The Origin of the Archegonium [1].

BY

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With two Figures in the Text.

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THE gap between the Thallophytes and those groups of higher plants which may collectively be called the Archegoniates is perhaps the most difficult of all to bridge when one attempts to trace the evolution of the plant kingdom. The problems chiefly concern the relation of the sexual organs in the two groups, or more precisely the origin of the archegonium and antheridium of the Bryophytes.

The presence of a well-defined sporophyte generation in the Bryophytes, while an important distinguishing character, gives less difficulty, because studies among the Thallophytes in recent years have indicated the possibility of a very general tendency towards the development of a sporophyte in this group. It is probably shown at low levels of the Confervales (*Ulothrix*), in the Conjugales and the Oedogoniaceae, while *Coleochaete*, the Rhodophyceae, and perhaps the Ascomycetes, present sporophyte generations that in complexity may fairly be compared with the simplest Bryophytes.

But the archegonium and antheridium have no parallel in the sexual organs of the higher Thallophytes, i.e. those groups

which have advanced to the level of sexual evolution termed heterogamy.

The sexual elements of heterogamous Algae are almost universally formed in single cells. These cells are generally called oogonia when they contain eggs, and antheridia if they produce antherozoids or sperms. Sometimes a collection of sperm-producing cells, with or without accompanying sterile tissue, is called an antheridium. This term has therefore ceased to have exact morphological value, and is applied to structures widely different in their degree of complexity, some being unicellular and some multicellular.

This vagueness in terminology has led to a recent protest by Vuillemin [1], especially with reference to the term 'sporangium,' which is now applied to any organ bearing spores, regardless of its structure, whether multicellular or unicellular. Vuillemin suggests a terminology that will clearly show the morphology of the reproductive organs of Thallophytes in contrast to conditions among the higher plants. He proposes the following names for unicellular reproductive organs :—

Sporocyst, an unicellular structure, producing asexual spores.
Gametocyst, „ „ „ gametes.
Oocyst, „ „ developing eggs.
Antherocyst, „ „ „ antherozoids or sperms.

These unicellular structures may then all be removed from the group of multicellular reproductive organs, which will then retain the old terms of—

Sporangium, a multicellular organ, producing spores.
Gametangium, „ „ „ gametes.
Archegonium, „ „ peculiar to higher plants, developing eggs.
Antheridium, „ „ developing antherozoids or sperms.

The question of terminology may seem to some a minor

[1] Vuillemin, Bull. d. l. Soc. Bot. d. France, xlix, 16, 1902.

matter, but it becomes of utmost importance when it rests on a clear morphological basis. It seems to the writer that the peculiarities of the reproductive organs of most Thallophytes justify a most careful consideration of the above suggestions, and he will employ the terminology throughout this paper as the best means of making clear the fundamental distinctions between the archegonium and antheridium of the Bryophytes and the reproductive organs of most Algae.

There are of course no archegonia in the Thallophytes, and antheridia in the narrower use of the expression (i. e. multicellular organs) are only represented by such structures as are found in the Characeae, and less conspicuously in groups of sperm-producing cells occasionally found among the green and brown Algae (e. g. *Oedogonium, Dictyota*).

Logically, the term ' antheridium ' should be strictly reserved for such multicellular structures as have clearly developed from a single cell whose activities produce tissues with a definite form and function. The antheridium of *Chara* is such an example, and the antheridia of all plants above the Thallophytes illustrate clearly the point. On the contrary, many so-called antheridia of Algae, especially among the Rhodophyceae, are simply groups of antherocysts, independent cells that happen to be associated together but are not tissues.

The antheridia of Bryophytes present clearly the distinctions between the antherocyst, a single cell, and the tissue with definite form whose co-operating cells establish an organ. The method of development of the antheridium is the basis of these fundamental distinctions. A superficial cell generally begins the process by several oblique divisions, which frequently result in the differentiation of a terminal cell that plays an important part in defining the form of the structure. This apical cell, if present, cuts off segments that build up the antheridium from above. If there is no clearly differentiated apical cell, the structure increases in size by various cell-divisions in its mass. Finally, periclinal walls separate a sterile layer of cells on the exterior from a central group. The latter divide by walls at right angles to one another into small cubical cells,

each of which develops a sperm. The antheridium is then a capsule of sterile tissue enclosing a mass of fertile cells.

The archegonium presents peculiarities of form and certain structural features that obscure its fundamental agreement in structure with the antheridium, but a close study of its development makes the homology of these organs clear. The archegonium, like the antheridium, arises from a single superficial cell, which divides in such a manner that a growing point is generally established, sometimes with a single apical cell, sometimes terminated by a group. This growing point, acting as a whole, builds up the archegonium, which is thus a unit from its earliest inception. At maturity the archegonium is a long narrow capsule, whose outer layer of cells encloses a central group. This central mass is a line of cells, sometimes numerous, running the entire length of the structure. Of these only the lower cell develops a gamete, its contents rounding off as an egg. The other cells (canal-cells) break down.

Generally the cells of the central mass form a single row, but Mr. G. M. Holferty has recently found among the Mosses that there may be two or more rows of canal-cells at various levels of the archegonium, but especially near the tip. His results have not yet been published, but their bearings on the present problem are so important that I have asked the privilege of announcing them in advance. Such conditions are identical with certain stages in the development of the antheridium, and establish clearly the homologies between these sexual organs. It seems almost certain that the canal-cells at one time produced gametes, and are therefore homologous with one another and also with the cell that develops the egg. The entire group, canal-cells and the egg, is homologous with the mass of sperm-producing tissue of the antheridium.

The archegonium is therefore a gametangium which has passed through an evolution characterized by such extensive sterilization of the reproductive cells that finally only one gamete is formed in the structure. The sterilization was progressive from the terminal region backwards, so that

the selected egg lies at the bottom of the capsule in the position most favourable for its own nourishment and for the protection and assistance offered to the young sporophyte.

The primitive archegonium and antheridium, then, agree in all essentials of structure, and are homologous. They are both multicellular from the beginning, the form is generally determined by a growing point, and the final result is a sterile capsule enclosing a mass of gamete mother-cells, very numerous in the antheridium, but so reduced in the archegonium that only one gamete matures.

It is not necessary in this discussion to consider the changes that come over the archegonium and antheridium in the higher groups of the Pteridophytes and in the Spermatophytes. The general trend is always towards the simplification and reduction of cell structure until many features of the primitive organs are lost. We are not concerned with these later conditions, but only with the older, more generalized form of organ, best illustrated to-day among the Liverworts and Mosses.

A comparison of the archegonium with the sexual organs of heterogamous Algae brings out great and fundamental differences. *Chara* and *Coleochaete* are the forms naturally considered in this connexion, because their sexual organs become invested with a cellular envelope, so that the eggs either before or after fertilization lie in a capsule. But the development of these organs shows clearly that the final structure is not a unit, but a composite of several independent elements. The eggs are produced in oocysts after the method usual to Algae. The enveloping capsules are formed of independent filaments which, arising from cells below the oocysts, have absolutely no organic relation to the latter.

The conditions in the Charales are further complicated by the peculiar small cells (Wendungszellen) that are cut off from the egg-cell before its maturity. The significance of these accessory cells has long been a matter of conjecture. There appears to be no reduction of the chromosomes with their

development. Götz [1] believes them to stand for the walls of
a reduced archegonium, thus removing this sexual organ of
the Charales from the category of the gametocyst and regard-
ing it as a degenerate archegonium plus the enveloping whorl
of filaments that surrounds the egg and forms the crown.
Götz calls the Charales Phycobryophytes, and does not con-
sider them to be directly connected with the Algae. This is
a very interesting suggestion, although objections present
themselves in the complexity of the processes required to
bring about the degeneration of such a well-established organ
as the archegonium and its displacement by an equally
elaborate envelope of filaments. It seems to the writer that
the accessory cells (Wendungszellen) may be nothing more
than the final and somewhat irregular expression of the vege-
tative activities of a growing point that is about to become
transformed into a sexual organ. In any event all botanists
will probably agree with Götz and others that the female
sexual organ of the Charales is not a primitive archegonium.

There seems to be, then, no sexual organ of the hetero-
gamous Algae from which the gametangium (multicellular) of
the Bryophytes could have arisen. We are forced to seek for
clues in other groups and among other structures than these
gametocysts (unicellular).

The structure of the archegonium and antheridium would
suggest a derivation from some multicellular organ, a sporan-
gium or gametangium. But unfortunately few structures of
this character are known among the Chlorophyceae, that
group of Thallophytes which naturally is considered nearest
to the Bryophytes. We should be forced to assume a more
extensive existence of such multicellular structures in groups,
now extinct, which were much nearer the main line of ascent
to the Bryophytes than any surviving Algae.

To what extent would we be justified in placing all the
heterogamous green Algae far away from such a main line,
and in recognizing a region of extinct groups with sexual

[1] Götz, Ueber die Entwickelung der Eiknospe bei den Characeen. Bot. Zeit.
lvii, 1, 1899.

organs unlike any existing Thallophytes ? The justification could only be the theoretical working-out of a very plausible series of stages in types whose previous existence, while entirely speculative, would do no violence to the position and arrangement of existing groups of Algae.

The assemblage of plants called the Thallophytes is much better understood with the advances of recent years. Although correlative with three other branches of the plant kingdom (Bryophytes, Pteridophytes, and Spermatophytes), the Thallophytes are peculiar in quite lacking common morphological characters of the sort that make these assemblages of higher plants very natural groups. The bonds of union in the Thallophytes are negative characters. Its members do not have the various positive marks of the higher groups. The association of the Thallophytes together because the vegetative structure is generally undifferentiated into stem, root, and leaf, is very similar to that old grouping of several independent branches of the animal kingdom under the head Invertebrata because they lacked the character of the highest subdivision.

The Thallophytes include an immensely more diverse assemblage of subclasses and orders than any other great class of plants. These groups are in certain regions so distantly related to one another that the gaps can only be bridged by assuming the previous existence of whole orders now entirely extinct or represented only by an occasional stray remnant. And the ages that brought about this fragmentary condition, with its remarkable forward developments in various directions, have left us in the structure of the surviving forms little or no evidence of the exact steps in the process. It is necessary to state this standpoint with respect to the Thallophytes so that the reader will clearly understand the possibilities of the theory that will be discussed presently, and which perhaps demands such preliminary explanation to justify its speculations.

The Chlorophyceae, as we have said, present no multicellular organs from which the archegonium or antheridium can be easily derived. But one region of the Thallophytes

gives us a structure that may throw some light on our problem. This structure is the plurilocular sporangium, and it is found in a number of the lower groups of the Phaeophyceae. The lower Phaeophyceae are represented by a number of families whose vegetative structure is diverse, but which agree in having one or both of two types of reproductive organs. There is the unilocular sporangium, a sporocyst, whose products are asexual zoospores ; and there is the plurilocular sporangium whose products, likewise biciliate zoospores, are known to be sexual in many forms.

The sexuality of the plurilocular sporangium, while well established in certain types, is nevertheless far from universal in the group. It is well known from studies among the Ectocarpaceae that the zoospores from plurilocular sporangia may germinate without conjugation, and the external factors that determine sexuality are in part understood. So in considering the plurilocular sporangium we are dealing with a very simple and primitive type of sexual organ. The plurilocular sporangium is plainly a modified filament or branch. It consists at first of a row of cells, but shortly most or all of these begin to divide by walls in three planes, until the space originally occupied by one large cell is divided up into very many small cubical compartments (loculi), which give the structure a curious checkerboard-like appearance. A biciliate zoospore or gamete is formed in each of these compartments. Certain cells generally remain undivided at the base of the branch, constituting a stalk ; and sometimes the tip remains sterile as a hair-like continuation of the axis.

Such is the structure of the simplest plurilocular sporangium. The higher types of this organ present some important modifications. The sterile tip is transformed entirely into reproductive tissue, so that the structure has less the appearance of a modified branch and more that of a specialized reproductive organ. There is also presented in certain forms (best known from studies among the Ectocarpaceae) a wide range of variation in the size and number of the compartments. Some of the sporangia have rather large compartments, and their

products are well-developed zoospores, deeply coloured by the brown chromatophores. The compartments of other sporangia are much smaller, and develop minute zoospores that are sometimes almost colourless. These conditions are shown in Fig. 21, a. Between these extremes there is frequently a sporangium with medium-sized cells whose products strike an average between the large and small zoospores.

The large and medium-sized zoospores may germinate directly if the conditions are not favourable for sexuality. The small zoospores have been known to settle down and germinate, but the results were feeble sporelings that could not live long. When sexuality is present the conjugation is usually between the large and small zoospores. The large gametes swim much more slowly than the small, and in certain forms (*Ectocarpus siliculosus*, *E. secundus*, and *Cutleria*) settle down as motionless cells which are fertilized by the small motile gametes. The latter have evidently reached a stage in their differentiation very similar to sperms both as to structure and behaviour.

It is evident that the plurilocular sporangium was not established from the first as a gametangium, because there is such a large amount of parthenogenetic development among its products. The structure at the outset was probably asexual. But it is evident that with sex once established the evolutionary direction is along lines exactly parallel with the history, so well understood, for several divergent and independent lines of Algae. Briefly stated, we observe the tendency to differentiate the gametes as to size resulting in small male and large sluggish female cells. The latter even behave like eggs in certain forms at the time of fertilization, when they are motionless. Although the type of sexual reproduction is isogamous, because the gametes are identical in form at the time of their discharge from the gametangia, still the conditions at the moment of fertilization are physiologically those of heterogamy.

Another peculiarity of the plurilocular sporangium should

be noted, and then we shall be ready to consider it in relation to our problem of the origin of the archegonium. The zoospores or gametes from plurilocular sporangia escape in various ways. There is extensive dissolution of the walls forming the compartments, and the zoospores are in this manner set free. But it has been observed in some species that the zoospores make their exit from the tip of the structure. It seems that the walls in the interior of the sporangium may break down more rapidly than those on the outside, so that the zoospores come to lie almost free in the interior, and are therefore able to escape from the opening first formed, which is generally at the tip.

We shall now take up some speculations on the fate of such a structure as the plurilocular sporangium under certain environmental conditions and in relation to the principles of sexual evolution. We shall try to show that the archegonium and antheridium might have been derived from such a structure.

It should be clearly understood that this is not stating a belief that the Phaeophyceae were the progenitors of the Bryophytes. We are using the plurilocular sporangium of the brown Algae simply as an illustrative type of a reproductive organ. To relate such an organ to the archegonium and antheridium we shall probably have to assume the existence of groups of green Algae with plurilocular sporangia of which no trace is left among living forms. This point will be considered later.

However, it is well to point out that a few Chlorophyceae have structures identical with the very simplest types of plurilocular sporangia, although with nothing approaching the complexities of the higher conditions. In *Schizomeris Leibleinii* portions of a filament, at times terminal, may become transformed into a thickened region several cells in diameter, all of which develop zoospores. And again, in *Draparnaldia* and some related forms the reproductive cells of lateral branches sometimes divide longitudinally to produce a branch which departs from the structure of a single row of

cells, and, since the cells develop zoospores simultaneously, strikingly resembles a plurilocular sporangium. The conditions among the lower Ectocarpaceae, especially in *Pylaiella*, are no more complex than in *Schizomeris* ; so we have in the Chlorophyceae structures that might readily be the forerunners of well-differentiated plurilocular sporangia.

A plurilocular sporangium is subject to two sets of factors that may influence its form and structure, together with the character of the sexual cells. There are, first, the general laws underlying all sexual evolution in its advance from isogamy to heterogamy. And in addition to these developments there are the changes possible in any multicellular organ, because it is a cell-complex, and may be differentiated into tissues. A gametocyst (single cell) is by its simplicity barred from the complications possible to a gametangium.

The differentiation of the gametes into eggs and sperms is readily understood along the line that we have already suggested, which is a well-known path of development, and has been travelled by many groups of Algae. We know that the gametes vary in size, and that the larger female elements are sluggish and tend to settle down before fertilization as quiescent cells, to which the male gametes are attracted. Should the sluggishness of the female gametes be intensified some of them might not be able to leave the gametangium, but would remain there as eggs, retained on the parent plant, to which the male gametes must make their way. It is not at all uncommon for zoospores of various Algae to be mechanically held within a parent sporangium and, unable to escape, to germinate there. Such habits on the part of female gametes of plurilocular sporangia would finally result in heterogamy, with the retention of the eggs within the parent gametangium.

What are the possibilities of modifications in form and structure of the plurilocular sporangia themselves? These would depend on two important factors, first the sterilization of portions of the structure, and second the differentiation of regions of exit or entrance for the gametes. Modifications

of the first sort are very significant, those of the second would be readily understood in relation to them.

Sterilization of reproductive tissue is a well-known tendency among plants. It results in the sacrifice of certain reproductive cells or tissues, either in relation to environmental conditions, or through the conservation of food-material by which certain cells are favoured in their nourishment at the expense of others. The latter condition is illustrated very extensively in the asexual reproductive tissue of the sporophyte, and among sexual cells notably by the sacrifice of the nuclei in the oocysts of the Fucaceae (e.g. *Pelvetia*), and during oogenesis in certain Phycomycetes (e.g. *Albugo*, *Peronospora*, &c.). It is of course a fundamental principle in oogenesis among animals. If, as seems very probable, the canal-cells in the archegonium are degenerate gamete mother-cells, this principle finds an admirable illustration, for they are sacrificed with obvious advantage to the egg at the bottom of the structure, not only for its nourishment but also in relation to the mechanics by which the neck of the archegonium is opened and the sperms brought to the egg.

Sterilization of reproductive tissue in relation to environmental conditions implies such changes as are obviously a response to external factors. They are frequently involved at the same time with the conservation of food, but this is of secondary importance. The most powerful external factor affecting an organ is the medium in which it lies. If this be air the structure must provide itself with effective protective coverings, for the drying action of the atmosphere is perhaps the most serious difficulty with which the land plant contends. Desiccation must have been the chief danger that aquatic plants faced when they left the water, and very little advance in internal structure could have been possible until this problem was solved by the development of suitable external coverings.

Now let us consider what would happen to plurilocular gametangia of aquatic Thallophytes if such forms should gradually adopt terrestrial habits. The general protection

against desiccation demanded by the plant would sooner or later affect the details of structure. The plurilocular sporangia would respond to the conditions and become modified with other organs of the plant. Probably the first change would be the differentiation of an external protective tissue. This would require the sterilization of the outer layer of gamete mother-cells which would form a capsule enclosing the remainder of the tissue. The structure of such an organ is diagrammed in Fig. 21, b. An advance of this character would place the plurilocular sporangium in the same group of organs as the antheridium and archegonium.

After such a modification of the plurilocular sporangium the more special peculiarities of the archegonium and antheridium would seem insignificant. The structure would of course all along have been under the influence of the principles that regulate the evolution of sex. The gametes might already have reached some degree of sexual differentiation ; or, if not, they would constantly tend in that direction ; and the results would eventually be heterogamy, with the continued specialization of male and female organs. The female gametangium would retain its gametes as eggs, and the male would discharge its sperms under the proper conditions of moisture. The highest development would be attained in the female organ when, through the sterilization of the gamete mother-cells, all but one were sacrificed to the advantage of a specialized egg (see Fig. 21, c).

And in this connexion we may again refer to Mr. Holferty's unpublished observations upon the archegonium of Mosses. When the canal-cells form two or more rows at various levels in this structure, we have conditions exactly like those diagrammed in Fig. 21, b and c. So these important stages in the evolution of the archegonium which we have assumed as necessary to the hypothesis are actually present, except of course that in the archegonium the canal-cells normally do not develop gametes[1]. But the evidence that the canal-cells are

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[1] Since the above was written, W. C. Coker has described and figured (Botanical Gazette, XXXV, 136, 1903) an archegonium with two eggs, lying one above the

degenerate gamete mother-cells can hardly be stronger, apart from the actual existence of such a series of organs as we have postulated.

To complete the agreement between such structures and the archegonium and antheridium we have only to understand the manner in which the terminal openings of these organs would be differentiated. These points of exit and entrance are conveniently situated, but there are probably more important reasons for their selection. The apex of the plurilocular sporangium is the situation where the gametes first mature and from which they first escape. And this would probably lead to the choice of such a point of dehiscence if the archegonium and antheridium were derived from this structure.

We have, naturally, very little direct evidence bearing on such evolutionary processes as we have just discussed. But the writer can see nothing in the structure, development, or behaviour of the archegonium, antheridium, or plurilocular sporangium that offers serious objections to the hypothesis presented. The difficulties are in the absence of intermediate stages, which cannot of course be presented unless forms exist that illustrate these conditions. The value of the hypothesis lies largely in its suggestiveness for further research, but it seems to the writer to offer an explanation far more acceptable than other views. Attempts to relate the archegonium to the oocysts of heterogamous Algae do violence to the fundamental character of their organization, as was shown at the beginning of the paper. This hypothesis, which carries the origin of the archegonium much farther back in point of time, seems safe in its reasoning and thoroughly consistent with the evolutionary principles of sex and tissue-differentiation.

To make the chief points in this paper clearer, and also as a summary, we have constructed diagrams (Fig. 21) illustrating

other and each with a ventral canal-cell. It was evident that the upper egg had developed from the lowest canal-cell. Such abnormalities are to be expected, according to our theory of the archegonium. Mr. Holferty has observed similar examples.

the evolutionary stages required by this theory of the origin of the archegonium and antheridium. And at the end (Fig. 22) we have arranged certain groups of Algae in relation to one another and to a problematical region of extinct forms which are supposed to have existed and been directly responsible for the Bryophytes.
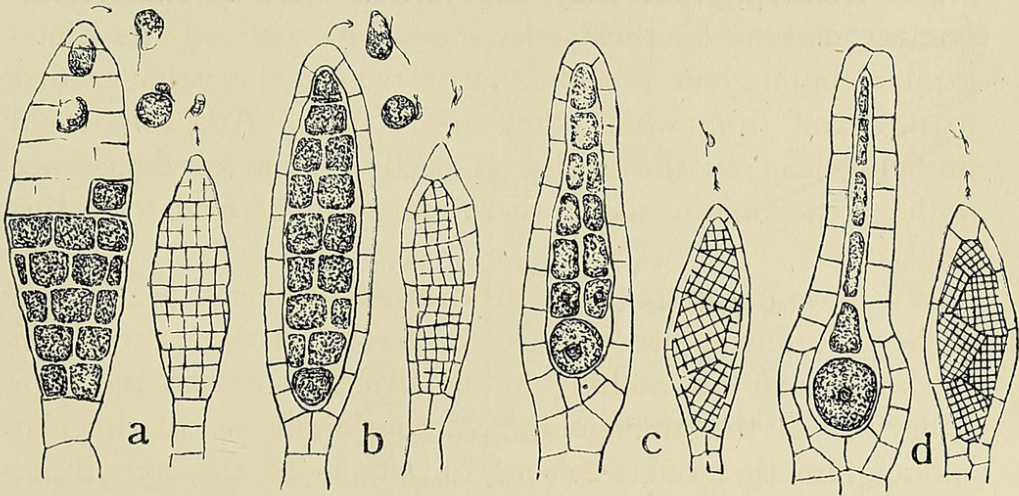
The families Ulothricaceae, Chaetophoraceae, and Coleo-

FIG. 21.—Diagrams illustrating the possible evolution of the archegonium and antheridium from the plurilocular sporangium. *a*. Plurilocular sporangia, with large and small gametes discharged from the apex, after the habit found in certain Phaeophyceae (e. g. *Chilionema Nathaliae*[1], *Ectocarpus virescens*[2], &c.). *b*. Plurilocular gametangia of a hypothetical algal type which has adopted terrestrial habits. The outer layer of gamete mother-cells has become sterilized as a protective capsule enclosing the fertile tissue. The gametes are differentiated in sex but both are still motile. *c*. Plurilocular gametangia of somewhat higher hypothetical forms at the level of heterogamy. Sterilization has proceeded so far in the female gametangium that only a few gametes are matured at the base of the organ, and these are eggs. *d*. Simple types of archegonium and antheridium. The female gametes are reduced to one, while the number of male gametes is greatly increased, and these cells are smaller and more highly specialized than in the earlier conditions.

chaetaceae of the Confervales are closely related to one another and seem to constitute a line of ascent. Among the lower representatives of these families are several forms (*Schizomeris, Draparnaldia*, &c.) whose zoospores are pro-

[1] Sauvageau, ' Sur quelques Myrionémacées.' Ann. d. Sci. Nat., 8° sér., v, 103, 1898.
[2] Id., ' Sur *l'Ectocarpus virescens*, Thuret.' Jour. d. Bot., x, 17, 1896.

duced in special regions of the filaments, sometimes con-
siderably thickened, which resemble the simplest types of
plurilocular sporangia. The presence of such structures
among the Chlorophyceae is important, since it tends to
overcome the difficulties in our assumption of a region of
extinct green Algae with plurilocular sporangia which we have
supposed to be the ancestors of the Bryophytes.

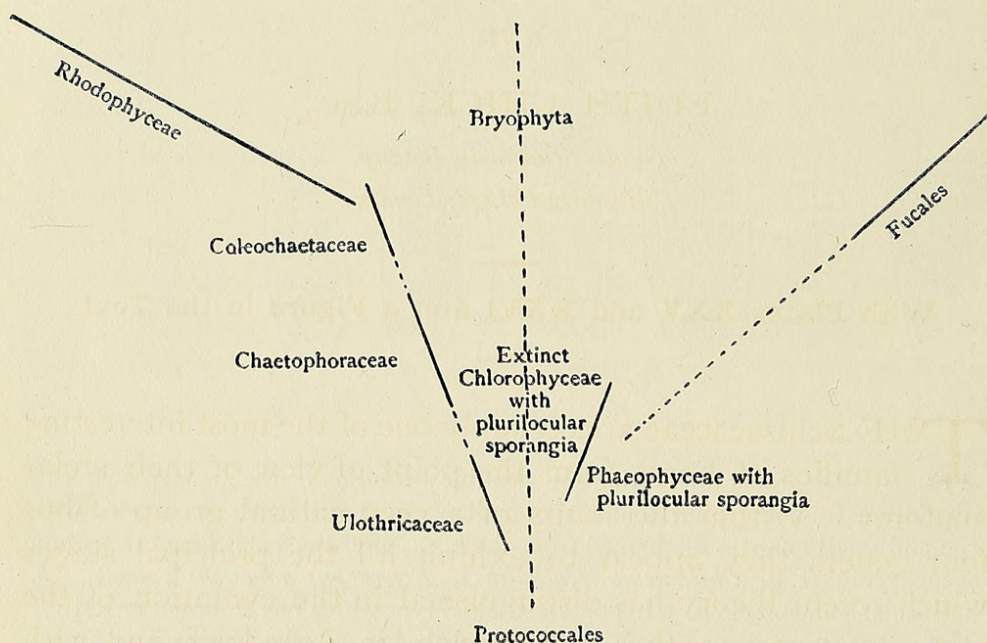The Rhodophyceae may have arisen close to the Coleo-
chaetaceae.

FIG. 22.—Diagram showing the position of a hypothetical group of extinct
Chlorophyceae with plurilocular sporangia, supposed to be the progenitors of the
Bryophytes, in relation to the algae most intimately concerned with this discussion.

The lower Phaeophyceae can hardly be supposed to have
given direct origin to the Bryophytes, although this is con-
ceivable. They have been arranged at the side of a hypo-
thetical region of extinct Chlorophyceae. The Fucales are
far to one side. Their sexual organs are gametocysts, and
must have had their origin from unilocular sporangia.