# On antithetic as distinct from homologous Alternation of Generations in Plants.

BY

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THERE are few subjects within the scope of Biology which have given rise to so much divergence of opinion, and at the same time so great obscurity of conception as that of 'alternation of generations.' For more than half a century the fact that within the narrow limit of the ontogenetic cycle, like does not always directly produce like, has been known and discussed, the discussion most frequently taking the form of mere comparison of the successive phases of various organisms, with but slight reference, if any, to the external circumstances under which the organisms grow, or to their relationships by descent. At the present time, knowing as we do how profoundly the environment affects the conformation of the organism, it is imperative that in the discussion of the phenomena of alternation such considerations should be constantly kept in mind, and especially the differences of external conditions of the organisms in which alternation is seen.

Before the days of the theory of evolution, when the idea of uniformity of type in organic creation held stronger sway over the minds of biologists than now, it was natural that the attempt should be made, by coercing facts into correspondence, to draw comparisons where they are not warranted: even among those who accept evolutionary views, the tendency

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remains—perhaps in order to simplify matters—to regard as homologous and truly comparable all such similar forms and phases as have not been actually demonstrated to be diverse in origin or nature. So with the study of alternation of generations; this term, the very sound of which has an insidious attractiveness, has been commonly used in a very extended sense, and applied with little discrimination to the succession of phases of life of different organisms, whether these be truly similar to, or dissimilar from, one another; and thus there has grown up the idea that an alternation of generations is due to some quality inherent in many organisms, and especially in plants, which leads them to pass through certain definite phases in the progress of their individual life. Such a view was at least implied by Sachs when he said [1] that the doctrine of alternation has the object of reducing to one scheme the main phases of life of all plants which bear sexual organs; such an object involves the presumption of a much greater uniformity of organic nature than can be justified by known facts. We must rather be prepared to find and to recognise in our classification of such phenomena various results of the impress of different external conditions upon diverse organisms, and avoid, rather than press forward, the reduction of phases of life of all organisms which show sexuality to one rigid scheme.

I am convinced that a merely formal comparison of different organisms, or of their successive stages one with another, will not suffice for the solution of the question as to the real nature of alternation. In order to gain a true conception of the meaning of alternation as a wide-spread biological phenomenon, the question should be approached from the physiological rather than the purely morphological point of view, while the conclusions thus arrived at are to be checked in accordance with what is known of phylogeny [2].

[1] Lehrbuch, 4th ed. p. 234.

[2] It will be unnecessary to quote and compare the diverse views of different writers on the subject of alternation: it will rather be my object to state briefly my own opinion, comparing it incidentally with those of others, where strong divergence exists.

Taking first, as the most prominent example, the Fern, we shall enquire what is the meaning of the alternation as we see it there. The gametophyte or prothallus of Ferns shows in its more delicate structure and its habit, as well as in the way in which the sexual process is effected, an adaptation to moist conditions, under which it grows best, while its ultimate function, that of sexual reproduction, cannot be carried out without the presence of external fluid water: it is, in fact, typically semi-aquatic in its nature, sharing its main characters with the Algae from which we have every reason to believe that the land-flora originated. The sporophyte, on the other hand, is fitted by its more robust texture as well as by its differentiation of tissues for successfully enduring exposure to the air under comparatively dry circumstances, while dry weather is important for the dispersal of the spores which it is the final function of the sporophyte to produce: thus the Fern, as we normally see it, is an organism with, so to speak, one foot in the water, the other on land.

Calling in also such evidence from phylogeny as we can command, it will, I think, be generally accepted that the gametophyte is the older and pre-existent generation[1]; it corresponds to the gametophyte as seen in the Liverworts, or in the green Algae, and if we trace the descent of the great archegoniate series from some green Algal forms, we may recognise that the gametophyte of the Ferns retains the chief Algal characters, as regards both its texture and its sexual process. The sporophyte, on the other hand, is the younger generation: among the present green Algae, which must undoubtedly have been in some measure related to the progenitors of the Archegoniatae, there is hardly any body strictly comparable to the sporophyte, nor is it to be expected that there should be, if as above stated the sporophyte is typically sub-aerial in its characters, while the green Algae are typically aquatic. A comparison of the successive families of the archegoniate series demonstrates

[1] This view was definitely stated by A. Braun, Ber. d. k. Akad. zu Berlin, 1875, p. 297.

the progress of the sporophyte from small beginnings in the lower Bryophytes to large size and great complexity of form and structure in the Vascular Cryptogams and Gymnosperms; its advance is accompanied by a corresponding reduction of the oophyte, and the whole is to be correlated with a progression from the aquatic or semi-aquatic habit of the lower forms, to the very distinctly sub-aerial habit of the higher. Taking all these points into our general view, it may be concluded that the alternation which is so prominent in the main archegoniate series is the result of adaptation of originally aquatic organisms to sub-aerial conditions of life: it may, in fact, be distinguished physiologically as an *amphibious alternation*, which finds its morphological expression in the difference of external form and internal structure between the more ancient gametophyte and the more recent sporophyte.

Regarding the archegoniate series from the point of view of descent, it is seen that the alternation must have been the result of *interpolation* of a new development between successive gametophytes, an intercalation of a new stage more especially adapted to life in air rather than in water —that intercalated stage being what we recognise as the sporophyte: this being so it is no matter for surprise that it should usually differ from the gametophyte in external form, though it may at times simulate it to a greater or less degree. Accordingly this alternation in the archegoniate series may from the phylogenetic point of view be styled an *alternation by interpolation* of a new sub-aerial phase between the pre-existent semi-aquatic ones: or, if the introduction of new terms be thought undesirable, this alternation may be called after Celakovsky[1] an *antithetic alternation.*

It is a direct outcome of this view of the origin of the sporophyte by interpolation of a new phase, which edged its way in, so to speak, between successive gametophytes, that it cannot itself be a gametophyte which has undergone a

[1] Sitz. d. Ges. d. Wiss. in Prag, 1874, p. 30.

change of form: this latter view has however found acceptance with more than one writer: Strasburger[1] and Pringsheim[2] both contemplated the possibility of the sporophyte having originated as a modification of a gametophyte: thus Strasburger wrote as follows[3]: 'For all plants from the Mosses upwards it appears to me probable that we have to do merely with a differentiation of a single original generation, that is with a Strophogenesis, and that if a developmental cycle consists of more than one independent, living, i. e. physiological, individual (according to Haeckel's definition), these individuals owe their origin only to individualisation of certain members of a single generation'; while Pringsheim wrote[4]: 'The alternation of generations of the Mosses appears accordingly as a contracted form of the alternation of generations of the Thallophytes, in which the neutral generations are reduced to one, and this one remains in inseparable connection with the sexual.—The great apparent difference in habit of the Moss sporogonium and the Moss plant thus reduces itself to the feeble development of the vegetative part, i. e. the axis, which is connected with the early formation of the sporangium upon it.—In the true Mosses in which the axis (of the sporangium) is less feebly developed than in the Liverworts, the identity between it and the Moss stem is expressed even in the anatomical structure.' This identity Professor Pringsheim considers to be demonstrated by the production of protonemal filaments from the seta itself (apospory), and he suggests it as not improbable that teratological conditions of the Moss sporogonium may be found bearing rudimentary leaves. Here there is propounded a view which is entirely at issue with that above stated; but the support of it appears to me to amount to little more than mere surmise or to be based upon the facts of apospory, a rare phenomenon which we have every reason to regard as teratological: against it has to be placed the whole weight of evidence of descent of the arche-

[1] Jenaische Zeitschr., 1874, p. 69. [2] Pringsh., Jahrb., Bd. IX. p. 43, 1878.
[3] l. c., p. 69. [4] l. c., p. 43.

goniate series, in which the progress of the sporophyte from a minute, indifferentiated body to the large independent plant may be followed; and though the evidence concerning the evolution of the Archegoniatae must naturally fall short of actual demonstration, it is at least sufficiently satisfactory to substantiate the view that the sporophyte is a result of interpolation of a new stage between successive gametophytes, rather than a result of formal modification of the gametophyte itself[1].

Accordingly it may be concluded that in the first and most prominent case of alternation of generations (that in fact which is recognised by botanists as *par excellence* the typical alternation) the origin of the alternation may be correlated with a change of habit from aquatic to sub-aerial life, and the neutral generation or sporophyte may on phylogenetic grounds be viewed as an interpolation of a new, and essentially sub-aerial phase between successive gametophytes: we will next enquire whether any other type of alternation, differing in nature or in origin, occurs among other plants.

On this point we find in the Text-book of Sachs[2] a direct expression of opinion: it is there stated that a comparison of the development of the Thallophytes with that of the Muscineae and Vascular plants will show 'that the development of all plants which possess sexual organs may be divided into two stages which correspond in all essential points to the two generations in the life-history of a Fern: and that there is, therefore, in the whole vegetable kingdom only one type of alternation of generations so far as it is brought about by sexual organs.' In his later published Lectures Professor Sachs does not materially alter this opinion. In the same year as the above passage was published, Celakovsky had however given an address[3] on alternation, which states very clearly the reasons for his drawing a distinction between different types of alternation; the chief point which he there insisted

[1] This view is clearly stated by Naegeli, Abstammungslehre, pp. 474, 475.

[2] Second English Edition, p. 229, or fourth German Edition, p. 234.

[3] Sitz. d. k. Böhm. Ges. d. Wiss., March 6, 1874.

upon was subsequently accepted by Alexander Braun[1]: but his views, which will now be considered afresh, were as regards the majority of European botanists completely overshadowed by the authoritative dictum of Sachs: while we recognise the great merits of the Text-book which ensured to it a cosmopolitan circulation, it is nevertheless to be remarked that the almost dogmatic attitude, which the author adopted with regard to alternation of generations, has prevented the spread of Celakovsky's views in quarters where their merits should have ensured acceptance.

Putting on one side the subject of 'alternation of shoots' to which Celakovsky devoted much attention, and which is suitably referred to by Sachs[2] as a phenomenon of minor importance, we recognise as the great contribution which Celakovsky made to this subject, that he drew a broad distinction between *antithetic alternation*, and *homologous alternation*[3]. The former term he applied to that alternation which is seen in the archegoniate series: he clearly recognised that in the archegoniate series the sexual was pre-existent from the point of view of descent, and called it the 'Protophyt,' while the neutral he styled the 'Antiphyt': it is unnecessary for us to adopt these terms, as the words gametophyte and sporophyte are suitable and firmly established. The term *homologous alternation* was applied by Celakovsky to that type of alternation which, though a much less clearly defined phenomenon, commonly occurs in the Thallophytes, and the term implies the basis of distinction between this and antithetic alternation[4]: it consists in a differentiation *inter se* of homo-

[1] Sitz. d. k. Akad. zu Berlin, 1876, pp. 289, &c.

[2] Text-book, 2nd Eng. Ed. p. 228, last paragraph. [3] l. c., p. 30.

[4] There will doubtless be found some botanists who will object to these phenomena being included in the term alternation; I think however that it is desirable that they should be, for two reasons: first, because the original use of the term as applied to animals covered and indeed referred chiefly to such phenomena as these, the antithetic alternation finding no counterpart at all in the animal kingdom:—this has been pointed out by A. Braun (l. c., p. 296); and secondly, because I think it is desirable, even at the risk of less simplicity of classification, to accentuate the difference between the antithetic alternation, and those phenomena in the lower plants and in animals, to which the term alternation was first applied by Steenstrup. Botanists are apt to lose sight of the original use of the term alterna-

logous generations which are fundamentally alike as regards descent; the differentiation may be simply as regards the character of the reproductive organs which they bear, or there may also be a differentiation of them as regards form, which, though clearly seen in some animals (e.g. the Medusae), is among plants of more rare occurrence. As in the case of antithetic alternation, so also may the homologous alternation be correlated with changes of external condition, and in some of the more protean forms the interdependence would appear to come out clearly: a series of examples will now be discussed by way of illustration of what is meant by homologous as distinct from antithetic alternation.

Taking first the Siphoneae, this protean family will prove most instructive. Though not the simplest of these plants in its sexual process, *Vaucheria* has a comparatively straightforward life-history: the zygote after a resting period germinates directly into a new *Vaucheria* plant, which may reproduce itself by brood-cells throughout a series of generations, which are similar to one another: finally on plants resembling these in every respect except in the reproductive organs which they bear, the oogonia and antheridia are produced and fresh zygotes formed. Now here is a series of generations similar in all essentials except one: there is no reason to regard them as showing a true or antithetic alternation, but they should all be recognised as potential gametophytes[1], a differentiation of them *inter se* having taken place to the extent that some produce only brood-cells, others sexual organs: in a similar manner the gametophyte of a *Marchantia* or *Tetraphis* may for a series of generations reproduce itself by gemmae (gametophytic budding) and the last generation bear sexual organs. If we are to recognise the sporophyte at all, it is in *Vaucheria* represented only by the zygote:

tion, in view of the more striking phenomena of antithetic alternation in plants, while on the other hand Zoologists are apt to regard the latter as on a par with alternation in animals. Both these dangers are avoided by retaining the words in their original sense. Compare De Bary, Fungi, p. 125.

[1] 'Potential oophores' is a term applied to the corresponding generations of *Coleochaete* by Vines, Lectures on Physiology, p. 632.

thus inasmuch as there is a differentiation as regards the mode of reproduction, we may in a sense distinguish an alternation of generations; but since such generations are similar to one another in every other respect, they are all to be considered as potential gametophytes, and homologous one with another: *Vaucheria* may thus be taken as a simple example of *homologous alternation* of non-sexual and sexual gametophytes.

In addition to the above phases of life a resting stage has also been described by Stahl[1], the *Gongrosira* stage, which appears to result from conditions of drought: the separate protoplasmic masses, produced by fragmentation, are each surrounded by a gelatinous cell-wall, and may undergo a period of rest: they germinate on exposure to suitable conditions, either by direct formation of new *Vaucheria* tubes, or by division of the protoplasmic body, and escape of the portions as separate amoeboid bodies, which ultimately develope into new *Vaucheria* tubes. Here is a peculiar adaptation to peculiar circumstances, but there is no reason to see in it more than a variant upon the structure of the ordinary gametophyte, and it may be ranked with other developments of the gametophyte. If the *Gongrosira* form be dignified by being styled an alternate generation, it is simply a generation homologous with the gametophyte.

If we compare other examples of the Siphoneae, even where an alternation has been recognised by others, it will be seen that it is nothing more than an *homologous alternation*: thus in *Botrydium*, in which Rostafinski and Woronin have described such various forms of reproduction[2], the life-history, though complicated, falls into the same plan. The gametes (here similar to one another) after conjugation form the resting zygote, which corresponds to the zygote of *Vaucheria*: this on germination, as in *Vaucheria*, produces the vegetative *Botrydium* plant. Under divers circumstances this may reproduce itself vegetatively in very different ways: by the formation of swarm-spores, which may be produced in four

[1] Bot. Zeit., 1879, p. 129.

[2] Bot. Zeit., 1877, pp. 663, &c.

different ways, or by fragmentation of the protoplasmic contents, these rounding off and forming cell-walls round each of the portions. In the formation of the swarm-spores the processes are essentially similar in nature, though different in detail, from those in *Vaucheria*, while in the various forms of resting spores, and even in those spores from which the gametes are derived, I think we see developments more or less closely comparable to the *Gongrosira* stage of *Vaucheria*. They may all be placed in the category of adaptations of the gametophyte itself to external circumstances, and at best we have here only an alternation of adaptive stages resulting from the differentiation of generations, *homologous with one another*—all being potential gametophytes. But Rostafinski and Woronin took a different view[1]: they styled the vegetative plant a 'sporophore generation,' while the 'oosphore' is represented by the sexual gametes which form the zygote, this being itself the limit of the two generations[2]. Comparing *Botrydium* with other Chlorosporeae they say that '*Botrydium* affords us an alternation of generations in which the existence of the vegetative plant falls in the post-embryonal period of life, as in the Ferns. In all other Chlorosporeae it is otherwise, as in the Moss; the vegetative plant arises from the spore, not from the ovum.' Hence we are to conclude that within the natural family of the Siphoneae the *Vaucheria* plant is the gametophyte, and the *Botrydium* plant the sporophyte, the comparison being strengthened by allusions to the Ferns and Mosses! I have chosen this example because it brings out very clearly the fundamental fallacy which underlies such a comparison: the term spore is by these authors applied to certain round bodies produced within the *Botrydium* plant under certain circumstances: it is assumed that, because they are round, limited by a cell-wall, and that from them the gametes are derived, therefore they are comparable to the spores of the Mosses or Ferns. But why should there be anything in the life-history of Botrydium strictly comparable to the spore of the Moss or Fern? It is exactly this assump-

[1] l. c., p. 666. [2] l. c., p. 663.

tion that there is, which underlies much of the misconception regarding alternation, and it comes out incidentally in the paper above quoted that this assumption is made: after stating that these spores of *Botrydium* close the first or sporophore generation, while the zygote is the second limit between the two generations, the authors remark, 'Alles Uebrige sind Anpassungs-Erscheinungen': '*All other phenomena are phenomena of adaptation.*' Are then sexuality and spore-formation not phenomena of adaptation? Are both the stages, like the laws of the Medes and Persians, fixed and unalterable for all time and in all plants?—most certainly not. It is found convenient and for the present reasonable to assume that sexuality is a uniform process throughout such organisms as show it, and the result of sexuality, the *zygote*, may therefore be assumed to be homologous in different forms, and be taken as a fixed comparable point in their life-cycle. For purposes of clearness of comparison, if not on other grounds also, this will I think be generally conceded. Are we justified in assigning a similar fixed position and general homology to the spore? When a comparison is made of the archegoniate series, the stage of spore-formation is found (with certain rare exceptions) to recur constantly, and for that particular series, on phylogenetic grounds as above stated, the recognition of spores as homologous is perfectly justified; even there however the formation of spores is to be regarded as a phenomenon of adaptation fixed by heredity, so that it recurs as a constant period in the antithetic alternation. But the question is whether this fixed character of the sporal stage is also to be found constantly in the Thallophytes. Those who, like Rostafinski and Woronin[1], draw close comparisons between alternation in *Botrydium*, and that in Mosses or Ferns, assume that it is: to my mind, there is abundant evidence, even within the Siphoneae, to show that it is not: the mere fact of the presence of these 'spores' in *Botrydium*, and their absence in the sexually higher

[1] l. c., p. 664. The authors have pointed out in the most interesting way the dependence of the several stages upon external conditions.

*Vaucheria*, shows their inconstancy, and if the 'spores' are of inconstant occurrence within the *Siphoneae*, how can we draw secure comparisons between those which are only occasionally present in the Siphoneae and those in the remotely distant Mosses and Ferns? Accordingly the sporal stage comparable to that in Mosses or Ferns must be abandoned as a fixed point in the life-cycle of such Thallophytes as *Botrydium, and the zygote alone remains as a point of fixed homology for comparative purposes*[1]. It follows necessarily that the tracing of an alternation comparable to that of the Archegoniatae in such a plant as *Botrydium* is a mere mental fiction. Such alternation as there is appears in this plant to be very directly dependent upon external conditions, and is to be recognised as a complicated form of alternation of homologous gametophytes, brought about by repeated and varied gametophytic budding. What has now been said of *Botrydium* will apply in all essential points equally well to *Acetabularia*.

Other groups of Algae also display phenomena comparable to these: but it will, I think, be unnecessary to follow the similar lines of reasoning out for all the main groups: it will suffice to remark that gametophytic budding appears to be absent, or at least rare, in certain cases (e.g. *Fucus*), but it is usually present; thus in *Oedogonium* and *Coleochaete* swarm-spores are formed, in *Volvox* the special cells of the coenobium which give rise to new coenobia, in Florideae the tetraspores, &c.: in all these cases the vegetative reproduction is a gametophytic budding, and such alternation as occurs *is an alternation of homologous generations*, which may frequently be correlated directly with season, or other external circumstances.

Turning to the Fungi, similar reasons to those above stated in the case of certain Algae may be found for recognising in them an alternation of homologous generations, derived one from another by a propagative process which may be styled gametophytic budding: reference will be made to certain

[1] Compare De Bary, Fungi, Eng. Ed., p. 121.

examples. *Mucor* has frequently been referred to as showing an alternation, and it has been pointed out how from the zygospore one or more thick hyphal tubes are formed, which are non-sexual, and at once form gonidiophores; that the mycelia derived from these gonidia may again propagate by gonidia, until finally a formation of zygospores may take place. In such a life-cycle an homologous alternation of potential gametophytes[1] is to be seen, similar in its main aspects to that in *Vaucheria*, the gonidia being examples of gametophytic budding, not a true spore-formation such as that in Ferns or Mosses. It is further to be noted in support of this that while in *Mucor* the hyphae which germinate from the zygospore are non-sexual, in *Sporodinia* they may directly produce fresh zygospores[2].

Brefeld[3] has discussed the dependence of the Mucorini, as also of Fungi at large, upon changes of external condition, as regards the formation of sexual and non-sexual organs of reproduction: he has pointed out that where sexual and non-sexual modes of reproduction occur on the same individual, external conditions may take part in determining the preponderance of the one or the other: starving may encourage sexuality, while high feeding encourages non-sexual reproduction; but he points out that in certain forms sexuality has so far fallen into abeyance, that suitable external conditions are insufficient to induce it with certainty; but this point, which is applicable for large families of Fungi (and, as he shows, to the Mucorini themselves), need not interfere with the general conclusion that in these organisms also the alternating modes of reproduction are to be viewed as originally the outcome of alternating external conditions, and not as in any sense absolutely fixed stages. Other reasons may have supervened to make one stage or the other more prominent in the life-cycle of a given species or family[4], or even lead to

[1] Vines' Lectures, p. 634.
[2] De Bary, Fungi, p. 147.
[3] Schimmelpilze, Heft IV, 1881, p. 74.
[4] With regard to the abeyance of sexuality in Fungi, compare Marshall Ward, Q. J. M. S., 1884, pp. 305, &c.

complete suppression; but still there is sufficient closeness of sequence between changes of external condition and modes of propagation in such a group as the *Mucorini* to justify the above conclusion. Similarly in the case of other Fungi, accepting the homologies indicated by De Bary[1], into the details of which it is unnecessary at present to enter, those reproductive cells which he has styled gonidia are collectively to be viewed as mere vegetative amplifications of the life-cycle, and comparable to that gametophytic budding, which has been so styled in the Algae, and also in the Mosses and Ferns. Further, the comprehensive view given by De Bary of the occurrence or non-occurrence of such budding within certain families[2] falls in with the corresponding irregularity of its occurrence in the Archegoniatae, and in the Algae.

It has now been pointed out that an antithetic alternation such as that in the archegoniate series is absent from the life-cycle of certain Algae and Fungi, in which the attempt has been made by some writers to trace it: the further question remains whether or not there is an antithetic alternation in any of the Thallophytes. Taking first the green Algae, well-known cases of formation of the fruit body with spores, or rather *carpospores* in the sense of De Bary[3], have long been recognised in *Oedogonium* and *Coleochaete* and probably also in *Ulothrix*, &c., and in a minor degree in some Desmids: here the zygote, instead of remaining undivided, and germinating directly into a new oophyte, undergoes a process of segmentation to form two, four, or more *carpospores* each of which may grow into a new individual gametophyte. As regards their origin and their position in the life-cycle, these correspond to the true spores (or carpospores) of the Liverwort, or Moss, or Fern; but there the similarity ends, for they differ in the circumstances under which they are formed, as well as in the bodies immediately produced from them, which are in the one case motile, in the other fixed. I should be disposed, therefore, while classifying these spores as *carpospores* in

[1] Fungi, Eng. Ed., p. 223. [2] Fungi, pp. 224, 337, &c.
[3] Fungi, p. 129.

De Bary's sense, not to regard them as phylogenetically identical with those of the archegoniate series, but rather as a parallel development—a similar response to a somewhat similar stress of circumstances: the rationale of formation of carpospores is the multiplication of the species without a corresponding repetition of the sexual process, in fact an economy of sexuality together with a uniform distribution of the effect of the sexual process: this may doubtless have been of importance both in the Archegoniatae and in the green filamentous Algae, and it is reasonable to think that both series may have developed in a somewhat similar direction, though by a distinct evolutionary sequence.

The same line of reasoning will also apply to the case of the Florideae, which are undoubtedly less closely allied to the Archegoniatae than are the Confervoideae: in these there is a more obvious interpolation of an intermediate growth between the successive gametophytes. The gametophytes may reproduce their like by tetraspores (gametophytic budding), which are often borne on distinct sexual plants; ultimately, as the result of fertilization of the procarps (borne often on distinct sexual plants), a growth of a more or less extensive nature is produced either from the actual cell fertilized (*Nemalion*, *Batrachospermum*), or from an adjoining cell or cells of the procarp (*Lejolisia*, &c.), or even more indirectly, from adjoining procarps to which the fertilizing effect is handed on (*Corallina*, *Dudresnaya*, &c.), and this results in the formation of carpospores. We may allow the use of this term, and recognise in the carpospores the result of a growth succeeding a sexual act, and differing in form and mode of production from the tetraspores: a comparison of different members of the Florideae will also suggest how such developments may have resulted from an interpolation of a developmental stage in a manner to some degree comparable to the interpolation of the sporophyte in the archegoniate series.

It is hardly necessary to point out that much the same is the case for the Ascomycetous Fungi, and that the series of ascogenous hyphae (e. g. in *Ascobolus* or *Eurotium*), upon

which the asci and ascospores are produced, may be regarded as an interpolated stage in the life-cycle; but all these examples might probably be classed with greater propriety as instances of analogy, than of strict phylogenetic homology.

Having recognised that though analogies as regards alternation are to be found between certain Thallophytes and the Archegoniatae, the identity is not a close one, we may now return to the consideration of the main archegoniate series of Plants: as above noted it is an important fact that in them the antithetic alternation is constant, though the balance of the two generations may vary: the very constancy of the phenomenon makes us enquire why it should be so: the circumstances which have led to this constancy seem to me to have been these. The archegoniate series is undoubtedly of Algal origin, and this their gametophytes amply bear out: they probably sprang from filamentous green aquatic forms, inhabiting, as so many of the green Algae now do, shallow fresh water, or the higher levels between the marine tide-marks[1]: the sexual reproduction was effected through the means of external water, and if other conditions were favourable it could be effected at any time through the water which was always present. Certain forms, perhaps thereby escaping from competition, spread to the land, where access of water was only an occasional occurrence: in these the sexual process could only be effected at time of rains or floods, or copious dews, and even then might not take place unless the sexual organs were fully mature: thus less dependence could be placed upon sexuality for propagation, and an alternative method of increase of individuals had to be substituted. This was done by the production of the sporophyte from the zygote: once fertilized a zygote might in these plants divide up into a number of portions (carpospores) each of which would then serve as a starting-point of a new individual, and dry circumstances, under which they would be powdery, would favour their dispersion, as in the lower Liverworts. In proportion as these plants spread to higher and drier levels

[1] Compare Weissmann's statement that 'the birthplace of all animal and plant life lay in the sea.' Nature, 1882, p. 564.

(in accordance with the advantage which they gained from escape from competition, and more free exposure to light for assimilation) the chance of a frequent recurrence of the circumstances necessary for sexual reproduction would be diminished, and the dependence upon carpospores for propagation would increase: consequently the number of spores produced by each sexually formed sporophyte must be larger, if the race is to survive, and be in a position to compete. Any increase in the number of spores entails greater supply of external nourishment during their formation; this in the phylum of the Bryophytes is chiefly supplied from the gametophyte, which shows distinct adaptation to sub-aerial habit, while the means of nutrition on the part of the sporophyte itself are in these plants very limited, and the external morphological complexity of it very slight. In other distinct phyla, however, such as the Filicinae, Lycopodinae, and Equisetinae, the sporophyte itself assumed the function of nutrition: a higher morphological differentiation of parts followed, and a more clear distinction between the organs which were to supply the nutriment (stem, leaves, roots) and the parts devoted to the formation of spores (sporangia): this for the first time stamped the sporophyte with a character of independence and permanence, while the number of spores produced might now be practically unlimited: in these respects the Vascular Cryptogams are immeasurably superior to the Bryophytes. One strange point in the whole story is, however, the tenacity with which these plants (under the obvious disadvantages which it entails when their habit is sub-aerial) retained their aquatic type of fertilization; it is only when we reach the Phanerogams, where the sporophyte reaches its climax while the gametophyte is almost abortive, that we see the sexual process accommodated to that sub-aerial life which had led to the dominant position of the sporophyte; for in them the fertilization is siphonogamic, being carried on by the pollen tube: these plants are therefore independent of external fluid water for their fertilization, and this fact has doubtless contributed largely to their present

ascendency. When, as in the preceding sketch, we consider what the results of the migration from water to land must have been, the permanence and constancy of the antithetic alternation explains itself. The permanence or morphological fixity of a phenomenon in any phylum is in a sense proportional to its importance in the well-being of the organisms: given a conservatism in the mode of fertilization (which I confess is difficult to explain), the rise and progress of the sporophyte in the archegoniate series, and the constant recurrence of the antithetic alternation, appear to me to be a natural outcome of the migration from water to land[1].

It is much more difficult in the Florideae and Ascomycetous Fungi to recognise or suggest what circumstances may have led to the interpolation of the neutral phase in their life-cycle: it is out of the question that the conditions have been the same as those which, according to the above view, conduced to the antithetic alternation in the Archegoniatae: while we recognise the chief determining conditions for these, the absence of such in the case of the Florideae and Fungi would be an additional reason for not considering the interpolated phase in them as strictly comparable to that in the Arche-

[1] Professor Geddes, in his recent work on the 'Evolution of Sex,' writes concerning the rationale of alternation as follows (p. 214):—

'A survey, in fact, of the conditions and characteristics of the two sets of forms, inevitably leads us to regard the asexual generation as the expression of predominant anabolism, and the sexual is equally emphatically katabolic. Alternation of generations is, in fine, a rhythm between a relatively anabolic and katabolic preponderance.'

I leave zoologists to deal with this generalisation from the zoological point of view; as applied to plants I dissent from it entirely. If we regard only the Fern, I will admit that the prothallus is *smaller* than the Fern-plant, and that the two follow one another in alternate succession; if this be all that is meant by the turgid phrase 'a rhythm between a relatively anabolic and katabolic preponderance,' the above quotation may in a sense be accepted as applicable to *Ferns*. But how is the above statement to be applied in the case of the Moss or Liverwort? It is obviously absurd to say that the large green assimilating gametophyte of *Marchantia* shows 'relatively katabolic preponderance,' while the minute parasitic sporophyte is the expression of 'relatively anabolic preponderance.' Professor Geddes appears to me to have made his generalisation while he had only the Fern in view, and his conclusion is entirely inapplicable to alternation in plants at large.

goniatae. I cannot here do more than suggest to those who make these organisms their more special study, that in alternations of external conditions of temperature, light, exposure to air, varying supply of nutrition either as regards quantity or quality (heteroecism), the circumstances may sooner or later be recognised which led to the interpolation of a new phase in these plants. It is to be remarked that the Thallophytes as a whole appear to be more directly affected by external circumstances than the higher forms: the hereditary stamp[1] seems to be less rigidly fixed upon them than upon the main archegoniate series: naturally this will greatly increase the difficulty of their comparative treatment, and should make us all the less ready to subject them to forcible comparison with the latter. I have above pointed out that there is in the sexual Thallophytes only one fixed comparable point—the zygote: and it is clearly to be understood that even the recognition of that as a fixed point depends upon an assumption, viz. that sexuality is a process uniform in its origin throughout sexual plants: in this we are at present justified. Reasons have been above given for not recognising the spore as an alternate fixed point for all sexual plants, and therefore for dissenting from the stiff views of alternation propounded by Sachs. Alternation is, like other phenomena of organic life, to be looked upon as a result of adaptation, not in any sense a matter of necessity: the external conditions to which plants are exposed are not, and have not been all uniform, and, therefore, if we admit that alternation is a result of adaptation, we have no right to assume uniformity in type of alternation throughout the whole vegetable kingdom.

I have dwelt at some length on the marked character of the antithetic alternation as seen in the archegoniate series of plants, because it is the most prominent case of alternation to

[1] It is quite apart from the object of this paper to discuss whether hereditary characters be the result of accumulation of the effects of external circumstances upon successive individuals, or of the mere selection of the favourable peculiarities of individuals of a variable race: the expressions used are not intended to convey any view on this question one way or the other.

be found either in animals or plants: there is, as far as I am aware, nothing which corresponds to it in the animal kingdom, while among plants, though such developments as those above referred to in the Confervoideae, Florideae, and Ascomycetous Fungi may be noted as occupying a similar position in the life-cycle, they need not be accepted as strictly comparable. Thus the phenomena which accompanied, or we may rather say conduced to, the rise of the higher sub-aerial forms of plants from the lower aquatic types, stand alone in the organic world.

As regards terminology, what has been above written calls for very little change: the main points have been satisfactorily settled by De Bary [1], and his definitions of *spore* and *carpospore* will stand. I would suggest, however, as an important addition too long deferred, that we should adopt the terms *antithetic alternation* and *homologous alternation* in the sense in which they were introduced by Celakovsky [2]: by so doing the true alternation of sporophyte and gametophyte is distinguished from the much less distinct phenomena of alternation in animals and in certain of the lower plants: thus alternations would be classified as follows:—

(*a*) *Antithetic alternation* of two generations phylogenetically distinct, i.e. where a new stage (sporophyte) has been interpolated between pre-existing generations (gametophytes): this has probably arisen independently in several distinct phyla, and the results are to be regarded as not perfectly comparable with one another.

(i) In the Archegoniatae.

(ii) In the green Confervoideae, &c.

(iii) In the Florideae.

(iv) In the Ascomycetous Fungi.

(*b*) *Homologous alternation* of two or more generations phylogenetically similar to one another, but differing in the presence or absence of sexual organs. To such alter-

[1] Fungi, pp. 119, &c.

[2] Sitz. d. k. Ges. d. Wiss. in Prag., 1874, p. 30.

nation the term 'alternation of generations' was first applied in animals: it is found in the Thallophytes, and might be described as a mere differentiation—often a very slight one—of successive gametophytes.

Thus, where an antithetic alternation occurs (though not in all plants which show sexuality), there are two points in the life-cycle, which we may regard as fixed, and comparable in different plants, viz. the *zygote*, and the *carpospore*: the generation which intervenes (e.g. in the Fern or Moss) between the zygote and the carpospore, will collectively fall under the term *sporophyte*; that between the carpospore and zygote is termed the *gametophyte*. Now the sporophyte may, in those organisms where it is of considerable size, reproduce itself in a vegetative manner by gemmae or buds (e.g. Lycopods, various Ferns and Phanerogams): to these modes of propagation the term *sporophytic budding* may be applied, and they may be represented graphically as an eddy in the main cycle of life, being mere vegetative amplifications. Such means of propagation naturally do not exist among the lower forms, where the sporophyte is absent or very rudimentary; but in these the gametophyte may multiply by the formation of gemmae of various kinds—e.g. Liverworts and Mosses (gemmae), Florideae (tetraspores), various Fungi (conidia), and Algae (brood cells), &c.—all these are mere vegetative propagations of the gametophyte, and may be ranged together under the heading of *gametophytic budding*: they are doubtless of independent origin, but in their results they are practically identical. In special cases more than a single form of gametophytic budding may take place in a single family or organism: thus, in the Mosses, a formation of gemmae may take place on the protonema, and other gemmae be formed on the Moss plant; again, in the Uredineae, various types of conidial reproduction are known, which are yet none the less mere repeated gametophytic buddings.

Besides these processes by which amplifications of the life-cycle appear, certain stages may be eliminated by apogamy

and apospory[1]: it will be unnecessary to describe these peculiarities afresh, but a word must be said as to the application of the terms. In the strict sense of the terms (that, in fact, in which they were first applied), these phenomena consist in the direct vegetative transition from one generation to the other *in cases where antithetic alternation is present*, and I think it is desirable to maintain them in this sense. The more promiscuous use of them among those Thallophytes in which a true antithetic alternation does not occur will only lead to confusion[2], even though the phenomena so described may be more or less analogous to the true type.

The mere fact that apogamy and apospory may occur, will suggest that the distinction between the two antithetic generations is not so clear a one as that indicated above: and some will be disposed, like Pringsheim, to conclude, from observations of apospory, that since the direct vegetative transition from the one generation to the other has been demonstrated in certain individuals, their distinctness of phylogenetic origin cannot be maintained. But against this conclusion is to be placed the fact that both apogamy and apospory are decidedly rare phenomena; that they appear for the most part in plants of variable species, and, in the case of apogamy at least, under conditions of cultivation which are not those natural to the plants. Moreover, attempts to induce apospory, though successful in certain Mosses, have been entirely without result in Ferns[3]. These facts, taken together with the results of comparison of the Archegoniatae, which point clearly to the view that the sporophyte originated by interpolation, lead me to conclude that these are phenomena of a teratological nature, and are not to be taken as evidence with regard to the evolutionary relations of the sporophyte and the gametophyte.

Finally, if such a view of the origin and true meaning of antithetic alternation as that above put forward be accepted,

[1] Linn. Trans., vol. ii. part 14, 1887, p. 302.
[2] Compare MacNab, Proc. Roy. Dub. Soc., n. s., vol. iv. pp. 466, &c.
[3] Annals of Botany, vol. iv. p. 168.

then the position adopted by me in a previous article in this journal is the natural consequence[1]. I have there insisted upon the conclusion that the axis and leaf of the gametophyte (i.e. in the Moss) are not the true homologues by descent of the axis and leaf in the sporophyte (e.g. Fern or Lycopod): both are doubtless similar from the physiological point of view, for both are to be regarded as a means of enlargement of surface, and of its exposure to air and light, in order that nutrition may the more freely go on; but in discussing their nature, and in classifying such parts, we are bound to take a general rather than a one-sided view; and while recognising the external form and physiological significance of the leaf, it is necessary also to take into consideration its origin by descent: once concede that the alternation in the archegoniate series is by interpolation of a new stage—the sporophyte—and it must necessarily follow that this, the newer generation, cannot be the result of a mere transformation of the old one, and consequently also the parts of the pre-existent generation—the gametophyte—cannot be strictly comparable to the parts of the interpolated generation, that is, of the sporophyte. The foliar differentiation must have taken place in the two quite independently, though as a similar response to the needs and external conditions of the plants. I have suggested that this point should be indicated in the terms used, and that while the axis and leaf of the sporophyte are styled the true caulome and phyllome, the terms phyllidium and caulidium should be applied to the correspondingly differentiated parts of the gametophyte. This suggestion was made, not as a mere effort of terminology, but rather as indicating a distinction of the first importance as regards the history of evolution of the main series of plants. I am disposed to think that, as our knowledge becomes more assured, it may be found necessary to subject the gametophyte and the sporophyte to an entirely distinct and separate morphological treatment, notwithstanding the many points of analogy between them as regards the form

[1] Annals of Botany, vol. i. p. 133.

and function of their parts: a step would thus be made towards a system of morphology which must be regarded as the ideal, viz. one based upon descent, the homologies being those of strictly lineal kinship.

## POSTSCRIPT.

After the above was written the MS. of the late Mr. Vaizey's paper, as printed below (p. 371), came to my hands: I had been present in 1887, at the meeting when this paper was read, but was surprised on reading it afresh to find how closely his views there expressed coincided with my own as laid down in the above pages. How far his paper served to suggest the line of thought here followed out I am unable to state at this distance of time, but I wish here to point out that the views above enunciated at length by myself coincide substantially with those on the seventh page of his paper of 1887. Under the circumstances it is satisfactory that the Editors have decided to print the paper at length, and so do justice to the memory of Mr. Vaizey.

F. O. B.

*June*, 1890.