# THE ALGAL ANCESTRY OF THE HIGHER PLANTS.[1]

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[With Two Figures in the Text].

IN all of the groups, above the level of the Thallophyta, the life-cycle is characterised by the succession of two individuals—the one sexual, the other asexual—in regular alternation, and the origin of these two alternating generations has long been the subject of discussion. One group of Botanists, with whom we may couple the names of Pringsheim and Scott,[2] have held that the two generations are homologous, having arisen by gradual differentiation from an indifferent generation bearing both asexual and sexual organs, such as is commonly found in the Algæ at the present day.

Other authorities, especially Celakovsky and Bower,[3] hold that the sporophyte is a new intercalation in the life-history, originating by a gradual elaboration of the zygote, *i.e.*, it is antithetic to the gametophyte.

Such evidence as has been adduced speaks neither for the one nor for the other view; in the case of the Pteridophyta the balance is, perhaps, in favour of the homologous theory, in the case of the Bryophyta more in favour of the antithetic. Nor does it seem necessary to postulate the same mode of origin for the two groups, a point of view that has not, perhaps, received sufficient consideration.[4] The differences between the sporophyte in Bryophyta and Pteridophyta are very marked; in fact, the only important resemblance is the differentiation of stomata of a similar type.[5]

In 1909, Lang[6] put forward a theory of alternation, the essence of which is to explain the differences between the two generations as being due to the retention of the spore (whether asexually or sexually produced) within the body of the parent-organism for a longer or shorter space of time. Lang's theory would appear to

[1] Presidential Address to the Intercollegiate Botanical Society, University of London.

[2] cf. Presid. Address, Bot. Sect., Brit. Assoc., Liverpool, 1896.

[3] Annals of Botany, IV., 1890, p. 347.

[4] cf. however Tansley, in New Phytologist, XI., 1912, p. 216.

[5] Recalling the development of structures closely resembling the sieve-tubes of the Angiosperms in such Laminariaceæ as *Macrocystis*, it is evident that like demands may lead to the differentiation of similar structures, without implying any close relationship.

[6] W. H. Lang. A theory of alternation of generations in Archegoniate plants based upon the ontogeny. New Phytologist, VIII., 1909, p. 1.

favour essentially the homologous view of alternation, and obviously opens up many possibilities for experimental research into this vexed question.

The writer has no intention of discussing the relative merits of these different theories. The purpose of the present communication is, in the first place, to sift the ground for the characters of the ancestral group from which the higher plants may have arisen. No one is probably prepared to dispute that the latter have a common origin, and that their ancestors were of the type of the present-day Thallophyta. Since all the groups above the level of the latter have pure green chloroplasts, with starch as a customary product of assimilation, it is to be presumed that their ancestors exhibited these features. Moreover, the spermatozoids appear invariably to be isokontan. This leads us inevitably to look for the ancestry of the higher forms among the Isokontæ.[1] The two generations in the higher groups are in general characterised by certain prominent features, in considering which we may leave the highly specialised Phanerogams out of the realm of our discussion.

The gametophyte is evidently typically prostrate and dorsiventral, the assumption of a radial construction being rare, and a mark of specialisation. The sexual organs seem primitively to have been borne on the upper surface, as we see it at the present day in most of the Hepaticæ, although tending to shift to the lower side, where more ample protection is obtainable. In practically all the Pteridophyta and all those Bryophyta regarded as the more primitive, the gametophyte retains a thalloid differentiation.

The sporophyte, on the other hand, is typically upright, and radial in organisation. This is quite patent in the Bryophyta, and it appears to be generally accepted that the sporophyte, in the Pteridophyta, was primitively radial.[2] A second feature of the sporophyte, in the Archegoniatæ, is the tendency to differentiate a main axis, with lateral appendages subservient to assimilation and the production of the asexual cells.

The two generations of Archegoniatæ may, therefore, be briefly characterised as follows:—The gametophyte a dorsiventral prostrate thallus, with the reproductive organs primitively on the upper surface; the sporophyte an upright structure, with radial organisation and a tendency towards peripheral placing of the assimilatory

[1] For a discussion of Schenck's hypothesis as to the origin of the Archegoniates from the Phæophyceæ, see p. 13.

[2] cf. Bower, The Origin of a Land Flora, 1908, pp. 363 and 625.

and reproductive tissues and gradual assertion of a main axis. A likely algal ancestry might, therefore, be expected to display these tendencies:— Differentiation of prostrate dorsiventral and radial upright systems, assertion of a main axis in the latter, and restriction of sexual organs to the prostrate portion, and of asexual organs to the appendages of the upright system. We may, perhaps, add to this, evidence of a terrestrial tendency, with corresponding adaptations.

The filamentous Algæ among the Isokontæ, to which we may now turn, include a number of separate series, viz., Ulotrichales, Chætophorales, Siphonales, Œdogoniales, and Conjugatæ. The last three are obviously specialised along lines of their own, in fact, some algologists are inclined to regard the last two as originating from ancestries independent of that of the remaining Isokontæ, a view which the writer does not share. Ruling out these three groups we are left with the Ulotrichales and Chætophorales, which are probably best regarded as distinct, though closely related, series.[1] The former are, on the whole, very uniform, and display little morphological differentiation, and what there is is scarcely relevant in the present connection. In the Chætophorales, on the other hand, we have a group with very considerable morphological differentiation and one, moreover, showing a very wide range of construction and a great diversity of habitat.

As a relatively primitive and central member of this group, we may regard the genus *Myxonema* (*Stigeoclonium*). In this genus the typical thallus consists of two portions, a prostrate system attached to the substratum (in the following, briefly referred to as the creeping base), and a more or less elaborate, branched, upright part, arising from the base and extending out into the water (Fig. 1, *a*); the former is dorsiventral, the latter essentially radial. Among the known species of *Myxonema* there are all possible variations in the degree of relative development of the base and the upright system. In some (*e.g.*, *M. tenue* (Fig. 1, *a*), *M. falk*-

[1] It will probably be useful to give the following outline sketch of the classification of the Chætophorales:—

(*a*) *Chætophoraceæ*:—Myxonema (Stigeoclonium), Chætophora, Draparnaldia, Gongrosira, Protoderma, Endoderma, Gomontia, Tellamia, Acrochæte, Ectochæte, Pseudochæte, Ochlochæte, Pringsheimia, Aphanochæte, etc.

(*b*) *Chætosphæridiaceæ*:—Chætosphæridium, etc.

(*c*) *Chætopeltidaceæ*:—Chætopeltis, etc.

(*d*) *Coleochætaceæ*:—Coleochæte.

(*e*) *Chætosiphonaceæ*:—Chætosiphon.

(*f*) *Trentepohliaceæ*:—Trentepohlia, Cephaleuros, etc.

*landicum*), the base is relatively insignificant, whilst the upright portion attains to considerable development; in others (*e.g.*, *M. farctum*, Berthold[1]) the base (Fig. 1, *b*) is predominant and of considerable extent, whilst the upright system is reduced to short filaments and hairs, the filaments being but little branched. The writer has recently described a *Myxonema prostratum*,[2] in which the creeping base (Fig. 1, *e*) is of still greater extent (covering several square millimetres of the substratum); large areas of this base are without any upright system whatsoever (apart from very scanty hairs), but at remote intervals there arise tufts of 3-5-celled branchlets.

From the available evidence it seems that one and the same species of *Myxonema* may exhibit a very varied relative development of base and upright system under different circumstances, *i.e.*, a species may be prevalently upright or prevalently prostrate, according to the conditions of the habitat. An investigation of the methods of germination of the zoospores in this genus has shown that whereas some first form a creeping base, from which the upright threads subsequently grow out, others only form upright threads, either lacking the base altogether, or only producing it at a later stage,[3] phenomena which again illustrate the varying importance or the two parts of the thallus in this genus.

Before proceeding, it will be well to refer to one feature of the Chætophorales, to which undue value might be attributed, viz., the production of hairs. These are, undoubtedly, a marked characteristic of the group, although completely lacking in some forms, and of very varying development in many. The tendency towards differentiation of the ends of the branches as hairs may be regarded as one indication of morphological elaboration. We can, however, also look upon it as an expression of the tendency towards reduction of the upright system, of which the hairs become the sole representatives in the almost completely prostrate forms to be dealt with in the following. It is questionable whether the peculiar sheathed hairs, characteristic of such forms as *Coleochæte* and *Chætosphæridium*, are to be considered as belonging to the same morphological category as the simple hairs of other Chætophorales. It is not out of the question that the different types of hairs may

[1] Nov. Act. K. Leop.-Carol. Ak. d. Naturf., XL., No. 5, 1878, pp. 201, 202.

[2] F. E. Fritsch, in Annals of the S. Afr. Museum, IX., 1917,

[3] cf. Berthold, *loc. cit.*, also Fritsch, in Beih. Bot. Centralbl., XIII., 1903, p. 372, etc.

have some biological significance that has as yet escaped recognition, but in any case we must regard them as a special development, which may not interfere with our perspective in estimating the remaining morphological characters of this group.

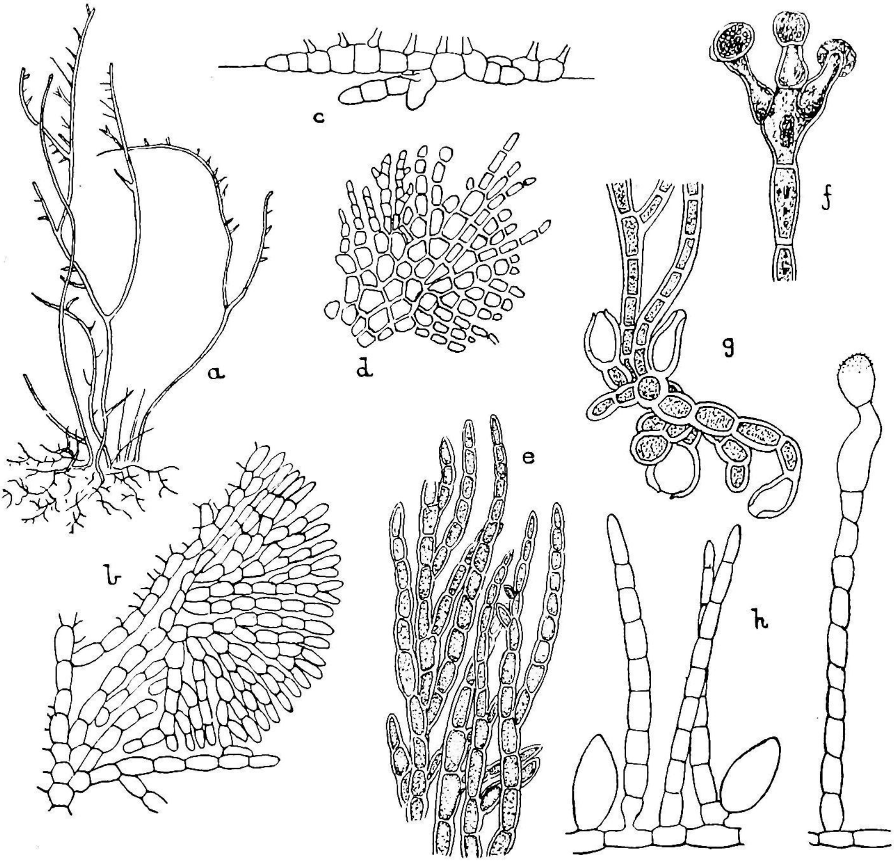


FIG. 1. *a*, *Myxonema tenue*, habit (after Huber); *b*. *M. farctum*, small portion of the creeping base (after Berthold); *e*. *M. prostratum*, a portion of the base; *d*, *Protoderma viride* (after West); *c*, *Aphanochæte repens* (after West), only the bases of the hairs are shown; *f*, *Trentepohlia umbrina*, end of an upright thread with three zoosporangia (after Oltmanns); *g*, *T. aurea*, base and erect system, the former with three gametangia (after Brand); *h*, *T*, *ellipsicarpa*, Schmidle, var. *africana*, Schmidle (after Schmidle).

The height of morphological differentiation among the Chætophorales, in fact among the filamentous Isokontæ generally, is attained by the genus *Draparnaldia*, a fact first brought out clearly by Berthold.[1] The elaboration in this case concerns the upright system, and, in correspondence with this, the creeping base is poorly developed; in some cases, according to Berthold, it is com-

[1] Berthold, *loc. cit.*, p. 202 *et seq.*

pletely wanting, the upright filaments being attached merely by the basal cell, strengthened by the outgrowth of rhizoids from some of the lower cells of the upright axes. The radial upright system exhibits a sharp differentiation into long and short branches. The former consist of large, slightly barrel-shaped cells, with a small chloroplast forming an equatorial girdle in the otherwise colourless cell. The short branches arise in dense, often more or less whorled tufts, are richly branched, and consist of short cells, each occupied by a large chloroplast; the different branches terminate in more or less marked hairs. It is plain that the short lateral branch-systems are the seat of the main assimilatory activity, and the production of swarmers and other reproductive cells appears to be confined to them. The large-celled long axes are probably in the main supporting and possibly also serve for purposes of storage. The differentiation of this Alga into main axes and lateral assimilatory and reproductive appendages is most marked.

In contrast to *Draparnaldia*, with its elaborate upright system, a large number of Chætophorales exhibit more or less complete reduction of the erect portion, whilst the dorsiventral creeping base remains highly developed. In some (*e.g.*, *Gongrosira*) there is still a considerable development of upright branches, although these are short and commonly combine with the densely branched pseudoparenchymatous base to form a convex cushion. In others, the upright system is represented only by hairs (e.g., *Aphanochæte*, Fig. 1 *c*, *Ochlochæte*, *Ectochæte*). Lastly, there are forms in which the upright portion of the thallus is completely suppressed, the whole consisting merely of the creeping base (e.g., *Protoderma*, Fig. 1 *d*, *Pringsheimia*). It should be pointed out that, in referring to these forms in this order, no probable line of evolution whatsoever is implied; in fact, it seems likely that there are several distinct series of reduction of the upright system in the Chætophorales. The instances are merely given as examples of varying morphological differentiation.

Among the terrestrial Trentepohliaceæ we encounter similar features. The genus *Trentepohlia* (*Chroolepus*) has a thallus differentiated into creeping base and upright threads (Fig. 1, *g*), the two varying somewhat in relative development in the different species, whilst in *Phycopeltis* and *Cephaleuros* the upright system is much reduced.

In all the more extreme prostrate forms the base shows a tendency to become pseudoparenchymatous, a feature well seen in

*Pringsheimia* and *Protoderma* (Fig. 1, *d*), but, in both of these cases, the origin from a system of branched threads is plainly evident, and this is also quite distinct in the discoid *Coleochætes*. There are, however, a number of Algæ which probably belong to this series (many of them not yet properly described), in which this origin from a filamentous condition is unrecognisable in the mature state.

Returning for a moment to our original statement as to what we may expect to find in the algal ancestry of the higher plants (p. 4), it will be seen that the Chætophorales satisfy all requirements, with one exception. They are a group displaying differentiation of the thallus into prostrate dorsiventral and radial upright systems; one genus (*Draparnaldia*) shows a predominant upright system, with a distinct main axis and laterals subservient to assimilation and reproduction; a considerable number of forms show reduction of the upright system, so that the thallus comes to consist largely or entirely of the prostrate portion. The only one of our expectations that is not fulfilled is the existence of forms, having sexual organs on the prostrate base and asexual organs on the upright threads. As regards this latter point it may first be noticed that, in the aquatic Chætophorales, as long as there is a properly developed upright system, the reproductive organs are usually confined to it; but, with the reduction of the upright system, they are relegated to the prostrate base (cp. for instance, *Coleochæte pulvinata* with *C. scutata*).

It is, however, among the terrestrial Trentepohliaceæ that we meet with the most important indications in this connection. In the genus *Trentepohlia* the zoosporangia are pedicellate, being provided with a stalk-cell of a characteristic knee-like form (Fig. 1, *f*), whilst the gametangia are sessile (Fig. 1, *g*). The two kinds of reproductive organs are, therefore, readily distinguishable, but it should be added that it is not yet certain that these structures are definitely asexual and sexual respectively in all the species of the genus; in several, however, this has been established beyond doubt, and it is to be presumed that it obtains in most, if not in all cases. In many species both kinds of reproductive organs are borne on the upright system, but especially in those forms in which the base is strongly developed, the gametangia tend to arise from the base (Fig. 1, *g*), whilst the sporangia are found on the upright threads [1] (Fig. 1, *f*). Very good instances are afforded by *T. diffusa*, De

[1] Oltmanns, Morph. u. Biol. d. Algen, I, 1904, p. 252.

Wildeman,[1] and *T. ellipsicarpa*, Schmidle var. *africana*, Schmidle[2] (Fig. 1, *h*).

We can see in this phenomenon a necessary result of the terrestrial habitat. The zoosporangia are detached as a whole, dispersed by the wind, and only liberate the contained swarmers when they come to lie on some moist substratum. The gametangia, on the other hand, liberate their gametes *in situ*, and thus the most favourable position for them will be on the creeping base, in close contact with the substratum, where inundation must be a frequent phenomenon.

It should also be noted that zoosporangia and gametangia are n some cases found on distinct, though similar, individuals.[3] There are thus all the necessary indications for the gradual differentiation of two alternating generations, of which the one bears the asexual organs on the upright system, the other bears the sexual organs on the creeping base. Disappearance of the base in the former, and of the upright system in the latter (both phenomena which are known to occur among the Chætophorales) will give two different generations, resembling those of the Archegoniatæ in all essential respects (cf. also the case of *Cutleria* discussed on p. 15).

From such a group as the Chætophorales, then, we could suppose two alternating generations like those of the higher plants to have arisen. We have to picture an ancestor, with well-developed base and upright system, from which the two generations gradually diverged in the way just indicated. Such an origin, of course, amounts to an homologous one, although presumably of a somewhat different kind to that in the minds of the adherents to the homologous theory; and the writer may appear, after taking an impartial attitude at the beginning, to be caught in the delinquency of favouring this view. It does not seem to him, however, that the above mode of origin is applicable to the Bryophyta, with their completely dependent sporophyte, without forced assumptions. It is propounded for the case of the Pteridophyta, and the writer realises that he, as little as anyone else, is able to bridge the gap between them and their ancestry.

There is, however, no necessity to seek a separate algal ancestry for the Bryophyta, as the group of the Chætophorales also

[1] Les Algues de la Flore de Buitenzorg, 1900, p. 72.

[2] Schmidle, in Engler's Bot. Jahrb., XXX., 1902, p. 63, Tab. II., Fig. 8-10.

[3] cf. J. Bonnet, in Progressus Rei Botanicæ, V., 1914, p. 101; Oltmanns, *oc. cit.*, p. 253.

affords indications of another possible mode of origin for the two alternating generations, an antithetic one, that seems most applicable to the case of the Bryophyta. This concerns the much-discussed *Coleochæte*. Here alone among the Isokontæ do we get any pronounced indication of an intercalated phase, due to the elaboration of the zygote, although minor instances are afforded by several other filamentous members (e.g. *Ulothrix*, *Oedogonium*). Comparisons between *Coleochæte* and *Riccia*, the Liverwort with the simplest type of sporophyte known, have been instituted by many Botanists, and it is unnecessary to enter into details here.

The value of *Coleochæte*, in relation to the origin of the two alternating generations in the higher plants, has been called into question by many in recent years, because the cytological features are not in accord with those obtaining in the latter. Allen[1] has shown that reduction in chromosome-number takes place on the germination of the oospore, so that the 16-32-celled plantlet arising from the latter corresponds cytologically with the ordinary sexual-organ-bearing thallus, and not with the diploid sporophyte of the higher plants. Should this, however, be taken as in any way invalidating the value of *Coleochæte* as an instance of the intercalation of a new generation in the life-cycle by the elaboration of the zygote? In the group of the Algæ everything is still in a condition of fluctuation, and we know that reduction in chromosome-number occurs at varying points in the life-cycle, sometimes on gametogenesis, sometimes after sexual fusion.[2] Thus reduction rendered necessary by the occurrence of sexuality will have taken place at different stages and will only gradually have become fixed at the stage of sporogenesis. Perhaps it was only with the establishment of the tetrad-division, so typical for the production of spores in the higher plants (as well as in *Dictyota* and many Rhodophyceæ), that reduction became located at a definite point in the life-cycle.

In considering the possible origin of the sporophyte in Bryophyta by gradual elaboration of the zygote, as we see it indicated in *Coleochæte*, it is not even necessary to ignore the essential construction of the thallus in the Chætophorales as a whole. The two main groups of the Bryophyta appear to have diverged at a

[1] Ber. deutsch. Bot. Ges., XXIII., 1905, p. 285.

[2] Reduction takes place on gametogenesis, for instance, in Fucaceæ. To regard the thallus in this group as being a sporophyte, on this basis, is surely the height of absurdity! cf. also Farmer, in New Phytologist, VIII., 1909, pp. 112-114; and Tansley, in New Phytologist, XI., 1912, p. 216.

very early stage, the thallus of the Hepaticæ arising from the creeping base, that of the Musci from the upright system. The Moss-protonema appears as a relict of the original creeping base, bearing, as it does, the upright and radial Moss-plant as a lateral branch. There is no difficulty at all in making these assumptions with the facts given in the foregoing pages before us.

The derivation of Bryophyta and Pteridophyta from one common ancestral algal group, although their further development is presumed to have proceeded on very different lines, is quite sufficient to explain the resemblances between sexual organs, etc. in the two cases. Moreover it should be noted that these resemblances are much more pronounced in the gametophyte (whose origin is assumed to be very similar in the two groups) than in the sporophyte (whose origin is regarded as very different in the two cases).

Looked at from the point of view of a group betraying characteristics indicative of the probable origin of the higher plants, it is significant that the Chætophorales exhibit more potentialities than any other group of the Isokontæ. A brief summary will suffice to illustrate this point :—

1. Great range of morphological construction.

2. The most highly differentiated sexual organs encountered among the Isokontæ (in *Coleochæte*).

3. The most marked development of the zygote as an independent generation (in *Coleochæte*).

4. Although the bulk of the present-day forms are found in freshwater (a fact which is not insignificant when we consider that the higher plants are likely to have had an origin from freshwater forms), a certain number are marine (e.g. *Pringsheimia*).

5. One whole series, the Trentepohliaceæ, are terrestrial.

6. A number of forms have become endophytic, being either subcuticular (*Endoderma*) or intercellular.

7. There is further great diversity of habitat; thus, *Tellamia* penetrates into the shells of Molluscs, *Gomontia* into calcareous substrata, whilst *Dermatophyton* grows on the testa of freshwater tortoises. The species of *Trentepohlia* play a part in the formation of Lichens.

8. Some forms (e.g. *Cephaleuros*, *Acrochæte parasitica*) are parasitic.

9. A number become encrusted with carbonate of lime (e.g. *Gongrosira*).

It must be confessed that, in this series, almost every conceivable type of growth-form and habitat has been realised. It does not, therefore, appear a forced assumption to seek in a group with such unlimited potentialities those evolutionary tendencies which gave rise to the higher plants.

In discussing the alternation of generations of the Archegoniatæ, much use has been made of representatives belonging to other groups of the Algæ, in particular of the Phæophyceæ. The latter show many interesting parallels with the Isokontæ and afford very useful data in connection with the probable mode of origin of the higher plants, but in utilising the information derived from this group it is necessary to maintain the proper perspective and to realise that the Brown Algæ cannot be regarded as anything else than a side-line of evolution (cf. below). In many respects, morphological and anatomical complexity of the thallus, differentiation of the sexual organs, and development of well-marked alternation, they have gone much further than the Isokontæ, and it is just in the evidence to be derived from these more advanced characteristics that the value of the Brown Algæ lies. We may suppose that the more advanced types among the Isokontæ were lost during the vicissitudes that must necessarily have accompanied establishment on dry land, whilst the Phæophyceæ, which have remained a marine group, have preserved numerous traces of this more advanced development. It is certainly significant that the Isokontæ show but little of the morphological elaboration seen in the Brown and Red Algæ.

At this point reference may be made to Schenck's attempt to derive the Archegoniatæ and the Characeæ from a Phæophyceous ancestry.[1] Whilst in no way underestimating the value of the detailed comparisons which he makes between vegetative and reproductive organs in the Brown Algæ and the higher groups, the writer cannot go with him to the extent of actually deriving the latter from this group of Algæ. The Phæophyceæ as a whole are distinguished from the Isokontæ and the higher plants alike by different pigmentation of the chloroplasts, different products of assimilation, and especially by a very characteristic type of motile element. In particular stress may be laid upon the motile element (whether zoospore or gamete) which is characterised by its laterally attached cilia, the one pointing forwards, the other backwards, and the close relation between their position and that of the

[1] Engler's Bot. Jahrb. XLII., 1909, pp. 1-37.

chloroplast and eye-spot. Moreover the Phæophyceæ are essentially marine. If we look at Schenck's work from the point of view of parallel development, however, it is exceedingly instructive. A detailed discussion is unfortunately impossible.

Before dealing with the established cases of alternation among the Brown Algæ, it will be well to examine a little more closely the lowest series of this group, viz., the Ectocarpales. This may probably be regarded as displaying many of the more primitive characteristics of the Phæophyceæ, and in many respects affords an astonishing degree of parallel with the Chætophorales. The simple filamentous *Ectocarpus* has a thallus differentiated into the same two portions as a *Myxonema*, i.e., there is a creeping base and an upright system, the branches of the latter often terminating in hairs. There are a large number of forms (*Ascocyclus*, Fig. 2, *d*, etc.) in

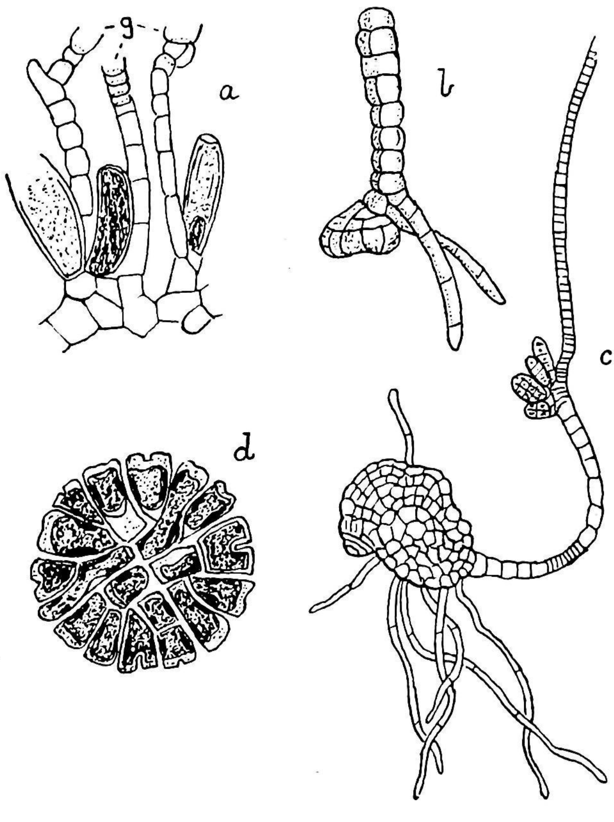


FIG. 2. *a*, *Myrionema vulgare*, showing zoosporangia and gametangia (g) (after Sauvageau); *b*, young *Aglaozonia*-thallus (from Oltmanns); *c*, abnormal *Cutleria* (from Oltmanns); *d*, *Ascocyclus secundus*, a young thallus (after Reinke).

which only the prostrate portion is developed, and there is the same diversity of habit as in the Chætophorales, though a terrestrial series is lacking. In many of the forms with a well-developed base, there is a tendency for the asexual (unilocular) sporangia to appear as lateral branches from the base of the upright threads, whilst the gametangia (plurilocular sporangia) are borne near their apex; this is well seen in *Myrionema vulgare*[1] (Fig. 2, *a*). It will be noticed that this arrangement is just the reverse of what obtains in *Trentepohlia*.

Throughout the Phæosporeæ the thallus betrays a more or less marked differentiation into prostrate and erect portions, although this is very much obscured in some cases. It appears, however, to be a safe assumption that this type of construction is the primitive one for the whole group.

The cases of alternation among the Brown Algæ that have been fully studied are those of *Cutleria*, *Zanardinia* and *Dictyota*, and a consideration of these will suffice. In *Dictyota*, the two generations,[2] indubitably identical in morphological construction as they are, could in no way be supposed to have arisen from different parts of an ancestral thallus; rather, they appear as two similar individuals, one of which has become sporogenetic, the other gametogenetic. The creeping base seems to have become completely suppressed in this case, although traces are seen in allied forms. *Dictyota* furnishes us with an instance of *strictly* homologous alternation, and the writer would put this case in a special category and does not regard it as directly comparable to the kind of homologous alternation that is supposed to have arisen in the line of evolution of the Pteridophyta. *Zanardinia*[3] seems to display the same kind of alternation as *Dictyota*, although here, possibly, it is the creeping system that has persisted and that has furnished the two homologous individuals. The two cases just cited are probably instances of the numerous modifications in the method of alternation which we may expect to find in so plastic and primitive a group as that of the Algæ.

The case of *Cutleria* is different. Here, apparently, we have a good instance of antithetic alternation, but appearances are deceptive. The life-cycle, whose cytology has been investigated by

[1] cf. Oltmanns, *loc. cit.*, p. 383, fig. 235; Sauvageau in Ann. sci. nat., Bot., 8 sér., V, 1898.

[2] cf. especially Lloyd Williams, in Annals of Botany, XVIII, 1904, pp. 141, 183; Hoyt, in Bot. Gaz., L, 1910, p. 55.

[3] cf. Yamanouchi, in Bot. Gaz., LVI, 1913, pp. 1—35.

Yamanouchi,[1] with the result that the features of reduction correspond closely with those obtaining among the higher plants, includes the erect sexual *Cutleria*-plant and the prostrate asexual *Aglaozonia*-plant, normally following one another in definite alternation. Parthenogenesis is a rather frequent phenomenon, the parthenospores, however, giving rise to more or less distinct *Aglaozonia*-stages. But there are numerous other important abnormalities. Thus, the zoospores, whilst often growing into typical *Cutleria*-thalli, occasionally[2] afford dwarfed thalli or even only simple, or more rarely branched, threads; these abnormal individuals (Fig. 2, *c*) sometimes produce gametangia on the erect system, but almost invariably grow out into *Aglaozonia*-like discs at their base. Oltmanns[3] interprets such stages as instances of a secondary formation of *Aglaozonias* by budding from the *Cutleria*-plant, but the writer would like to place a totally different interpretation upon them.

It seems likely that the ancestor of these forms had a thallus differentiated into the usual prostrate base and erect portion (cf. p. 14), in fact in the normal *Aglaozonia*-stage this is quite apparent. the base being represented by the *Aglaozonia*-disc and the upright system by the small erect column which invariably arises in the germination of the *Aglaozonia*-plant (Fig. 2, *b*). Young *Cutleria*-plants also seem to display some indications of a creeping basal system. It may be suggested, therefore, that the ancestor of *Cutleria* had a thallus bearing asexual organs near the base and sexual organs on the upright system, as we find it in *Myrionema*, etc., among the present day Ectocarpales (p. 14). With the development of these organs at different periods, they became segregated on distinct individuals, the asexual ones practically losing the upright system and the sexual ones the prostrate portion. The erect column of the *Aglaozonia*-stage would thus be a relict of the original erect system, whilst the abnormal stages above described would merely be a return to the ancestral condition. Sauvageau[4] has described stages which appear as transitions between young *Cutleria*-plants and the column of the *Aglaozonia*-stage, and these are quite in accord with the above hypothesis. All the evidence seems to point to the conclusion that the two generations of *Cutleria*

[1] cf. Yamanouchi, in Bot. Gaz., XLVIII, 1909, pp. 380—387.

[2] Church, "Polymorphy of *Cutleria multifida*," Ann. of Bot., XII, 1898, p.75; Kuckuck, in Wiss. Meeresunters. Abt. Heligoland, III, 1900, pp. 61—79; cf. also Oltmanns, *loc. cit.*, p. 403.

[3] *loc. cit.*, p. 403.

[4] Ann. sci. nat., bot., 8 sér., X, 1899, p. 265.

are merely diverging developments from a common ancestral sporogenetic and gametogenetic thallus.

Such a view is, moreover, quite in accord with the hypothesis put forward above in connection with the origin of the two generations of the Pteridophyta from a Chætophoraceous ancestry, and we have here a good illustration of how diverse the two diverging generations may soon become. It is interesting to note that the morphological origin of the two generations in *Cutleria* is just the reverse of that postulated in the Chætophorales, the sporophyte being prostrate, the gametophyte erect, a variation only too likely to occur in groups where alternation was in the making.

Finally, we may briefly consider the alternation that has been observed in the Red Algæ. In this group also, differentiation of the thallus into a creeping basal portion and an upright system is frequently observed, especially in the simpler forms (e.g., *Batrachospermum*, *Chantransia*), but in the vast majority it is the upright system that has been elaborated, with more or less complete elimination of the basal portion. Two types of alternation are known in the Red Algæ, *viz.*, the type characteristic of *Nemalion* and presumably of many of its immediate allies, and the complex alternation typical of the more advanced forms.

The case of *Nemalion* is very similar to that of *Coleochæte*, the sporophyte (as constituted by the sporogenous threads forming carpospores) appearing as an intercalated stage. Wolfe[1] came to the conclusion that reduction occurred at the end of this intercalated phase, *viz.*, on the formation of the carpospores. Svedelius[2] has, however, recently investigated *Scinaia furcellata*, another member of the Nemalionales, and finds that the oospore undergoes reduction-division at the inception of germination, three of the four nuclei produced aborting, whilst the remaining one is used in the formation of the sporogenous threads. It seems probable that this is the usual course of events among the Nemalionales, which therefore, as regards their life-cycle, are in almost complete agreement with *Coleochæte*. Presumably matters are the same in *Batrachospermum*; here, however, the carpospores, on germination, give rise to the well-known *Chantransia*-stage, that is a mainly prostrate system of creeping threads, from which the *Batrachospermum*-plant arises as a side-branch. This sequence is very similar to that occuring in Mosses, and here we have the state of affairs postulated on p. 12.

1 Annals of Botany, XVIII, 1904, p. 608.

2 Nov. Act. Reg. Soc. Scient. Upsala, sér. IV, Vol. IV, No. 4, 1915.

In the case of the more advanced Florideæ, several of which have been fully studied,[1] we have the most complicated instances of alternation known among the Algæ. We may take *Polysiphonia* as a type. Here we have first the production of a phase, which arises by the elaboration of the zygote and is constituted by the cystocarp. The carpospores of the latter give rise to a *Polysiphonia*, identical in all respects with the thallus bearing the sexual organs, except that it is diploid and produces only tetraspores. The latter again give rise to the sexual *Polysiphonia*, reduction having taken place during the tetrad-division in the tetrasporangium.[2] The numerous complications occurring in many forms and disclosed by the work of Oltmanns and others can be neglected here, where we are only concerned with the main facts.

In the life cycle of these Florideæ we therefore have two spore-bearing generations, *viz.*, (a) the cystocarp, parasitic on the gametophyte and propagating by carpospores; and (b) the ordinary *Polysiphonia*, independent and propagating by tetraspores. That reduction, which can only take place once in such a life-history, occurs on the second spore-producing generation is probably associated with the acquisition of a definite tetrad-stage in spore-formation (p. 11 ). The writer would regard these advanced Florideæ as exhibiting both an antithetic spore-producing generation and one which is strictly homologous.[3] If, as he has attempted to show, both antithetic and homologous alternation can occur among the Algæ, it is quite plausible that the two phenomena should be combined in the same life-cycle.[4]

Amongst all the cases of alternation among Algæ that have been considered, that of *Cutleria* certainly stands out as the most illuminating in connection with the main theory here propounded. Though the result in this case is just the opposite, *viz.*, a prostrate sporophyte and an erect gametophyte, it fully illustrates the course of events here suggested.

In conclusion, some of the main features may be briefly summarised as follows:—

[1] cf. Yamanouchi, in Bot. Gaz. XLI, 1906, p. 425 and XLII, 1907, p. 401; Lewis, in Ann. of Bot., XXIII, 1909, p. 639; Svedelius, in Svensk. Bot. Sidsskrift V, 1911; VI, 1912; VIII, 1914; also Ber. deutsch. bot. Ges. XXXII, 1914.

[2] cf. Yamanouchi, *loc. cit.*

[3] The strict homology of the sexual and tetraspore-bearing generations is shown by the occurrence of abortive tetrasporangia on sexual plants and of abortive carpogonia on tetraspore-bearing plants; for details, see Svedelius and Lewis, *loc. cit.*

[4] cf. also Tansley, in New Phytologist, XI, 1912, pp. 213—216.

(1) In all the more advanced groups of the Algæ, the thallus exhibits frequent differentiation into a creeping base and an upright system.

(2) Among the Chætophorales, which plainly show such a differentiation of the thallus, there are evidences of unlimited potentialities; we also find in this group (a) a whole series of terrestrial forms, (b) the only member of the Isokontæ with a distinct main axis bearing laterals which carry on assimilation and reproduction and (c) in the species of *Trentepohlia*, forms showing relegation of the sexual organs to the base and of asexual organs to the upright system.

(3) The available evidence is regarded as pointing to the Isokontæ for the ancestry of the higher plants, and for the reasons mentioned under (2) this ancestry is thought to lie among forms resembling the Chætophorales.

(4) The Pteridophyta are supposed to have arisen from such forms by the gradual divergence of two generations, the sexual derived from the creeping base, the asexual from the upright system. The Bryophyta are supposed to have arisen from forms resembling *Coleochæte* by gradual elaboration of the zygote.

(5) *Cutleria*, in a side-line of evolution, fully illustrates the way in which two generations can be derived from the type of thallus common in all the main groups of the Algæ, after the manner postulated for the case of the Pteridophyta.

(6) The cases of alternation among the Algæ may be distinguished as follows:—

(a) The two generations arise from different parts of the ancestral sporo- and gametogenetic thallus (*pseudo-homologous alternation*):—

(1) The gametophyte is prostrate, the sporophyte erect (Pteridophyta, possible cases to be found among the Chætophorales).

(2) The gametophyte is erect, the sporophyte prostrate (*Cutleria*).

(b) The two generations arise from the same part of the ancestral thallus, the other portion aborting (*strictly homologous alternation*):—

(1) The two generations arise from the upright system (*Dictyota*).

(2) The two generations arise from the prostrate system (*Zanardinia ?*).

(c) The sporophyte arises as an intercalated stage in the life-history, due to the elaboration of the zygote (*antithetic alternation*):—

(1) The gametophyte arises from the prostrate system (*Coleochæte*, Hepaticæ).

(2) The gametophyte arises from the erect system (Nemalionales).

(3) The gametophyte retains both the prostrate and erect systems (*Batrachospermum*, Musci).

(d) There are two spore-producing generations, the one an intercalated phase produced from the zygote, the other strictly homologous (*Polysiphonia*, *Griffithsia* and other advanced Florideæ).

East London College,
*November 28th, 1916.*

## THE ORIGIN OF SPHAGNUM ATOLLS.

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IN connection with the study of the development of the climax vegetation of Minnesota, opportunity has been afforded the writer to investigate the sphagnum atolls of the state and particularly the Anderson and Ballard atolls of Crow Wing County which MacMillan (1) described in 1894. A sphagnum atoll is any bog surrounded by a trench of stagnant water. In the centre of the bog the remains of the original pond may be present in which case the name atoll is quite applicable. Such bogs are to be found in northern and central Minnesota and are said to occur in Wisconsin, Michigan, and New York.

MacMillan (1) endeavoured to explain their development and suggested probable causes of their formation. He attributed their development primarily to the rise and fall of the water level of the original pond, and summarises the process as follows: "The origin of the sphagnum atolls in the cases studied may be ascribed to a season of gradual recession of the waters of the pond, followed by a season of comparatively rapid increase in area and level. The atolls first appear as annular floating bogs separated from the shoreward turf as a result of the original zonal distribution of littoral plants and the rise of the waters together with the favourable concurrence of a group of special and necessary conditions. Some of the apparent conditions of the atoll-formation are (*a*) a definite maximum size and depth of the parent pond; (*b*) considerable