ALTERNATION OF GENERATIONS IN THE THALLOPHYTES.—Since the pioneering investigations of Hofmeister, it has been generally recognized in Botany that the Archegoniatae are characterized by a definite form of alternation of generations. It consists in the regular alternation of a part which bears the sexual organs—the gametophyte—and of a non-sexual part which produces the spores—the sporophyte. An essential difference separates the two divisions of the Archegoniatae. In the Pteridophyta the gametophyte is a delicate, short-lived, thalloid structure, the sporophyte is a well-developed, leafy plant. In the Bryophyta, however, the gametophyte appears as a leafy plant, while the sporophyte is represented by a leafless stalked capsule, which lives as it were parasitically on the gametophyte.

In sharp contrast to the harmonious unanimity which has hitherto been the rule in Botany as regards this alternation of generations in the Archegoniatae, is the lively contest of contradictory views as to the alternation of generations in the lower plants. With regard to these the question arises, first, whether a regular alternation of definitely characterized generations is to be observed; and secondly, what in that case is the connexion between this alternation, should it turn out to be a fact, with that of the Archegoniatae. I shall not deal exhaustively here with the many different opinions on this question; I shall briefly touch upon those views only which are important in point of principle.

The first clear carrying out of the idea of a regular alternation of generations in the Thallophytes is in the Text-book of Sachs (1874), who there endeavoured to make the course of development of Algae and Fungi fit with that which holds in the Mosses. The life of *Vaucheria*, *Mucor*, an Ascomycete, or one of the Florideae, is divided according to Sachs into two sharply separated parts, of which one is characterized by the appearance of sexual organs, the other by the spore-bearing tissue which springs from the fertilized ovum. Thus the mycelium of a *Mucor* which bears the sexual organs, the thallus of *Vaucheria*, or of the Florideae, represent what we now term the gametophyte; the fruit-body of Ascomycetes or of Florideae, the zygospore of *Mucor*, the oospore of *Vaucheria*, represent the second non-sexual generation—the sporophyte. The alternation of generations of the Thallophytes is therefore, according to Sachs, essentially similar to that in the Archegoniatae. The

propagation by zoospores, conidia, &c., corresponds to the propagation by buds in the Mosses and Ferns, and is not taken into account as regards the actual alternation of generations.

Pringsheim takes up a quite opposite point of view (1876, 1878). According to his opinion the fruit of the Ascomycetes and Florideae has not the value of a special generation, but is only to be regarded as a part of the mother-plant sexually influenced. The true alternation of generations of the Thallophytes consists, according to Pringsheim, in the regular succession of independent so-called neutral generations, having non-sexual propagation, and a single sexual generation. Thus, zoospore-forming generations of *Vaucheria*, or *Oedogonium*, alternate with a generation which bears the sexual organs. Both kinds of generations are of essentially similar structure; they are distinguished by the form of their propagation. Only the first generation, which springs from the fertilized ovum, has often properties which differ from those which follow, e.g. in *Coleochaete*. In the Mosses this first non-sexual generation is much more sharply characterized; it is developed as the sporogonium, and is the only neutral generation; it differs from the sexual generation only by the scanty development of the vegetative part.

While the views of Sachs on the one hand, and of Pringsheim on the other, were showing some tendency to spread, other views appeared in opposition, now to one, and now to the other. Vines (1879) held that most of the Thallophytes have no alternation of generations at all, since their mode of propagation, whether sexual or non-sexual, is directly dependent upon external conditions; that a definite alternation of generations, comparable to that of the Mosses, is only found in *Coleochaete* and *Chara*. Celakovsky (1877), however, was more in accordance with Pringsheim in his conception of the Thallophytes, for like him he accepts an alternation of neutral and sexual generations. Celakovsky designates this alternation of generations as homologous, since the successive generations are equivalent to one another. Celakovsky opposes Pringsheim in his conception of the alternation of generations in the Archegoniatae, which he designates as the antithetic. Here the two alternating generations are not homologous, but essentially different; the non-sexual generation has also phylogenetically nothing to do with the neutral generations of the Thallophytes. This conception of Celakovsky was at first neglected, but was taken up again by Bower

(1890), and put on a footing of detail. Bower holds that the antithetic alternation came about by the intercalation of the non-sexual generation, the sporophyte, as a quite new development between two gametophytes. This interpolation of a special sporophyte probably took place in the alga-like ancestors of the Archegoniatae, as they passed from a life in water to a life upon the land. In the series of the Thallophytes there are, in addition to the homologous alternation of generations, more or less advanced beginnings of an antithetic alternation, as for instance in *Coleochaete*, the Ascomycetes, and Florideae.

All these various conceptions of alternation of generations in the Thallophytes rest on morphological comparison of the hitherto known facts of the life-history, while still very little was known of the behaviour of these organisms in open nature, or in long-continued cultures. Yet by such observations only is it possible to decide whether an alternation of generations can be proved at all, and how the influence of the outer world, so often assumed, really affects the course of life of the Thallophytes. These questions were the point of departure for my investigations on the conditions of propagation in Thallophytes. The investigation had to be extended in two directions: in the first place, it was necessary to decide whether there is a regular alternation of free and independent generations; secondly, whether a non-sexual generation characterized by special qualities arises of inner necessity from the fertilized ovum.

The first question receives its answer, according to the results of my investigations, that no regular alternation of neutral and sexual generations exists in any of the Thallophytes which have been tested. They possess two or several kinds of propagation, each of which is directly dependent upon quite definite external conditions. If we take any vegetative stage we please, a filament of a *Vaucheria*, an *Oedogonium*, a piece of mycelium of a *Sporodinia* or *Ascoidea*, there are then present in each part the specific potentialities of sexual and non-sexual propagation. In open nature the fortuitous conditions determine which of the potentialities is developed, and how the modes of propagation follow one another, whether upon the same individual, or on different individuals. An exact knowledge of the conditions gives the experimenter the secure control over the organism, which can at will be forced into any desired mode of propagation within the limits of its species. The problem becomes

more complex if other additional modes of propagation appear, as they do in many Fungi. In *Saprolegnia* we can distinguish four kinds of propagation: (1) by simple mycelial growth, that is, by breaking of the mycelium into pieces; (2) by zoospores; (3) by oospores; (4) by gemmae. The conditions for each of these four kinds of propagation are somewhat different, and it is thus possible, as my later investigations prove, to force the fungus at will into one or other of the four modes of propagation.

The potentialities for the several kinds of propagation in the Thallophytes, such as *Vaucheria*, *Oedogonium*, *Chlamydomonas*, *Sporodinia*, *Saprolegnia*, *Eurotium*, &c., are quite equivalent, i.e. there is no cause in the inner nature of the cell, or in the special organization of the potentiality, for one of these of its own initiative being developed earlier or later; nevertheless, according to the species, the special conditions which dominate the kinds of propagation may be more or less readily realized in open nature, as well as in the laboratory. In particular, the sexual propagation is often dependent upon more complex conditions than the non-sexual. While both can be induced without difficulty in *Sporodinia*, in other Mucorini it is most difficult to see the zygosporangia at all. I have not succeeded in my attempts to induce the formation of zygosporangia in the common and easily cultivated *Mucor racemosus*, though such formation doubtless exists.

In the works of Brefeld the idea is often expressed and tested of bringing a Fungus by culture through the most numerous successive conidium-forming generations to its higher fruit-form. This idea is connected with Brefeld's idea that inner causes are more important than external causes for the appearance of the fruit-form. The result of the serial cultures of Brefeld, whether positive or negative, was under all circumstances accidental. The experiments would prove the view of Brefeld only if the external conditions had really been always the same in all the numerous serial cultures. Since Brefeld, to judge from the meagre statements of his methods of culture, has not paid any attention to this constancy of the conditions, it will also have been a matter of chance whether they remained the same, or varied in such a way that another form of fruit took the place of that which preceded it. In any case, I may assert that if in Fungi such as *Sporodinia*, *Saprolegnia*, *Ascoidea*, *Eurotium*, those external conditions are maintained constantly which are characteristic for one of the forms of propagation, that same form only is produced. Hitherto

a vegetative growth of whatever duration, or a continued propagation in one form, has never of inner necessity led to the appearance of another.

We can now say that the majority of Algae and Fungi will behave like the species which have thus far been tested; in which behaviour the relation of dependence of the propagation, on each occasion, upon the outer world will vary extremely according to the species. If one recognizes thus far as operative factors light, temperature, moisture, oxygen, chemical composition of the nutritive medium, here is already at hand a great wealth of most various combinations of external stimuli which set the formative processes in motion. Further investigation will teach what a wealth of unexpected relations is here to be discovered between the outer world and organic life.

Despite all this, the possibility remains that in certain species a regular alternation of neutral and sexual generations does appear. That might be possible for the Florideae, in which the tetraspores and carpospores are often formed on special individuals. This simple fact proves nothing as yet, since it is faced by the other fact, that both kinds of propagation also appear from the like individual. The question remains open whether the tetraspores do not make their appearance at times, and seemingly on individuals other than do the carpospores, for the simple reason that the external conditions for the two of them are very dissimilar. The question cannot be decided till longer-continued cultures of the Florideae have been arranged. The answer will presumably not turn out differently from that in the case of other Algae. At the first glance an alternation of generations in Pringsheim's sense comes to much clearer expression in certain parasitic Fungi, especially in the Uredineae. If we leave aside the undecided question as to the occurrence of a sexual act, the observations and experiments teach that the life of a Fungus such as *Puccinia graminis* necessarily takes the course of the alternation of two independent generations living upon different host-plants, the one bearing teleutospores, the other forming aecidia. In addition there are still the subsidiary fruit-formations of the uredospores and of the spermogonia. In fact we have here a regular alternation of generations, such as appears in analogous form in the case of several of the lower animals; there is no obvious reason for avoiding the expression in this case, if one takes into account the actual circumstances of the case. But still it would be wrong to apprehend this alternation of

generations as if we had here an essentially new process, as against those other sorts of Fungi which are dimorphic or polymorphic. There are nearly allied Uredineae in which all the spore-forms appear one after another upon the same mycelium. In my view the condition for the different kinds of propagation will also be unlike, and the regular alternation of the fruit-forms would be explained by the fact that by the development of the host-plant itself, as by its dependence upon the seasons, changes in it necessarily go forward, which will serve as direct occasion for the growth of the different spore-formations of the parasite.

In *Uromyces Polygoni*, for instance, the aecidia appear only on the young plant, the uredospores and teleutospores on the older. In the heteroecismal Uredineae the special conditions for the individual fruit-formations are much more strongly distinguished still, so that other host-plants are necessary to bring the Fungus to the formation of aecidiospores or teleutospores. The time will probably come when these conditions may be more accurately recognized, and the Uredineae be cultivated on artificial substrata. Then it will appear whether these parasites do not behave just like the other Fungi, and cannot also be compelled to produce the different fruit-formations upon the same mycelium. A great obstacle to the cultivation of the Uredineae lies in our ignorance of the chemical composition of the host-plants. We are quite ignorant of the substances characteristic for the species, which, besides the usual food-stuffs, sugar, proteid, &c., are at any rate of decided importance for the development of the parasite.

In all the cases now mentioned we have to do with the alternation of several generations, each of which is characterized by special propagation. In the unicellular Thallophytes the non-sexual propagation coincides with the vegetative division. The propagation of the Desmidiaceae and Diatomeae by division corresponds to the propagation of *Chlamydomonas* by means of motile cells. In all of them the sexual process ensues after a series of divisions. Naegeli includes these processes under his conception of alternation of generations, and even extends it to the Bacteria in which, after a series of generations by division, the cycle is closed by the formation of endospores. But if the term alternation of generations be limited to organisms with dimorphic propagation, an alternation of shoots might be spoken of in this case.

Under all circumstances, whatever name the thing may bear, we must ask ourselves the same question as regards these phenomena as in the dimorphic Thallophytes; we must inquire whether a more or less definite number of cell-generations must be passed through before the fruit-generation can follow. In the *Bacillus* of anthrax (*Bacillus anthracis*), Buchner (1890) has already proved that it can be propagated as long as you please by division, and that at any moment the formation of spores can be induced by direct influence of the outer world. Schreiber (1896), who has closely investigated the conditions of spore-formation in several Bacteria, has been able to prove still more definitely that the spore-formation always begins as a direct consequence only of external conditions. Starting from the germinating spore, it was possible, after the third division, to induce spore-formation again. In *Chlamydomonas*, I was able to prove with certainty that the cells, through innumerable generations, propagated in an exclusively vegetative manner, but that at any time the formation of sexual swarm-spores can be attained with ease and certainty. Most probably the same holds for the Desmidiaceae, in which certain species may be propagated for many weeks together by division, but from the first were capable of sexual propagation when exposed to the conditions characteristic for it.

On the other hand, the Diatomeae seem to have a necessary alternation of generations, just as, according to the investigations of Maupas, the Ciliatae among the Infusoria. According to the theory founded by Pfitzer, the cells of the Diatomeae, whose silicified cell-wall consists of two parts fitted one within the other, do not grow in the direction which is usually styled longitudinal. The consequence of this is that on each division one of the daughter-cells maintains the length of the mother-cell, the other will necessarily be smaller by the thickness of the membrane. Thus by continued divisions the cells become smaller and smaller till, on reaching a certain minimum size, the process of auxospore-formation appears, by which the original maximum length is again attained. This generally acknowledged theory has been supported by the investigations of Miquel. He cultivated a number of Diatoms in artificial nutritive media, and noted in the successive generations a gradual lessening of the cells, till finally the formation of auxospores followed very freely. Thus, according to the statements of Pfitzer, Miquel, and others, the view might appear to be sufficiently established, that in

the Diatomeae the formation of auxospores follows only as a consequence of that organization of the cell which has been described after a number of divisions which may be almost mathematically defined, while the external conditions play no definite part in the process. But, meanwhile, we ought not to forget that this theory is in much need of further confirmation. The main point in the whole question is whether the cell-wall of both cells after division really does undergo no increase by growth in length to even a very small degree. Pfitzer himself has noted that such growth does occur in certain species, though this would be of no account for making up the loss of size which accompanies division. It ought to be distinctly proved, by direct and exact measurements, whether a growth in length takes place or not; above all, we ought to know precisely what influence the various external conditions exert upon the life of the Diatomeae. It may possibly be that under certain circumstances growth takes place, under others not. The fact, brought forward by Miquel and others, that it is by no means always the smallest cells which form auxospores, but also those of middle size, deserves consideration. Still more important are the statements made by Karsten, that *Melosira nummuloides* can be brought to the formation of auxospores simply by change of water, that in *Achnanthes longipes* the impending conjugation does not take place, but is replaced by vegetative growth when the cells are exposed to a cool temperature. If we assume that definite external conditions induce growth in length during division, others encourage auxospore-formation, the earlier observations on the smallness of the cells which form auxospores may thus be explained. In many Thallophytes the rule holds that in the stage of preparation for the higher fruit-form growth diminishes, or ceases, but division is still continued, so that, for instance, in the Desmidiaceae, *Spirogyra*, and *Chlamydomonas*, it is always the smallest cells which conjugate. This may also be the case on the formation of the auxospores of the Diatomeae, and the smallness of the cells would then be less the cause of auxospore-formation than the result of those external conditions which occasion this process. I bring this possibility forward in order to draw attention to the pressing need for accurately defining the conditions of the events in the life of the Diatomeae by the help of pure cultures, and by the use of physiological methods. Whichever way the decision may fall, the life-history of the Diatomeae gives no explanation of the wholly different alternation of generations

of the Archegoniatae, any more than does that of the other Thallophytes which have been mentioned.

But now the question arises whether there is not in many Thallophytes another form of alternation of generations, which presents nearer relations to the phenomena in the Archegoniatae. The fertilized ovum develops according to the statements of investigators in a definite way in certain species: thus, for instance, the zygospore of one of the Mucorineae, the oospore of *Vaucheria* and of *Saprolegnia*, usually germinate by formation of a short tube, which directly bears a sporangium. Pringsheim speaks, in such a case, of the first neutral generation: we might regard this as the actual spore-forming generation, corresponding to the sporophyte of the Mosses. Closer investigation shows that an oospore of *Vaucheria* shows no tendency in any way fixed by heredity to form a sporangium. It produces first a short germinal tube, which may either continue its vegetative growth, or may at once form zoospores, or sometimes sexual organs. That would depend alone on external conditions. De Bary and I myself have lately proved the same for the oospores of *Saprolegnia*, and Van Tieghem for the zygospores of the Mucorini. There is no true meaning in speaking of an alternation of generations in these cases, since the formation of the sporangia is not a peculiarity of germination, but follows the same conditions as it does subsequently. These plants do not behave differently in principle from the Fucaceae, or Conjugatae, in which the fertilized ovum passes more or less directly into the thallus, since no other propagation exists at all.

But there are perhaps other species in which the mode of germination of the oospores has become more definite. The zygotes of *Hydrodictyon* show, according to Pringsheim, a characteristic mode of germination, but it is not yet known exactly how far it is a constant process. In *Oedogonium* the germinating oospore forms four zoospores—a process which does not occur again in its later life. The manner of germination is not absolutely indispensable, since the oospore also passes over directly into a filament, though it appears to be the commoner case. Still more peculiar is the germination of *Coleochaete* as described by Pringsheim, in which the fertilized ovum divides and forms a tissue, from the cells of which zoospores arise, which then grow on into the typical thallus. There are no exact investigations whether this kind of germination is a constant phenomenon, since the germination has only been observed by Pringsheim, under conditions which were

apparently not very favourable. The formation of these bodies, which are like the zoospores formed elsewhere, from the tissue of the oospore, is perhaps a quite fortuitous circumstance, which differs in no way from the usual propagation. But the chief reason for comparison with the Mosses, and for the assumption of an alternation of generations, lies in the production of specially formed propagative cells from the oospore. It might be quite possible that the cells of the oospore in *Coleochaete scutata* should pass over directly into the thallus, but in *C. pulvinata* perhaps only after a change in the mode of growth. The essentially regular germination by help of a pro-embryo, as in *Chara*, will not be accepted as a formation of a special non-sexual generation. It is true that Vines has advanced such a conception, and compares the pro-embryo of *Chara* with the whole sporogonium of the Mosses. His view has not been taken up, since as a matter of fact in *Chara* a comparison seems permissible only with the protonema of the Mosses, or with the pro-embryo of *Batrachospermum*.

Next to *Coleochaete* it is the Ascomycetes and Florideae, the life-history of which has since the time of Sachs been compared with the alternation of generations in the Mosses, for in both the fertilized ovum has often a complicated development of its own; the last object of this is the formation of spores, which are clearly different from the usual propagative cells. As described by Schmitz, and according to the latest observations of Oltmanns (1898), the nature and method whereby the formation of the fruit depends on an intimate union of the fertilized egg-cell with definite auxiliary cells of the mother-plant is extremely peculiar. In the higher differentiated forms, e. g. *Callithamnion*, according to Oltmanns, a cell-derivative from the fertilized egg-cell—a cell-nucleus with some protoplasm—is united with a large auxiliary cell, and coalesces with it into a new cell-unit, whereupon the nucleus of the auxiliary cell is pushed aside as apparently functionless. This new cell, of which the wall and of which the plasma belong for the most part to the mother-plant, is stimulated by the 'egg-energid' to form the spores. In still more highly developed forms the mother-plant provides also for the enveloping of the spore-producing cells. Oltmanns compares the relation of egg-cell and mother-plant with that of a parasite and its host-plant, and sees therein a confirmation of the view that the fruit of the Florideae corresponds to the sporogonium of the Mosses. But

one may also designate the state of the facts with this expression : that the fruit of the higher Florideae is a product of the mother-plant that is stimulated by the fertilized egg-cell. Pringsheim, at least, might, in the far-reaching dependence of the fruit-formation upon the mother-plant, find a substantial support for his view, that the fruit of the Florideae has not the value of a special non-sexual generation. Finally we have to consider subjunctive interpretations. I myself should hold the comparison of the Floridean fruit with the sporophytes of the Mosses as quite justified. But one essential point in this matter ought not to be forgotten. One may compare the fruit of the simple Florideae with that of the simple Liverworts, and apprehend both as in some degree analogous structures. But a very important and interesting difference discloses itself, if one follows up the line of development in the two series. In the Mosses the effort is distinctly marked in the ascending series of forms to differentiate more highly the sporogonium as an immediate product of the fertilized ovum, and to make it more independent of the mother-plant in its nourishment. In the series of the Florideae the opposite tendency shows itself to make the development of the fertilized ovum constantly more strongly dependent on the mother-plant, and to attain the higher differentiation of the fruit by means of essential co-operation of the mother-plant. Beyond this no one will wish to assert a nearer relation of kinship between Mosses and Florideae.

It is still more difficult in the Ascomycetes to decide the question of the alternation of generations than in the Florideae. Notwithstanding the remarkable differences which are to be observed in them up to the origin of the ascus-fruit, we must still, with De Bary, regard the whole group as a single and united one. But we ought not to connect the Ascomycetes with the Phycomycetes, either with the Peronosporae after De Bary, or with the Mucorineae after Brefeld; but we should recognize in them a group which, with its simplest forms, sends out its roots into the lowest division, the Archimycetes, to which the Chytrideae and other Fungi belong. In quite simple Ascomycetes, e. g. *Ascoidea*, *Dipodascus*, *Endomyces*, there appears a striking difference in the mode of origin of the asci. In *Ascoidea* and *Endomyces*, according to Brefeld, each ascus arises directly from a mother-cell of the mycelium. In the nearly-related *Dipodascus*, according to Lagerheim, two cells coalesce, and it is the product which grows on into the ascus. In the one case—apparently the more common one—the

ascus is a direct product of the mother-plant; in the other forms we may speak of the beginning of a non-sexual generation. If we pass on to the fruit-bearing forms in some still relatively simple species, we find the asci as products of a fertilized ovum, e. g. in *Sphaerotheca* according to Harper, or the Laboulbeniaceae according to Thaxter. In others we may regard a structure homologous with the ovum, but not actually capable of fertilization, as the starting-point for the formation of asci, while other constituent parts of the fruit, such as the wall, and commonly the stalk, &c., are supplied by the mother-plant. In the highest forms the most complicated Pyrenomycetes, and the *Cladonias* among the Lichens, &c., the fruit is, according to our present knowledge, exclusively a product of the mother-mycelium, just as is the case according to Brefeld in the Basidiomycetes. It is only in case of the simpler forms that we can compare the ascus-fruit with the sporogonium of the Mosses, and, as Oltmanns has done, place it in relation to the processes in the Florideae. In the Ascomycetes it is still more clearly to be recognized than in these plants that the antithetic alternation of generations has stood still at the first attempts, and in the higher forms has been replaced by direct development of the fruit from the mycelium. As regards the solution of the question how the alternation of generations in the Archegoniatae came into existence, the Ascomycetes can contribute far less than the Florideae.

Taking a general view of the department of the Thallophytes thus traversed, the following cases may be distinguished as relating to the question of the appearance of an alternation of generations:—

1. The majority of the Algae and Fungi have two or more kinds of propagation, each of which necessarily depends upon definite external conditions characteristic for it. According to the conditions, occurring fortuitously in open nature or in cultivation, the kinds of propagation may appear on the same or on different individuals, independently or in any succession. The fertilized ovum in sexual forms does not differ essentially on germination from another propagative cell. In none of these cases is there any reason for speaking of an alternation of generations.

2. In certain heteroecismal parasites, e. g. many Uredineae, the life-history of the species takes the course of a regular succession of different individuals with special modes of propagation; we may here speak of an alternation of several generations characterized by different

propagation. There would be in this case an alternation of homologous generations in the sense of Celakovsky and Bower. Here also we have essentially to deal only with Fungi which have dimorphic or polymorphic propagation, with the limitation that the external conditions for some of the forms of propagation are so different that, so far as experience yet goes, these are only developed upon separate host-plants.

3. In the unicellular Diatoms there is, according to the theory of the cause of auxospore-formation hitherto current, an alternation of generations in the sense that, after a definite number of cell-generations derived by division, the formation of auxospores follows by internal necessity. But it needs still more exact investigation, for it is quite possible that the formation of auxospores, like the formation of zygotes of the Desmidiaceae, is essentially dependent upon external conditions. In that case there would be no definite alternation of generations in the Diatomeae.

4. In a number of Thallophytes, some few Chlorophyceae, above all in the Florideae and Ascomycetes, a fruit arises from the fertilized ovum, or a body homologous with it, which produces, in a manner peculiar to it, non-sexual cells, the spores. This spore-bearing fruit may be compared with the sporogonium of the Mosses, and the alternation of the sexual plant with the spore-fruit may be regarded as an antithetic alternation. But this comparison does not extend further than the establishment of a certain analogy.

In the two series of the Florideae and Ascomycetes, in contrast to the series of the Mosses, it appears that the fruit in the higher forms becomes constantly more dependent upon the mother-plant, and that the duty of higher differentiation of the fruit falls essentially upon the latter. The fruit there appears not as a special generation, but as a product of the mother-plant.

What, then, remains from which to derive the alternation of generations of the Mosses and Ferns? Only *Coleochaete*, which, since Pringsheim's celebrated investigation, has been quoted as a connecting link between Algae and Archegoniatae. But it has never been proved that the zoospores of the germinating oospore are to be regarded as a characteristic product of the fruit, and, accordingly, as a form of propagation homologous with the Moss-spores. But, on the other hand, it makes no great demand on our imagination to figure to ourselves how, in the *Coleochaete*-like ancestors of the Mosses, this step

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 ARCHÉGONIATAE.—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 Meeting¹. 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.

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