests a comparison with the sporophyte of the simpler archegoniate plants. While in many Thallophytes the fertilized ovum or the zygospore develops directly into an independent plant resembling the parent, in these it first divides into a number of cells, which are usually motile spores, but may form a small mass of tissue from the cells of which swarm-spores arise. It is sufficient to mention *Oedogonium*, *Cystopus* and *Coleochaete* as organisms which show this clearly. In the life-history of *Sphaeroplea* only sexual individuals and the group of swarm-spores, which results from division of the oospore, alternate, independent asexual individuals not being found.

If we now consider how this second form of alternation in Thallophytes might have come about, without for the moment extending

our view to archegoniate plants, the essential distinction of the antithetic and homologous theories will become plain. Further, we shall here be dealing with a problem with regard to which the work of Professor Klebs justifies the anticipation that direct evidence will sooner or later be obtained. The main question at issue is, In what relation does the group of spores in *Oedogonium*, or the small mass of tissue resulting from the division of the fertilized ovum in *Coleochaete*, stand to the asexual individuals of the same species? There is some evidence that in this stage we see the representative of an asexual individual, the vegetative body of which has become more or less completely reduced. Thus occasionally in *Oedogonium* a vegetative individual develops from the zygote; in *Uothrix* the zygospore develops a rhizoid, but the contents of what appears to be a rudimentary plant are wholly devoted to the formation of motile spores. On this view the cell-mass in *Coleochaete* would be regarded as a reduced thallus, all the cells of which form spores asexually. The reduced generation which proceeds from the zygote would genealogically correspond to an independent asexual individual, and just as the latter is homologous with a sexual individual, so would the four spores in *Oedogonium* or the cell-mass in *Coleochaete* be. This would be homologous alternation of generations.

But the same facts can be viewed in another light. In all these cases the advantage to the plant in producing almost at once a number of individuals instead of one as the result of the sexual act is obvious. The division of the ovum may have originated as a special adaptation to this end, and not represent a reduced first neutral generation at all. In the life-history of these plants there would then be a stage not represented in the majority of the Thallophytes, which may in this sense be spoken of as interpolated. The cell-mass of *Coleochaete* upon this view would not represent a less reduced neutral generation, but a more complicated development of the interpolated stage, which is seen in its simplest form in *Oedogonium*. This stage would not correspond to, or be homologous with, the independent asexual individuals, and leaving these out of account, only one individual, and the result of elaboration of its zygote would be represented in the life-history. The alternation would not be homologous but antithetic.

If we now proceed to apply these two points of view to the facts of alternation in the Archegoniatae, the problem in its most general

form is this: Is the sporophyte in the Bryophytes and the Vascular Cryptogams to be ultimately traced back to modification of a genealogical individual homologous with the gametophyte, or is it the result of still further elaboration of an interpolated stage more or less like that seen in *Coleochaete*? On the antithetic theory the sporophyte is traced increasing in complexity through a series of forms illustrated by *Oedogonium*, *Coleochaete*, *Riccia*, *Marchantia*, *Anthoceros*, and the simplest sporophytes of the Vascular Cryptogams are regarded as having been derived from a sporogonium, which already possessed a considerable amount of sterile tissue. If, on the other hand, we apply the homologous theory, several alternatives present themselves. The first, which is not widely different from the antithetic theory, is that in the course of its descent the sporophyte of the Vascular Cryptogams has passed through a stage resembling the Bryophyte sporogonium, but that the origin of this second generation in the ancestral Algae was homologous. But the homologous theory does not necessarily assume the existence of the sporogonial stage. The sporophyte of the Vascular Cryptogams may have had an independent origin from that of the Bryophyta, and have resulted from the modification of individuals, which were never reduced to the condition of a fruit body.

As to the circumstances which led to alternation of generations, the two theories are in essential agreement. We owe to Professor Bower the general statement, which must serve as the starting-point of any explanation, that the origin of the alternation may be correlated with a change of habit from aquatic to sub-aerial life. This holds whether the second generation is considered to be homologous with the first, or to be the result of interpolation. On the latter view, which is that elaborated by Professor Bower, the importance of the drier conditions of life is sought in the prevention of repeated acts of fertilization. It would thus have been an advantage to the organism to produce many individuals as the result of one sexual act, and this is seen to be effected with increasing perfection as we pass from the simpler to the more complex Bryophyte sporogonia, and from these to the Pteridophyta. The same change of environment may, however, have initiated the modification of individuals, which were originally potential sexual plants, into spore-bearing forms. We shall return to this when discussing apogamy.

We have seen that the facts of morphology do not of themselves

indicate decisively which theory is the correct one. The reasons which render one or the other view the more probable are bound up with the more general question of the course of descent in the vegetable kingdom. The question of the relationship between the main groups of plants is a very complex one. All that we need do here, however, is to recognize the existence of several alternative views, and the bearing of these on the two theories of alternation. The indications of alternation in the Thallophytes may be first referred to. These seem closely comparable to the simplest Liverwort sporogonia, but it has not been suggested that any direct relationship exists in any case. The existence of these rudimentary sporophytes in various Green Algae, in *Cystopus*, and in an analogous, though distinct form in Ascomycetes and Florideae, is indeed strongly suggestive of their independent origin in the Thallophytes of the present day, and justifies us in considering it probable that similar developments may have occurred in the ancestral Algal forms from which the Archegoniates arose. But the further recognition of the possibility that the origin of the Archegoniatae may have been polyphyletic, and in particular that the Vascular Cryptogams may have had a line of descent from Thallophytes perfectly distinct from that of the Bryophyta, has a much more important bearing on the nature of alternation. The gap between Bryophytes and Pteridophytes is wide, and on this view would be an essentially natural one; any attempt to bridge it would involve misleading conclusions. I do not wish to enter into the question of the polyphyletic origin of archegoniate plants further than to show that its possibility must be borne in mind in considering the nature of alternation. It may be pointed out, however, that such a view would appear to follow naturally from the supposition that the origin of the sporophyte was correlated with the spread of aquatic organisms to the land. It may be considered probable that a number of organisms in different places would have undergone more or less similar modifications. The homologies which exist between the spore-bearing generations of Mosses and Ferns are no less possible results of homoplastic developments than others in favour of which direct evidence exists. If the origin of the Pteridophyta has not been from the Bryophyta, the comparison between the sporogonia of the latter and the simpler sporophytes of the Vascular Cryptogams would lose much of its weight, since the two may have proceeded, as Goebel

suggested, on distinct lines from the beginning. It is therefore advisable to ascertain if any evidence exists which may indicate how the Vascular Cryptogams could have been derived directly from Algal forms. Something of the kind, as we shall see, may possibly be afforded by the facts of apogamy.

So far we have seen no reason to regard the nature of alternation and the views on descent which underlie it as anything but open questions. There are, however, two important classes of facts, which have been regarded as affording more direct evidence in favour of the antithetic and homologous theories respectively. These are the cytological differences between the two generations, and the deviations from the normal life-history known as apospory and apogamy.

The first of these will only be mentioned. The existence of the double number of chromosomes, which results from the sexual fusion, in the nuclei of the sporophyte, throughout Bryophyta, Ferns, and the higher plants, certainly appears to lend support to the view that the sporophyte is an interpolated stage in the life-history. From the cytological point of view the intercalation is between the doubling of the number of chromosomes by the sexual fusion and the reduction in number in the spore mother-cells. Facts are wanting as to the nuclear changes in Thallophytes, and also in apogamy and apospory.

These latter phenomena are the last element in the problem that can be referred to at length. We saw that in the case of the alternation of clearly homologous generations in the Thallophyta it had been shown that the assumption of the sexual or asexual form depends on the external conditions. This experimental study needs to be extended to the rudimentary sporophytes of the Green Algae, but with regard to these it is already known that in *Oedogonium* the fertilized ovum may grow out directly into a vegetative plant, instead of dividing into spores. In the Archegoniatae this complete substitution of one generation for another is not known to occur; no variations in the external conditions are known to induce a Fern-spore to develop into a Fern-plant, or the fertilized ovum to give rise directly to a prothallus. But the facts as to the direct development of the one generation from the tissues of the other, and the existence of structures which may fairly be described as intermediate between gametophyte and sporophyte are sufficiently striking.

The main facts with regard to apospory, the vegetative origin of the

gametophyte from the tissues of the sporophyte, are briefly these. In Mosses cut portions of the seta or capsule have been induced to give rise to protonemal filaments; in one case this is known to have occurred in nature while the capsule was still attached to the Moss plant. In a number of Ferns the production of prothalli from the sporangia, the placenta, the surface of the leaf or the leaf margin, takes place. In *Scolopendrium vulgare* and *Nephrodium Filix-mas* varieties are known in which the first leaves of the young sporophyte exhibit this capability of producing prothalli. The causation of this phenomenon is still obscure. In a number of cases sporal arrest has been shown with probability to be of importance, notably in the case of *Onoclea*, in which apospory occurred on fertile leaves which had been experimentally induced to assume the vegetative form. Further, the fact that conditions of life favourable to the gametophyte, such as laying the fronds on damp soil, determine the growth of prothalli from the tissues of some aposporous Ferns may be mentioned. As to the weight to be attached to apospory it must be borne in mind that the phenomenon is little more wonderful than the fact of the spore, a cell isolated from the sporophyte, producing a prothallus. Here, as in the case of apogamy, the investigation of the cytological details is urgently needed.

The deviations from the normal life-history, which are classed as apogamy, may be considered to possess more importance as suggesting the homology of the two generations in the Ferns. Though as yet only known in this group of plants, apogamy has been found in more than twenty species. In some the young Fern-plant arises on the under surface of the prothallus, which in these cases often bears few or no sexual organs. But in cases in which apogamy has been induced the characters of the two generations may be much more intimately blended. Thus tracheides may occur in a prothallus more or less modified in external form. This may grow on as a bud, or may bear isolated members of the sporophyte, leaves, roots, ramenta, or sporangia. The characters of the two generations are here united in the same individual in a way that at least suggests a gradual transition from gametophyte to sporophyte.

It is to be hoped that the further study of these deviations from the normal development will lead to their causation being made clear. This may minimize the importance to be attached to them, especially should they be found to depend on a nuclear change. The facts

regarding the cytology of these new growths are still unknown; it is not even certain that the cells of the aposporously produced prothalli possess the half number of chromosomes, and those of the apogamously produced sporophytes the double number, though this may be assumed to be probable. Apospory at least might be readily explainable by such a nuclear change.

With regard to apogamy, however, some general conclusions may fairly be drawn even in the absence of observations on the nuclei. For whatever change may take place in the latter, it is certain that the transition from prothallus to sporophyte, or from prothalloid to sporophytic tissue, takes place without relation to the sexual fusion, and is so far comparable to an ordinary variation. Further, it is to be noted that the change takes place, so far as the conditions are known, when, by preventing the access of fluid water, fertilization is delayed, and when in other ways the conditions approach those favourable to the sporophyte rather than the gametophyte. These modifications of the conditions are of the kind to which aquatic organisms would be exposed on assuming a terrestrial habit. It is, therefore, possible to view the changes which take place in prothalli under these circumstances, not as reversions, but as indications of the capability of the gametophyte to assume the characters of the sporophyte under suitable conditions. If there is any truth in this way of regarding the facts of apogamy, they become of value in enabling us to picture the steps by which the Fern-sporophyte may have arisen by changes in individuals homologous with the original sexual form. The prothallus, especially in the Ferns, must have departed much less widely from the ancestral Algal form than the sporophyte; this may be connected partly with the conditions to which it remains adapted, and partly with the fact of its growth being in nature cut short by the early formation of the embryo upon it. The various cases of apogamy which have been observed form an almost complete series of transitions between prothallus and sporophyte, and have been used to frame a provisional hypothesis of how the alternation in the Ferns might have arisen, if it did not come about in the way suggested by the antithetic theory.

All such use of the facts of apogamy and apospory is liable to the criticism that they are teratological in their nature, and are not a safe guide in a morphological question of this sort. There are many facts which go far to justify such a view, but we should, I venture to think,

be unwise to leave the consideration of these phenomena altogether on one side. Not only can no sharp line be drawn between variations (the use of which in evolutionary questions none will deny) and monstrosities, but, apart from the particular organic forms which result, we appear to be dealing with a capability of many—perhaps all—Fern-prothalli to assume characters of the sporophyte; a general property of the gametophyte of this kind cannot be disregarded A fuller knowledge than we possess of the causes of apogamy is, however, necessary before the bearing of the phenomena on the nature of alternation can be properly estimated; such knowledge may lead to an explanation more in accordance with the antithetic theory than any which has yet been given.

Whether the homologous or the antithetic theory is to be considered the more probable has an obvious bearing on morphology. But there is a wide difference between considering the two generations homologous with one another in the sense that the spore-bearing generation is ultimately to be traced back to modification of the sexual, and the view that any special structure of the sporophyte is strictly homologous by descent with any structure in the gametophyte. Special evidence would be necessary before such a conclusion could be drawn, and, so far as I am aware, no such case has been shown to exist. Not only, then, does the question of the nature of alternation of generations in the Archegoniates appear to be an open one, but there seems no reason to apprehend confusion in comparative morphology, whichever of the two theories be adopted as a working hypothesis.

In concluding this account of some of the main factors in the problem which is the subject of this discussion, three subsidiary questions may be suggested—the probable line of descent in archegoniate plants, the bearing of the cytological facts on the question, and the significance to be attached to apospory and apogamy. None of these questions, any more than the general one of the nature of alternation, may admit of a decided answer. It can, however, hardly fail to be productive of good if this discussion enables us to see our way more clearly to the directions in which the answers to these problems must be sought.

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