THE MOST PRIMITIVE LIVING REPRESENTATIVE OF THE ANCESTORS OF THE PLANT KINGDOM.

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There is but little doubt among botanists that the land flora as it now exists has originated from aquatic ancestors. Both from the morphologic and palæontologic standpoints the evidence corroborates this view. Indeed, the dependence of land plants upon an adequate water supply, together with the fact that in such groups as the Mosses and Ferns, fertilization itself can only be accomplished in the presence of water supplied from some external source, gave rise to the conclusion that the origin of the vegetable kingdom was from primitive plants living in the water, long before there was the more conclusive evidence now existing.

It would be interesting to inquire into the life histories of certain transitional groups with a view to tracing this migration from water to land. For modern morphological and physiological investigations has enabled us to do this with a considerable degree of certainty. Not only would we be able to show that the establishment of the higher representatives of our land flora had been brought about by certain methods of specialization in lower aquatic or semi-aquatic forms, but it would be possible to indicate to a certain extent at least how this process had been carried on. However such an inquiry would lead us entirely too far afield at this time and it will be necessary to grant without further discussion that the facts are sufficient to sustain the aquatic origin of the higher plants.

Naturally, in seeking for the primitive ancestors of the vegetable kingdom, attention is at once directed to the algæ, the group of plants which to a very considerable extent is more dependant upon the presence of external water for the carrying on of its vital processes than any other. Furthermore, in the present state of our knowledge, such an investigation would not be devoted to the more

highly differentiated brown or red algæ, but rather to the green algæ, in which group there exists the closest resemblances to the structure of the lower land plants. The problem thus becomes one of discovering as nearly as may be possible the most primitive member of the green algæ. And by "*primitive,*" of course, is not necessarily meant the simplest form, but that plant which seems to be nearest to the starting point of the phylogenetic tree and from which certain definite lines of ascent can be traced.

In considering the origin of the green algæ, numerous theories have been held and it would be impossible to give even a mere outline of the various improbable suggestions which have been advanced regarding the evolution of this group. During the past ten years, however, a great deal of light has been thrown upon the phylogenetic relationship of the algæ. Not only has the increase in our knowledge of the life histories of the algæ been considerable, but the discovery of many new genera and species has made clear the affinities of various families as never before. Of the 275 good genera now recognized among the green algæ, one fourth have been discovered and described since the appearance of Engler and Prantl's "Pflanzenfamilien"—the last complete work on the subject and still the recognized authority. The addition of so many new and in many cases important links to the chain of development of these plants, has reduced the former chaotic condition to something like order and it is no longer quite such a matter of speculation regarding the origin of the main group of the green algæ.

Ten years ago Chodat derived the green algæ from the simplest, unicellular, non-motile forms then known, namely, the Palmellaceæ. Within this family he included four genera whose simple life history showed three principal stages. From these so-called "conditions," as Chodat pointed out, developed the three important and ruling tendencies which have dominated the lower green algæ.

These are: (1) The *zoöspore condition,* or the unicellular motile stage, with the other two conditions transient or subordinate. (2) The *sporangium condition,* that is, the unicellular *non*-motile stage, with the other two conditions accidental or transient. (3) The *tetraspora condition,* where the non-motile cells are connected at right angles by the increasing consistency of the walls, giving rise

to the formation of a tissue or filament. The other two conditions are reduced or transient.

Having established these three principal "conditions," Chodat proceeded to establish the phylogeny of the green algæ along these lines and succeeded in clearing up considerable obscurity which had previously existed. However, the starting point selected by Chodat has been open to some criticism and it remained for Blackman to suggest the most satisfactory explanation of the origin of this group. He, while following in a general way the theory of Chodat, took the position that the three "tendencies" had their origin *not* in the non-moile *Palmella* form, but in the motile *Chlamydomonas* type.

I have had the genus *Chlamydomonas* under investigation for several years, observing its various species for the most part in pure cultures grown upon both solid and liquid media. The vegetative cells of *Chlamydomonas* are variable in both size and shape; in general, however, they are from 20–35 μ in length and 10–20 μ in breadth, being elliptic or pyriform in outline. One end of the cell is usually produced into a colorless beak, from which two cilia always protrude. The chloroplast is quite variable in form and with one exception is provided with a single pyrenoid. Non-sexual reproduction is by means of zoöspores, which are formed by the division of the contents of the mother cell, after it has come to rest. Sexual reproduction is usually by the conjugation of naked motile gametes of similar size and in no way distinguishable from each other. It is interesting to note, however, that in addition to this method there may also be the conjugation of unequal motile gametes and in one species—to be referred to later—there takes place the conjugation of dissimilar gametes, one of which, the larger, comes to rest before conjugation. We thus have within the limits of this well defined and natural genus, not only the most primitive form of gamogenesis, but through anisogamous conjugation a gradual approach to true oögamy—the highest type of sexual reproduction developed among the algæ.

In abandoning the starting point of Chodat's theory of the development of the green algæ, it is not necessary to replace his idea relative to the three predominating tendencies manifest in the lower members of this group. While different names are attached to these

conditions as recognized at the present time, they are essentially those pointed out by Chodat, namely:

1. A tendency towards the aggregation of motile vegetative cells, with a gradually larger and more specialized motile colony. This is the *Volvox* type and in no place in the plant kingdom do we have a more perfect series of development than from the simple *Chlamydomonas* form to the complex and highly differentiated *Volvox* type.

2. A tendency towards the formation of an aggregation of non-motile cells into a filament or tissue by the repeated vegetative division of an original mother cell. This is the *Tetraspora type.*

3. The *Endosphæra* type, where the tendency towards the formation of vegetative divisions and septate cell formation is reduced to a minimum. This is, of course, Chodat's *sporangium* tendency, although not so much importance is attached to it.

Without going into details it may be said that various species of *Chlamydomonas* (of which there are about thirty, all remarkably constant as regards their cytological characters), taken collectively, exhibit all these three tendencies and that the simpler forms of algæ which possess but a *single* tendency, seem clearly to have diverged from some one species of this genus.

The endosphærine tendency in *Chlamydomonas* has given rise to a single family, *Endosphæra.* This is naturally strictly unicellular and with no vegetative divisions; the reproduction of the species can take place only by the formation of zoöspores or gametes. A family so restricted as to its vegetative habit could hardly be expected to develop very far and it is interesting to note that practically all the genera are epiphytic upon other algæ or aquatic plants, and that this habit of life has undoubtedly given rise to a distinct group of fungi. The suggestion has been made that the peculiar Siphonales may have developed from this *Endosphæra type,* and while such a view is reasonable, it must necessarily, at the present time, be a mere matter of speculation.

But one family, the Volvocaceæ, has resulted from the development of the volvocine tendency. While the evolution of sex in this group has been carried to the highest possible degree, the restrictions of an enforced motile vegetative condition did not permit this family to give rise to anything further.

It is the tetrasporine tendency which has been the permanent one and has resulted in producing the higher green plants. This condition in *Chlamydomonas* resulted in the production of a series of plants which gradually replaced the formation of zoöspores by that of vegetative cell division. The resulting family was the Palmellaceæ, the one which formed the starting point in the development of the algæ, according to Chodat. While there seems to be but little question that the Palmellaceæ have given rise to most of the other families of the green algæ, there is every evidence that it was itself derived from *Chlamydomonas,* rather than the reverse, as contended by Chodat.

It is impossible at this time to even indicate the development of the higher algæ from the Palmellaceæ. With the exception of the Confervales, which seems to have developed independently of the typical green algæ, and the Conjugales, which apparently have arisen directly from the *Chlamydomonas* type, all the higher green algæ can be traced back through the Palmellaceæ with considerable certainty to their *Chalmydomonas* ancestor. The Conjugales have always been a stumbling block in constructing any developmental line of the algæ from primitive forms. But granting that the filamentous Conjugales, as well as the desmids, are unicellular (the reasons for which can not now be given) it is comparatively easy to find the origin of the conjugation habit so emphasized in this group, in *Chlamydomonas Braunii.* In this species the female or receptive cell comes absolutely to rest before fertilization and the smaller or male cell becomes attached to it. Then the entire contents of the male cell passes into the female cell, leaving behind the empty cell wall, just as in some of the desmids and in most of the filamentous-like Conjugales.

The more the genus is studied the more reasonable becomes the conclusion that *Chlamydomonas* has not only given rise to such an aberrent group as the Conjugales, but that it may safely be regarded as the phylogenetic starting point of the various lines of ascent in the true green algæ. At present in the higher algæ the *Chlamydomonas* stage is, of course, retained in the zoöspore and the gamete, a vegetative non-motile generation being interpolated between either

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a sexual or non-sexual motile stage. In the very highest type of reproduction in the green algæ the male gamete alone represents the *Chlamydomonas* stage. Indeed, we may well assume that the motile male gamete of the mosses and ferns constitutes the last remaining type of the original *Chlamydomonas* condition, which with other more positive evidence points to the origin of such land forms from a *Chlamydomonas*-like ancestor.

Although practically all the evidence for the position taken has necessarily been omitted, it is hoped that enough has been said to at least indicate the unique and important position occupied in the plant kingdom by the alga *Chlamydomonas.*