# BIOLOGICAL LECTURES DELIVERED AT THE MARINE BIOLOGICAL LABORATORY OF WOOD'S HOLL, 1899; PP. 1-280

Published @ 2017 Trieste Publishing Pty Ltd

ISBN 9780649074389

Biological Lectures Delivered at the Marine Biological Laboratory of Wood's Holl, 1899; pp. 1-280 by Various



Edited by Trieste Publishing Pty Ltd.
Cover @ 2017



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# BIOLOGICAL LECTURES DELIVERED AT THE MARINE BIOLOGICAL LABORATORY OF WOOD'S HOLL, 1899; PP. 1-280

Trieste

# FIRST LECTURE.

## THE EVOLUTION OF THE SPOROPHYTE IN THE HIGHER PLANTS.

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THE questions relating to the origin of organic structures must always possess great interest for the biologist, and when I was asked to speak before the students at Woods Holl, it seemed to me that a discussion of recent views bearing on the development of the spore-producing structures of the higher plants, *i.e.*, the Archegoniates and seed-bearing plants, would not be inappropriate.

There is good reason to suppose that among plants, as among animals, the most primitive forms were aquatic; and it is highly probable that many existing fresh-water algæ are but slightly modified descendants of these ancestral types. This is evinced by the great uniformity shown by existing green algæ all over the world. Most genera and many species are cosmopolitan, and they exhibit far less variety than is shown by their larger and more specialized marine relations. Presumably the conditions in fresh water have changed but little, and as the more specialized forms have taken to the land, or have developed in the sea, the few that remained in their primitive environment have been subjected to much less competition, and have probably persisted with but little change from very remote times.

Leaving aside certain forms of doubtful affinities, like the bacteria and blue-green algæ, the existing forms which represent most nearly the ancestors of the higher plants are the Volvocineæ and Protococcaceæ. The former are, as all botanists know, free-swimming green organisms which show resemblances on the one hand to low animals, and on the other are very like the free-swimming reproductive cells, or zoöspores, of many of the higher algæ. The latter probably originated from forms like the simpler Volvocineæ by the loss of motility associated with the development of a continuous cellulose membrane about the vegetative cells. This stage in the evolution of the green algæ is represented by some of the simpler Protococcaceæ. Above these unicellular forms are a number of filamentous plants, single rows of nearly uniform cells. Such plants are Œdogonium or Conferva, which well represent the next step in the evolution of the plant body.

The differentiation of the reproductive cells in the algæ, while it offers one of the most interesting and instructive examples of the evolution of plant structures, must be passed over here. It may be mentioned, however, that the differentiation of the sexual cells has evidently taken place quite independently in several groups of algæ.

In the further development of plant types two very important factors are to be considered. First, the adaptation to a marine existence, and, second, the exchange of an aquatic for a terrestrial life.

The conditions in the ocean are markedly different from those in fresh water, and most plants which have adapted themselves to life in the sea have become decidedly changed. The salinity of the water has no doubt been one of the factors in these changes, but more important is probably the question of light. The two most characteristic groups of sea plants, the red and brown seaweeds, are provided with special pigments in addition to the chlorophyll, and there is little question that these pigments are developed, in part at least, in response to changed light conditions.

As the conditions of light and temperature in a marine environment are far more constant than those in fresh water, we find, as a rule, that marine algæ, especially those inhabiting the deeper water, are more susceptible to changes of light and temperature than are most fresh-water forms.

While certain seaweeds growing between tide-marks are subject to exposure to the air, it is only for a short time, and we find in most such algæ a development of mucilaginous tissue which prevents their complete desiccation.

These seaweeds have adapted themselves perfectly to their peculiar environment, and such highly specialized forms as the great kelps and many red algæ probably represent the highest types of these marine plants. They have diverged widely from the simpler fresh-water algæ, and there is no reason to suppose that they have given rise to any higher types.

The simple fresh-water green algæ, which, so far as we know, most nearly represent the ancestors of the terrestrial green plants, differ much in their conditions of life from the seaweeds. Most bodies of fresh water are subject to great fluctuations of depth, often drying up completely for long periods, or sometimes being frozen. It is obvious that plants living under such conditions must be very resistant, and we find that such is the case among most green algæ. Not only, as a rule, are they capable of enduring a great range of temperature, but usually at the end of their vegetative period they produce special cells, "spores," which can endure complete desiccation without injury, and are also uninjured by freezing. By means of these "resting-spores" the plant is carried over from one growing period to the next, and when the conditions are favorable, the spores germinate and give rise to a new generation. This production of resting-spores is one of the most striking differences between these fresh-water algæ and their red and brown relations in the sea, where there is usually no necessity for such resting-spores.

Certain green algæ, like some species of the common genus Vaucheria, may be considered amphibious, as they do not actually grow in the water, but are exposed to the air on the surface of moist earth, from which they absorb the water necessary for their growth. The ability to thus grow with a diminished water supply is an evident advantage, and in some such way as this it is probable that the first strictly terrestrial plants originated from some originally aquatic algal ancestors.

We can imagine some such forms gradually becoming better and better able to vegetate on the mud left by the subsidence of the water, and finally becoming adapted to life on land. The lower liverworts, which represent the simplest types of existing land plants, probably originated in some such way. There are still existing certain amphibious liverworts, species of Riccia, which live for the most part as floating aquatics, but sometimes settle down in the mud left by the subsiding water, or even creep up the muddy banks and establish themselves as land plants. This seems to be most commonly done before the development of the reproductive organs. It is very likely that the individual history of these liverworts illustrates the origin of the typical forms from their aquatic ancestors.

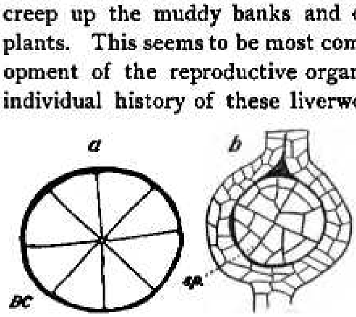


FIG. 1. — *a*, Diagram of a section through the germinated resting-spore of an alga (Coleochæte), showing the mass of cells within. Each cell of the rudimentary sporophyte produces a single zoöspore. *b*, Longitudinal section of the lower part of the fertilized archegonium of a liverwort (Riccia), showing the contained sporophyte, *sp.*, developed from the egg-cell. Each cell of the sporophyte, except the outside ones, gives rise later to four non-motile spores.

Among those algæ which approach most nearly to the lower liverworts there is a hint of the characteristic alternation of generations so conspicuous in the mosses and ferns. The egg-cell in such algæ, on being fertilized, produces a resting-spore which may be invested with a protective envelope of cells. This resting-spore (oöspore) does not, on germination, produce a new plant at once, but a globular cellular mass is formed (Fig. 1, *a*), each cell of which gives rise to a motile zoöspore, which then grows into a plant like the parent one.

This alternation of sexual and non-sexual plants becomes, as is well known, very prominent in the mosses and ferns, or Archegoniates as they are called on account of the peculiar female organ, the archegonium.

While there is unmistakable evidence of relationship between the lower liverworts and the green algæ, it must be admitted that at present the gap between the two groups is a very great one, and we are not in a position to state positively just where is the point of contact between Archegoniates and algæ.

The structure of the archegonium (Fig. 2) is very constant throughout the Archegoniates, but has very little in common with the much simpler oögonium, or female organ of the green algæ, and its origin is still a matter of conjecture.

Aside from the character of the sexual organs, there is no difficulty in homologizing the sexual plant (gametophyte) of the lower liverworts and that of certain green algæ.

As a result of the change from the aquatic to an aërial environment, we find the tissues of the gametophyte in the liverworts more resistant to loss of water than is the case in the algæ. The outer cell-walls are cuticularized, and there is more or less specialization of the inner tissues, and this specialization may be very pronounced, as we find in such large liverworts as Marchantia. Finally, in the leafy liverworts and true mosses, the gametophyte develops a definite axis and special assimilating organs, leaves.

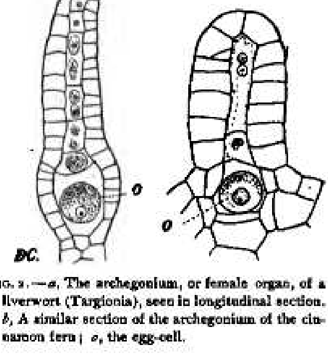

FIG. 2.—*a*, The archegonium, or female organ, of a liverwort (Targionia), seen in longitudinal section. *b*, A similar section of the archegonium of the cinnamon fern; *o*, the egg-cell.

It is the sporophyte, however, or non-sexual plant, developed from the fertilized egg within the archegonium, that we wish especially to consider. We have already intimated that in certain algæ the oöspore, on germination, gives rise to a globular cell-mass (Fig. 1, *a*), each cell of which produces a zoöspore. In the lowest liverworts, *e.g.*, Riccia (Fig. 1, *b*), a similar globular cell-mass is produced from the fertilized egg, but there is a much shorter period intervening between fertilization and the germination of the spore. This cell-mass, while directly comparable to the corresponding structure in Coleochæte, differs from it in two important particulars. In the first place, a single external layer of cells in the sporophyte of Riccia (Fig. 3, *a*) remains sterile, and, secondly, each cell of the interior sporogenous tissues, instead of producing a single zoöspore, gives rise to four non-motile, thick-walled spores, which do not germinate immediately, but are capable of becoming quite dry without losing their vitality, thus answering physiologically to the single oöspore of the algæ. In short, the resting period is here shortened, owing to the power of the gametophyte to grow on land, and for the protection of the growing sporophyte within the archegonium.

It must be remembered, however, that for fertilization to be effected, the gametophyte must be covered with water, or, as it were, go back to the original aquatic condition, since in all Archegoniates water is necessary for the opening of the sexual organs, as well as for conveying the ciliated spermatozoids to the archegonium.

This amphibious habit of the gametophyte is retained throughout the whole group of Archegoniates, and is even found in the lowest seed plants, *e.g.*, Cycas.

As the archegoniate type becomes better developed, we find a change taking place in the relative importance of gametophyte and sporophyte. While in certain groups like the leafy liverworts and the true mosses there is a considerable amount of specialization in the gametophyte, in other types, especially those which seem to lead up to the ferns, the gametophyte is much simpler in structure, and it is the sporophyte which becomes the conspicuous phase. We must remember, however, that in these forms the sexual organs, archegonium and antheridium, are essentially the same as in the lower liverworts and true mosses, and like them require water in order that fertilization may occur.

As every botanist knows, the fern spore on germination produces, not the fern as we ordinarily understand it, but the inconspicuous liverwort-like gametophyte, or "prothallium," which not only closely resembles in general appearance a simple liverwort, but also bears reproductive organs of very similar structure.

The change in the relative importance of gametophyte and sporophyte has evidently been a very gradual one and is well illustrated in the existing Archegoniates.

It is safe to assume that the most primitive Archegoniates had a sporophyte in which all the cells were sporogenous as they are in Coleochæte, but no such primitive forms are known to exist at present. The simplest known type of sporophyte is that of Riccia (Fig. 3, *a*), already referred to. Here, although a thin peripheral layer of cells is sterile, much the greater part of the sporophyte is composed of sporogenous tissue, all of whose cells produce spores.

There are still existing a number of low liverworts which very clearly show the mode of progression from the simple capsule filled with spores, found in Riccia, to the more highly organised sporophyte of the higher forms. The first step in the development of the sporophyte is the separation of the

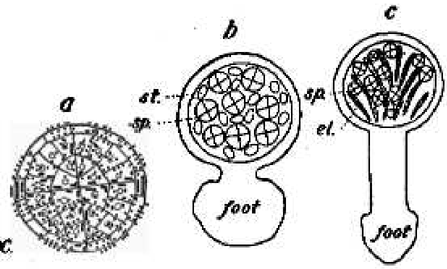


FIG. 3. — Diagram showing the evolution of the sporophyte in the typical liverworts. *a*, Riccia; *b*, Sphærocarpus; *c*, Porella. In Riccia all but the single outer layer of cells produce spores; in Sphærocarpus an absorbent organ or foot is present, and some of the sporogenous tissue remains sterile, forming the sterile cells, *st.*; in Porella a stalk is developed between the foot and the capsule, and the sterile cells within the capsule develop into elaters, *el.*; *sp.*, tetrads of spores.

upper spore-bearing portion from a lower part, which becomes an organ of absorption, — the foot, — and thus the sporophyte begins to assume the character of an individual plant with both vegetative and reproductive tissues. This stage is well shown by the little liverwort Sphærocarpus (Fig. 3, *b*). Here the upper part of the sporophyte becomes differentiated into a globular capsule, with a well-developed wall enclosing the sporogenous tissue, some of whose cells remain undivided and serve to nourish the growing spores derived from the other sporogenous cells.

In the higher liverworts (Fig. 3, *c*) the foot is well developed, and a stalk is usually formed between it and the capsule. In the latter the sterile cells form the curious spirally