FLOWERLESS PLANTS

BY THE LATE

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EXTENSIVELY REVISED BY

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PREFACE TO THE TWELFTH EDITION

IN preparing a new edition of FLOWERLESS PLANTS there have been two aims: the modernization of the work so that it may be generally useful to students as an introduction to Cryptogamic Botany, and the preservation of Scott's unsurpassed exposition of morphology and anatomy. The latter aim has been achieved by making little change in the earlier part dealing with Archegoniate Plants, although for the first time the concept of the haploid and diploid conditions has been introduced and the position of meiosis stressed. The first part is almost pure Scott. To further the other aim, considerable changes have been made in the two chapters on Algæ and Fungi. A number of the types considered in earlier editions do not now normally appear in Botany courses for first-year students, and so it has been thought best to substitute *Fucus* for *Pelvetia*, *Mucor* for *Pilobolus*, to leave out such types as *Ectocarpus*, *Callithamnion*, *Nostoc* and *Puccinia*, and to omit the chapters on Myxomycetes and Flagellata. A considerable number of new illustrations have been added, especially in the chapters on Algæ and Fungi.

The account of *Lycopodium selago*, added by the late Professor F. T. Brooks as an appendix iu the Eleventh Edition, has been incorporated in the body of the book following *Selaginella*.

Thanks are due to Messrs. Longmans, Green & Co. for permission to reproduce two figures (Figs. 125 and 126) from Buller's *Researches on Fungi.*

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INTRODUCTION

LIFE-CYCLES OF FLOWERLESS PLANTS

BEFORE considering a series of types representing the range of structure and life-history encountered amongst Flowerless Plants, certain features concerning life-cycles in general require brief discussion.

In any species of plant the number of chromosomes in each nucleus is either n or $2n$, where n is a number constant for the species. The sexual cells or *gametes* have nuclei with n chromosomes. In the act of fertilization two gametes of opposite sex unite and their nuclei fuse, so that the zygote has a nucleus with $2n$ chromosomes. A cell with a nucleus containing n chromosomes is termed haploid and one with $2n$ is called diploid.

During the course of ordinary vegetative cell-division the number of chromosomes in the nucleus remains unchanged. Thus, when a diploid cell containing a nucleus with $2n$ chromosomes divides both the nuclei of the two daughter cells have $2n$ chromosomes. Similarly if a haploid cell divides the daughter cells are also haploid. Vegetative cell division in which the chromosome number remains unchanged is known as *mitosis.*

In every organism in which a sexual process occurs there is at some stage in the life-cycle another kind of division called *meiosis*. Only a diploid cell containing $2n$ chromosomes can undergo meiosis. In this process the cell divides once and then, immediately, each daughter cell divides again. The result of these two divisions is to give four haploid cells. Meiosis is, perhaps, best defined as two divisions of the nucleus with only one division of the chromosomes. It is an elaborate process and need not be further discussed here. It should be emphasised that the term meiosis refers to the two divisions. The group of four haploid cells, derived by meiosis from a diploid cell, is called a *tetrad.*

In the life-cycle of any organism it is just as important to know where meiosis occurs as it is to know at what point sexual fusion takes place. In plants there are three positions in the life-cycle at which meiosis may happen. Firstly, it may occur at gamete formation. This is known in *Fucus* and in a few other Algæ, but is the normal state of affairs in animals. Where meiosis occurs at this stage the body of the organism is diploid. Secondly, meiosis may take place at the germination of the zygote. If this happens, the plant body is haploid and the zygote is the only diploid stage in the life-cycle. This arrangement is commonly found in the freshwater Green Algæ (*e.g. Spirogyra*). Thirdly, meiosis may be associated with spore production. This is the most usual condition in plants. It is found in many Algæ (*e.g. Laminaria*, *Dictyota*, *Ulva*) and in all green plants above the level of the Algæ. Where meiosis occurs at spore formation the life-cycle is clearly divisible into two parts: a haploid phase or *gametophyte* which bears the sexual organs, and a diploid phase or *sporophyte* on which the spores are produced. The life-cycle is then said to show an *alternation of generations*. Alternation of generations is characteristic not only of liverworts, mosses, ferns, club-mosses, horsetails and seed-plants but also of many Algæ.

CHAPTER I

THE VASCULAR CRYPTOGAMS OR PTERIDOPHYTA

SELAGINELLA KRAUSSIANA

Selaginella is a large genus containing about five hundred species most of which inhabit the damp forests of tropical countries. A few are natives of Europe, and one, *Selaginella selaginoides* (L.) Link, grows in our own country, on boggy moors, or in mountainous districts. Some of the tropical species are grown in hothouses. Both *Selaginella* and the allied genus *Lycopodium* belong to the Class *Lycopodiales* or Club Mosses.

In general appearance the Selaginellas resemble large Mosses, for they have long, usually creeping, stems, thickly clothed with numerous small leaves. With the true Mosses, however, which we shall describe later on, they have nothing whatever to do.

Selaginella is chosen as our first flowerless or Cryptogamic type, because in its reproduction and general course of development the genus comes as near to Flowering Plants as any other Cryptogam[1] now living. In other respects, such as its vegetative anatomy, the structure of *Selaginella* is peculiar to itself. We shall pass rapidly over this part of its organisation, and give most of our attention to the reproductive processes. We will, however, begin by examining the external characters of one or two of the species.

I. *EXTERNAL CHARACTERS*

A. VEGETATIVE ORGANS

Selaginella kraussiana, A. Br.,[2] a native of S. Africa, Madeira, and the Azores, and the commonest species cultivated in greenhouses, has

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[1] The word *Cryptogams*, constantly used for Flowerless Plants, dates from Linnæus, who lived in the eighteenth century. It implies that in these plants the process of fertilisation is hidden, while in Flowering Plants (*Phanerogams*) it is manifest. This distinction no longer holds good, for, with the help of the microscope, fertilisation is at least as easy to observe in Cryptogams as in Phanerogams. The names, however, are still kept up.

[2] Alexander Braun, the authority for the name.

a creeping stem, which, however, rises a little above the surface of the ground (Fig. 1). The main stem is repeatedly forked, and the two branches arising at each bifurcation are alike. From the principal shoots other smaller branches are given off laterally, and these again bear still finer ramifications. The origin of the branches is really the same all through the plant, for all branches are really lateral, but they are formed so near the growing-point that the latter seems to give rise to two equal shoots. In the earlier ramifications both shoots develop similarly, so that we cannot distinguish between the main axis and the branch. This is not so with the later-formed branches, which are evidently different from the axis which bears them. When a growing-point gives rise to two perfectly equal shoots, the branching is said to be *dichotomous*. In *Selaginella*, the branching is not really dichotomous, but it comes very near to being so.

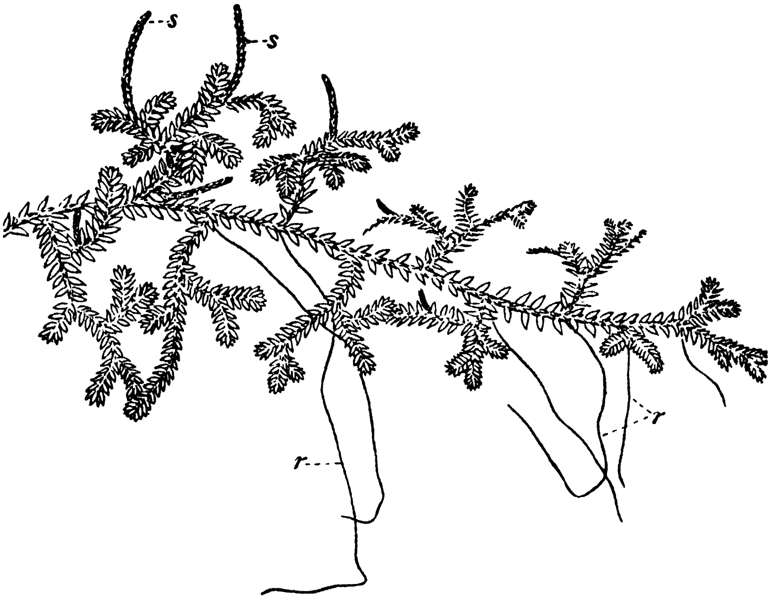

FIG. 1.—*Selaginella kraussiana*; general view. *r*, rhizophores; *s*, spikes or cones. (Reduced slightly.)

The stem bears very numerous small leaves, which are separated by distinct internodes on the older parts, but are crowded together towards the growing-points. The leaves are arranged in four rows, two of which spring from the lower and two from the upper side of the stem. The leaves on the lower side are much larger than those on the upper (see Fig. 2).

The arrangement, if carefully examined, is found to be in pairs, each pair consisting of one of the large lower leaves and one of the small upper ones, which are exactly opposite each other. The leaves live for several years.

Each leaf bears on its upper surface and close to the base, a small membranous outgrowth, *the ligule*, which is best observed on the very young leaves (see Figs. 10 and 16), as it soon withers and disappears. This ligule is characteristic of the whole genus *Selaginella*, and one other living genus, *Isoëtes*, and, unimportant as it seems, is a very ancient character, for it is found in a large group of fossil plants of the coal period (*Lepidodendreæ*).

At each ramification of the stem, a root-like organ is given off, which arises at the side of the stem, just below the fork (see Figs. 1 and 3). These organs, the *rhizophores*, are colourless and destitute of leaves; they grow straight down to the soil and resemble roots, but have no root-caps. On coming into contact with the ground they branch, giving rise to subterranean rootlets, which have root-caps as usual.

If the plant which we examine is fruiting, we shall find that some of the branches, instead of creeping along near the ground, grow straight upwards; it is these vertical branches which form the terminal spikes or cones. The cones bear the reproductive organs; they differ from the vegetative branches in the fact that all their leaves are of the same size (see Figs. 1 and 3).

Other species of *Selaginella* differ very widely from that just described.

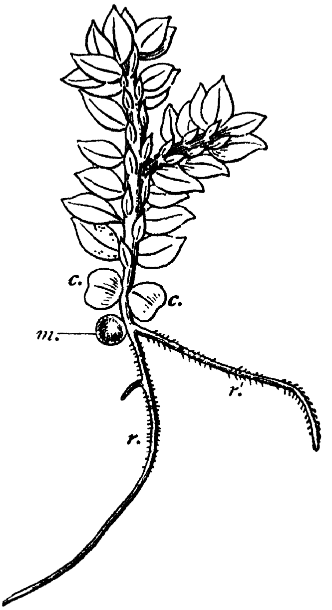

Fig. 2.—*Selaginella kraussiana*; young plant. *m*, megaspore still in connection with plant; *c*, two cotyledons; *r*, main root; *r'*, first lateral root. Note the two kinds of leaves. Magnified 6 diameters. (R.S.)

Some are minute creeping plants of almost microscopic dimensions, with unbranched stems (*S. simplex*); others have climbing stems, which ascend tall trees, and may attain a length of 60 feet (*S. exaltata*); while in others again the stem is stiff and erect, rising vertically to a height of three feet from the ground (*S. grandis*).

A still more important variation is in the arrangement of the leaves. The majority of species agree with *S. kraussiana* and *S. helvetica* (see Fig. 3), in having four rows of leaves, two large and two small, in the vegetative region, while in the spikes all the leaves are alike. In another group, however, to which our native species (*S. selaginoides*) belongs (see Fig. 5), the leaves are all similar, and are arranged spirally, both on the ordinary stem and on the spike. In certain foreign species again, the case is just opposite, for the leaves of the spike, like those of the vegetative stem, are of two kinds.

B. REPRODUCTIVE ORGANS

The *Selaginella* plant is a diploid sporophyte. The reproductive organs are the *sporangia*, containing the spores. Each sporangium is a stalked sac, reaching a diameter of about a millimetre, and is borne in the axil of one of the leaves of the cone (see Figs. 4 and 5).

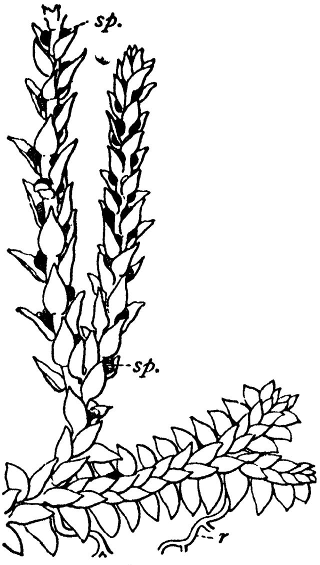

FIG. 3.—*Selaginella helvetica*, showing procumbent stem and two fertile spikes. *r*, rhizophore; *sp*, sporangia. Slightly magnified. (After Dodel-Port.)

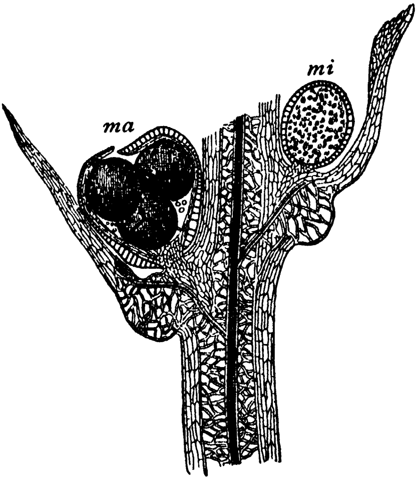

FIG. 4.—*Selaginella helvetica*; part of longitudinal section through spike, showing two sporophylls. *ma*, megasporangium dehiscing; three out of four megaspores visible; note abortive mother-cells; *mi*, microsporangium with numerous microspores. Magnified about 15 diameters. (After Dodel-Port.)

The sporangia are of two kinds: the one kind (the *microsporangium*) contains very numerous small *spores*[1] (*microspores*), comparable in size to pollen-grains. The other kind (the *megasporangium* or *macrosporangium*) contains only four spores, *megaspores* or *macrospores*, but these spores are so large that the sporangium which contains them has to be much larger than that which holds the innumerable microspores (see Fig. 4).

Both kinds of sporangia are borne on the same cone; generally the

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[1] The word *spore* is applied to any single cell which becomes isolated from the parent plant for reproductive purposes.

microsporangia are the more numerous, and occupy the axils of all the upper leaves of the cone, while the few megasporangia are found at the base of the cone only. The arrangement, however, varies in different species. The development and structure of the sporangia will be further described below.

II. *INTERNAL CHARACTERS OF THE VEGETATIVE ORGANS*

a. The Stem

It will be convenient to begin with a short description of the anatomy of our native species, *S. selaginoides*, which, though exceptional in the genus, illustrates several points of importance.

In the upper part of the ascending branches the stem has the structure shown in transverse section in Fig. 6.

There is a single central cylinder traversing the middle of the stem. This is surrounded by a wide intercellular space, which is bridged over at intervals by long radiating cells connecting the stele with the cortex. The latter is thick and of ordinary parenchymatous structure, and is bounded externally by a large-celled epidermis without stomata. Now, returning to the stele, we find the whole interior of the cylinder occupied by solid wood consisting entirely of lignified tracheids. The development of this central mass of wood is also peculiar, for the first-formed elements or protoxylem groups lie at the outside of the wood; in this particular case there are seven such groups, and it is from these points that the development of the xylem starts; so we see that in this stem the wood develops centripetally, just as it does in the root of other plants. This is a very important difference from Flowering Plants.

This centripetal development of the xylem holds good as a general rule for the stems of the Selaginellas and their allies.


FIG. 5.—*Selaginella selaginoides*; fertile spike. Magnified 1½ diameters. (W. C. W.)

Surrounding the xylem is a ring of phloëm, consisting of parenchyma and sieve-tubes, but with no companion-cells. The sieve-tubes, like those of the Conifers, have their sieve-plates on the lateral walls. The whole stele is bordered by a layer of cells containing starch. Outside this layer is the intercellular space. Each of the cells, which stretch across the space, has a Casparian band; these cells represent the endodermis.

This type of stele is a very ancient one: many of the plants of the coal period (*Lepidodendron*, etc.) had a vascular system almost exactly like that of *S. selaginoides*, though on a much larger scale.

From each angle of the stele in *S. selaginoides*, where the protoxylem is situated, a slender bundle runs out to a leaf, which it traverses from end to end without branching.

As we have already mentioned, the structure of this species is exceptional in the genus; its interest lies chiefly in the resemblance to so many fossil forms, from which we may probably infer that it is a very primitive type of structure. A great many Selaginellas, like *S. selaginoides*, have only a single vascular cylinder, or, in other words, are *monostelic*.

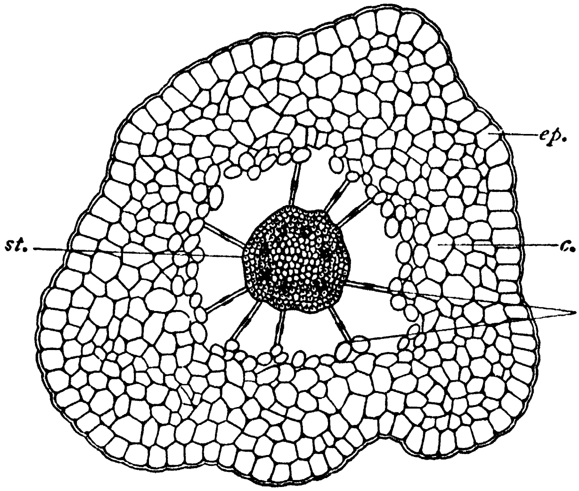

FIG. 6.—*Selaginella selaginoides*; transverse section of stem. *ep*, epidermis; *en*, trabeculæ representing endodermis; *c*, external cortex; *st*, stele; the seven dark groups are protoxylem. Magnified about 35 diameters. (After Harvey Gibson.)

If we now return to the species, *S. kraussiana*, with which we started, we find a totally different arrangement. In this species, the stem is traversed by two parallel steles, each of which has a single protoxylem-group. The structure of these steles, their course through the stem, and their relation to the leaves, are sufficiently indicated in Figs. 7 and 8. In other species the steles are more numerous and are sometimes fused together in a complicated manner. The anatomical peculiarities of the stem of the genus *Selaginella* may be summed up as follows:

(1) The stele usually contains no pith.

(2) The vascular tissue of the stele is not divided into distinct bundles.

(3) The xylem is usually developed centripetally.

(4) In many species there is more than one stele.

As regards the details of the tissues, it is only necessary to add that the tracheids of the protoxylem are annular or spiral. The other tracheids usually have long transverse pits, and are called scalariform (see Fig. 27), from the ladder-like appearance which these pits give to their walls. We shall find this form of tracheid very general among the higher Cryptogams, and shall study it more fully in the Ferns. In one or two species of *Selaginella* true vessels, arising by cell-fusion, occur in the wood.

The growing-point of the stem in *Selaginella* differs from that in Flowering Plants in the fact that the meristem at the apex shows no trace of stratification, *i.e.* of any arrangement in distinct layers In many species, among which is *S. kraussiana*, we find at the apex a single cell, larger than its neighbours, from the divisions of which all the new tissues and organs are ultimately produced. The presence of this single *apical cell*, as it is called, is very general, though not universal, among Cryptogams, and contrasts sharply with the small-celled meristem characteristic of the Flowering Plants. We shall, however, have better opportunities of studying growth by an apical cell when we come to other groups of Cryptogams, so we will defer the further consideration of this subject.

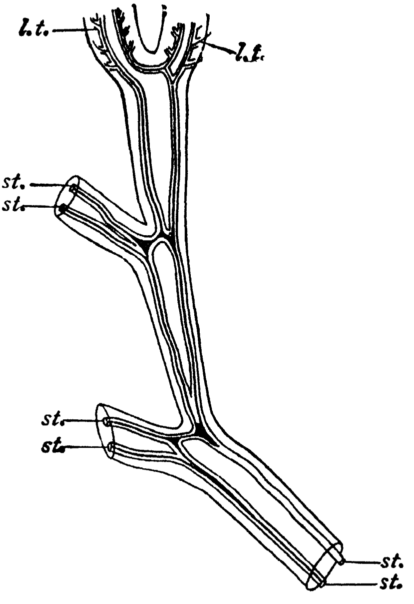

FIG. 7.—*Selaginella kraussiana*; diagrammatic transparent view of stem. *st*, the two steles, anastomosing at base of branches; *l.t*, leaf-trace bundles, only shown in upper part. (After Harvey Gibson.)

b. The Leaves

The leaves of *Selaginella* are of excessively simple structure; each leaf, as we have seen, receives a single vascular bundle from the stem. The bundle traverses the leaf from end to end, forming the midrib;

it has no branches, neither is there any transfusion-tissue, which in Conifers takes the place of the branched veins. The bundle consists of a slender strand of tracheids surrounded by a thin layer of phloëm. Around the whole is a bundle-sheath.

The mesophyll of the leaf is very slightly differentiated, the intercellular spaces being a little larger towards the lower surface. The epidermis, like the mesophyll, contains chlorophyll; the chloroplasts in each cell are few and unusually large.

The stomata, which have the ordinary structure, are usually found on the under-side of the leaf only, and especially in the neighbourhood of the midrib. The membranous ligule at the base of the leaf on its upper surface has already been mentioned.

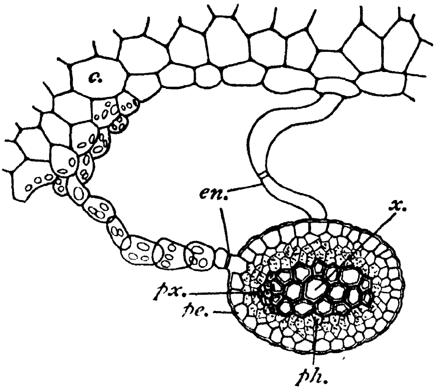

FIG. 8.—*Selaginella kraussiana*; part of transverse section of stem showing one stele. *x*, the wood; *px*, protoxylem; *ph*, phloëm; *pe*, pericycle; *en*, endodermal cells forming the whole or part of trabeculæ; *c*, inner layers of cortex. Magnified about 100 diameters. (After Harvey Gibson.)

c. The Rhizophores and the Roots

The rhizophores in fact may be regarded as roots which have not yet begun to from a root-cap. The anatomical structure is simple, but unlike that in most other roots. There is a single stele, which contains only one group of xylem and one of phloëm. This structure, which may be called *monarch*, is pretty general in *Selaginella* and its allies. It is a very ancient character, for the rootlets of the fossil relations of *Selaginella*, which lived in the Carboniferous epoch, had an almost identical structure. The rhizophore, as distinguished from the root, of *S. kraussiana* is peculiar in having central protoxylem.

III. *REPRODUCTION AND LIFE-HISTORY*

a. The Sporangia and Spores

We have already learnt that *Selaginella* is reproduced by spores which are of two kinds. The organ in which the spores are immediately produced is the *sporangium*. In *Selaginella* a single sporangium is borne in the axil of each fertile leaf or *sporophyll* of the cone. The sporophyll associated with the microsporangium is a *microsporophyll* and that associated with the megaspore is the *megasporophyll.* The cone is a vertical shoot differing but little from the ordinary vegetative shoots of the plant, and bearing many sporophylls (see Figs. 3, 4, and 5).

We will now trace the development of a single sporangium. It does not matter whether we take a microsporangium or a megasporangium, for up to a certain point they develop in the same way.

Each sporangium arises, just below the growing-point of the cone, from the outgrowth of a little group of meristematic cells, situated either exactly in the axil between leaf and stem or rather higher up, on the stem itself. A little ridge of tissue is thus produced, which at first consists of uniform cells. Very soon, however, a few cells in the middle of the young sporangium, lying immediately below its epidermis, begin to be distinguished by their more abundant protoplasm (see Fig. 9, *B*). Only one or two such cells are visible in a radial section such as that shown in the figure. This little group of cells is called the *archesporium,* for ultimately, after much growth and numerous cell divisions, it produces the spores. The archesporium soon becomes surrounded by a well-marked layer of cells, the *tapetum,* formed partly from the surrounding tissue, and partly from the archesporium itself (see Fig. 9, *A* and *B*, *t*). The whole sporangium continues to grow and its cells to divide. At the stage shown in Fig. 9, *A*, it already has a short stalk, and the archesporium has given rise to a many-celled tissue.

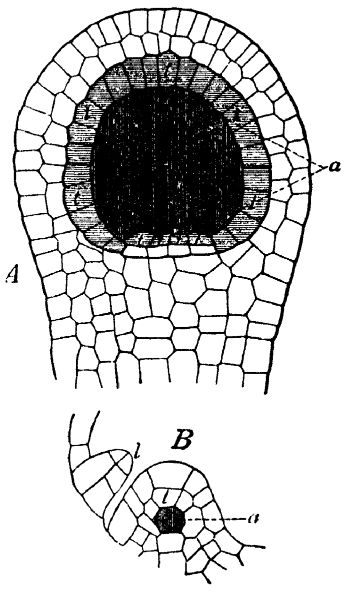

FIG. 9. — *Selaginella selaginoides. A*, young microsporangium in longitudinal section; *t*, tapetum; *a* (darkly shaded), mass of sporogenous cells derived from archesporium. *B*, very young megasporangium; *t*, tapetum; *a*, archesporium; *l*, ligule of sporophyll. Magnified about 300 diameters. (After Goebel.)

Up to this point both kinds of sporangia behave exactly alike. The reader will at once see that, thus far, the development of the young sporangium is in all respects similar to that of a pollen-sac.

Henceforth it will be necessary to distinguish between a microsporangium and a megasporangium. We will first describe the former.

The divisions of the archesporial cells of a microsporangium give rise to a mass of spore-producing tissue, each cell of which now rounds itself off and becomes a *spore mother-cell.* The spore mother-cells, like the other cells of the plant, are diploid. Each now undergoes meiosis, thus producing four haploid cells. The four daughter-cells become the *microspores*. Each group of four is tetrahedrally arranged. The microspore acquires a cell-wall of its own, the outer layer of which is thickened and cuticularised.

The microsporangium is now ripe, and the space within is filled with microspores (Fig. 10), for the mother-cell walls have broken down.

We see that in every respect the *microsporangium*, throughout its whole development, closely resembles a *pollen-sac*, while the *microspores*, in their structure and mode of origin, precisely correspond to the *pollen-grains*.

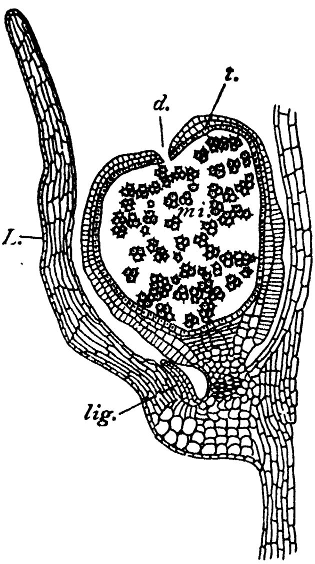

FIG. 10.—*Selaginella selaginoides*; microsporangium in radial section. *L*, sporophyll; *lig*, ligule of sporophyll; *mi*, microspores still grouped in tetrads inside the sporangium; *t*, persistent tapetum; *d*, place of dehiscence. Magnified about 40 diameters. (R. S.)

We will consider the further destiny of the microspores later on, and will now pass to the megasporangium.

Up to the time when the spore mother-cells become isolated from one another, the development of the megasporangium goes on in just the same way as that of the microsporangium. Now, however, a striking difference manifests itself. In the megasporangium, out of all the numerous mother-cells, only a single one undergoes meiosis; all the rest remain undivided and are abortive (see Fig. 4).

The one favoured mother-cell divides into four tetrahedrally arranged haploid daughter-cells; each daughter-cell becomes a *megaspore*. The four megaspores develop enormously, and gradually displace and absorb all the remaining mother-cells, which, however, can be seen for a long time lying inert in the sporangial cavity. The four megaspores, as they grow, gradually take possession of the whole interior of the sporangium, which itself grows to a greater size than the microsporangium (see Figs. 4 and 11). The megaspores acquire greatly thickened cell-walls, the outer layers of which are cuticularised, and often have a rough and warty surface.

We see then that a megasporangium differs from a microsporangium in the fact that only one mother-cell divides, and that its daughter-cells occupy the whole sporangium, which thus contains four spores only.

The megaspores, the diameter of which is about twenty times that of the microspores, attain their great dimensions at the expense of the abortive mother-cells.

We cannot understand the relation of the microspores and megaspores to each other, or to the reproductive cells of Seed Plants, until we are made acquainted with their further history. We will therefore now go on to describe the changes which take place in the spores, on their germination.

b. Germination of the Microspores

The microsporangium, when ripe, opens by longitudinal dehiscence, the wall splitting along a line parallel to the surface of the adjoining leaf (see Fig. 10). The microspores are set free violently and thereby scattered, and if they fall on damp earth germination takes place.

The first thing that happens is that the spore divides into two cells of very unequal size. A very small cell is cut off on one side of the spore (see Fig. 12, *A*, *p*). This little cell takes no further part in the development, and may be called the *prothallus-cell*. The large cell now divides into two equal parts (see Fig. 12, *A*); each half undergoes several further divisions. The final result is that we find the spore divided up into about a dozen cells. One of these is the little prothallus-cell first formed, which remains unaltered. Of the remainder, eight form an external layer, within which the central cells are enclosed, their number being either two or four according to the species. In *S. kraussiana* there are four (Fig. 12, *B*, *c*). While these divisions are in progress, the spore grows a little, becomes more spherical, and bursts its outer hard membrane, so that its contents are now enclosed only by its inner cellulose wall. The central cells next undergo several successive divisions; the small cells thus formed become rounded and lie freely in the space enclosed by the external layer (Fig. 12, *C*). At this stage the haploid male prothallus derived from the microspore consists of a prothallial cell and an antheridium. The wall of this consists of

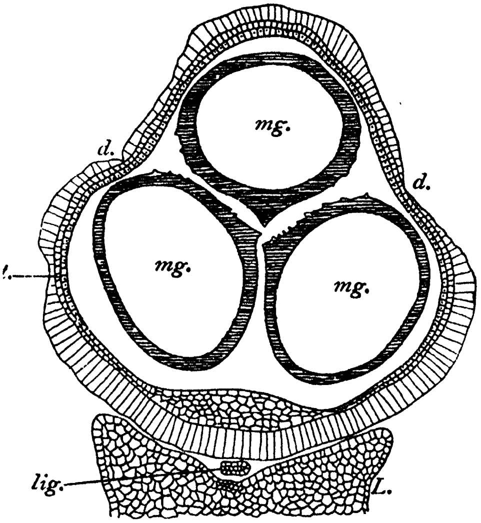

FIG. 11.—*Selaginella selaginoides*; megasporangium from same cone in tangential section (transverse to sporophyll); *mg*, megaspores, three out of the four are visible; *t*, persistent tapetum; *d*, line of dehiscence; *lig*, ligule; *L*, sporophyll. Magnified about 40 diameters. (R. S.)

a layer of cells and within this wall are the sperm mother-cells. Subsequently the wall-cells become disorganised, their contents contributing to the nutrition of the central group. The prothallus-cell, however, persists all through. The round central cells (sperm mother-cells) are alone concerned in the further development.

When the external layer becomes disorganised, its cell-walls disappear and the contents flow together into a structureless mass, in which the round cells are embedded. In the meantime important changes go on in the contents of these cells. The large nucleus, which each cell contains, becomes converted into a long, rather club-shaped body, which has a spiral twist. At the thin end of this body there is a little cytoplasm, and at this point two excessively fine cytoplasmic threads are attached (see Fig. 12, *D*). The whole body now constitutes a *spermatozoid*, and the cytoplasmic threads are its *cilia* or *flagella*. The cell in which a spermatozoid is formed is called its *mother-cell*. The surrounding cells having completely broken down, the spermatozoid mother-cells are let loose into the water, for the whole process of the germination of the microspores can only go on in water. The microspores are, however, so small that a very little water is sufficient, such as we should find on the surface of the ground after rain or heavy dew.

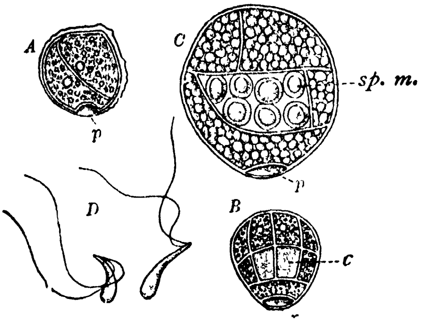

FIG. 12.—*Selaginella*; germinating microspores. *A*, young stage; *p*, prothallus-cell; first wall formed in antheridium. *B*, more advanced stage; *c*, central cells which will form spermatozoids. *C*, mature stage; *sp. m*, spermatozoid mother-cells, surrounded by cells of wall of antheridium. *D*, free spermatozoids, each with two cilia. *A*, magnified 290 diameters; *B*, magnified 290 diameters; *C*, magnified 640 diameters; *D*, magnified 780 diameters. (After Belayeff.)

The spermatozoids next become free from their mother-cells, the walls of which dissolve. As soon as the spermatozoids are at liberty, or even sooner, their cilia begin to lash about in the water, and when free the spermatozoid sets off in active locomotion. The movement is a double one: the spermatozoid travels through the water with its narrow ciliated end foremost, and at the same time it rotates about its own axis.

We must remember that the spermatozoids are of a very minute size; the body is about 0.012 mm. long, the cilia about twice that length.

The spermatozoids are the bodies which perform the act of fertilisation. Each spermatozoid corresponds to one of the generative cells in the pollen-tube of Flowering Plants. We know that the generative cell chiefly consists of a very large nucleus, with only a little cytoplasm. This is also true of the spermatozoid, which is all nucleus, except the small part at the pointed end and the cilia, which are cytoplasmic. The spermatozoid is an actively moving cell, which swims off on its own account, and may eventually find its way to an ovum. It thus differs from the generative cell of the higher plants, which, except in some of the Gymnosperms, is conveyed passively to its destination by the growth of the pollen-tube.

c. Germination of the Megaspores

Unlike the microspores, the megaspores of *Selaginella* begin to germinate while still in the sporangium. Each of the four megaspores is tetrahedral in shape, like a microspore. It contains at first a single haploid nucleus and abundant cytoplasm, in which is a large vacuole containing oil. The nucleus lies near the angle, where the megaspore joins its three sister-cells. We will call this angle the *apex* of the megaspore. The first sign of germination is the division of the nucleus into two. The divisions are repeated many times, and soon cell-walls begin to appear in the cytoplasm, between the daughter-nuclei. The cell-formation is at first limited to the apical part of the spore, but it gradually spreads downwards and inwards. In Fig. 13 a megaspore is shown which is already nearly half filled with tissue. As a rule, the cell-division extends so far that the tissue fills the whole cavity of the spore. In some species this process is completed even before the megaspores are set free from the sporangium, while in others the lower part of the tissue is developed after the spores have fallen on the ground.

The tissue which fills the megaspore is called the *prothallus.* The prothallus, which is haploid, gives rise to the *archegonia,* or female organs. A cell at the apical end of the prothallus grows larger than the rest, and divides into two by a wall parallel to the outer surface. The upper cell divides by two longitudinal walls, crossing each other at right angles, into four, and each of these four cells divides by a transverse wall into two. Thus a neck is formed, consisting of eight cells arranged in two tiers (see Fig. 14, *n, n*). (Of course only four of the cells can be seen in longitudinal section.)

In the meantime the lower cell, which has so far remained undivided, forms an outgrowth which penetrates between the cells of the neck. This outgrowth is cut off as a distinct cell, called the *neck canal-cell.* Another smaller cell, the ventral canal-cell, is cut off below it; the remaining lower portion of the original central cell is the *ovum* (cf. Fern-archegonium, Fig. 40). In *Selaginella* a real canal is formed, for the canal-cells break down, and an open passage, containing only mucilage, is left between the cells of the neck leading down to the ovum within (see Fig. 14).

The first archegonium is sometimes formed before the megaspore is shed.[1] After the dehiscence of the megasporangium, which takes place violently[2] by a longitudinal slit, the megaspores are shed on the ground. The growth of the prothallus continues, the coats of the megaspore are ruptured at its apical end, and so the upper part of the prothallus becomes exposed, turns green, and grows a little beyond the limits of the megaspore (see Fig. 15).

Other archegonia are formed around the first one, and a few rhizoids grow out from the prothallus. Thus the prothallus is the gametophyte and, like most gametophytes, is haploid.

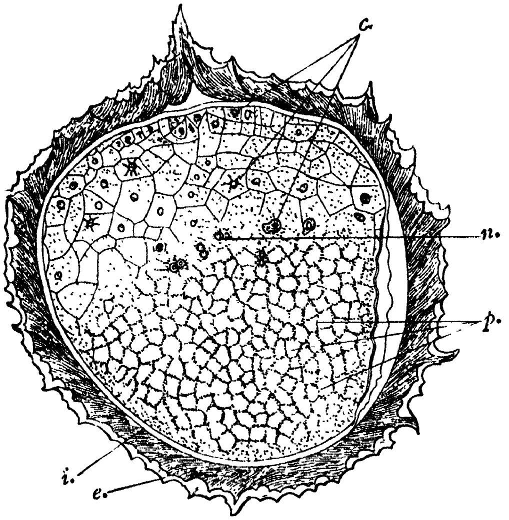

FIG. 13.—*Selaginella martensii*; germinating megaspore. *c*, cellular tissue of prothallus, only complete in upper part of spore; *n*, free nuclei; *p*, undivided protoplasm of spore forming a network; *i*, inner, *e*, outer, layer of cell-wall of spore. Magnified 335 diameters. (After Heinsen.)

d. Fertilisation and Embryology

The archegonia are fertilised by spermatozoids; this takes place under water. The spermatozoids, when liberated from the ruptured antheridia, swim actively through the film of water covering the damp earth, and some of them are attracted to the archegonia of any female prothallus which lies near enough. The probable nature of the attraction will be considered when we come to the Ferns (see p. 49). At this time the mucilage formed from the disorganised canal-cells not only fills the canal of the archegonium, but spreads a little beyond its opening (see Fig. 14, *m*). The details of fertilisation are not so well

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[1] It has occasionally been observed that fertilisation takes place and the embryos develop while the megaspores are still retained in their sporangium.

[2] The mechanism of spore discharge is the same in both microsporangium and megasporangium, and is clearly similar to the mechanism of the fern sporangium which will be described later.

known in *Selaginella* as in the Ferns, but there is no doubt that the spermatozoid becomes caught in the mucilaginous drop and then passes down through the canal to the ovum below. In other plants it has been proved that the spermatozoid unites with the ovum, the nucleus of the former fusing with that of the latter.

The fertilised ovum is, of course, diploid. It surrounds itself with a cell-wall of its own, and soon divides by a transverse septum into two cells. The upper cell, *i.e.* that lying next to the neck of the archegonium, becomes the suspensor, which may undergo a few further cell-divisions (see Figs. 15 and 16, *S*). The lower cell develops into the embryo itself. Owing to the growth of the suspensor in length, the embryo is carried deep down into the tissue of the prothallus (see Fig. 15). The embryonic cell undergoes segmentation, and very soon the first organs of the embryo are marked out. The two first leaves or cotyledons lie on either side of the stem apex. One side of the hypocotyl grows out into a temporary organ, the *foot* (see Figs. 15 and 16). This organ serves to absorb food for the young plant from the tissues of the prothallus. The first root appears a little later, between the foot and the suspensor. Fig. 15 gives a general idea of the position of these organs, and their relation to the prothallus. In Fig. 16 a slightly more advanced embryo is shown in greater detail. At this stage the young stele, consisting of procambial tissue, can already be traced from the apex of the stem to that of the root. It will be noticed that the cotyledons, like all the other leaves of the plant, possess ligules.

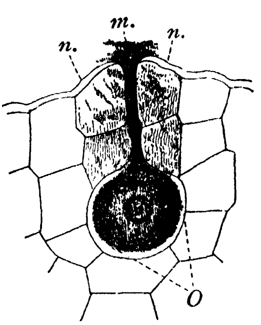

FIG. 14. — *Selaginella*; archegonium ready for fertilisation. *O*, ovum; *n*, cells of neck; *m*, mucilage in canal. Magnified about 500 diameters. (After Pfeffer.)

The stem begins to branch while the embryo is still enclosed in the prothallus. A young plant of *Selaginella kraussiana* after germination is shown in Fig. 2. It is still attached by its foot to the megaspore, or rather to the prothallus inside it.

Comparison between Selaginella and the Gymnosperms

At first sight the differences between even the highest Flowerless Plants, such as *Selaginella*, and the Seed Plants, seem so great that we see little in common between them. In the Cryptogams we find no obvious flowers and no seeds, while fertilisation takes place in a totally different way from that which prevails among typical Phanerogams. If, however, we carefully compare the development of *Selaginella* with that of a Gymnosperm, we shall find it quite possible to trace the corresponding stages in their life-history; and, having accomplished this for the Gymnosperms and the higher Cryptogams, it will not be impossible to extend the comparison further so as to include the Angiosperms on the one hand, and the simpler Cryptogams on the other.

We have found that the development and structure of the microsporangium of *Selaginella* agree very closely with that of a pollen-sac in the Seed Plants. The microspores produced in the former are developed precisely in the same way, and have the same essential structure as the pollen-grains formed in the latter. When the microspore germinates it begins by cutting off a little inactive cell (the prothallus-cell), and the pollen-grain of a Gymnosperm does the same. The subsequent divisions lead to the formation of the spermatozoids in the Cryptogam, and of the generative cells in the Gymnosperm. In both cases these are the bodies which effect fertilisation. That the generative cells are homologous with spermatozoids has long been recognised. In a few of the Gymnosperms the generative cells become converted into actively moving spermatozoids comparable to those of the Ferns. The antheridium, *i.e.* the organ in which the male cells are formed, is more complex in *Selaginella* than in the Gymnosperms, for in the latter it has almost become reduced to its most essential part, the generative cells themselves. The comparison of the development gives us then the following chief results:

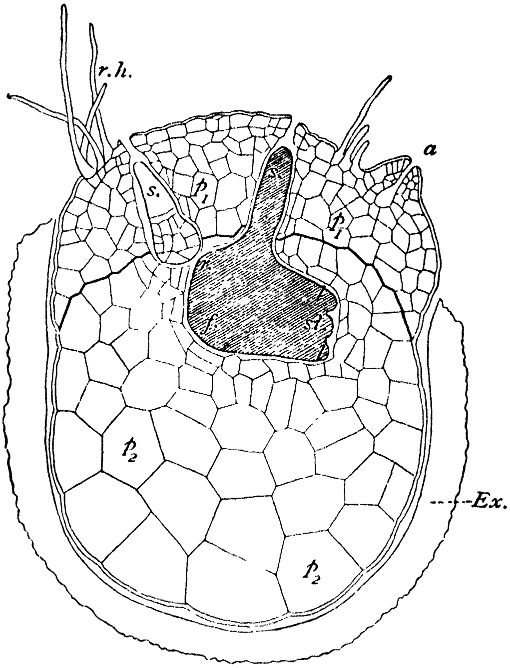

FIG. 15.—*Selaginella martensii;* longitudinal section through old prothallus showing two embryos. p_1 and p_2, prothallus; *a*, unfertilised archegonium; *r.h*, rhizoids; *s*, suspensors of embryos; larger embryo shaded, no cells shown; *r*, root; *f*, foot; *st*, stem; *l*, *l*, cotyledons; *Ex*, wall of megaspore. Magnified 165 diameters. (After Pfeffer.)

Selaginella.		*Gymnosperm.*
1. Microsporangium	=	Pollen-sac.
2. Microspore	=	Pollen-grain.
3. Spermatozoids	=	Generative cells.

The female prothallus of *Selaginella* corresponds to the female prothallus (endosperm) of a Gymnosperm. The only real difference is that in *Selaginella* the prothallus grows a little way out from the megaspore, becomes partly green, and forms a few rhizoids. It is, in fact, a more independent structure in the case of the Cryptogam, developing freely on the ground, instead of within the closed tissues of the ovule.

Now the cell in which the prothallus of *Selaginella* develops is the *megaspore*, while that in which the "endosperm" of a Gymnosperm arises is the *embryo-sac*. We therefore arrive at a new term in the comparison; the megaspore is the equivalent of the embryo-sac.

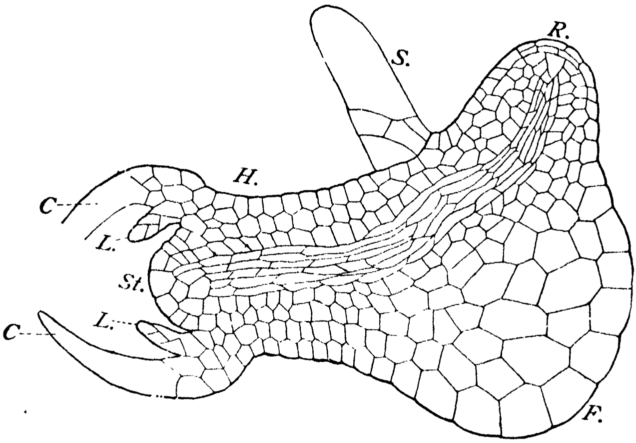

FIG. 16.—*Selaginella*; advanced embryo in longitudinal section. *S*, suspensor; *R*, root; *F*, foot; *C*, cotyledons (cell-walls omitted); *L*, ligules; *St*, apex of stem; *H*, hypocotyl. Magnified 165 diameters. (After Pfeffer.)

There are some differences, however, to be dealt with at this point: in normal cases the megaspore is set free and completes its development on the ground, while the embryo-sac remains always enclosed in the ovule or seed. We must remember, however, that the megaspore itself begins its germination while still in the megasporangium, and, in exceptional cases, even the embryo-plant may be developed in this position. The thick cuticularised wall of the megaspore is obviously a necessity for its protection when it becomes freely exposed.

A more serious difficulty is that there are four mesgapores in *Selaginella*, and only one embryo-sac in the Gymnosperm. In most Gymnosperms the three sister-cells of the embryo-sac become abortive at an early stage of their development, as is the case also with the sister-cells of the fertile megaspore in some fossil relations of *Selaginella*, exceptionally in species of *Selaginella* itself, and constantly in the heterosporous Water-Ferns.

The organ in which the megaspores are produced is a megasporangium; that in which the embryo-sac develops is the ovule. Both organs arise in the same way from a group of cells near the growing-point. We infer, then, that the megasporangium corresponds to the ovule, or more strictly to the nucellus of the ovule, for the megasporangium has no integument.

We have found, however, that the megasporangium and microsporangium are just alike in the earlier stages of their growth; the former, as we have seen, corresponds to the nucellus of an ovule, the latter to a pollen-sac. Hence we must draw the conclusion that a pollen-sac and the nucellus of an ovule are equivalent structures—a result which could only have been arrived at by a comparison with Cryptogams. We may sum up our inferences as to the relations of the female organs in the two types thus:

Selaginella.		*Gymnosperm.*
1. Ovum	=	1. Ovum.
2. Archegonium	=	2. Archegonium.
3. Prothallus	=	3. Endosperm.
4. Megaspore	=	4. Embryo-sac.
5. Megasporangium	=	5. Nucellus of ovule.

If we try to carry this comparison farther, and to find the equivalent in the Cryptogam of the carpels and stamens of the Seed Plant, we find that the microsporophyll corresponds to the stamen and the megasporophyll to the carpel.

We see then, that although Cryptogams and Phanerogams appear to differ so completely from one another, we can yet successfully compare them together and determine the relations between their organs.

Organs which resemble each other in their development and their place in life-history, so that we regard them as morphologically the same organ, are said to be *homologous* one with another. Organs, on the other hand, which are morphologically different, but are adapted to the same physiological function, are said to be *analogous*. In our comparison between *Selaginella* and a Gymnosperm we have aimed at establishing the *homologies* of the various organs; such comparisons are essential in order to determine the relationships of different groups of plants, for it is only by tracing the homology or morphological equivalence of organs that we can form any idea of the probable modifications which may have taken place during the course of descent.

The proof in 1851 that the reproductive organs in Flowering Plants and Pteridophytes are homologous was due to the German botanist

Hofmeister, and is one of the greatest discoveries ever made in morphology. We have every reason to believe that the Seed Plants are descended from Cryptogams, which resembled *Selaginella* in having two kinds of spores. Their actual ancestors, however, which have been extinct for millions of years, were no doubt totally different in all other respects from any Cryptogams now living.

One point remains: we have not yet considered the homologies of the seed. One part of the seed, the testa, is not represented in *Selaginella*, for the megasporangium is without integuments. The megasporangium itself corresponds to the nucellus of an ovule, as we have already seen, but it never develops into anything of the nature of a seed. This is because the megaspores are normally set free from the megasporangium before fertilisation takes place, so that the seed-stage is never reached. The megaspore, when it is filled with prothallus and contains an embryo, bears a certain resemblance to a seed, but there is no complete homology; for, as we have already seen, the development shows that the megaspore is homologous with the embryo-sac only.

The typical seed, such as we find in the Flowering Plants, represents a persistent, integumented megasporangium, containing a single megaspore, which produces a prothallus, and, after fertilisation, an embryo, while still *in situ*. The shedding of the seed thus corresponds to the detachment of the entire megasporangium, together with its integument and contents. Bodies closely analogous with seeds are found in some fossil Lycopods allied to *Selaginella*, but the true seeds of the higher plants appear to have been evolved from other stock.

LYCOPODIUM SELAGO

In describing *Selaginella kraussiana* (p. 1) it was pointed out that *Selaginella* and *Lycopodium* are the chief living genera of the Class of Vascular Cryptogams (Pteridophyta) known as the *Lycopodiales* or Club Mosses, a Class which was a dominant feature of the vegetation of the world in remote geological ages, *e.g.* when the Coal Measures were being formed. Although closely related to *Selaginella*, *Lycopodium* differs in important respects, so it is desirable to describe it in order to make our account of the Club Mosses more complete. *Lycopodium* comprises some hundred species most of which live in the tropics or sub-tropics either as terrestrial plants or as epiphytes. Only a few species occur in Britain, and these are rarely abundant except locally. The species we shall describe is *L. selago* L., which is confined to moorland tracts in mountainous districts of this and other parts of the world, often at a considerable elevation.

I. *EXTERNAL CHARACTERS*

A mature plant which, as in *Selaginella*, is a diploid sporophyte, is about three to six inches high and consists of a short prostrate base, from which the slender forked roots arise, and stiffly erect shoots which branch dichotomously (see Fig. 17).

The stems bear crowded small green leaves of simple form, spirally arranged. The leaves are stiff and terminate in a sharp point; they are attached to the stem by a rather broad base. The leaves, as in all species of *Lycopodium*, have no ligule, and in this respect are unlike those of *Selaginella*. In an oldish plant a small yellowish blob will be seen in the axils of most of the upper leaves. These blobs are the sporangia, which, unlike those of *Selaginella*, are all of one kind. The distribution of the sporangia on the erect shoots is somewhat varied:

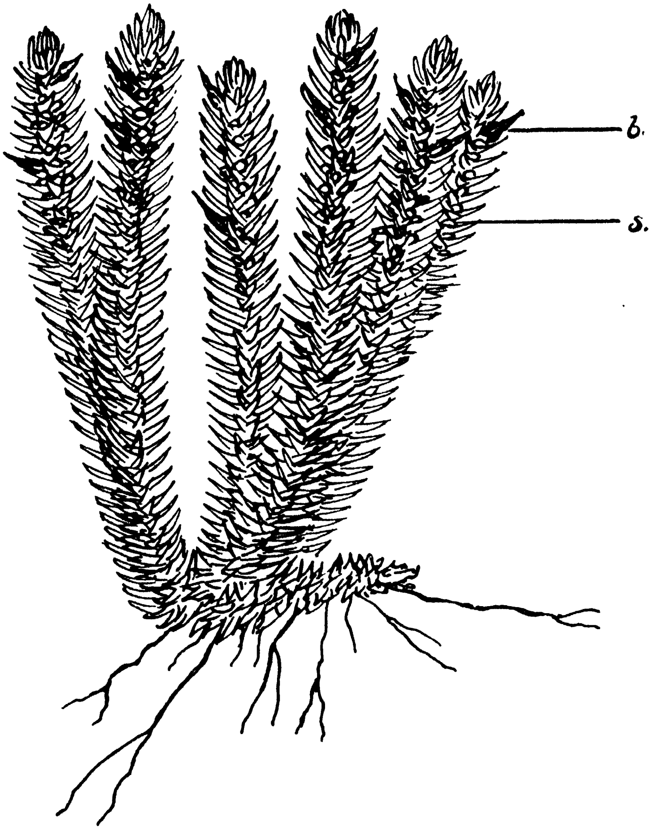

FIG. 17.—*Lycopodium selago*; mature plant. *b*, bulbil; *s*, sporangium. (W. J. Dowson.)

of the spiral (see Fig. 21, *c*). Everyone who has ever watched a Fern coming up in spring must have noticed the form of the young leaves. Each leaflet is coiled up in a similar way. This mode of folding of the young leaf is called *circinate* or crosier-like *vernation*, vernation being a general word for the folding of a leaf in the bud. When the leaf finally expands, the inner side grows more rapidly than the outer, so that the curves become straightened out. Circinate vernation is characteristic of the Ferns generally. The leaves usually die in winter.

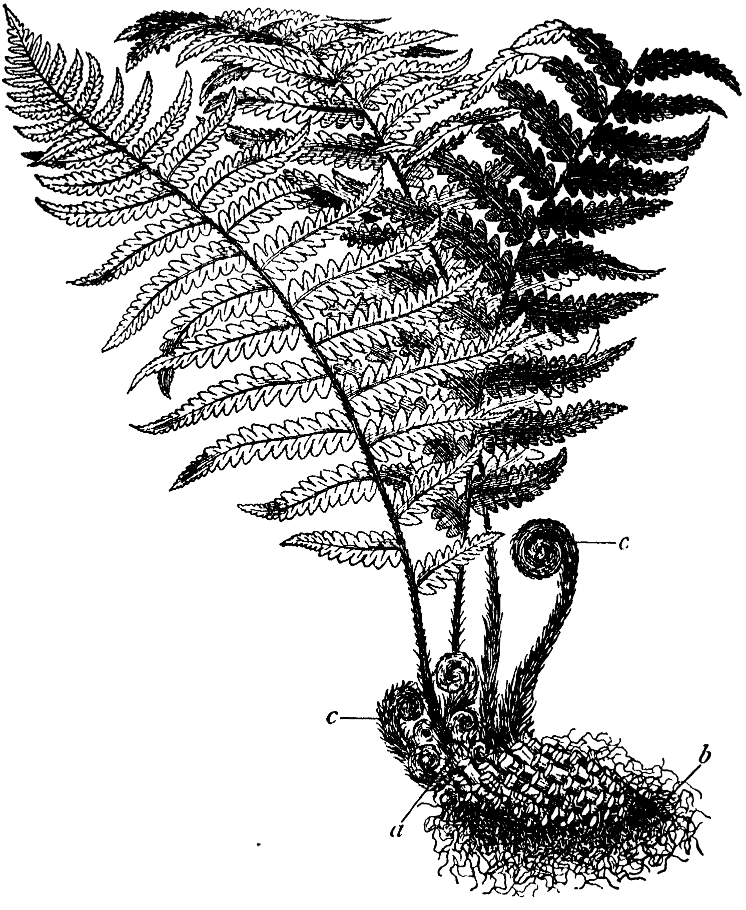

FIG. 21.—General view of the Male Fern. *a*, apex; *b*, base of stem, which is covered with the remains of old leaves, and bears numerous adventitious roots; *c*, *c*, young leaves, showing circinate vernation. Greatly reduced.

The branching of the stem in this Fern is peculiar; no branches at all are formed at the growing-point, but buds arise on the petioles of some of the leaves, springing from their outer sides a little above the base. These buds, though their first origin takes place very early, only develop into branches at a much later time, and often not until the upper part of the leaf has died off. Few branches are formed in this particular Fern.

Ferns vary very much as regards their branching; in some, as in the Bracken Fern, the stem forks at the apex; in a few, as in some Filmy Ferns, the branching is axillary like that of Flowering Plants, while in others, as in some of the Tree Ferns, the stem does not branch at all.

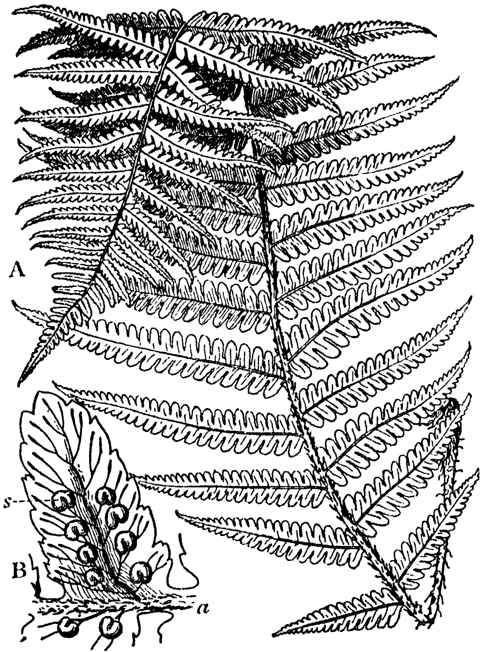

Fig. 22.—A, leaf of Male Fern (much reduced). B, part of a fertile pinna seen from below; *a*, midrib; *s*, sorus. Magnified. (After Luerssen.)

The *roots* which we find on an ordinary full-grown plant are all adventitious, for the original main root of the embryo dies away very early. The adventitious roots, which arise at the bases of the leaves, usually three below each leaf, are very slender and much branched. An old stem is densely clothed with a matted growth of adventitious roots (see Fig. 21).

B. Reproductive Organs

The ordinary Fern plant, such as we have described, is purely asexual. Like *Selaginella*, it is a diploid sporophyte and bears sporangia only, but, unlike that genus, the sporangia and the spores which they contain are all of one kind. The sporangia of the Male Fern and of most other Ferns are borne on the lower surface of the ordinary foliage leaves, so that here there is no difference between vegetative leaves and sporophylls.

If we examine one of the fertile leaves in summer, the clusters of sporangia, or *sori*, as they are called, are very conspicuous on the under-surface. They are usually absent from the basal part of the leaf. On the larger segments, the sori are arranged in two short rows, one on each side of the midrib (see Fig. 22, B), while on the smaller segments there may be only one or two sori altogether. Each sorus is covered by a kidney-shaped membranous envelope called the *indusium*, and is seated just over one of the lateral veins. The individual sporangia which cannot be distinguished without the aid of a lens, are very numerous in each sorus, and every sporangium contains a large number of spores.

On germination, each spore gives rise to a *prothallus*, which is a much larger structure here than in *Selaginella*, and leads quite an independent existence (see Fig. 36). The prothallus is a flat, green, heart-shaped body, sometimes as much as half an inch in diameter, attached to the soil by the rhizoids, on its under-surface. Prothalli may be found in abundance covering the damp ground where Ferns are growing. In Ferns the same prothallus usually bears both kinds of sexual organs, the antheridia and archegonia. After fertilisation the ovum formed in one of the archegonia becomes an embryo, which eventually grows up to be a new Fern plant.

In Ferns, then, we have, in normal cases, a sharp *alternation of generations*. The Fern plant is the asexual generation, or *sporophyte*, producing the sporangia, and ultimately the spores. The prothallus is the sexual generation, or *gametophyte*,[1] producing the antheridia and archegonia, in which the sexual cells are developed.

The sporophyte is diploid and the gametophyte is haploid. Meiosis occurs at spore formation.

II. *INTERNAL STRUCTURE OF THE SPOROPHYTE*

A. The Vegetative Organs

1. The Stem or Rhizome

a. The Vascular System

In the Male Fern and most other Ferns a single simple stele (*protostele*) is present only when the stem is still quite young. As the growing-point strengthens, and the crowded leaves are formed, a very complex structure is gradually built up so that a network of vascular strands or *dictyostele* arises. In fact the simple *protostelic* structure is only found at the very base or oldest portion of the stem; this part soon dies away altogether, so the whole stem of a Male Fern, as soon as it is once fairly established in the ground, is dictyostelic. This is true for the majority of Ferns, but a few retain a protostelic structure throughout life.

If we examine with the naked eye, or with the aid of a lens, the transverse section of the mature stem of the Male Fern, we see the cut ends of the apparently separate steles, embedded in ground tissue (see Fig. 25).

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[1] The word *gamete* means a sexual cell.

In order to understand the arrangement it is necessary to make a dissection, carefully removing the parenchyma and leaving behind the vascular skeleton only. Such a preparation is shown in Fig. 24. The apparently separate steles form a hollow network, with large diamond-shaped meshes. Each mesh corresponds to the base of a leaf; the strands bordering the mesh give off branches, the leaf-traces, which enter the petiole (see Figs. 23, 24). As the leaf-traces of the Male Fern cover the surface of the stem, and no internodes are developed, every transverse section must necessarily be surrounded by the bases of leaves, cut across at various levels, and showing the stelar tissues entering them from the stem (see Fig. 25).

FIG. 23.—Longitudinal section of small stem of Male Fern. *a*, apex; *l*, *l*, bases of leaves; *st*, stem; *g*, leaf gap. Natural size. (After Sachs.)

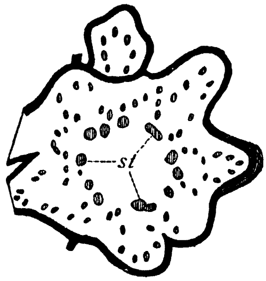

FIG. 25.—Transverse section of stem of Male Fern, showing the bases of leaves. *st*, principal strands of the stem. (After De Bary.)

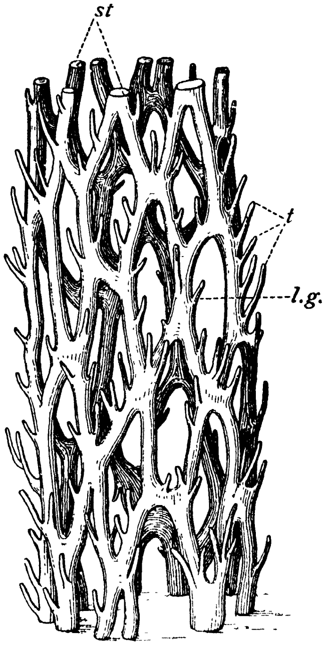

FIG. 24.—Stelar system of the Male Fern dissected out. *st*, principal strands of the stem; *l.g*, leaf gap corresponding to the insertion of a leaf; *t*, strands passing out into the leaf. Magnified. (After Reinke.)

Every strand of the stele consists of a central mass of wood surrounded by a somewhat incomplete ring of phloëm (see Fig. 26). This arrangement is usual in Ferns, and vascular strands of this kind are often called concentric bundles. Each of them almost exactly repeats the structure of the whole vascular cylinder of the embryonic stem.

The wood consists of tracheids and parenchyma; the tracheids of Ferns are generally of the kind called *scalariform*, or ladder-like, from the peculiar structure of their walls, shown in Fig. 27. This structure depends on the form of the pits, which are slightly bordered and much elongated in the transverse direction, so that the thickened ridges between them resemble the rungs of a ladder.

In the strand figured (see Fig. 26) there is only one group of protoxylem (*px*) lying on one side of the wood. In the larger strands of the stem there are usually two or three such groups. Spiral tracheids occur at these points, but usually become destroyed very early as the stem grows in length. Surrounding the wood is a layer of parenchyma containing starch, and then we come to the phloëm-zone, consisting of sieve-tubes and parenchyma. The former have their sieve-plates on the lateral as well as on the oblique terminal walls.

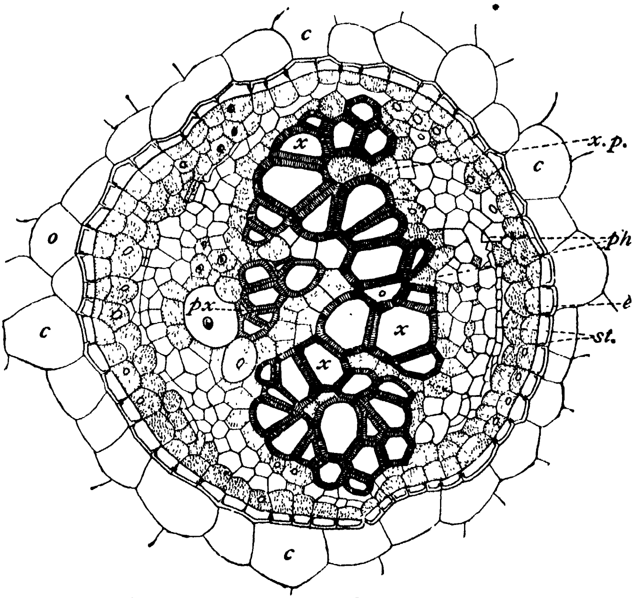

FIG. 26.—Transverse section of small strand or bundle from petiole of Male Fern. *c*, *c*, cortical cells; *e*, endodermis; *st*, starch sheath, made up of inner endodermis and pericycle; *ph*, phloëm; *x*, *x*, xylem; *px*, protoxylem; *x.p*, xylem-parenchyma. Magnified 200 diameters. (R. S.)

The phloëm again is surrounded by a belt of parenchyma very rich in starch, beyond which we come to the endodermis. The endodermis is really two cells thick, but its inner layer cannot be distinguished from the pericycle except by the fact that its cells fit on exactly to those of the outer endodermal layer. This outer layer alone has the usual structure of an endodermis and becomes thick-walled.

β. *Other Tissues of the Stem*

The great mass of the ground-tissue, in which the steles are embedded, consists of ordinary parenchyma containing abundant starch. The outer cells have thicker walls, and those nearest the epidermis are narrow and fibrous. The epidermis itself has a thick brown outer wall, and otherwise presents no peculiarities. It bears flat chaffy scales, or *ramenta*, which are very characteristic of the plant, and indeed of almost all Ferns. They are sometimes of large size, reaching half an inch in length, and consist of a plate of tissue one cell thick, attached to the epidermis at one end; they arise each from the growth and division of a single epidermal cell.

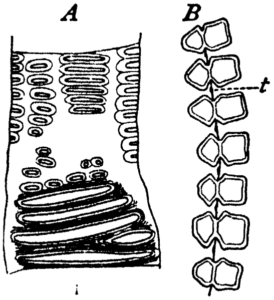

FIG. 27. — Portions of scalariform tracheids. *A*, part of wall in surface view. Magnified 187 diameters. *B*, part of wall in section, showing bordered pits; *t*, torus on closing membrane. Magnified 375 diameters. (After De Bary.)

2. The Leaf

As we have seen, each leaf, at least in the mature plant, receives several vascular strands from the stem (see Figs. 23, 24, and 25). The structure of the petiole is simple enough. The strands (see Fig. 25), as seen in transverse section, are arranged in a horseshoe, embedded in ground tissue, the outer layers of which consist of very thick-walled cells. The basal part of the petiole is densely clothed with chaffy ramenta, which are more scattered higher up on the leaf.

A bundle enters each pinna of the leaf, branching off from one of the two larger strands which are situated near the upper surface of the leaf-stalk. This bundle gives off branches to the right and left, which enter the successive segments of the lamina, and by their further ramifications supply its vascular system (see Fig. 22, B). As we trace the bundles into the finer veins of the leaf, we find that the upper part of the phloëm gradually dies out, so that the ultimate branches of the bundle system come to be collateral instead of concentric. This is general in Ferns.

The structure of the leaf is distinctly bifacial. The mesophyll towards the upper surface consists of closely packed squarish cells, forming a kind of palisade-parenchyma, though the palisade form is not well marked. The lower portion of the mesophyll, on the other hand, is made up of irregularly branched cells, attached to each other by only small parts of their surface, so that large intercellular spaces are left between them. This tissue is thus a typical spongy parenchyma. All the cells of the mesophyll contain abundant chloroplasts (see Fig. 32, *A*).

The epidermis of the lower surface alone bears the stomata, which are very numerous (see Fig. 28).

The cells of the epidermis on both surfaces of the leaf have undulating cell-walls fitting closely together. The cells contain chlorophyll, as is general in the epidermis of Ferns, though much less usual among Flowering Plants.

3. The Root

The adventitious roots of the Male Fern arise, as we have already seen, at the bases of the leaves, though they are in direct connection with the principal steles of the stem.

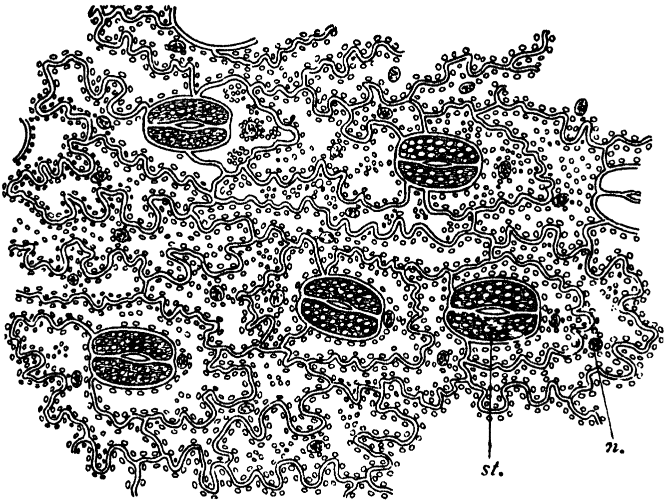

FIG. 28.—Part of epidermis from the under-side of leaf of Male Fern. Note the undulating cell-walls and numerous chloroplasts. *n*, nucleus of epidermal cell; *st*, stoma. Magnified 105. (R. S.)

The structure of the root in Ferns is, with one or two exceptions, essentially similar to that of the root in Seed Plants. In the Male Fern and in many other Ferns the vascular cylinder of the root is diarch (see Fig. 29). The first-formed elements of the wood, protoxylem, lie at the two ends of the xylem plate, and the development of the wood advances from these two points in centripetal direction to the middle of the cylinder.

The small first-formed tracheids are spirally thickened, the larger elements, developed later, are scalariform. On either side of the xylem-plate, and therefore alternating with the protoxylem-groups, are two strands of phloëm. The whole is surrounded by a single layer of pericycle, and this again by the endodermis, which has the usual fatty bands on its radial cell-walls. The cortex consists of two zones—an inner thick-walled region forming a firm sheath round the cylinder, and an outer portion in which the cells have thinner walls. We often find that the cell-walls of the inner zone are not uniformly thickened; at the points opposite the two ends of the xylem-plate, the cells remain comparatively thin-walled so as to leave a free passage, through which the water absorbed from the soil can reach the wood, and thus pass upwards to the stem and leaves. At the exterior of the whole root is the piliferous layer, which bears numerous unicellular root-hairs.

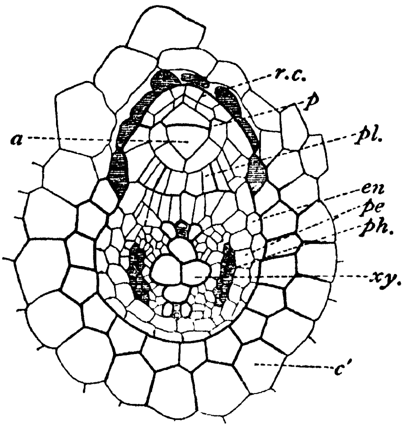

Fig. 29.—Transverse section of central part of young root of a Fern, showing origin of rootlet. *xy*, diarch xylem; *ph*, phloëm; *pe*, pericycle; *en*, endodermis; *c'*, cortical cells; *a*, apical cell of rootlet; *r.c*, root-cap; *p*, cortex of rootlet; *pl*, stele of rootlet. Magnified about 150 diameters. (After Van Tieghem.)

4. The Growing-points

α. *The Stem*

With rare exceptions, the development of both stem and root in Ferns can be referred to a single apical cell, from the divisions of which all tissues and organs arise. This important cell can be easily distinguished from its neighbours, which are derived from it, by its larger size and characteristic form. In the Male Fern and most other members of the class, the apical cell of the stem has the form of an inverted three-sided pyramid or tetrahedron, with its curved base directed outwards (see Fig. 30, which is taken from a simpler Fern-stem, but illustrates the essential features).

In longitudinal section, therefore, the cell appears triangular; its three sides are in contact with the adjacent tissue, while the curved base is free and faces outwards. The apical cell divides in regular order by walls successively parallel to each of its three sides. The cells thus cut off are called segments (see Fig. 30). By the growth and repeated subdivision of the three rows of segments all the tissues of the stem are produced.

β. *The Root*

The root, like the stem, carries on its apical growth by means of a single cell, which here also has the form of an inverted three-sided pyramid. The essential difference between the divisions in the apical cell of the root and in that of the stem is that, in the former, cell-walls are not only formed parallel to the three sides, but also parallel to the base of the pyramid. The segments thus cut off from the outer end of the apical cell (see Fig. 31) go to form the root-cap; those cut off laterally build up the tissues of the root itself, in much the same way as in the case of a stem with a simple monostele.

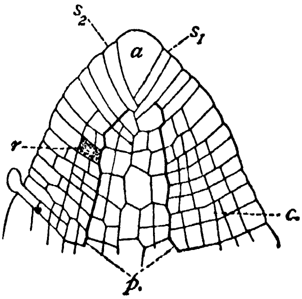

FIG. 30.—Apex of stem of a Fern (stolon of *Nephrolepis*) in longitudinal section. *a*, apical cell; s_1, s_2, segments; *c*, cortex; *p*, stele; *r*, cell from which a root will arise. Magnified 80 diameters. (After Van Tieghem.)

The mode of branching of the root in Ferns differs in one important respect from that in the higher plants. In Ferns each rootlet arises, not from the pericycle, but from the endodermis, and in fact its origin can always be traced to a single endodermal cell, lying opposite one of the groups of protoxylem. The cells destined to give rise to rootlets can be distinguished by their larger size. The cell in question divides up by inclined walls, so as to form at once a pyramidal apical cell, by means of which the further development of the rootlet is carried on (see Fig. 29).

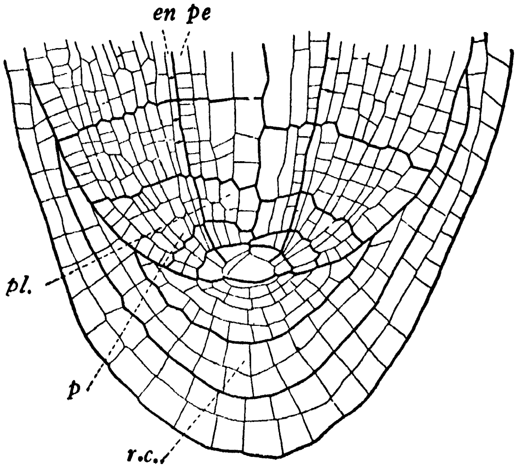

FIG. 31.—Apex of root of a Fern in longitudinal section, showing triangular apical cell. *pl*, stele; *pe*, pericycle; *en*, endodermis; *p*, cortex; *r.c*, root-cap. The dark lines mark out the cell-groups, each formed from a single segment. Magnified 120 diameters. (After Van Tieghem.)

The origin of the adventitious roots, which play so important a part in the organisation of Ferns, follows the same rule which holds good for the rootlets. Every adventitious root arises from an endodermal cell bordering on one of the strands of the stem. In Fig. 30, for example, the shaded cell marked *r* is destined to produce a root. We see from this that the first differentiation of the root-forming cells in the stem takes place very early.

γ. *The Leaf*

The development of the leaf in Ferns, like that of the stem and root, goes on at the apex, whereas in most Flowering Plants the growth of the leaf chiefly takes place at the base. It is only when still very young that a Fern leaf grows by means of a single apical cell. This cell soon divides up so as to form a row of marginal cells, all of which take equal parts in the subsequent cell-formation.

B. REPRODUCTIVE ORGANS OF THE SPOROPHYTE

We have already seen that the sporangia of the Male Fern are grouped in sori, and that the sori are seated on the back of the leaf, under the lateral veins of a segment or pinnule (see Fig. 22, B).

Beneath each sorus is a prominent mass of tissue, which we may call the *placenta* (see Fig. 32, *r*). This receives a short branch from the vascular bundle immediately below it. The placenta grows out at its summit into the kidney-shaped indusium, which consists of a membrane, one cell in thickness, attached to the placenta by a massive stalk (see Fig. 32, *i*). The sporangia spring from the sides of the placenta, and are all roofed in by the indusium. Each sporangium consists of a long slender stalk, made up of two or three rows of cells, bearing the terminal spore-case or capsule (see Fig. 32, *B*, *C*, *E*). A club-shaped glandular hair is usually borne on the stalk. The capsule is not spherical but much flattened, resembling the case of a watch in form; its wall when mature consists of a single layer of cells; its interior is occupied by the spores, forty-eight to sixty-four in number, which are of a brown colour when ripe.

The sides of the capsule are formed of cells with thin membranes, but around its edge runs a single row of larger cells with peculiarly thickened walls of a rich brown colour, forming a very conspicuous feature under the microscope, when the sporangium is ripe. This special row of cells is called the *annulus* (see Fig. 32, *B*, *C*, *E*). The annulus starts from the stalk at one side, passes over the crest of the capsule, and extends about half-way down on the other side. Here it suddenly comes to an end. The cells of the wall immediately below the termination of the annulus are broad and flat. It is here that the *stomium* occurs. This is the place where the capsule ultimately opens (see Fig. 32 *B* and *C*, *st*). In the annulus both the inner and the radial cell-walls are much thickened; the free outer walls of the cells, however, remain thin. The annulus is concerned with the dehiscence of the sporangium when ripe.

Each sporangium arises from *a single superficial cell* of the placenta;

in this respect it differs from the sporangia hitherto considered, namely, the sporangium of *Lycopodium* and the microsporangium and megasporangium of *Selaginella*. The great majority of Ferns are distinguished by the unicellular origin of their sporangia. A single cell, then, grows out from the surface of the placenta and soon begins to divide. One or two basal cells are often cut off, to begin with, by transverse walls, but they are of no great importance. The terminal cell next undergoes division by inclined walls (see Fig. 32, *G*), three of which are formed in succession, inclined to each other at an angle of 120°, as seen from above. In side view, as shown in the figure, only two of these walls can be seen, and they join each other at an acute angle. The result of these three divisions is to carve out a three-sided pyramidal cell with a free base, quite like the apical cell which we have already described in the stem and root. The next wall formed runs parallel to the free base of this pyramidal cell, so now we have a central cell surrounded on all four sides by the segments which have been cut off from it. The segments undergo a great many more divisions, and form the wall of the capsule, which remains only one cell thick, as all the cell-divisions are at right angles to its surface. The lateral segments also cut off cells below, which go to build up the stalk.

In the meantime the pyramidal cell has itself divided by walls parallel to its four sides, so that it is now surrounded by an inner layer of cells separating it from the wall of the capsule. These intermediate cells undergo further divisions in various directions and form the *tapetum*, the ultimate destiny of which is to afford food material to the developing spores (see Fig. 32, *F*, *iw*).

The central cell which remains is the essential part of the whole structure, for this is the *archesporium*, from which the spores themselves are produced (see Fig. 32, *F*, *c*). We see, then, that in this case the archesporium begins as a single cell. It undergoes several cell-divisions (see Fig. 32, *F*, *c*). The cells thus produced round themselves off and become the mother-cells of the spores. In many Ferns there are sixteen or more mother-cells in each sporangium, but in the Male Fern there are usually not quite so many.

The spore mother-cells are spherical; as the sporangium has grown more rapidly than they have, they do not fill the whole interior, but float freely in a half-liquid mass derived from the disorganised tapetal cells. Each mother-cell now divides twice so far as to form four cells (see Fig. 32, *D*). These two divisions represent meiosis so that the four daughter-cells, the spores, are haploid. As they ripen they become kidney-shaped, the convex side corresponding to the free outer surface of the mother-cell, while the concave edge of each spore represents the line of junction with its sister-cells. The spore membrane becomes

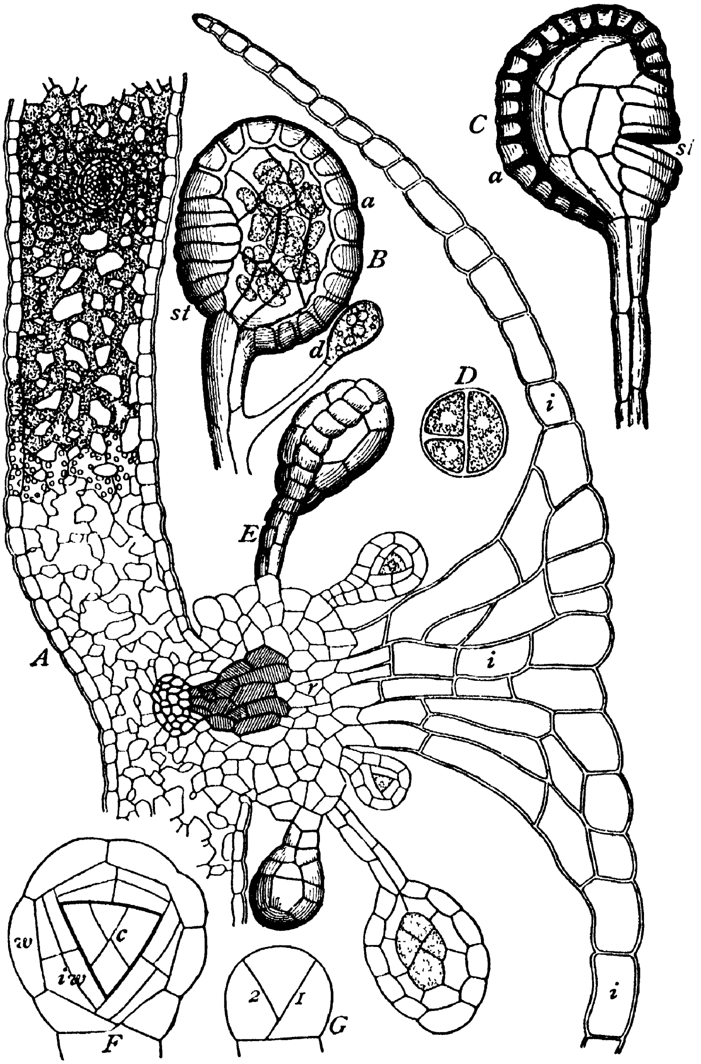

FIG. 32.—*A*, transverse section of portion of lamina of Male Fern passing through a sorus; *i*, indusium. Magnified 80 diameters. *B*, single sporangium in side view; *a*, annulus; *st*, cells which dehisce; *d*, glandular hair. *C*, sporangium dehiscing at *st*; *a*, annulus. *B* and *C* magnified 100 diameters. *D*, spore mother-cell divided (only three spores visible). Magnified 350 diameters. *E*, nearly ripe sporangium. *F*, young sporangium; *c*, sporogenous cells; *iw*, tapetum; *w*, wall. *G*, very young sporangium, showing first divisions. Magnified 260 diameters. (After Luerssen.)

much thickened, and consists of two layers, the outer of which is strongly cuticularised, and assumes a dark-brown colour.

By the time the sporangia are ripe the indusium has withered so that they are freely exposed. It is the annulus which causes the sporangium to

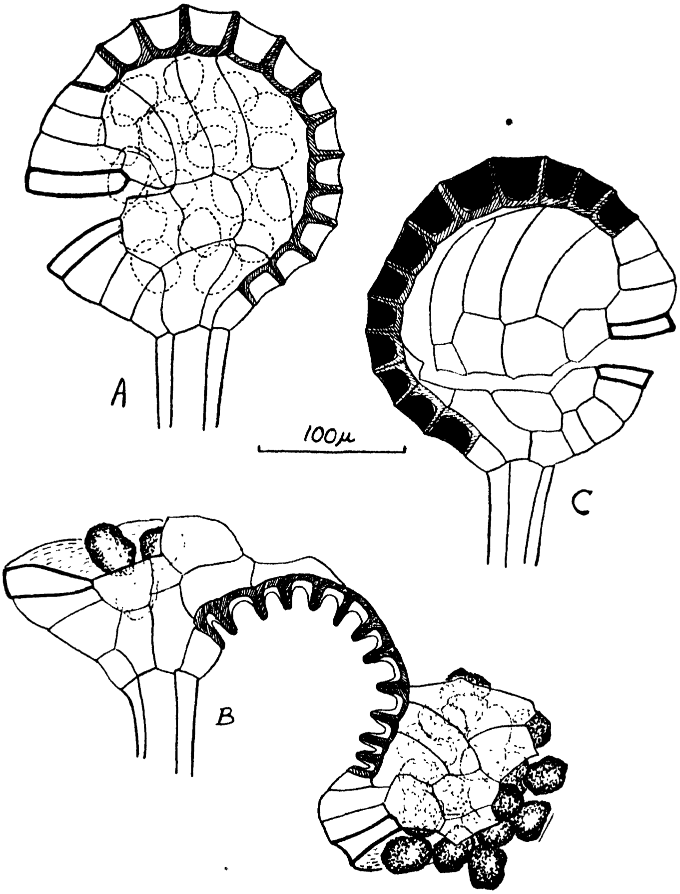

FIG. 33.—*Dryopteris* sp. A–C changes in sporangium on drying. In A the sporangium is just opening at the stomium; the spores are outlined by dotted lines. B, later stage with annulus bent backward. C, a little later after annulus has returned to its former position—the annulus cells are now largely filled with gas (shown black).

open (see Fig. 33). Dehiscence occurs when the ripe sporangium begins to dry. Water evaporates from the annulus cells, thus reducing their volume, with the result that the thin outer walls of the cells are sucked inwards so that they become concave instead of convex. Further reduction in volume, following further evaporation, is brought about by curvature of the inner thick wall of each annulus cell, in such a way that the two lateral thickened walls approach one another more closely and the concavity of the thin wall increases. At an early stage the curvature of the inner thick wall leads to rupture of the sporangium in the region of the stomium, and the annulus then gradually straightens out splitting the capsule into a lower and an upper cup with most of the spores in the latter. With still more evaporation the annulus slowly bends backwards. If we consider the conditions within an annulus cell at this stage, we find that its very much reduced aqueous contents are under tension. The curved inner thickened wall is tending all the time to return to its original shape, but this is prevented by the cohesion of the water molecules and by their adhesion to the cell walls. Eventually the tension on the water exceeds the breaking strain. A bubble of gas makes its appearance in the annulus cell which instantly returns to its former shape and size with a consequent enlargement of the gas bubble (probably a vacuum saturated with water vapour) which comes to occupy most of the cell-interior. The sudden jerk resulting from the appearance of a gas phase in one annulus cell probably leads to rupture of the unstable tensile fluid in all the other cells of the annulus, so that they all, more or less simultaneously, return to their original size. Thus the whole annulus suddenly springs back to its former position and, in so doing, catapults the spores into the air to a distance of several centimetres. In nature this process occurs in air. However, the same series of events can be brought about, and much more easily observed under the microscope, if water is withdrawn from the annulus cells not by subjecting them to dry air, but by mounting the sporangia in pure glycerine which removes water osmotically from the annulus cells. The viscosity of the medium slows down the movements so that they can easily be watched. Further when a gas phase replaces liquid in each annulus cell it appears black under the microscope.

It is a very general rule that the dehiscence of sporangia is so contrived as to take place in dry weather.

We have now traced the history of the reproductive process in the asexual generation. The most important points in which the Male Fern differs from *Selaginella* are the totally different arrangements of the sporangia, the origin of each sporangium from a single cell, and the fact that sporangia and spores are all of one kind.

As regards the two latter points, however, all Ferns do not agree with the Male Fern, for in some members of the class the sporangia have a multicellular origin, while others are heterosporous. It now remains for us to follow the germination of the spores, to see how the prothalli are produced from them, to learn how fertilisation is effected, and finally to study the origin of the embryo, which develops once more into the asexual Fern-plant, and thus completes the cycle of life.

III. *THE GAMETOPHYTE OR SEXUAL GENERATION*

A. DEVELOPMENT AND STRUCTURE OF THE PROTHALLUS

Fern spores can be sown successfully on ordinary garden earth, on peat, on sand, or even on pieces of tile. The last-mentioned material has the advantage that very clean cultures can thus be obtained. It is well to heat the soil, or whatever else is used, up to at least 100° C. (the boiling-point of water) before sowing the spores, so as to destroy the germs of other organisms, which are sure to be present, and might compete only too successfully with the young prothalli. It is important not to sow the spores too thickly, or else when they germinate the prothalli overcrowd each other. The cultures must, of course, be kept moist. It is best to cover them with a bell jar and to supply water from below.

After about a week, the beginning of germination may be observed; the spore starts growing and bursts its brown outer membrane. By this time the spores, which in their resting condition are without chlorophyll, will have begun to turn green. The first thing which the germinating spore does is to form a rhizoid. An outgrowth containing little or no chlorophyll arises from the spore, becomes cut off by a cell-wall, and grows down into the soil; the remaining larger part of the spore grows out towards the light, and divides at first transversely. A few more transverse walls are formed, the end cell being always the one to divide, so that the prothallus soon takes the form of a short green filament (see Fig. 34), any cell of which may produce a rhizoid. In most Ferns the rhizoids of the prothallus remain unicellular; in a few they become multicellular.

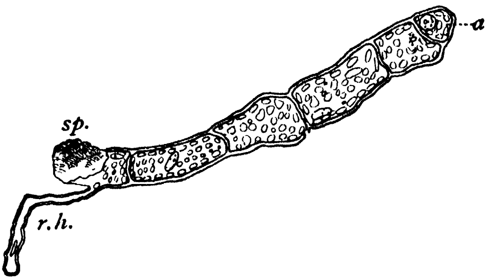

FIG. 34.—Very young prothallus of a *Dryopteris*. *sp*, membrane of spore; *r.h*, first rhizoid; *a*, apical cell. Magnified 210. (R. S.)

Soon the transverse divisions of the filament cease, an oblique wall appears in the terminal cell, followed by another at right angles to it, and thus a wedge-shaped apical cell is marked out. This goes on cutting off segments to the right and left, the segments divide up further, and soon the young prothallus becomes converted into a flat cellular plate, which for a time remains only one cell thick (see Fig. 35). As growth goes on, the prothallus tends to become heart-shaped, the growing-point lying at the base of a depression between two lobes. This is due to the fact that the apical meristem does not grow so fast as the older tissue which has been produced from it on either side.

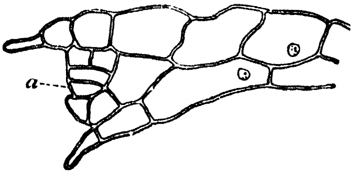

FIG. 35.—Apex of young prothallus of *Dryopteris*, older than in Fig. 34, seen in surface view. *a*, apical cell. Magnified 210. (R. S.)

The single apical cell does not long maintain its independence. It soon divides up into a row of equivalent initial cells, which all take a like share in the subsequent development. The prothallus, which for a short time grows vertically, soon assumes a horizontal position, and henceforth there is a marked difference between the lower side, which is in contact with the soil, and the free upper surface. It is from the under-side that the new rhizoids arise, and to this side also the sexual organs are limited.

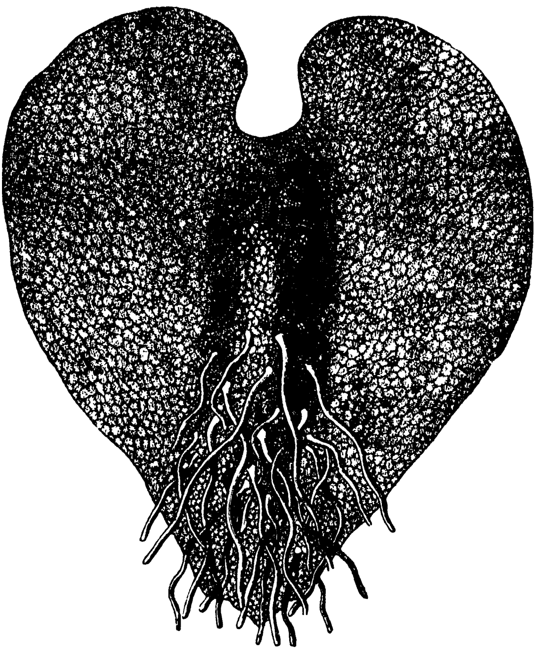

FIG. 36.—Full-grown prothallus seen from below, showing archegonia towards the apex, antheridia and rhizoids towards the base. Magnified about 25 diameters. (After Luerssen.)

A normal full-grown prothallus seen from below is shown in Fig. 36. The middle part, lying just behind the growing-point, forms a pad or cushion several cells in thickness, while the lateral portions or wings remain one cell thick.

The antheridia or male organs arise chiefly on the older basal part of the prothallus and sometimes also on the wings. The female organs or archegonia are limited to the cushion. Usually the prothallus is monœcious, bearing both kinds of sexual organs; but this is not always so. Male prothalli are not uncommon, and are generally of small size. Sometimes a prothallus at the earliest stage of its development, while still in the form of a short filament, begins to form antheridia. A filamentous prothallus, bearing male organs only, is shown in Fig. 37, but still smaller ones occur.

Specimens with archegonia only are rarer, and are of the ordinary form.

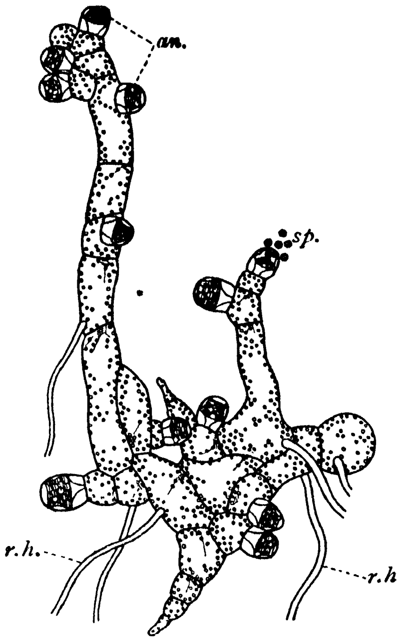

FIG. 37.—Young male prothallus of Male Fern. *an*, antheridia; *sp*, spermatozoids escaping; *r.h*, rhizoids. Magnified about 70 diameters. (After Kny.)

B. DEVELOPMENT AND STRUCTURE OF THE SEXUAL ORGANS

1. The Antheridia

Each antheridium arises from a single cell, the upper part of which grows slightly beyond the general surface of the prothallus, and is cut off by a transverse wall. It then undergoes a few divisions, so that the antheridium comes to consist of a central cell, surrounded by two ring-shaped cells, one above the other, and covered in on the top by a cap-cell. Some of the stages of development are shown in Fig. 38, A.

The central cell divides up repeatedly, and gives rise to the spermatozoid mother-cells, the number of which in each antheridium averages about twenty (see Fig. 38, B). In each mother-cell one spermatozoid is formed. The mature spermatozoid consists of a spirally coiled body like a corkscrew, but thicker at one end than the other. Near the thin end a number of excessively fine cilia (contractile protoplasmic threads) are attached (see Fig. 38, C).

The development has been very exactly followed; it is known that the greater part of the body of the spermatozoid is formed from the *nucleus* of the mother-cell; the cilia, however, and the part of the body

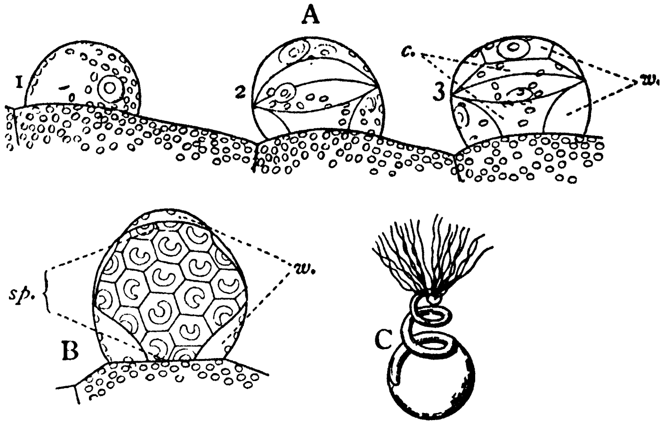

FIG. 38.—Antheridia of Male Fern. A, 1, 2 and 3, antheridia three successive stages seated on prothallus; *c*, central cell; *w*, wall. B, older antheridium; *sp*, mass of spermatozoid mother-cells; *w*, wall. C, a single spermatozoid. Magnified, A and B about 300, C about 700 diameters. (After Kny.)

to which they are attached, are derived from the cytoplasm. In Fig. 38, B, the young spermatozoids are shown enclosed in their mother-cells.

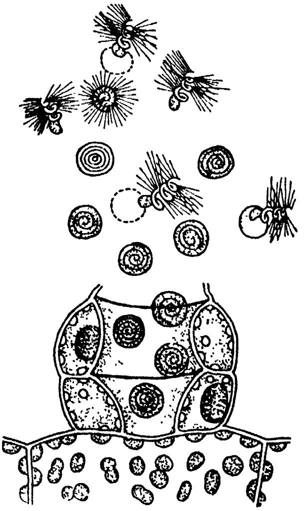

FIG. 39.—Ripe antheridium, showing spermatozoids escaping. Magnified 350 diameters. (After Luerssen.)

In the ripe antheridium every mother-cell contains its spermatozoid curled up inside it; as soon as a drop of water comes into contact with the antheridia, they open, by the bursting of their cap-cells (see Fig. 39). The pressure which brings this about is due partly to the swelling of the mother-cells themselves, and partly to that of the ring-cells, which absorb water and press upon the mass of mother-cells, squeezing them out from the antheridium. The whole mass of mother-cells is now set free, but each spermatozoid is still imprisoned within its own mother-cell. The membranes of the latter, however, are soon dissolved, and now the spermatozoids are able to escape, and begin their active career. Each spermatozoid drags with it, attached to the hinder end, a bladder-like sac, which is derived from the inner part of the cytoplasm of the mother-cell (see Figs. 38, C, and 39). The locomotion is very active; the little spermatozoids go wriggling through the water in all directions, always keeping their thin ciliated ends foremost; they revolve on their axes, and advance at the same time, not in straight lines, but in varying curved paths. Sometimes the little bladders are left behind, sometimes they hang on all the time, until an archegonium is reached. Before describing the ultimate fate of the spermatozoids, we must now turn our attention to the archegonia.

2. The Archegonia

As we have already mentioned, the archegonia do not rise so indiscriminately on different parts of the prothallus as the antheridia do, but are limited to the sides of the thickened cushion. An archegonium, like an antheridium, arises from a single cell, which at first projects only slightly above the level of the neighbouring tissue. It divides by two transverse walls into three cells: the lowest or basal cell undergoes a few divisions, but takes no important part in the further development; the middle cell ultimately forms the ovum and the two canal-cells; while the uppermost of the three grows and divides to form the neck (see Fig. 40). The neck is the only part which projects beyond the surface of the cushion.

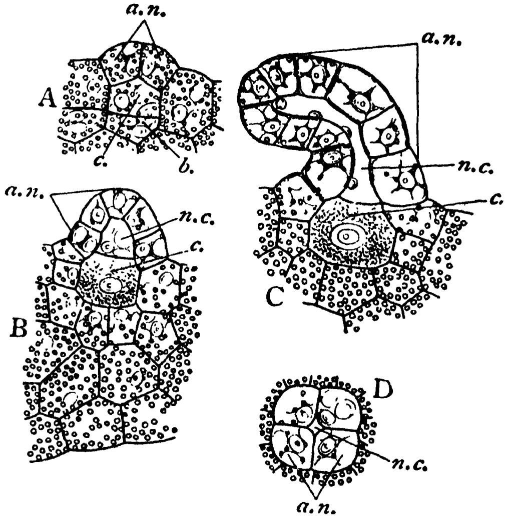

FIG. 40.—Development of archegonium of Male Fern. A, very young; *a.n*, neck of archegonium; *c*, central cell; *b*, basal cell. B, rather older; *n.c*, neck canal. C, nearly ripe; *n.c*, canal cells disorganised. A. B. C, in longitudinal section. D, neck seen from above. Magnified about 250 diameters. (After Kny.)

The neck-cell first divides, by two longitudinal walls at right angles to each other, into four cells placed crosswise, as seen in surface view (see Fig. 40, D). Each of these four cells then divides up repeatedly by approximately transverse walls, so that the neck is finally made up of four rows of cells. While these divisions are going on, the neck is increasing in length, and at the same time the central cell grows up between the four rows of neck-cells (see Fig. 40, A and B), which separate a little to make way for the outgrowth. The projecting part of the central cell is presently cut off by a wall, and forms the *canal* of the neck. This canal-cell may itself undergo one or two further divisions, but they are usually incomplete, no cell-walls being formed. A second canal-cell is now cut off below the first; the remaining part of the central cell rounds off its protoplasm, and now constitutes the *ovum*. The archegonium has by this time reached its complete development. The neck is not straight, but is sharply curved backwards, *i.e.* towards the basal end of the prothallus (see Figs. 40 and 41).

We see that the archegonia are really quite similar to those of *Selaginella*, and also have much in common with the archegonia of Conifers.

C. FERTILISATION

In Ferns, as in Cryptogams generally, fertilisation can only take place under water. In nature this happens after rain or heavy dew, when the under-sides of the prothalli are thoroughly wetted. When we are cultivating prothalli it is necessary to sprinkle them with water from above, when the sexual organs are ripe, if we wish to obtain embryos. We have already seen how the antheridia open under water, and how the active spermatozoids are set free. In like manner the archegonia, when moistened, open to receive them. This happens because the protoplasm of the canal-cells swells up and becomes converted into mucilage, which exercises a pressure on the neck, and causes it to open at the top, the four rows of cells being forced apart. The mucilage now more than fills the canal, and forms a viscid drop at the mouth of the archegonium (see Fig. 41).

The spermatozoids swimming through the water are attracted by the archegonia. This remarkable fact, which long remained an absolute mystery, is now so far explained that we have good evidence as to the nature of the substance which attracts them. When a spermatozoid, as it makes its devious way through the water, comes within a short distance of the neck of an open archegonium, it turns aside from its course, and makes for the opening. Here it finds the mucilaginous drop, and promptly plunges into it, Its movements do not cease, though in the denser fluid they go on more slowly; the spermatozoid wriggles its way down the neck, through the mucilage which fills it, and so at last reaches the ovum below. Quite a number of spermatozoids may be seen swarming around the opening of a ripe archegonium and several may penetrate down the canal, but only one succeeds in uniting with the ovum.

Now it has been shown by experiment that the spermatozoids of Ferns are attracted by certain chemical substances, and especially by malic acid. If artificial archegonia are prepared (consisting of tiny capillary glass tubes) and filled with a mucilage to which a small quantity of this acid has been added, they are found when placed in water containing fern-spermatozoids, to exercise the same attraction upon them which the real archegonia exercise in nature. The malic acid gradually diffuses out into the water, and the spermatozoids are influenced by it, so that they move in the direction in which the substance is more concentrated, *i.e.* towards the tube. Although it cannot be proved that the archegonia themselves contain malic acid, as they are too small for a recognisable quantity to be obtained from them, yet this substance is known to be present in the prothallus as a whole; so there can be little doubt that the natural archegonia owe their attractive influence to the same chemical agent which has proved efficacious in experiment.

We see, then, that these minute protoplasmic bodies, the spermatozoids, are not only capable of active movement, but also possess a certain power of perception, by which their movements are guided.

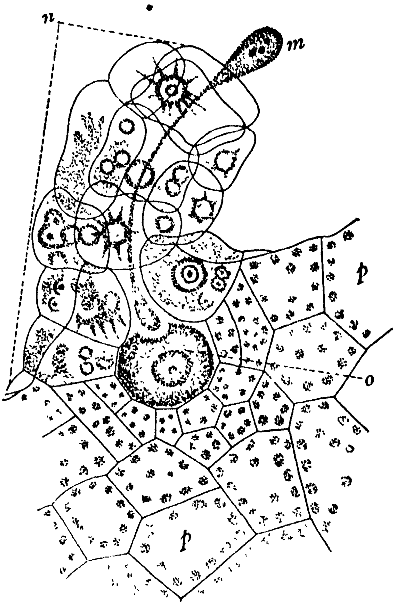

FIG. 41.—Archegonium ready for fertilisation. *o*, ovum; *n*, neck; *m*, mucilage extruded from canal; *p*, cells of prothallus. Magnified 350. (After Strasburger.)

Now that we have learnt how fertilisation is brought about, we will go on to consider its results.

D. EMBRYOLOGY

The first change after fertilisation is the formation of a cell-wall around the protoplasm of the diploid fertilised ovum. It now at once begins to grow and divide, becoming the embryo, or young plant, of the sporophyte generation.

The embryo of a Fern differs from that of the plants hitherto described, in having no suspensor; the whole of the fertilised ovum goes to form the embryo. Throughout the Fern-group there is considerable uniformity in the manner of development of the embryo from the ovum. The first wall (called the basal wall) runs nearly parallel to the axis of the archegonium, and at right angles to the axis of the whole prothallus. This divides the young embryo into an *epibasal* and a *hypobasal* half; the former faces the apex and the latter the base of the whole prothallus. Two more cell walls then appear, all three being at right angles to each other, so that the embryo is now cut up into eight parts or octants. From the epibasal half the apex of the stem and the first leaf arise, while the hypobasal part produces the apex of the root, and an organ called the *foot*, which is of a temporary character and serves to attach the young plant to the prothallus and to take up food from it until the embryonic stage is past (see Fig. 42, *f*).

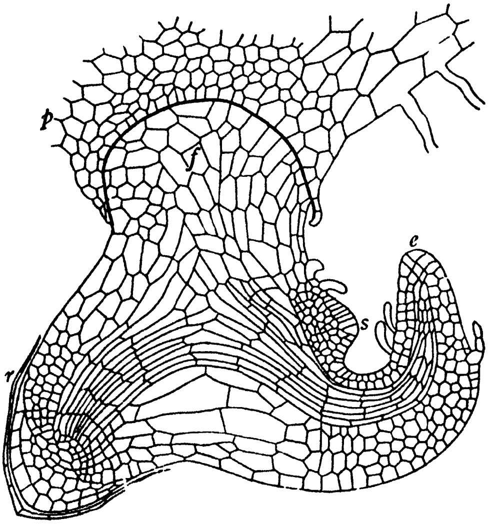

FIG. 42.—Embryo of a Fern (*Pteris*) in median section. *s*, apex of stem; *e*, first leaf; *r*, root; *f*, foot by which embryo is attached to prothallus; *p*, prothallus. Magnified 150. (After Hofmeister.)

Growth and accompanying cell-division go on rapidly; the parts which develop quickest are the root and first leaf; for a long time the stem remains very rudimentary. The ventral part of the archegonium becomes much enlarged, to make room for the developing embryo. The root is the first part to break through, whereupon it makes its way down into the soil. It is soon followed by the first leaf, which turns upwards between the lobes of the prothallus, and spreads out its blade to the light. Meanwhile the foot is absorbing the food produced by the prothallus but this is soon exhausted, and then the embryo becomes an independent plant, which continues its growth, producing fresh leaves and roots. The leaves which are first formed are always of a comparatively simple shape, and it is only gradually that the successive leaves assume the form characteristic of the species. At the same time the stem increases in bulk, and its anatomical structure becomes more complex.

We have now traced the normal life-cycle through its complete course, and have got back to the asexual generation, or diploid sporophyte, from which we started.

E. COMPARISON BETWEEN THE LIFE-HISTORY OF FERNS AND THAT OF THE HIGHER PLANTS

In the Ferns, the occurrence of a distinct alternation of generations is manifest. In these plants the prothallus, though small, is just as distinct an individual, and leads just as independent a life, as does the asexual Fern-plant itself. In fact, we may even say that the prothallus is the more independent of the two, for while the young Fern-plant is for a time dependent for its nutrition on the prothallus, the latter is never dependent in any way on the Fern-plant. At any rate we have in normal Ferns two perfectly definite generations, as distinct as possible from each other; one, the gametophyte, bearing the sexual, and the other, the sporophyte, the asexual organs of reproduction, and in the ordinayr course of life these two generations succeed each other in regular alternation. It was in fact from the Ferns that the idea of alternation of generations among plants first arose, though it had been recognised in the animal kingdom long before.

Of course the same phenomenon really occurs in *Selaginella* and in Seed Plants, but in all these it is much less conspicuous.

The regular alternation of sexual and asexual individuals is often modified in special cases among Ferns. The modification may either result in a lengthening or a shortening of the ordinary life-cycle. The life-cycle is lengthened when we get vegetative propagation of the Fern-plant so that the number of asexual generations interposed between two sexual ones is increased. This happens in those Ferns which form buds on their leaves; the buds become detached and give rise to new plants, as may easily be seen in *Asplenium bulbiferum* var. *viviparum*, so commonly grown in greenhouses. Everybody must have noticed the minute Fern-plants which are dotted about on the fronds of these Ferns, and which in the form of their little leaves are so different from full-grown speciments.

Another way in which the life-cycle may be extended is by vegetative reproduction of the prothallus—just the converse of the process already described. In this case a number of additional *sexual* generations may be introduced into the life-history. This is pretty common among Filmy Ferns, and in some tropical species, in which the prothallus produces little buds from which new prothalli arise, so that the number of sexual individuals may increase indefinitely without the intervention of the sporophyte generation.

So much for the *lengthening* of the life-history. In other cases, it is cut short—that is to say, the one generation passes over into the other, without the aid of the regular sexual or asexual reproductive organs.

There are two possible cases of this kind; either the sexual generation may give rise directly to the asexual (*apogamy*), or conversely the asexual generation may give rise directly to the sexual (*apospory*). We have no space to go into the details of these exceptional modes of development, but it is necessary to mention them, because it is very important to learn at starting that the distinction between the two generations is not absolute, but that the one may sometimes pass directly into the other.

We thus see that we must regard the regular alternation of sexual and asexual reproduction as the normal course of life-history in Ferns and their allies, but not as a cast-iron scheme which can never be departed from.

THE COMMON HORSETAIL (*Equisetum arvense* L.)

The existing Vascular Cryptogams belong chiefly to three great stocks or Classes. We have already examined representatives of two of them—namely, Club Mosses and a Fern. It still remains for us to make the acquaintance of the third Class, that of the Horsetails (*Equisetales*). The latter are not now a very important group, for there is only one living genus, containing about twenty-five species. But small as the Class is in these days, it is a very ancient one, and seems to stand quite apart from its neighbours among the Ferns and Club Mosses. In early geological times, especially in the far-off period when the coal-beds were being formed, the Horsetails were in the height of their glory, and were represented by a number of very diverse forms, many of which grew into trees. Hence this good old stock, though now so reduced, is quite as worthy of our study as its more prosperous fellows.

Several species of Horsetail are natives of England, and some are very common. In general habit they all bear a strong family likeness to each other, all having stiff, upright, jointed stems, with whorls of little-developed leaves, those of each whorl being united to form a sheath around the stem. If the stem is branched, its branches are also in whorls, the whole plant having a very formal and regular appearance (see Fig. 43). The fructification is in the form of cones, each of which is borne at the end of an upright stem, or of a branch. In some species (see Fig. 43) there are special fertile stems which only bear the cones, but do not branch, and are not green. In others, the cones are borne on the ordinary green vegetative stems. Underground, the plant has a much-branched rhizome, which penetrates to a great depth in the soil, and makes these plants most obstinate weeds. If such a species as *E. arvense* or *E. maximum* has once established itself in garden ground, it is almost impossible to get it out again, for its rhizome goes

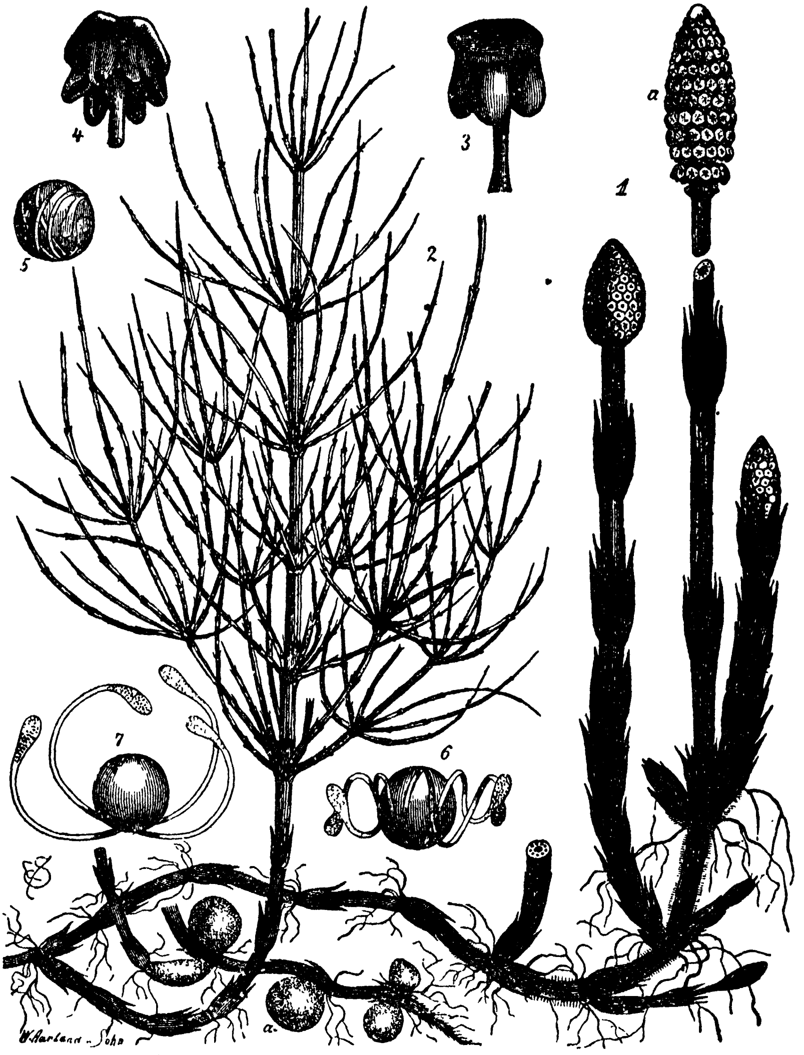

FIG. 43.—*Equisetum arvense.* 1 and 2, general view of plant, showing underground rhizome, bearing roots, with fertile and sterile aërial stems. 1, Fertile stems; *a*, ripe cone. 2, much branded sterile stem; *a* (on rhizome), tubers. 3, single peltate scale from cone, showing sporangia. 4, similar scale below; sporangia dehiscing. 5, young spore, with elaters not yet expanded. 6, mature spore in damp condition; elaters curled up. 7, the same in dry condition; elaters expanded. Figs. 1 and 2 reduced; Figs. 3 and 4 magnified slightly; Figs. 5, 6 and 7 very highly magnified. (After Wossidlo, from Strasburger.)

too deep to be easily dug up, and is perpetually giving rise to new shoots.

Equisetum, as we shall find, resembles other Pteridophyta in having a sharply marked alternation of generations. The plant, as we see it, is the asexual diploid sporophyte, and with this we will begin.

I. *EXTERNAL CHARACTERS OF THE SPOROPHYTE*

A. VEGETATIVE ORGANS

The general habit of the commonest British species, *E. arvense*, is well shown in Fig. 43, but only some of the upper branches of the rhizome are represented. We must picture to ourselves the main part of the rhizome deep down in the soil, perhaps three feet below the surface, sending up branches which alone are visible in the figure. The characteristic leaf-sheaths are obvious on all the stems whether above or below the ground; on the older parts of the rhizome, however, they often wither away. Each sheath consists of a whorl of coherent leaves, the free parts of which are represented only by the teeth at the top of the sheath.

The rhizome bears numerous slender adventitious roots, arising at the nodes, and in this species also produces round tubers, each of which represents a short branch consisting of a single swollen internode. These tubers are capable of giving rise to new plants, and thus form a means of vegetative propagation (see Fig. 43, 2, *a*).

The characters of the stem are best studied in detail on the shoots which rise above the ground. The surface is ribbed lengthwise, each rib lying in the same straight line as one of the leaves of the node next above. Both ribs and leaves alternate regularly in successive internodes. The stems above ground are in this species (*E. arvense*) of two kinds. First, we have the fertile shoots, which show themselves in spring (March) and have no other function than to bear the cones (Fig. 43, 1). These fertile shoots are unbranched, and are of a pale colour, containing little or no chlorophyll. They die down as soon as the spores are shed. The other shoots are sterile, and their branches constitute the assimilating apparatus of the plant, for the leaves are of little importance in this respect (Fig. 43, 2). They are of a deep green colour, and are repeatedly branched, the branches breaking out from the stem through the lower part of the leaf-sheaths. In each whorl the branches are equal in number to the leaves, and alternate with them. The ultimate ramifications are very slender, and only have from three to five ribs, while the main stem may have as many as twenty. The surface of the aerial shoots is very hard and somewhat rough, especially at the ridges.

We see then that our plant has a very characteristic habit, marked partly by the small development of the leaves and partly by the great, regularity of the whorled branches. Other species differ considerably from this type; many have only one kind of stem, the cones being borne on ordinary vegetative shoots, while in others the aërial shoots branch little, or not at all. In *E. maximum*, the largest British species, the barren stems sometimes attain a height of six feet, but some of the tropical kinds, such as *E. giganteum*, a native of tropical South America, are much taller, even, it is said, reaching forty feet.

B. Reproductive Organs

The cone of an *Equisetum* is unlike the fructification of any other living plant, and cannot be mistaken when once seen, though the male cones of some Coniferæ, such as the Yew, are found to bear a certain resemblance to it when closely examined. The cone is terminal. It consists of a fairly stout axis, giving rise to densely crowded alternating whorls of peltate scales (*sporangiophores*) on which the sporangia are borne (see Fig. 43, 1, *a*). The scales of the cone are usually called *sporophylls*, and their mode of development agrees well with their leaf-nature, but some of the fossil forms throw a certain amount of doubt on this interpretation, so we prefer to call them simply *sporangiophores*, sporangium-bearers. In each whorl there are a considerable number of sporangiophores—often about twenty. Each has a short cylindrical stalk, and expands at the end into a flat disc, to the under-side of which five to ten sporangia are attached. The peltate heads of the sporangiophores are in such close contact that they usually become hexagonal from mutual pressure. The sporangia extend inwards as far as the axis. They contain very numerous spores, which are all of one kind. At the bottom of the whole cone is a ring of abortive leaves, called the annulus (see Fig. 43, 1, *a*); sometimes there are two such rings. These rudimentary structures are of some interest, because in many of the fossil forms there are whorls of barren leaves or bracts between the whorls of sporangiophores. It is possible that we find the last remnants of these bracts in the annulus of living Horsetails.

II. *INTERNAL STRUCTURE AND DEVELOPMENT OF THE SPOROPHYTE*

1. Vegetative Organs

a. The Stem

The general structure of the stem in the genus *Equisetum* is at once simple and characteristic. Among all the Cryptogams now living, these plants approach most nearly, as regards their anatomy, and especially that of the stem, to the simpler Gymnosperms and Dicotyledons, though in other respects they differ widely from them. The stem of *Equisetum* is invariably traversed by a number of collateral leaf-trace bundles, arranged in a single circle. The course of these bundles is excessively simple; a single one enters the stem from each leaf, *i.e.* from each tooth of the coherent sheath. It passes straight down the whole length of the internode, without joining on to any other bundle until it reaches the node below. Here it forks into two, and the forks attach themselves to the two adjoining bundles coming up from below, just where they are beginning to bend out into the leaves; consequently every internode contains just as many bundles as there are leaves at the node above, and as the leaves alternate with each other at successive nodes, so also do the bundles in the corresponding internodes. As all the bundles enter the stem to the same depth, and then turn vertically downwards, it follows that, as seen in transverse section, they always form a single ring. It will be seen that the bundle-system is just of the kind typical for Conifers and Dicotyledons, but it is one of the very simplest examples of this type. The stem is always ridged on the surface, as mentioned above. Each of the ridges corresponds in position to one of the vascular bundles (see Fig. 44).

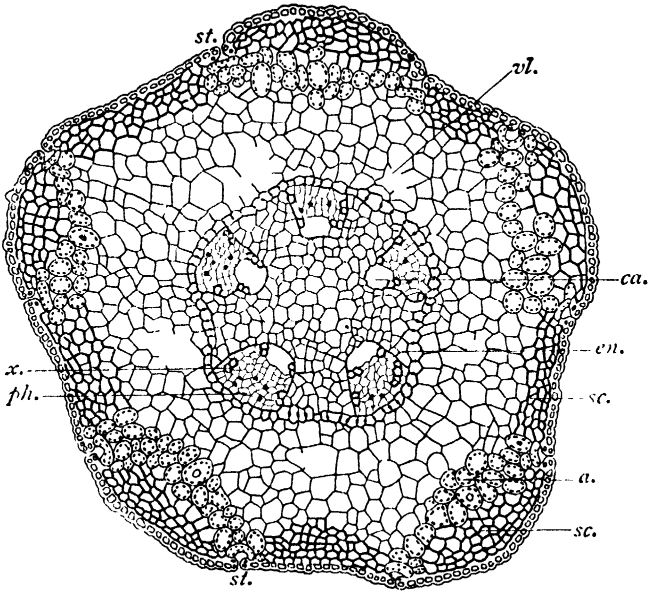

FIG. 44.—*Equisetum arvense*; transverse section of a branch of sterile stem. *x*, xylem; *ph*, phloëm; *ca*, carinal cavity; *en*, endodermis; *sc*, sclerenchyma; *a*, assimilating tissue; *vl*, vallecular cavities (imperfectly formed); *st*, stomata. Magnified 45 diameters. (R. S.)

The Equiseta are characterised by a great development of intercellular spaces, which have a very definite arrangement. There is usually a ring of large spaces in the cortex, and these cortical cavities are alternate in position with the bundles, and thus lie opposite the depressions or furrows of the external surface. For this reason they bear the name of *vallecular cavities.* Another ring of intercellular canals accompany the bundles, one on the inner side of each; these lie opposite the ridges of the stem, and are consequently called the *carinal cavities.* We shall see presently how they arise. These canals are interrupted at the nodes. Lastly, the whole interior of the pith of the internodes often becomes hollow, leaving only a persistent diaphragm at each node. This almost always happens in the main aerial stems; but in the finer aerial branches (see Fig. 44) and in the rhizome the pith often remains solid, as is the case in *E. arvense.* The intercellular spaces do not all fulfil the same function; the carinal cavities contain water, while the vallecular cavities are always full of air. The central cavity usually contains air, but may become partly filled with water. Many species grow in swamps or badly drained situations.

In *E. arvense* and some other species the central cylinder is well defined, a common endodermis surrounding the whole ring of vascular bundles on their outer side. In other species, however, there is a separate endodermis round each individual bundle, as in *E. limosum* (Fig. 45).

In others again there is an intermediate state of things, for a common endodermis is present *inside* the ring of bundles, as well as outside them (*E. variegatum*). These differences, however, do not otherwise affect the anatomy. Although the same general structure is maintained throughout the shoot, yet in the minute ultimate branches the number of bundles becomes much reduced, often down to three, and then the appearance of the transverse section may be very different from that of a main stem or larger branch (see Fig. 45).

We will now consider the tissues rather more in detail, and will begin with the vascular bundles. Each bundle is normally collateral, *i.e.* with xylem on its inner and phloëm on its outer side. The carinal cavity marks the position of the *protoxylem* or first-formed tracheids of the bundle (see Fig. 44). Here a few tracheids have become thickened (in an annular or spiral manner) at very early stage of growth; consequently they cannot follow the expansion of the surrounding tissues, and a rupture takes place, forming the cavity. Projecting from the walls of this cavity we see the rings or spirals of the disorganised tracheids (see Fig. 44). The later-formed part of the xylem, consisting of a few scalariform tracheids (not vessels), is usually separated from the protoxylem by a little parenchyma, and forms two groups to the right and left of the bundle. The whole wood, therefore, if continuous and not disturbed by the carinal cavity, would form, as seen in transverse section, a V with the point inwards and the limbs outwards. The phloëm lies between the limbs of the V (see Fig. 44, *ph*). It consists of sieve-tubes (with sieve-plates on their oblique transverse walls) and parenchyma. Beyond this, on the outer side, we come to the pericycle and then to the endodermis (with well-marked Casparian bands on its radial walls) which marks the beginning of the cortex (Fig. 44). The xylem is often very little developed, especially in the rhizomes and the stems of aquatic species. The pith, or what remains of it, when the stem is fistular, consists of ordinary parenchyma, and presents no features of interest.

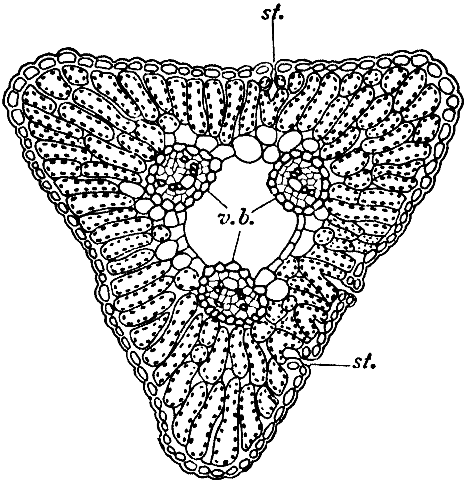

FIG. 45.—*Equisetum limosum*; transverse section of an ultimate branch of the aërial stem. *v.b*, the three vascular bundles, each with its own endodermis; *st*, the depressed stomata. The pith is hollow, but there are no vallecular cavities. Almost the whole cortex is assimilating palisade-tissue. Magnified 100 diameters. (R. S.)

The cortex, however, at least in the aerial stems and branches, is highly differentiated, as indeed we might expect, considering that it has here to perform the assimilating function usually assigned to the leaves. The inner cortical layers consist of large-celled parenchyma traversed by the air-containing vallecular spaces. The outer cortex is made up of two kinds of tissue, namely, sclerenchyma, fulfilling the mechanical function of strengthening the stem, and chlorophyll-tissue, to which the function of photosynthesis belongs (see Fig. 44). Now both these tissues need to be as near the surface as possible, in order to do their work to the best advantage. The mechanical tissue offers the greater resistance to bending strain, the further it is removed from the centre-line, or "neutral axis," as it is called in mechanics, of the column, here represented by the stem. For this reason we know that iron columns are always made hollow, for the same amount of material can be used to better advantage if brought as near the exterior as possible, than if distributed all over the transverse section. This mechanical principle is constantly illustrated in the construction of plants. Again, the assimilating tissue obviously requires to be as near the surface as possible, so as to be fully exposed to light, without which its work cannot go on.

Now we will see how in the stem or in a branch of *Equisetum* a ompromise is made between these two competing interests. Each rominent ridge of the stem is occupied by a strand of sclerenchyma, nd there are an equal number of additional strands placed at the ottom of the furrows (see Fig. 44, *sc*). The assimilating tissue occurs 1 curved bands, each of which lies behind one of the sclerenchymatous idges, and reaches the surface on either side of it, between the nechanical tissue of the ridge and that of the furrow (see Fig. 44, *a*). 'he epidermis has stomata at those places only where the chlorophyll-issue reaches the surface, so they are placed where they are most eeded. In the very minute ultimate branches, such as that of which transverse section is shown in Fig. 45, things are simplified. Here here is little need for mechanical strength, as the weight of the branch ; trifling, and so we find the whole cortex utilised for carbon assimila-ion.

The epidermis is chiefly remarkable for its strongly silicified outer ell-walls, which make the surface extremely hard. If all the organic natter be completely burnt away, a perfect skeleton of silica, still howing every marking on the cell-walls, is left behind. The stomata re peculiar, because the guard-cells are completely covered in on the op by the subsidiary cells, so that a double pair of guard-cells, one bove the other, seems to be present.

The description of the structure of the stem, which we have just iven, refers more especially to the sterile shoots growing above ground. 'oth the underground rhizomes and the fertile shoots are somewhat nodified in structure. In the former the epidermis is destitute of tomata, and the cortex of chlorophyll-tissue, while mechanical tissues re little developed: thus the whole differentiation of the outer tissues ; much reduced.

In *E. arvense* the pith of the rhizome is solid, and this is often so 1 the smaller aerial branches, as shown in our Fig. 44. The tubers onsist simply of parenchyma crowded with starch, and traversed by few reduced vascular bundles; each tuber corresponds to a single nternode.

b. The Leaves

The vascular bundles of the lead-sheaths are of simple collateral tructure, and do not have carinal canals. Each bundle is surrounded y its own endodermis, whether this is so in the stem or not. As in ne stem, the bundles correspond in position to the ridges of the sheath; utside each bundle lies a strand of sclerenchyma. A narrow band of hlorophyll-containing tissue lies between the sclerenchyma and the ascular bundle, and approaches the surface on either side of the ridge. The stomata are placed where the assimilating cells reach the epidermis, so that there are two longitudinal series of stomata corresponding to each vascular bundle. The rest of the leaf-sheath consists of ordinary parenchyma, which thins out between the ridges. The teeth, which alone represent the free part of the leaves, are still further simplified; a vascular bundle enters each tooth, but gradually dies out. The leaves are of little importance as organs of photosynthesis.

c. The Roots

The roots of *Equisetum* are always very slender, and must not be confused with the underground parts of the stem, which are much larger (see Fig. 43). All the roots seen on a mature plant are adventitious; the main root of the embryo only lasts a short time; its structure is like that of the adventitious roots, and our Fig. 46, which was drawn from the main root, will serve to represent either. The young parts of the root bear numerous root-hairs. There is a wide cortex, enclosing a small and simple central cylinder, the structure of which is usually either triarch or tetrarch.

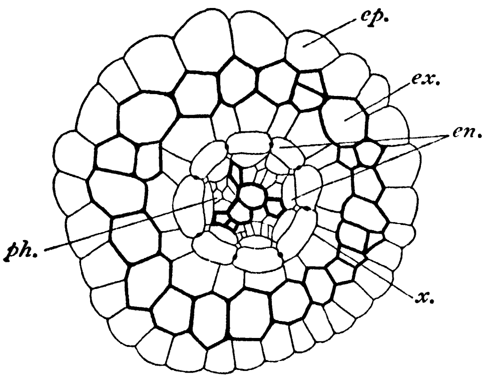

FIG. 46.—*Equisetum*; transverse section of main root. *x*, triarch xylem; *ph*, phloëm (three groups); *en*, double endodermis; *ex*, thick-walled exodermis; *ep*, epidermis. Magnified about 100 diameters. (After Buchtien.)

The arrangement of the xylem- and phloëm-groups is that usual in roots; the centre is occupied by a large tracheid. The chief peculiarity of the root is its double endodermis; the inner layer taking the place of a pericycle, which is quite absent. That this layer is really part of the endodermis is proved by the development, and by the fact that its cells fit on accurately to those of the outer sheath, which alone has the usual endodermal structure (see Fig. 46, *en*). The origin and mode of growth of the root will be considered in the next section. Apart from the peculiarity in the endodermis, the structure quite agrees with that of a simple root in the higher plants.

d. Growing-points and Branching

The growing-points of *Equisetum* afford perhaps the very best examples of growth by means of a single apical cell, by the divisions of which all the tissues arise. The apex of the stem is acutely conical (see Fig. 47), and the top of the cone is occupied by the large apical cell which has the form, so common in apical cells, of an inverted three-sided pyramid, of which the curved base is free, while the three sides are adjacent to the surrounding meristematic tissue. Divisions take place in the apical cell by walls formed in succession parallel to each of its three sides; each segment cut off is then divided into two by a wall parallel to the first.

The cells thus formed are again divided by approximately radial walls, and then for the first time division takes place in a plane parallel to the external surface of the growing-point. We now have an outer and an inner set of cells. The former, by their further growth and subdivision, give rise to the whole of the vascular tissue, cortex and epidermis; the inner cells only form the pith, which in the main stem soon becomes hollow. The ring of vascular bundles is only marked out at a long distance below the growing-point. About the fifth internode from the apex we find a small-celled zone of tissue, derived from the inner part of the outer layer. This zone gives rise to the vascular bundles, and to the medullary rays between them.

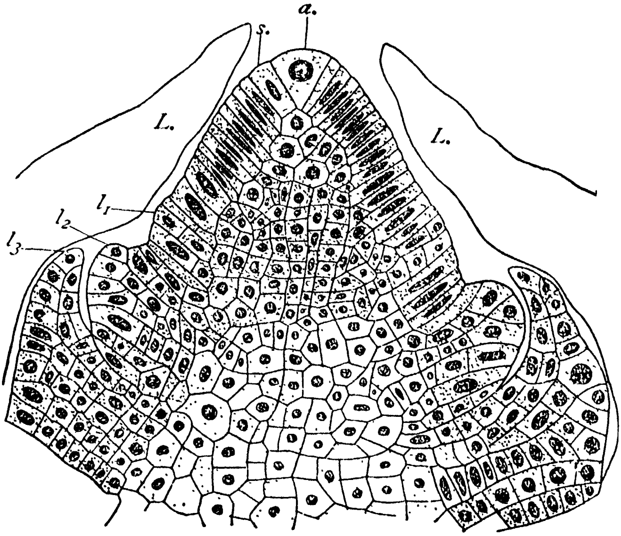

FIG. 47.—*Equisetum arvense*; longitudinal median section of the apex of the stem. *a*, apical cell; *s*, segment cut off from it; l_1, l_2, l_3, youngest leaves in order of age. *L*, outline of older leaves. Magnified 180 diameters. (R. S.)

The whorls of leaves are at first crowded closely together; the internodes between them only begin to lengthen some way down the stem. Each whorl arises from the outgrowth of a ring of tissue which extends all round the stem. The circular ridge thus produced, which is at first of equal height all the way round (see Fig. 47, l_1 and l_2), is the young sheath, and soon grows out at certain places to form the leaf-teeth. We see then that the sheath is formed first, and the free part of the leaves later.

The development of the branches in *Equisetum* is peculiar. They are apparently of endogenous origin, and for a long time were thought really to arise below the surface. The branches are arranged in whorls in the axil of each sheath, but alternating with the leaf-teeth. The buds arise near the growing-point, each from a single superficial cell, lying immediately above the junction between leaf-sheath and stem (see Fig. 48).

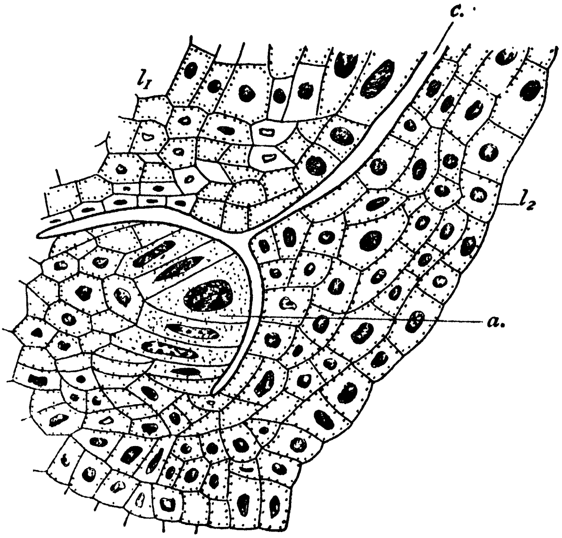

FIG. 48.—*Equisetum arvense*; part of a radial section of stem, just below the apex, to show exogenous origin of branch, *a*, apical cell of branch; l_1, cortex of stem; l_2, base of leaf below branch; *c*, crevice between them, about to close up. Magnified 360 diameters. (R. S.)

This cell divides up so as to carve out a pyramidal apical cell like that of the main stem, and the growth of the branch now goes on in the usual way. But while it still consists of a very few cells only, the leaf-sheath grows out above it, and joins on to the tissue of the stem on the upper side of the bud, so as completely to shut it in. Our figure shows the bud just before it is quite enclosed, while there is still a crevice left above it, between the stem and the leaf-sheath. When this passage is once shut, it never opens again; the bud goes on developing within a closed chamber. It lives to some extent at the expense of the surrounding tissue, and eventually breaks through the base of the leaf-sheath, and at last reaches the light of day. Seen from outside, these branches appear to arise below the node. Endogenous buds are very rare, and we see that those of *Equisetum* are not among them, but only become enclosed after they have started in the usual way, as superficial outgrowths.

Another peculiarity in *Equisetum* is the arrangement of the adventitious roots, which do not grow on the main stems, but are always in connection with lateral buds. As a rule, one root (occasionally more) is formed at the base of each branch, arising on its lower side, just below its first leaf-sheath. On the aërial branches these roots generally remain undeveloped, while the branch goes on growing. On the rhizome the reverse is the case, for, as a rule, the buds themselves are abortive, while the roots which they bear grow vigorously. The root grows at the apex by means of a single apical cell of the same pyramidal shape as that of the stem, from which it differs, however, in forming walls parallel to the free base, in addition to those parallel to the sides. The cells thus cut off at the end increase and multiply very rapidly, and form the root-cap. All the rest of the root is formed from the segments cut off from the three sides of the apical cell. The mode of growth is much the same as in the Fern-root, shown in Fig. 31.

The roots of *Equisetum* branch freely; the origin of the branches, as in other roots, is deep-seated or endogenous. It is from the inner layer of the double endodermis that the rootlets are formed, each of them arising from a single cell which lies just on one side of a protoxylem-group. This cell divides up so as to form an apical cell of the usual pyramidal form. The rootlet has to make its way through the whole thickness of the cortex.

2. Reproductive Organs of the Sporophyte

We have already learnt the main points in the structure of a cone of *Equisetum* so far as they can be seen with the naked eye or a pocket lens It remains for us to make ourselves acquainted with the more minute characters. The anatomy of the axis of the cone is in all essentials just the same as that of a vegetative stem, and the development takes place in the same manner, though the growth of the cone is limited. The whorls of sporangiophores are in origin somewhat similar to the whorls of vegetative leaves, but in the fertile cone scarcely any sheath is developed, so that sporangiophores are separate outgrowths almost from the first. The upper part of the sporangiophore soon begins to grow in diameter more rapidly than its base, which thus becomes constricted, so that the mature peltate form is already indicated. At about the same time the sporangia begin to show themselves as slight outgrowths projecting from the under-side of the expanded portion. Each of the sporangia, of which there are many, arises from the growth of a little group of cells. The essential part, however, can all be traced to a single superficial cell which by its repeated divisions gives rise both to the archesporium and to that part of the wall lying over it.

At the stage shown in Fig. 49 the archesporium has already grown and divided up, so as to form a good-sized mass of spore-producing tissue. The wall is several cells in thickness. The layer of cells which immediately surrounds the spore-producing tissue on all sides, and may be called the tapetum, is soon used up for nutritive purposes, and the intermediate layers also disappear, so that the wall of the ripe sporangium is only one cell thick. In the meantime the sporogenous tissue goes on increasing, but all its cells do not become mother-cells; a good many break down and give up their contents, which serve, together with the tapetum, to feed the survivors.

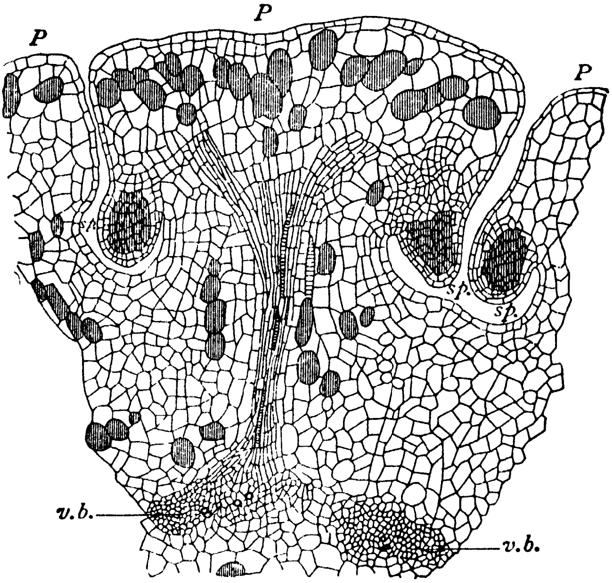

FIG. 49.—*Equisetum maximum*; part of transverse section of young cone, showing one complete peltate scale, and parts of two others (*P*). *sp*, sporangia; the shaded part is the archesporium; *v.b*, vascular bundles; the scattered shaded cells are tannin sacs. Magnified 50 diameters. (W. C. W.)

The remaining mother-cells, of which there are a large number in the sporangium, then divide each into four, the nucleus dividing twice before the partition-walls are formed. These two divisions of the nucleus represent meiosis, so that, as in other members of the Pteridophyta, the spores are haploid. Finally, the four daughter-cells are arranged in a tetrahedron.

The young spores of *Equisetum*, when first formed, have a thin wall of cellulose only, but as they ripen the structure becomes very complicated and characteristic. The actual membrane of the spore consists of three layers, but outside all these we find structures quite peculiar to *Equisetum*, namely, the *elaters*. They are formed from the fourth or outermost layer of the membrane—the *epispore*, as it is called; this layer splits along spiral lines into two long bands (with flattened ends), which, until the spore is mature, remain closely wrapped round it (see Fig. 43, 5). When the spores are quite ripe and getting dry, however, the two elaters stretch themselves out, remaining attached only in the middle of their length, and at one point, so that they appear as four distinct appendages (Fig. 43, 7). If it is damp they coil themselves up again (Fig. 43, 6). These extraordinary hygroscopic movements may be repeated an indefinite number of times, as we can see by mounting some spores on a dry slide under the microscope, and then breathing on them. The moist air makes the elaters coil up, and as they dry they stretch out again, setting the spores in motion by their contraction and expansion.

There is some doubt whether these movements tend to disperse the spores. Possibly the chief function of the elaters is to help in the dehiscence of the sporangium. As this loses moisture the spores inside begin to stretch out their elaters; this causes the whole mass of spores to take up more room, and so to press on the wall of the sporangium, which they thus tend to burst. It has also been suggested that they cause the spores to keep entangled together, so that they are obliged to germinate in company. This might be of importance, as the prothalli are usually diœcious.

The outermost layer of the sporangial wall, which alone persists till maturity, consists of spirally thickened cells. Dehiscence takes place by a longitudinal slit (Fig. 43, 4).

The development of the cones, at least in some species of *Equisetum*, is remarkably slow. Thus the cone from which the section shown in Fig. 49 was made, would not have matured for two years. In this species (*E. maximum*, the largest in the British Flora) the cones of three successive years are present on the plant at the same time. In March, when the spores are shed, we have not only the ripe cones rising into the air on the fertile stems, but underground, still enclosed in buds, we find the cones of the next year, and the year after that too. In some species, however, as in *E. limosum*, the development is a great deal quicker.

The spores of *Equisetum* contain not only a nucleus, but chloroplasts. As is usually the case with green spores, they must be sown within a few days after ripening, or they will not germinate at all.

II. *DEVELOPMENT AND STRUCTURE OF THE SEXUAL GENERATION (GAMETOPHYTE)*

1. THE PROTHALLUS

The spore gives rise to the haploid gametophyte or prothallus (see Fig. 50). On the whole, the sexual generation of the Horsetails is much like that of the Ferns, though there are many differences in detail, and the mode of growth and ultimate form of the prothallus are less regular in *Equisetum* than in such Ferns as *Dryopteris*.

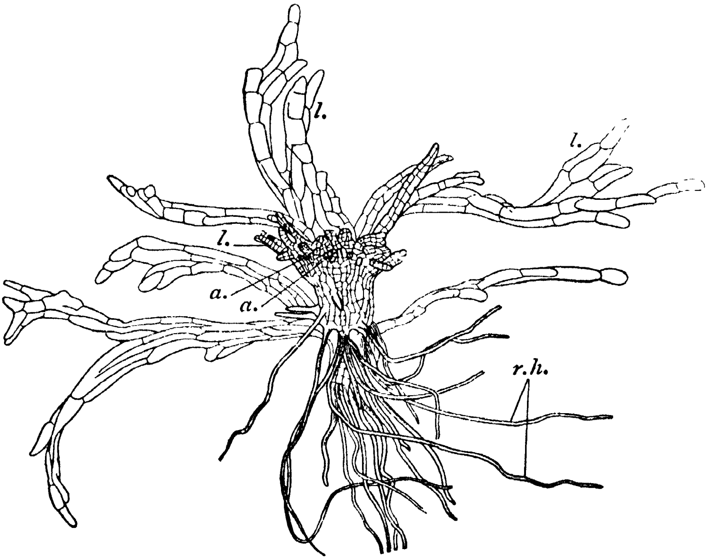

FIG. 50.—*Equisetum maximum*; large female prothallus, seen from below. *l*, *l*, lobes; *a*, *a*, archegonia; *r.h*, rhizoids. Magnified about 30 diameters. (After Buchtien.)

The most striking point about the prothallus of the Horsetails is its being usually (though not without exception) diœcious. We found that in the Ferns very small prothalli often form male organs only, while the better-grown individuals produce archegonia as well. In Horsetails this difference has gone farther and become more constant. Even in Horsetails, however, it is not fixed, but depends a great deal upon nutrition. Prothalli grown on a poor soil (*e.g.* damp sand) will only produce male organs, while those which are better treated will generally become females. The sexual organs of the prothallus need not be described, since in all essentials they agree with those of the fern prothallus.

2. The Embryo

Fertilisation, so far as is known, takes place in the Horsetails in the same way as in the Ferns. The spermatozoids, like those of Ferns, are sensitive to the presence of malic acid, and are no doubt thus enticed to seek the archegonia. The prothalli are by no means easy to cultivate, and only a few observers have succeeded in tracing the whole history. The prothalli generally grow healthily enough up to the time when the first antheridia are formed, but then they often begin to "damp off." However, the development has been followed throughout by a few botanists, so that we know how the embryo arises from the fertilised ovum. The latter first divides into two by a horizontal wall. The first division in the upper half (that towards the neck of the archegonium) is by a somewhat inclined wall, which separates the first leaf from the unicellular rudiment of the young stem. The latter at once cuts off two segments, which give rise to the second and third leaves. These three leaves form the first whorl of the young Horsetail. Though coherent at the base, they are more distinct from each other than the leaves of later-formed whorls. After these first divisions the apical cell of the stem has already assumed the pyramidal form which it keeps all through life.

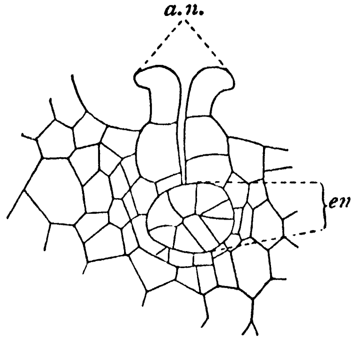

FIG. 51.—*Equisetum maximum*; fertilised archegonium. *a.n*, neck of archegonium; *em*, young embryo, showing first divisions. Magnified about 150 diameters. (After Buchtien.)

In the meantime similar divisions have taken place in the lower half of the young embryo. Here an inclined wall separates the cell destined to give rise to the main root from one which merely forms the *foot*, a comparatively unimportant structure in *Equisetum*. The root-cell, which lies exactly opposite that from which the stem is derived, divides up so as to form the usual pyramidal apical cell, from which, by a wall parallel to the free surface, the root-cap is marked off. Thus the young embryo of *Equisetum* is started, and even at this early stage shows something of the characters of the mature plant, such as the whorled leaves and pyramidal apical cells. Fig. 51 shows a very young embryo enclosed in the venter of the archegonium, when only a few divisions have taken place. In Fig. 52 we see the section of an embryo at a much more advanced stage, when two whorls of leaves are already formed.

Up to about this age the embryo remains within the cavity of the enlarged archegonium. So far, the root has not developed much, but now it grows rapidly and breaks through the tissue of the prothallus below it. It is followed by the stem, which bursts the neck of the archegonium. The young plant is now becoming independent, though for a time it remains connected, by means of the foot, with the prothallus. The main axis formed directly from the embryo has only a limited growth. It remains very slender, and stops growing after it has formed from ten to fifteen whorls of three leaves each. It is interesting to note that in the smallest species of *Equisetum*, *E. scirpoides*, three-leaved whorls are formed throughout life. At the base of the main stem a stouter lateral branch arises, and this again produces another still more vigorous shoot, and so on. Thus the mature form of the species is gradually built up by the production of successive branches, each more highly developed than the last. After a time one of the lateral shoots turns downwards and penetrates the ground, thus forming the first rhizome of the young plant. The main root is fairly well developed, though only a temporary organ, and shows the same structure as the subsequent adventitious roots.

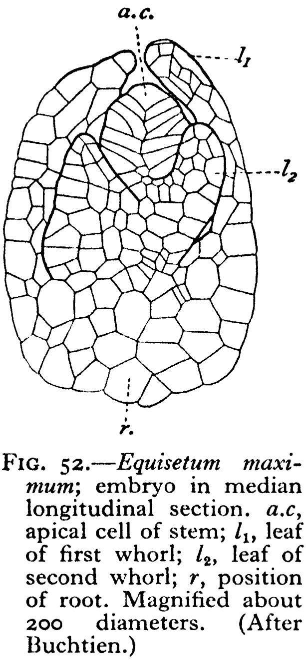

FIG. 52.—*Equisetum maximum*; embryo in median longitudinal section. *a.c*, apical cell of stem; l_1, leaf of first whorl; l_2, leaf of second whorl; *r*, position of root. Magnified about 200 diameters. (After Buchtien.)

SUMMARY

We have now traced a Horsetail through the complete cycle of its life. So far as the general course of development is concerned, we have found an essential agreement with that in the Ferns—namely, a sharply marked alternation of generations, spores of one kind, and a well-developed prothallus. Although the latter is usually diœcious, the distinction between male and female prothallus is not a fixed one, but is dependent to a great extent on external circumstances, especially nutrition. The prothallus is not unlike that of some Ferns, but the plant—the asexual generation—is as different as possible from Ferns and Lycopods, and this applies both to vegetative structure and spore-bearing organs. Evidently the Horsetails form a perfectly distinct class by themselves. As mentioned above, this class was once, in remote geological ages, an extensive and varied one. Many of its members not only grew into trees, but had the same mode of secondary growth by means of cambium, which is now almost entirely limited to Dicotyledons and Gymnosperms. Their fructifications showed a great variety, some few resembling those of *Equisetum*, while most of them were more complicated, and several produced spores of two kinds. In fact we can form a much better idea of the class *Equisetales* from the study of its extinct members, than from that of the small remnant which has survived to our own times.

We have now come to the end of our types of Vascular Cryptogams, and may very briefly sum up the characters of this great and ancient sub-kingdom of plants. They are quite easily characterised as plants with a clear alternation of sexual and asexual generations, each of which leads a more or less independent life, the asexual stage always being much the more highly developed of the two. The fertilisation by means of spermatozoids, which sometimes occurs even among the Gymnosperms, is here a constant character. The heterosporous Vascular Cryptogams come nearest to the Flowering Plants, as was fully explained in our chapter on *Selaginella*, which is the only heterosporous type which we have had space to describe. Heterospory, however, is by no means limited to the Lycopod series; it occurs also among Ferns, and, as we have already pointed out, among the fossil Equisetales. We cannot say for certain at present which of the heterosporous groups really comes nearest to the Phanerogams; probably none of those now living bear much resemblance to the real transitional forms (still altogether unknown), which existed at an enormously remote period. *Selaginella* serves as well as any other type to enable us to form an idea how Cryptogamic and Phanerogamic modes of reproduction are related.

CHAPTER II

BRYOPHYTA

THE sub-kingdom, with which we have now to deal, is characterised by the occurrence of a sharply defined alternation of generations, in which the sexual generation is the more important as regards vegetative development, the sporophyte being always dependent upon the gametophyte for a great part of its nutrition, and never becoming free. This sub-kingdom is that of the *Bryophyta*, or moss-like plants. It includes two great Classes, the true Mosses and the Liverworts. The Mosses, the general appearance of which is familiar to every one, have a vegetative growth much like that of the higher plants, with well-formed stems and leaves, but all these organs belong to the sexual generation, and so are not directly comparable with the leaves and stems of the higher plants, which belong to the asexual stage. The Liverworts, perhaps less generally known to those who are not botanists, sometimes have distinct leaves and stems not unlike those of the true Mosses, but many of them have a different organisation, the plant showing no distinction of leaf and stem, but consisting of an undifferentiated body performing the functions of both these organs, and called a *thallus*. We will take one of these thalloid Liverworts for our first type of Bryophyta, because its gametophyte generation is so much like the prothallus of a Fern, a fact which helps us at once to grasp the homologies between plants otherwise so different.

A. LIVERWORTS (HEPATICÆ)

PELLIA EPIPHYLLA

1. THE THALLUS

Pellia epiphylla Nees is a common Liverwort, growing in various non-calcareous habitats, sometimes by the sides of brooks or wells, or in damp woods and hedgerows, sometimes actually living under water; in other cases, however, it grows on comparatively dry sandy ground. The plant in its vegetative condition is a green, flat, lobed thallus, repeatedly branched, the lobes often overlapping each other (see Fig. 53).

The plants grow socially, and may collectively cover a considerable patch of ground. If we cut off a part of the thallus and examine it, we find that it forks repeatedly, all the branches lying nearly in the same plane. The thallus has an upper and under surface, the former darker green than the latter; it is traversed by a midrib, from which it thins off on either side towards the margins (Fig. 54). On the under-side numerous rhizoids are borne, which spring from the midrib and fix the plant to the ground; for *Pellia*, like other Bryophyta, possesses no true roots.

The whole character of the plant varies greatly according to the conditions under which it grows; so much so that its different forms would never be supposed to belong to the same species, if the transitional states had not been observed. Under water (where, by the by, *Pellia* never fruits) the thallus is long, narrow, and strap-shaped, branched at rather distant intervals, with a very distinct midrib, and very thin margins. On damp ground, where *Pellia* attains its greatest luxuriance, the thallus is much broader than in the aquatic form, but still elongated, with the branches spead out nearly flat, and the midrib very strongly marked. On dry sandy soil the plant assumes a very different form; the thallus remains short and stunted, with densely crowded branches overlapping each other. The whole plant is much thicker and tougher, and consequently the midrib becomes indistinct. Sometimes when the plants begin their new growth, they send out a great number of small crowded branches, giving a parsley-like appearance to the growing edge of the thallus.

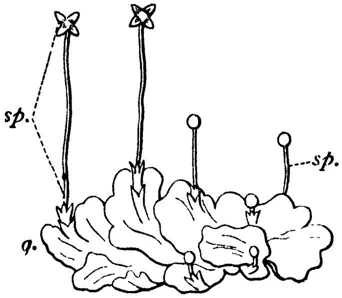

FIG. 53.—General view of a plant of *Pellia epiphylla*. *g*, the lobed thallus, constituting the gametophyte generation; *sp*, the sporophyte generation. The sporogonia to the left have opened; those to the right are younger and still closed. Half natural size. (After Cooke.)

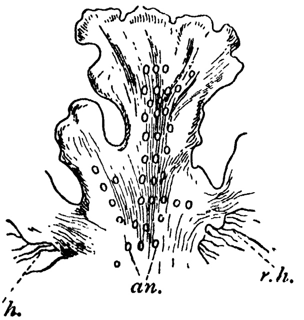

FIG. 54.—Part of the thallus of *Pellia*, seen from above. *an*, the numerous antheridia; *r.h*, the rhizoids. Slightly magnified. (R. S.)

The anatomical structure of the thallus is excessively simple. It consists entirely of parenchyma, the cells of which are elongated in the midrib, and polyhedral in the rest of the thallus. Chloroplasts occur chiefly in the more superficial cells. They are more abundant in the cells on the upper surface and in all cells of the thinner marginal portions. The whole tissue is rich in starch-grains and some cells contain oil. The epidermis has a thin cuticle, at least on the under surface of the thallus. In the interior of the middle part of the thallus there are sometimes vertical strands of cells with thickened walls. The walls, however, are of cellulose, and there is no lignification. The rhizoids are unicellular; the cell-walls of the older rhizoids have a brownish colour, but give cellulose reactions.

The growing-point of each branch lies as the base of a depression between the lobes, just as in the prothallus of a Fern. The growth here goes on by means of a single large apical cell, which cuts off segments both at its sides and base. The former build up, by their subsequent growth and divisions, the lateral parts of the thallus, while the basal segments are chiefly concerned in forming the midrib. The tissue derived laterally from the apical cell grows more rapidly than the apex itself, which consequently always lies in a recess of the margin.

The branching of the thallus, which as we have seen may take place very freely, is dichotomous, the original growing-point giving rise to two. The way this happens is that a new apical cell is formed near the old one, and then both the apical cells go on growing on their own account. The growing-point is surrounded by short glandular hairs, which secrete mucilage and so help to prevent the delicate tissues of this part from drying up.

We see, then, that the thallus of *Pellia* is both in external form and internal structure a very simple organism, bearing no resemblance to any of the plants hitherto considered, so far as their asexual generation is concerned. There is, on the other hand, a very marked agreement with the prothallus of a Fern in form, structure, and general mode of growth. In fact, as we shall find, *Pellia* and a Fern stand on nearly the same level as regards their sexual generations, though the sporophytes of the two are absolutely different.

2. The Sexual Organs

a. The Antheridia

The thallus of *Pellia* is a haploid gametophyte. It is monœcious, producing antheridia at first, and then beginning to form the archegonia. Although our plant bears a general resemblance to the prothallus of a Fern, we must not expect to find an exact agreement. In the position of the reproductive organs there is an important difference; in the Fern-prothallus they are usually limited to the lower surface, while in *Pellia* and the Liverworts generally it is always the upper side which bears them. The antheridia are easily seen with the naked eye, dotted over the upper surface on either side of the midrib (see Fig. 54).

The antheridia when mature are globular bodies, reaching 0·3 mm. in diameter, attached to the thallus below by a very short multicellular stalk. Each antheridium is enclosed singly in a flask-like sheath, leaving only a very narrow opening at the top (see Fig. 56). This sheath is formed by the gradual growing up of the thallus-tissue around the young antheridium. The development takes place in the following way: The antheridium arises from a single superficial cell situated on the upper side of the thallus, immediately behind the growing-point. This cell rises above the general level of the thallus, and divides by a transverse wall; the lower cell thus formed, after undergoing a few further divisions, forms the short stalk. The upper cell divides by a longitudinal wall into two cells, and these rapidly subdivide in such a manner as to form a single superficial layer enclosing a few central cells (see Fig. 55). The former constitute the wall of the antheridium, which remains one cell in thickness; the central cells undergo a great number of divisions, giving rise to a small-celled tissue, which, when mature, is entirely composed of the mother-cells of the spermatozoids (Fig. 56). During the cell-division rapid growth of the whole organ goes on, and in the meantime a wall of cells grows up around the antheridium, keeping pace with its development, and ultimately closing it in, except for a narrow opening at the top (Figs. 55 and 56).

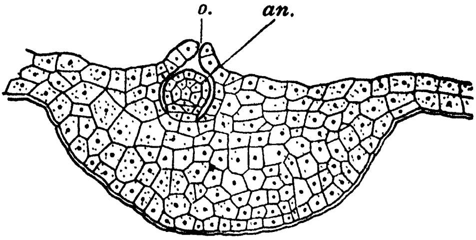

FIG. 55.—Transverse section through the midrib of the thallus of *Pellia*, showing a young antheridium. *an*, antheridium; *o*, opening of the sheath surrounding the antheridium. Magnified 80. (R. S.)

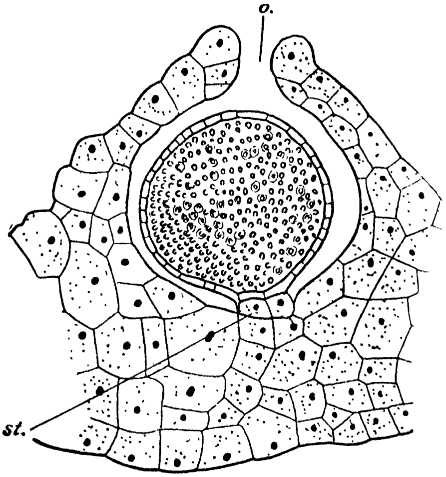

FIG. 56.—Part of a similar section showing a nearly ripe antheridium. *st*, stalk of antheridium; *o*, opening of sheath. Magnified 80. (R. S.)

This is the usual course of antheridial development in the Liverworts; the sheath, however, is not constantly present. There is also a fairly close agreement with the antheridia of Ferns, though there are some differences in the details of development as well as in size.

Each of the numerous cells of the central mass of tissue produces a single spermatozoid, just as in Vascular Cryptogams; the development is also just the same, for the body of the spermatozoid arises almost entirely from the nucleus, while the cilia, which are here two in number, are derived from the cytoplasm. The presence of two cilia only is constant throughout the Liverworts and Mosses. Among Vascular Cryptogams we find this number in the spermatozoids of most of the Club Mosses, as represented by *Selaginella*, while in the Ferns and Horsetails the cilia are much more numerous. In *Pellia* the body of the spermatozoid is spirally coiled, with the cilia attached just behind the thin end, which keeps in front while the spermatozoid is swimming (Fig. 57). Here also a little bladder, formed from the remains of the cytoplasm, hangs on to the spermatozoid when it is first set free.

b. The Archegonia

The female organs, which here, as in the Vascular Cryptogams, bear the name of archegonia, arise in large numbers just behind the growing-points of the older thalli on the upper side. The thallus always thickens where they are formed. The thickened part comes to a sudden end towards the margin of the thallus, and the archegonia thus come to be seated on a steep slope, facing towards the growing-point. In the meantime the thallus goes on growing below the thickened part, forming a thin membrane, while simultaneously a membranous out-growth arises above, behind the archegonia, and completely overlaps the whole group, which thus appears to be enclosed in a kind of pocket on the upper surface of the thallus. This pocket is called the *involucre*. The development of the involucre varies much according to the position in which the plant grows; in dry habitats it reaches a great length, while in wet places it remains short.

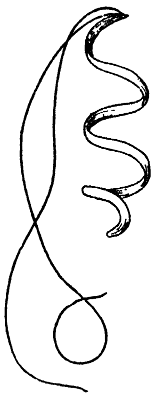

FIG. 57.—Single spermatozoid of *Pellia*, showing the spirally coiled body and the two long cilia. Magnified 1225. (After Guignard.)

We will now follow the development of the archegonium itself. Like the antheridium, it arises from a single superficial cell. This grows out and cuts off a basal cell by a transverse wall. From the upper cell the archegonium itself is developed. Three vertical walls are first formed, separating a central cell from three peripheral cells. A transverse wall cuts off a cap-cell from the top of the central cell. Then the peripheral cells, or some of them, divide vertically, so that we have a ring of about five cells surrounding the central one. Next, all the cells divide across by a transverse wall, cutting the whole archegonium into two halves, the lower being the venter and the upper the neck (Fig. 58). The principal parts are now marked out. The external cells of the lower ventral part grow and divide, giving rise to a wall two cells thick, while the central cell undergoes a single transverse division into two very unequal portions; the small upper part is the ventral canal-cell, the lower and larger cell becomes the *ovum* itself (Fig. 58). In the meantime the neck elongates greatly, and all its cells divide repeatedly by transverse walls, so that the ripe archegonium consists of a chimney-like neck, enclosing a row of canal-cells leading down to the ovum at the bottom (see Fig. 58). The cap-cell at the top of the neck divides into four by vertical walls crossing each other at right angles. We see that the archegonium of a Liverwort differs from the corresponding organ of a Fern or other Vascular Cryptogam, not only in the much greater length of the neck, but also in the origin of the neck-canal. In the Liverworts this is derived from the upper part of the archegonium, while in the Vascular Cryptogams it is formed from an outgrowth of the central cell. The final result, however, is much the same in both cases, and on the whole there is more reason to lay stress on the essential similarity of the sexual organs in plants so remote from each other, than to dwell on their somewhat minute differences.

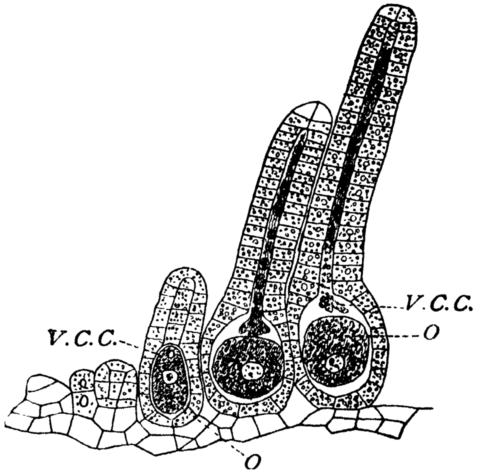

Fig. 58.—Archegonia of a Liverwort (*Marchantia*). The youngest stages are shown on the left. In the more mature archegonia, the venter, neck, and canal are clearly shown. *O*, ovum; *V.C.C*, ventral canal-cells. Magnified about 200.

When ready for fertilisation, the archegonium opens. This is due to the pressure of the mucilaginous substance in the canal, arising from the disorganised neck canal-cells. This substance takes up water, swells, and so forces the four cap-cells apart, causing the neck to open, while at the same time a portion of the mucilage protrudes through the opening.

c. Fertilisation

In *Pellia*, as in the Cryptogams generally, fertilisation must take place under water; after rain or dew the surface of the thallus is wet enough for the spermatozoids to accomplish their journey. The cells of the antheridial wall take up water, swell, and press upon the mass of spermatozoid mother-cells. The antheridium bursts, and its contents are set free. Due to surface-tension effects they spread out rapidly in all directions in the water film covering the thallus. Then, as soon as the spermatozoids are released from their mother-cells, they swim through the water, rotating as they go, in much the same way as those of a Fern. They are also drawn towards the archegonia as soon as they come within their "sphere of influence"; in another Liverwort (*Marchantia*) the spermatozoids are found to be attracted by soluble proteins, such as are doubtless present in the disorganised canal-cells. They are caught in the mucilage, wriggle down the neck of the archegonium, and one of them effects fertilisation by union with the ovum. In all this process there is exact agreement with the Vascular Cryptogams.

So much the more surprising is the remarkable difference in the ultimate product of fertilisation. The ovum when fertilised surrounds itself as usual with a cell-wall, and begins to divide. The result of this development will be considered in the next section.

3. The Sporophyte

a. External Characters

If we examine a fertile specimen of *Pellia* about February, we see the young sporophytes on the upper surface of the thallus. At this stage each sporophyte appears as a dark green ball, the *sporogonium* or *capsule*, about one-sixteenth of an inch in diameter, projecting from the involucre (Fig. 53). It is attached by a short, thick stalk of a lighter green colour, the bottom of which is tightly fixed in the body of the thallus. If we look at the sporophyte with a lens, we see that the upper spherical part—the capsule—is partly enclosed in a light-coloured membrane, the *calyptra*, which is just beginning to burst; the capsule, where its surface is exposed, is smooth and glossy. The stalk is called the *seta*.

Later in the season, about April, a great change happens. The seta elongates with great rapidity, and in three or four days attains a length of perhaps as much as three inches (see Fig. 53). The seta in its elongated condition is of a pure white colour, rather transparent, and bears the dark green, or now almost black, capsule aloft on its top, the whole looking like a thick pin with a round head (Fig. 53, on right). Shortly afterwards the dehiscence of the capsule takes place, by four longitudinal fissures, splitting the wall into four valves, which straighten themselves out, forming a horizontal cross on the top of the seta (see Fig. 53, on left). The spores are then set free. It is not long before the seta collapses, and the whole structure, when once the spores are shed, soon perishes. We will now go back to the fertilised ovum, and see how the sporophyte, which represents the asexual generation, is developed.

b. Development

Fertilisation may occur in all the archegonia within a single involucre, but normally only a single sporophyte is produced. Probably the first ovum to be fertilised monopolises the locally available food so that other fertilised eggs are prevented from further development.

The fertilised ovum within the archegonium is diploid and undergoes many divisions until a structure consisting of thousands of diploid cells is produced which is the sporophyte. While this development is taking place, the venter of the archegonium also grows to form the *calyptra* as a tightly fitting sheath around the sporophyte.

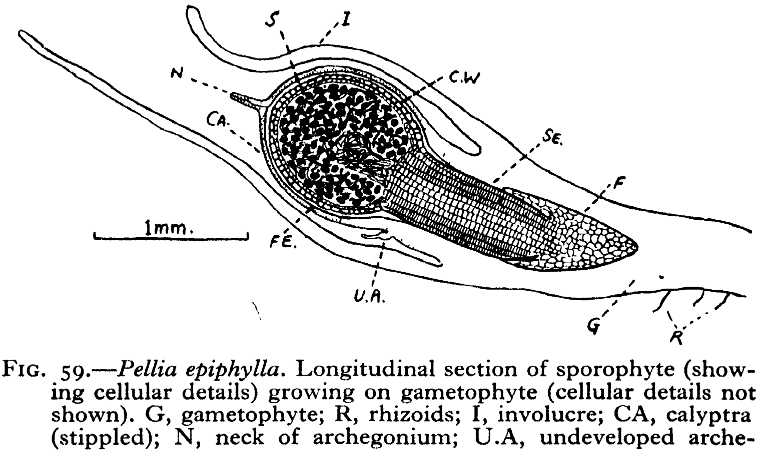

FIG. 59.—*Pellia epiphylla.* Longitudinal section of sporophyte (showing cellular details) growing on gametophyte (cellular details not shown). G, gametophyte; R, rhizoids; I, involucre; CA, calyptra (stippled); N, neck of archegonium; U.A, undeveloped archegonium; F, foot; SE, seta; C.W, capsule wall; F.E, fixed elaters in centre of capsule; S, spores and free elaters.

The fully-developed sporophyte, as it appears whilst still protected by the *calyptra*, consists of three parts (Fig. 59). First there is the *foot*, in form rather like an arrowhead pushed into the tissues of the gametophyte with which it is not in organic connection, but maintains intimate contact. The cells of the gametophyte around the foot are rich in starch and it seems clear that its function is the withdrawal of food, salts, and water from the gametophyte for the growth of the sporophyte. Secondly there is the *seta* or stalk consisting of very uniform short-celled parenchyma. Thirdly at the end of the seta is the *capsule* or sporangium with a wall consisting of several layers of cells inside which the sporogenous tissue occurs. However, the whole of this is not used up to form spore mother-cells. A certain number of the cells grow in length while remaining narrow and ultimately form long tubular structures with a double spiral of thickening reinforcing the wall internally. These curious elements—very characteristic of liverworts—are called *elaters*. In *Pellia* some of these elaters are fixed and radiate into the capsule from the top of the seta, but a large number are free.

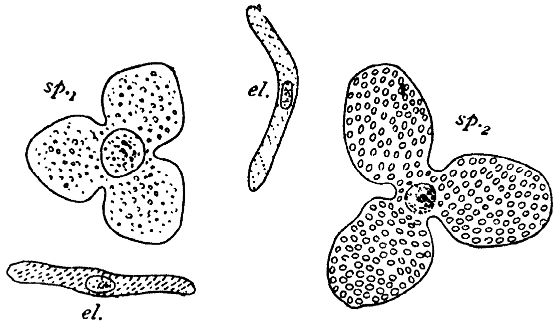

FIG. 60.—Elaters and spore mother-cells of *Pellia*. *sp.*$_1$ and *sp.*$_2$, spore mother-cells about to divide; *el*, *el*, young elaters with indications of spiral thickenings. Magnified 360. (R. S.)

Young free elaters, with the spiral bands just beginning to form, are shown in Fig. 60, and nearly mature ones are represented in Fig. 61 among the spores.

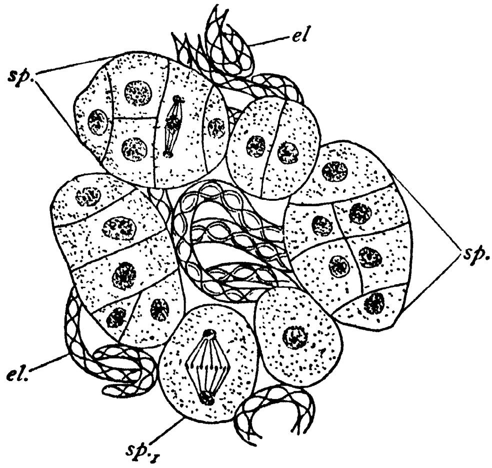

FIG. 61.—Spores and elaters from an almost ripe capsule of *Pellia*. Each spore (*sp.*) is dividing into several cells. At *sp.*$_1$, a stage of division is shown. *el*, *el*, elaters. Magnified 360. (R. S.)

The mother-cells of the spores, which are very numerous, are of a peculiar shape. At an early stage they become very deeply four-lobed, the lobes being tetrahedrally arranged, so that only three are seen in one plane (Fig. 60, *sp*). The lobes are connected in the middle by a quite narrow neck, in which the diploid nucleus, which remains for a long time undivided, is situated. Eventually the nucleus of the mother-cell divides twice to give four, each daughter-nucleus travelling out into one of the lobes, which now become separated from one another by cell-walls, so that the division is complete.

The two nuclear divisions represent meiosis, so that the four cells derived from the mother-cell form a tetrad of haploid cells. These are really the spores, but in *Pellia* a curious thing happens. The spores begin to germinate while still within the capsule, so that at the time of their liberation each is composed of six or eight cells containing chloroplasts (Fig. 61).

The whole structure of the sporophyte is already complete while the seta still remains quite short. Its elongation, as we have seen, is a comparatively sudden process, and is due to the great stretching of cells which are already formed. The calyptra, which was previously ruptured, is now left behind as a torn membrane at the base of the stalk.

As we have seen, the capsule splits on drying along four lines of weakness radiating from its apex. The four little teeth of capsule-wall thus delimited bend backwards exposing the mass of fixed and free elaters amongst which the spores are entangled. As this dries it expands into a fluffy mass from which the spores are blown away gradually and only by relatively strong gusts of wind (Fig. 62). The elaters show feeble hygroscopic movements. In many other liverworts, however, particularly the leafy ones, the elaters have much more powerful thickenings and perform very vigorous movements on drying which are responsible for the violent discharge of the spores.

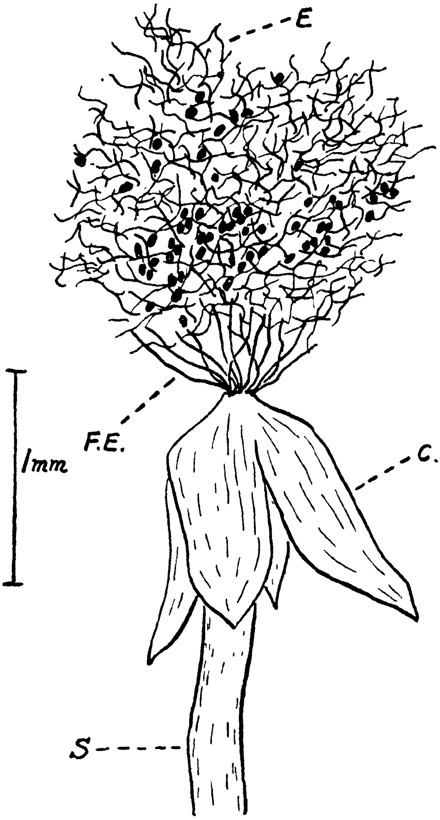

FIG. 62.—*Pellia epiphylla.* Dehisced capsule. S, seta; C.W, segment of capsule wall; F.E, fixed elaters; E, free elaters. The black dots are spores, but most have already been shed.

The development of the sporophyte of *Pellia* occupies a full year; when the spores are shed new archegonia are already ripe for fertilisation.

Falling in a suitable spot the spores are capable of germinating at once to give a new haploid gametophytic thallus.

SUMMARY

We have now completed the simple life-history of this Liverwort. We must not suppose that all Hepaticæ are equally simple; the class is a large one, said to include about five thousand species, and embraces a considerable variety of form and structure. In some (*e.g. Marchantia*) the thalloid form is retained, but a great complexity of anatomical structure exists, while at the same time the thallus bears highly modified branches for the production of the sexual organs. Special organs of vegetative propagation—gemmæ—are also very frequently present, which serve to reproduce the haploid thallus directly. In another very numerous series of Liverworts, we find, instead of a thallus, a delicate leafy stem of great beauty; in this group (which includes the majority of the species) we have a high external differentiation of the gametophyte, while the anatomical structure remains simple. We will now sum up the essential points in the development of Liverworts, as represented by our type.

The thallus of *Pellia* is obviously comparable to the prothallus of a Fern, while the antheridia and archegonia also are evidently of the same nature as the sexual organs of the Vascular Cryptogams. Fertilisation is accomplished in just the same way, but the product is totally different. In the Ferns the sexually produced embryo grows up into the plant itself, which goes through a long and vigorous course of purely vegetative development before it proceeds to form the asexual reproductive cells (spores). In *Pellia*, and Liverworts generally, the sexually produced embryo grows, not into an independent plant at all, but merely into a small sporophyte, which remains attached to and dependent upon the sexual individual. The capsule, it is true, contains chlorophyll in its outer layer, and so can do some assimilation on its own account, but for the bulk of its food it must rely on the store produced by the thallus. Spore-production is the one function of the sporophyte; all the parts—foot, seta, and capsule—are means subservient to this end; there is no vegetative development worth mentioning. This is the great characteristic, not merely of the Liverworts, but of the Bryophyta generally—the gametophyte is the prominent vegetative generation, while the sporophyte has little more to do than to discharge its purely reproductive functions as a spore-producing organ. The sporophyte is not always so simple as that of *Pellia*, but still the same rule holds good. We see, then, that in this sub-kingdom we have to do with plants in which the sexual generation is readily comparable to that of the higher Cryptogams, while the product of fertilisation—the sporophyte—is developed on entirely different lines. The Bryophyta are in fact plants with a well-marked alternation of generations, in which the *sexual* generation is the more conspicuous and independent. The distinction between Bryophyta and Vascular Cryptogams is so sharp and constant that the gulf between them has been spoken of as the widest in the vegetable kingdom.

B. THE MOSSES

FUNARIA HYGROMETRICA

The true Mosses, the general appearance of which will be familiar to everyone, are more highly organised plants than the Liverworts. Their greater complexity extends to both generations; the higher development of the gametophyte removes all obvious resemblance to the prothallus of a Fern, while the sporophyte, though complicated, is still only a stalked sporogonium, and in no way approaches the asexual generation of the Pteridophyta. The Mosses, unlike *Pellia*, never have their vegetative organs in the form of an undifferentiated thallus, but possess a perfectly distinct stem bearing spirally arranged leaves. In fact, the external characters of a Moss plant are essentially similar to those of vascular plants, but in the Mosses leaf and stem belong to the haploid sexual generation, while in the higher plants they form part of the diploid sporophyte.

The special Moss (*Funaria*) on which our description is based (Fig. 63), is a very common one, and usually grows on the ground, sometimes occurring on walls also, where, however, it is less abundant than some other kinds. It comes up in great quantities in places where there has been a fire. This Moss grows in close tufts of a bright green colour; in a single branched shoot we find that the slender stem is erect, reaching perhaps half an inch in height, and densely clothed with small simple leaves. The lower part, where the plant is kept from the light by the crowding of its fellows, is brown, the leaves here having lost their colour. The upper free part of the stem bears the bright green living leaves, and terminates in a bud. The stem is branched, but not very abundantly, the branches, like the main stem, growing in a vertical direction. At the base of the plant we find a number of attaching filaments or *rhizoids*, but there is no real root—an organ which does not exist in any of the Bryophyta.

The leaves are arranged in a spiral and are inserted on the stem with a fairly broad base; they are ovate in form, pointed at the tip, and traversed by a distinct midrib, though not otherwise veined. The septate rhizoids are hyaline when quite young, but soon become brown.

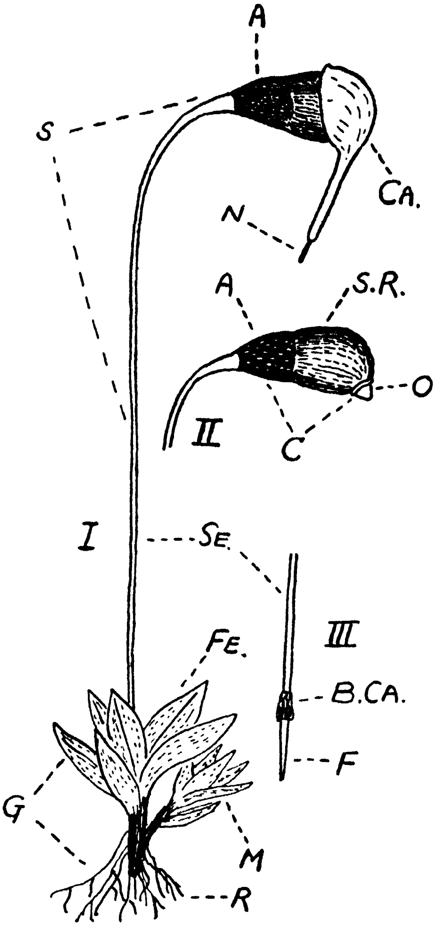

Fig. 63.—*Funaria hygrometrica.* Structure as seen with hand lens. I, whole plant; II, capsule after removal of calyptra; III, basal part of sporophyte pulled away from gametophyte. S, sporophyte; G, gametophyte; F, foot; B.CA, base of calyptra; CA, calyptra; N, neck of old archegonium; C, capsule; A, apophysis; S.R, spore-bearing region; O, operculum; S.E, seta; FE, female branch and M, male branch of gametophyte; R, rhizoids.

The above description applies especially to the barren stems; we shall refer more particularly later on to those which bear the reproductive organs.

1. The Leafy Stem

a. Structure

The anatomy of the Moss plant, as represented by *Funaria,* is simple, but yet shows a fairly well-marked differentiation of tissues. In the mature stem three distinct zones can be distinguished—epidermis, cortex, and central cylinder. The epidermis is one cell thick in most places, though here and there a double row of cells may be found. Its cells are small, and in the older part of the stem become very thick-walled. The cortex is of relatively great thickness, and made up of parenchyma, the outer cells having thicker walls than the inner. When young, the cortical cells contain chlorophyll. The central cylinder consists of a very sharply defined cylindrical strand of long, narrow, thin-walled cells, destitute of protoplasm. It is possible that this is a conducting tissue.

The leaves of *Funaria* are transversed by a conspicuous midrib while the rest of the leaf is only one cell thick. The cells of the thin part are uniform, except at the somewhat serrated edge, where they are narrower and have rather thicker walls. The midrib is several cells thick, and contains a small strand of narrow cells, like those in the central cylinder of the stem. Probably these cells conduct water and assimilated food, while the function of assimilation belongs to the thin part of the leaf, which is very rich in chloroplasts (Fig. 65, *d*). Moss leaves, by the by, are very favourable objects for observing the multiplication of the chloroplasts by division.

As we have said, a Moss possesses no true root. The functions of a root are performed by the *rhizoids*, as they are called, multicellular filaments springing from near the base of the stem (see Fig. 64, *r*). These rhizoids are different from the rhizoids of Liverworts, which are unicellular. The Moss rhizoids consist of a single chain of very long cells separated from one another by oblique walls. They grow entirely by means of the apical cell at the free end of each filament, and branch repeatedly, the diameter diminishing with the successive orders of branching, so that the final ramifications are very slender indeed in comparison with the main filaments. The whole simulates a regular root system, though totally different in structure.

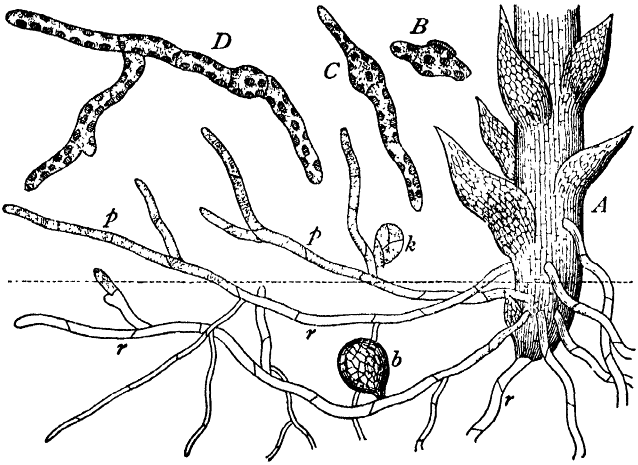

FIG. 64.—*A*, lower part of a Moss plant, bearing leaves and rhizoids (*r*), which grow up above the ground and form secondary protonemata (*p*). At *b* is an underground gemma or bulbil. At *k* is a bud from which a new leafy stem will grow. Magnified about 20. *B*, *C*, and *D*, successive stages of germination of a spore of *Funaria*, producing a primary protonema. Magnified 200. (After Luerssen.)

b. Apical Development

The stem of all Mosses grows by means of a single apical cell, and the plant is built up in the most regular manner from its segments. The cell is of the same inverted pyramidal form which we found in *Equisetum*, and divides at first in the same way by walls parallel (or nearly parallel) to the three sides. Each segment first divides into an inner and an outer cell. From the inner cells thus formed the greater part of the tissues of the stem is derived, while the outer cells give rise to leaves, buds, and the outside part of the stem. Each outer cell divides into an upper and a lower half; from the upper half the leaf is produced while the lateral buds, where they exist, owe their origin to the lower of the two cells. We see then that every segment produces a leaf, and that each lateral bud stands *below the leaf* to which it belongs, instead of in its axil—a striking difference from the higher plants. Later growth, however, may apparently displace this arrangement. Each leaf grows in length chiefly by means of a two-sided apical cell. The chief points then in the development of a Moss stem are the growth from an apical cell, the origin of a leaf from each segment, and the position of the lateral buds *beneath* the leaves to which they belong.

2. The Sexual Organs

The leafy moss plant is a haploid gametophyte. *Funaria* is monœcious, though this is not the case with all Mosses. The female shoots arise as lateral branches on the male. Later, however, the male branch is pushed to one side and appears lateral (Fig. 63). At the top of the male branch the leaves are crowded together to form a conspicuous rosette. This is not unlike a flower, especially as the middle part of the rosette is of a reddish colour. In some of the larger Mosses (such as *Polytrichum*, which includes some very conspicuous Mosses, common on heaths) the resemblance to a flower is still more striking. However, there is of course no direct homology, for these rosettes belong to the gametophyte, not to the sporophyte generation, and the organs which they enclose are antheridia, not stamens. On the growing-point, within the rosette, numerous antheridia arise in long-continued succession without any strict order. Both young and mature antheridia are shown in Fig. 65. As usual, the antheridium owes its origin to a single cell in which one or two transverse walls are formed, after which the growth goes on entirely by means of the apical cell, which cuts off two rows of segments. It is a good general rule in the Mosses that every organ, of whatever kind, grows by means of an apical cell, whereas this mode of growth is nothing like so general among the Liverworts. By further subdivisions of the segments, and finally of the apical cell itself, the antheridium is differentiated into an external wall one cell in thickness, and an internal tissue, each cell of which becomes the mother-cell of a spermatozoid (Fig. 65, *b*).

The mature antheridium is club-shaped and 0·3 mm. long, containing many mother-cells. The development of the spermatozoid is similar to that in Liverworts or Vascular Cryptogams. The antheridia open on access of water; the cells of the wall swell and press upon the mother-cells within, which are expelled, when the top of the sac ruptures, in a single mass. The mother-cells spread apart on the surface of water and are conveyed to the female branches by rain or dew. The mucilaginous walls of the mother-cells disappear, liberating the spermatozoids; each is spirally coiled with two cilia, as in the Liverworts (see Fig. 66, *C*). The antheridia are accompanied by multicellular hairs with large heads, called the *paraphyses*.

The female branches are, at first, very small; usually one such branch is present, springing from the male stem some distance below the rosette; sometimes more branches are produced. The leaves converge together at the top, forming a bud within which the archegonia are contained (Fig. 66, *A*). They arise from the cells of the growing-point, and the apical cell among others is itself used up to form an archegonium, so that no further direct growth of the vegetative axis is possible.

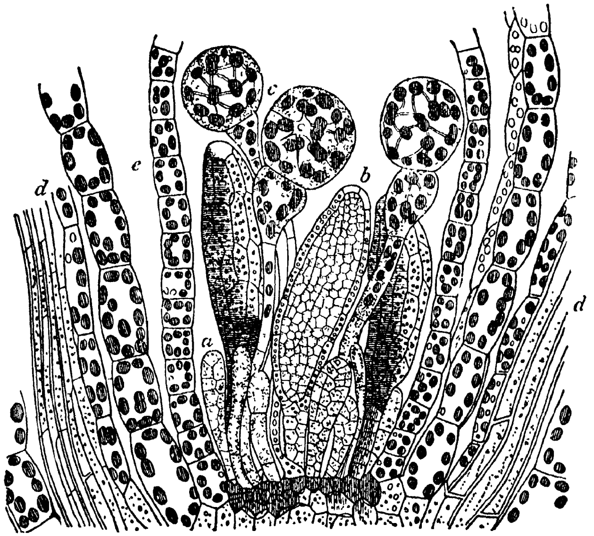

FIG. 65.—Longitudinal section through the apical bud of a male shoot of *Funaria*, *d*, leaves cut through the midrib; *e*, leaves cut through the lamina; *c*, paraphyses; several antheridia are shown; *a*, very young; *b*, nearly ripe antheridium. Magnified 300. (After Sachs.)

The cell from which an archegonium is to be formed first divides by a transverse wall. The further growth is by means of the apical cell, which in this case gives rise to four rows of segments, three of which are peripheral and form the wall of the archegonium, while the fourth row is central. From the lowest cell of the central row the ovum and ventral canal-cell (see Fig. 66, *B*) are produced; the rest of the series of central cells forms the canal of the neck. The external segments undergo further transverse and vertical divisions; the wall of the neck ultimately consists of six rows of cells surrounding the canal. The ventral part of the wall, enclosing the ovum, becomes two layers in thickness, and the whole archegonium is seated on a multicellular pedicel. Apart from this last point, the final form of the archegonium is similar to that in the Liverworts, the chief difference consisting in the marked apical growth which goes on in the archegonium, as in other organs, of the true Mosses. When ready for fertilisation the terminal cells of the neck separate widely from each other, leaving an open passage into the canal, which now only contains the mucilage derived from the disorganised canal-cells.

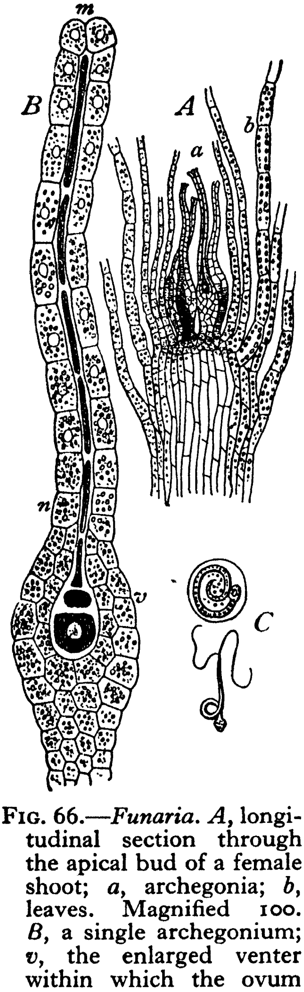

Fig. 66.—*Funaria. A*, longitudinal section through the apical bud of a female shoot; *a*, archegonia; *b*, leaves. Magnified 100. *B*, a single archegonium; *v*, the enlarged venter within which the ovum and ventral canal-cell are seen; from *n* to *m* is the neck, enclosing the neck-canal. Magnified 550. *C*, unripe spermatozoid in its mother-cell, and mature spermatozoid with two cilia. Magnified 800. (After Sachs.)

Fertilisation, as in Cryptogams generally, takes place under water. The male cells are brought near the female organs as already indicated; they may trickle down or be splashed on to the female branches in rain or dew. In some diœcious Mosses (*e.g. Polytrichum*), however, the spermatozoid mother-cells are often carried to the female plants by insects. The spermatozoids liberated from the mother-cells in the vicinity of the archegonia must accomplish the rest of their journey by their own movements. Experiments precisely similar to those described in the case of the Ferns have been successfully carried out on Mosses, and here also it appears that the archegonia attract the visits of the swarming sperm-cells by means of a chemical secretion. In Mosses, however, it is not malic acid, but sugar (cane-sugar), which forms the bait. The spermatozoids, having been thus lured to the archegonium, penetrate the neck-canal, and one of them ultimately reaches the ovum and effects fertilisation.

3. The Sporophyte

Funaria fruits very freely, and if we look at a patch of it, at any time of year, we are sure to find plenty of fructifying plants at one stage or another. In the mature state the sporophyte consists of a long red-brown stalk, bearing at its end a nodding pear-shaped capsule (see Fig. 63), which at first is green, but finally turns brown. Until almost the last the capsule carries on its top a conical hood (the *calyptra*) split along one side; at an earlier stage this completely envelops the capsule, and is only pushed off as it expands, remaining hanging for a long time. When the calyptra is removed we see the top of the capsule, which is closed by a neat conical lid. The stalk (*seta*), the base of which is pointed and is inserted into the gametophyte stem as a *foot*, and capsule (*sporogonium*) together constitute the diploid asexual, spore-bearing generation, and is derived from the fertilised ovum. The calyptra, however, is formed from the enlarged wall of the archegonium, which is split off at the base, and borne aloft on the capsule as it grows. The calyptra therefore is, by its origin, a portion of the sexual plant. We will now describe the structure of the sporophyte when fully formed, and then shortly trace its development from the ovum.

Beginning with the capsule, which is the essential part, containing the spores, we find that its base is solid, while the upper portion contains a large hollow space separating the central mass of tissue from the wall. (The longitudinal section shown in Fig. 67 is from a young capsule in which all the tissues are already marked out. Fig. 68 is a diagrammatic representation of the same structure.)

It is the upper part of the capsule which is fertile, while the basal solid portion (*apophysis*) performs nutritive functions. The whole capsule is covered by a well-marked epidermis which, on the apophysis, contains stomata. In the upper part of the capsule the hypodermal layers are colourless, while those towards the interior contain chlorophyll. Connected with these inner cells of the wall are filamentous strands, also containing chlorophyll, which extend across the intercellular space, and form a junction with the internal tissues. The central mass is narrow below and expanded above, assuming a barrel-like shape. It is from this part that the spores are produced. The archesporium forms at first a single cellular zone, which has a hollow cylindrical form, or, more accurately, is shaped just like a barrel with the ends knocked out (see Fig. 68, A). The archesporial layer is separated from the intercellular space by a zone of sterile tissue called the outer *spore-sac*. Within the archesporium is the large central mass of sterile colourless tissue (the *columella*), which is connected below by a thinner strand with the tissue of the apophysis. The layer between archesporium and columella is called the inner spore-sac. The lid (*operculum*) is at first continuous with the capsule, but eventually becomes detached by the severance of a ring of cells (the *annulus*) between lid and wall.

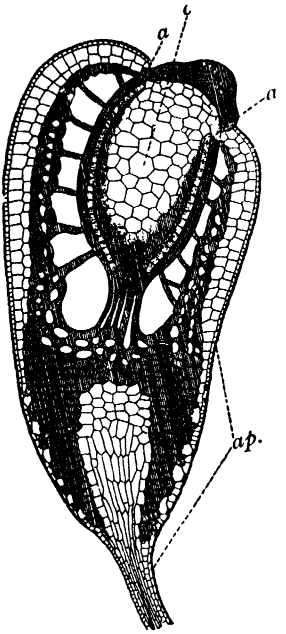

Fig. 67.—Capsule of *Funaria* in longitudinal section. *ap*, the apophysis; *a*, *a*, the archesporium, forming a single layer of cells (lightly shaded); it surrounds the columella, *c*. The green assimilating tissue is darkly shaded. The operculum closes the top of the capsule, above the columella; its individual cells are not shown. The dark spots in the epidermis of the apophysis indicate the stomata. Magnified 14. (After Haberlandt.)

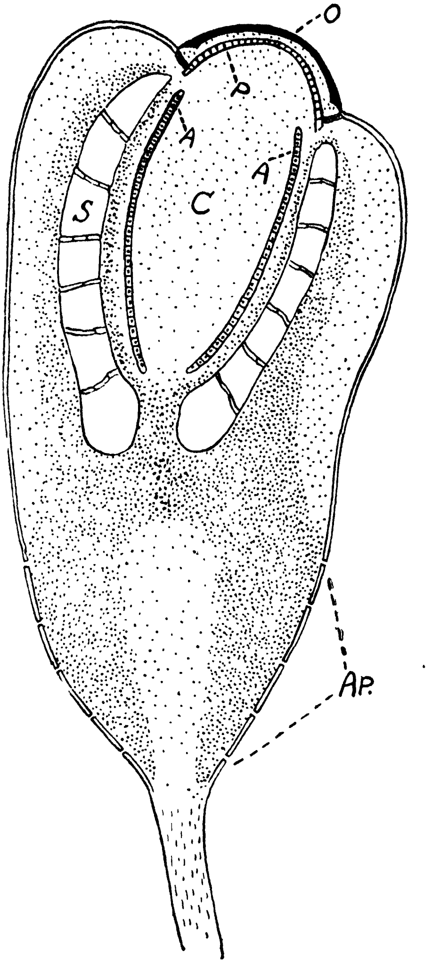

Fig. 68.—*Funaria*, diagram of capsule illustrated in Fig. 67. AP, apophysis (the gaps represent stomata); O, operculum; P, peristome; A, archesporium; C, columella; S, air-space crossed by trabeculæ.

The apophysis is essentially the assimilating part of the capsule; beneath the epidermis is a broad zone of chlorophyll-tissues, the cells of which are in many cases of the typical palisade form (see Fig. 69). The epidermis bears well-developed stomata, which are in essentials similar to those of the higher plants. In *Funaria*, however, they generally have the peculiarity that the wall between the two guard-cells breaks down at the two ends, so that the part enclosing the pore is left standing up in the middle of the fused guard-cells, like a chimney-shaft passing through a room (Fig. 70). At an earlier stage, however, the stoma is two-celled, just as in vascular plants, and in many Mosses it remains so all through. In other respects these Moss-stomata are quite typical. The guard-cells differ from the ordinary epidermal cells in containing abundant chloroplasts; the form of the cells, as seen both in surface view and in section, could be exactly matched in the stomata of flowering plants. Beneath each stoma is an intercellular space (Fig. 69). It is remarkable to find these organs so perfectly differentiated in plants like the Mosses, which in all other respects are so remote from the higher groups. A few Liverworts e.g. *Anthoceros*) also have well-formed stomata on the sporogonium. It is worth noting that typical stomata have in no case so far been found in the sexual generation; when the gametophyte bears organs with the same function (as in certain Liverworts), they are constructed on a totally different plan.

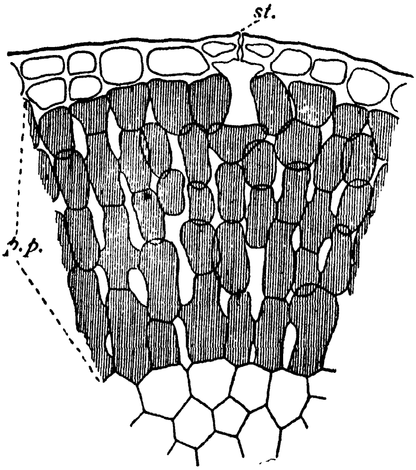

FIG. 69.—Part of the apophysis of a Moss (*Bryum*) in transverse section. *p.p*, the assimilating palisade parenchyma; *st*, stoma. Magnified 130. (After Haberlandt.)

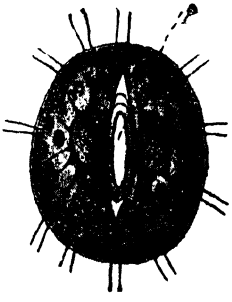

FIG. 70.—Stoma of *Funaria* in surface view. *p*, the pore. Note the nuclei and chloroplasts of the fused guard-cells. Magnified 630. (After Haberlandt).

It is evident from the anatomical structure that the sporophyte is capable of obtaining a great part of its food for itself, and this has been proved experimentally to be the case. So far as the assimilation of carbon is concerned, a sporogonium of *Funaria* is largely able to provide for itself, from the time when its assimilating tissue is developed. Water, with the mineral food-substances, is necessarily supplied through the stem of the Moss plant, and passes up to the capsule through the seta, which contains a central conducting cylinder, like that of the stem itself. The cortex of the seta consists of thick-walled tissue, and serves to give the mechanical strength necessary to enable this slender stalk to support the weight of the capsule. The bottom of the seta is fixed in the tissue of the gametophyte by a conical foot (Fig. 63), but although the contact is a very close one there is never any organic connection between the two generations.

We see then that the sporophytic generation of *Funaria* is in part parasitic on the sexual plant, in part independent. It resembles in this respect a green parasite such as the mistletoe, which, like the *Funaria* fruit, must obtain all its water and mineral food from the host-plant on which it grows, but can provide its carbonaceous food for itself.

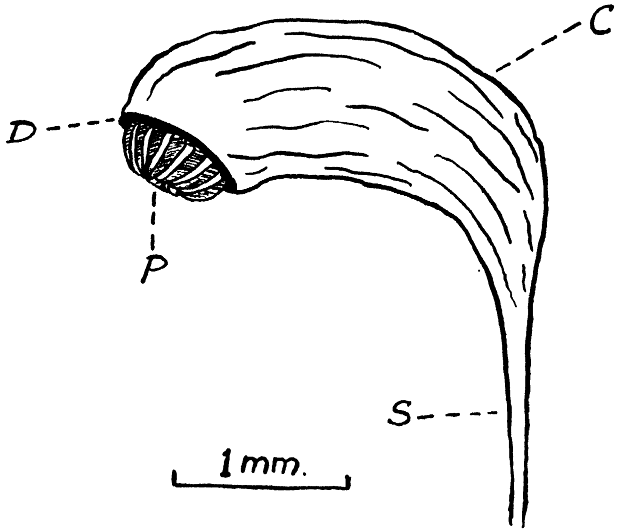

FIG. 71.—*Funaria hygrometrica.* Dry mature capsule after separation of the operculum. C, capsule; S, seta; D, diaphragm; P, peristome.

In some other Mosses, however, the sporophyte is destitute of chlorophyll, and so has to lead a completely parasitic existence, depending for the whole of its food on the leafy Moss plant.

We will now return to the essential part of the capsule, that, namely, in which the spores are formed. The archesporium is at first only a single layer of cells, and occupies but a small part of the capsule (Fig. 68). Repeated divisions now take place, and the archesporium increases in thickness. Ultimately each of the cells formed by it becomes a diploid spore mother-cell, which undergoes meiosis to form a tetrad of haploid spores. As soon as the spores are ripe the capsule begins to dry up. The columella and all the delicate tissues of the fruit collapse, and when the capsule is fully ripe it consists essentially of the wall only, filled with a mass of dark-green spores. The lid becomes detached, but the capsule after this is not left freely open, for in the meantime a double row of teeth (called the *peristome*) has been formed (Fig. 71 and Fig. 72). These teeth, which project from the edge of the capsule and partly close its mouth, are formed from strips of thickened cell-wall, all other parts of the cells involved having perished.

The spores are not all scattered at once; the dissemination is regulated by the teeth of the peristome, which, when the air is wet, completely close the mouth of the capsule. Thus spores escape only in dry weather.

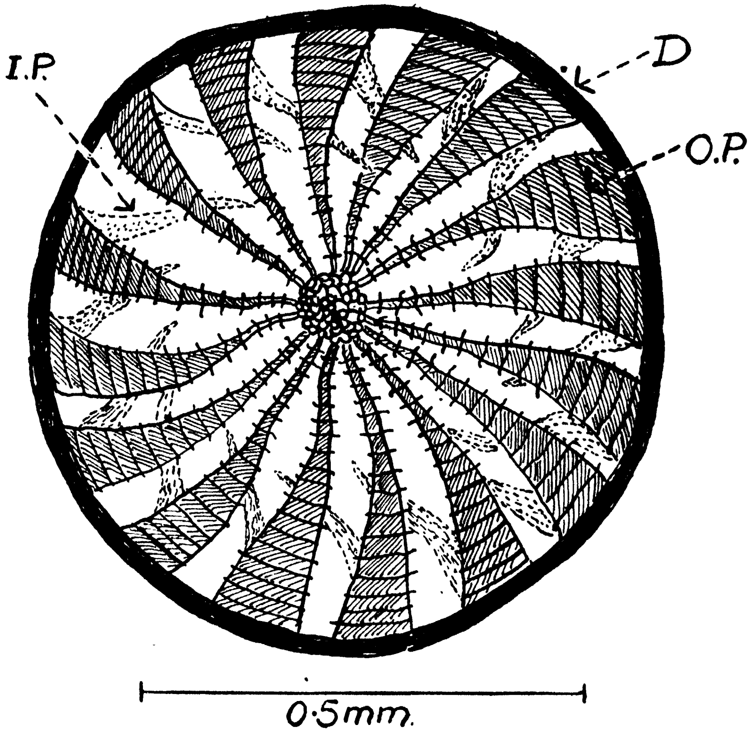

FIG. 72.—*Funaria hygrometrica.* Peristome as seen when looking directly into mouth of capsule. D, diaphragm; O.P, outer peristome tooth; I.P, inner peristome tooth.

4. GERMINATION OF THE SPORES

The spores themselves contain abundant chlorophyll, and also have a reserve of oil which serves to provide material for germination. When this takes place, the spore does not at once give rise to a Moss plant, but first of all produces a branched filamentous growth of very simple structure, much resembling some of the simpler plants (*Algæ*), as we shall find later on. This filamentous condition of the young Moss, which thus forms the first stage of the gametophyte generation, is called the *protonema* (see Fig. 64). The spore generally sends out filaments in two directions; one remains green and creeps along the surface of the ground, the other loses its chlorophyll and becomes the first rhizoid. The filaments grow in each case by an apical cell; they branch freely but remain only one cell in thickness; often the protonema develops to a great extent, forming a tangled green felt, which may cover several square inches of ground. The young Moss plants arise from the protonema as lateral buds (see Fig. 64, *k*). A cell of the protonema gives rise to a branch; the branch divides by inclined walls so as to form a tetrahedral apical cell, and as soon as this has taken place regular segmentation begins, and the leafy Moss plant is soon built up. The first leaves are simpler than those of the more mature plant, and may be destitute of a midrib.

The protonema which we have just described is formed directly from the spore, and is therefore called the *primary* protonema. It may also arise in a secondary way from any part of the plant—from rhizoids (see Fig. 64), or from the stem or leaves. The production of protonemata provides the plant with a most abundant means of vegetative propagation, for every growth of protonema is capable of giving rise to a number of Moss plants. Many Mosses produce special vegetative buds either on their stems or rhizoids (Fig. 64, *A*, *b*), or throw off certain of their leaves as organs of propagation. In most cases, whatever be the nature of the reproductive body, whether spore or bud, it begins by forming protonemata, from which the leafy plants arise at a later stage. This insertion of a filamentous stage of growth in the life-cycle, before the production of the typical form of gametophyte, is very characteristic of the true Mosses; in the Liverworts, the protonema is on the whole much less developed.

SUMMARY

If we now briefly sum up the characteristic points in the life-history of the true Mosses, we see that both generations are decidedly more highly organised than in the Liverworts. The gametophyte is here constantly developed as a leafy stem, quite comparable to that of the higher plants, though occupying a different place in the life-history. We find at the same time a considerable degree of anatomical complexity, corresponding to the higher external organisation. Similarly, the sporophyte, or asexual generation, is far more complex than in the Liverworts. Except in the one point of possessing true stomata, its complexity, however, is on quite different lines from that of the corresponding generation in the higher plants. The Mosses, in fact, constitute a remarkable and very isolated group, highly developed in their own way, but with no near affinities to other Classes of plants.

The Bryophyta, as a whole, form a perfectly well-defined sub-kingdom, characterised by the occurrence of a well-marked alternation of distinct generations, of which the sexual is the more highly developed, so far as the vegetative organs are concerned. The sexual organs—both archegonia and antheridia—are constituted on the same general plan as those of the higher Cryptogams, though differing in many details. The Vascular Cryptogams, together with the Bryophyta, are sometimes classes in one sub-kingdom under the name of *Archegoniatæ*, founded on the general similarity of the female organs all through these groups.

It is of interest to note that in the *Archegoniatæ* generally damp conditions are necessary for the proper functioning of the gametophyte and at a certain stage there must be free water in which the spermatozoids can swim to the archegonia, whilst dry conditions are necessary for the essential stage of spore-liberation from the sporophyte.

CHAPTER III

THE ALGÆ

THE sub-kingdom with which we have now to make ourselves acquainted differs profoundly from any of those of which representatives have been already considered. Seed plants, members of Pteridophyta and Bryophyta are fundamentally land plants, but Algæ are essentially aquatic. The members of the group most familiar to ordinary readers are the Seaweeds, for with very few exceptions all plants which grow in the sea belong to the Algæ. On the other hand, an immense number of species are inhabitants of fresh water. Generally speaking, the larger and more complex forms are marine; the fresh-water and terrestrial representatives are both smaller and simpler. Among Seaweeds there are species which rank with the most gigantic members of the Vegetable Kingdom, while there are other Algæ which are entirely invisible as individuals to the naked eye. The higher Algæ often show a complex external form, and, at the same time, their tissues are highly differentiated. On the other hand, the simplest Algæ consist of single isolated cells. Amid this vast range of forms it is evident that only a very few types can be dealt with here. As far as possible, our examples are selected with a view to illustrate the most striking variations in the life-history and mode of reproduction of Algæ.

The classification of the Algæ into their principal classes roughly follows the colour. It so happens, however, among these plants that differences in their pigments generally coincide with important morphological distinctions. We will begin with the pure green Algæ those, namely, in which the chlorophyll, like that of most of the higher plants, is not disguised by the presence of any other colouring matter. This class—the *Chlorophyceæ*—includes the majority of the fresh-water Algæ, as well as many Seaweeds. They are, on the whole, among the simpler Algæ, and many of the unicellular forms belong here. We will take as our first type a fresh-water Alga which, though anatomically simple, shows a very advanced form of reproduction.

A. THE GREEN ALGÆ (*Chlorophyceæ*)

ŒDOGONIUM

I. STRUCTURE

The genus *Œdogonium*, of which there are a great many species, includes some of the commonest fresh-water Algæ, and may be found in almost any pond or tank, though less common in running water. *Œdogonium* is filamentous, the individual threads being only just distinguishable by the naked eye, and grows attached when young to stones, piles, larger water-plants, or, in fact, to any submerged object, forming a dark-green downy coating upon it. In the mature condition the filaments usually float freely.

Fig. 73 shows the whole of a small plant of *Œdogonium ciliatum*, highly magnified; the specimen is much below the usual size. The main outlines of the structure, however, are always the same, the whole plant consisting of a single row of cylindrical cells, attached at one end, which we may call the radical end. The basal-cell contains less chlorophyll than the others. It is expanded into a flattened disc, which forms a holdfast, but probably does not take any special part in the absorption of food. Fresh-water Algæ absorb their food, mineral as well as gaseous, by their whole surface. Both the carbon-dioxide which they require for assimilation, and the oxygen necessary for their respiration, are present in a dissolved state in the water, which at the same time contains salts in solution quite sufficient to supply the needs of these plants.

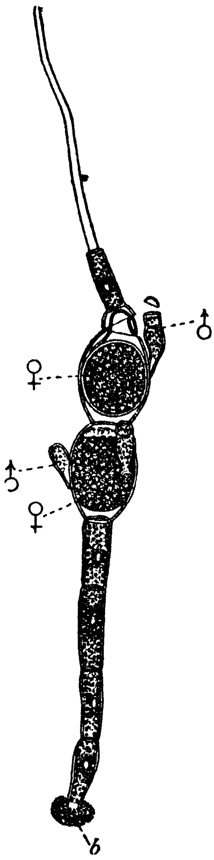

Fig. 73.—General view of a very small female plant of *Œdogonium ciliatum*. *b*, the attaching disc; ♀, ♀, two oögonia, the upper of which has opened by a lid at the top, and contains the fertilised oöspore; the lower is still closed, and the ovum unfertilised. ♂, ♂, dwarf males adhering to the oögonia. The uppermost has opened to discharge a spermatozoid. Magnified 166. (After Pringsheim.)

The structure of an ordinary vegetative cell of *Œdogonium* is as follows: Within the cellulose wall the cytoplasm forms a hollow sac—the primordial utricle—enclosing a large vacuole. The body containing the chlorophyll is very peculiar. In most plants the chloroplasts are small granules, numerous in each cell (though *Selaginella* forms an exception to this). In *Œdogonium*, however, there is only a single, very large chloroplast in each cell. It lies in the primordial utricle, and extends all round the cell, having the form of a hollow cylindrical network. It is so large as to give a green colour to the whole cell, when seen under low powers of the microscope. Within the chloroplast are several protein granules (the *pyrenoids*), around which starch-grains are deposited as a result of assimilation in sunlight. Each cell contains a single large nucleus embedded in the cytoplasm which lines the wall.

Œdogonium has no apical growing-point. In some species (such as that figured) the end cell grows out into a long hair, and takes no further part in the divisions. Certain cells of the filament, lying between the basal cell and the terminal hair, divide by transverse walls, as long as growth goes on. The formation of overlapping caps on the cell-wall, at the upper end of some of the cells, is due to the fact that after each division the wall of the mother-cell splits near the top, and a new piece of cell-wall is inserted between the broken edges as the daughter-cells grow. As the split takes place repeatedly near the same place, a succession of caps is formed, one corresponding to each cell-division.

We thus see that the vegetative structure of an *Œdogonium* is excessively simple—far simpler than that of any plant which we have hitherto described. We have now to consider the way in which the Alga reproduces itself.

In addition to fragmentation of the filaments there are two distinct methods—the one asexual, the other sexual. The former serves to propagate the plant rapidly during summer, or as long as the conditions are favourable to its growth; the latter has for its result the production of *resting-spores*, which can survive alike the cold of winter and the periods of drought to which *Œdogonium*, in common with other freshwater Algæ, is often exposed.

2. REPRODUCTION

a. Asexual

Any vegetative cell may serve as an organ of asexual reproduction and many individual plants only show this mode of propagation.

The entire contents of a cell are used up to form a single spore. The protoplasm gradually withdraws itself from the cell-wall, the whole mass assuming a rounded form. At the same time a clear, colourless spot appears on one side of the contracted protoplasmic body. From this clear portion of the protoplasm numerous cilia are developed. The cell-wall splits across and the crack opens widely at one side, that, namely, towards which the clear patch of protoplasm is turned. The spore now begins to pass out through the opening, changing its form as it does so, to adapt itself to the width of the passage (see Fig. 74, A). On first becoming free from the mother-cell, the spore is enclosed within a delicate mucilaginous membrane which soon disappears, so that now the reproductive cell is completely at liberty. In shape it resembles a pear, the more pointed end being colourless; the chloroplast occupies the wider part, in which also the nucleus is contained. There is no cell-wall, and the whole spore is a purely protoplasmic structure. The cilia form a fringe around the narrow end (see Fig. 74, B). Their oscillations set the spore in motion, and now it swims off through the water, rotating on its axis, and advancing with the pointed end foremost.

This is the first instance of an actively-moving *spore* that we have met with; among the higher Cryptogams already described it is only the male cells or spermatozoids which are capable of locomotion; in a large proportion of the Algæ this power extends also to the spores. On account of its active movements such a spore as that of *Œdogonium* is called a *zoospore.*

The zoospore swims about for some time (24 hours or so); it is sensitive to light, swimming towards light of moderate intensity, and retreating from it when too bright. As the zoospore becomes older it avoids the light more than before, and its movements are then directed towards the bottom of the water or solid objects contained in it; at last it comes to rest, and in doing so attaches itself by its pointed end to some solid body. It loses its cilia, and now for the first time forms a cell-wall of its own. The free end grows out, divides by a transverse wall, and thus starts a new *Œdogonium* filament, like that from which it was produced. This mode of reproduction by actively moving spores, capable of immediate germination, is extremely common among the Algæ. It is characteristic of most of the pure-green group, whether inhabitants of fresh water or of the sea, and extends also to certain other families.

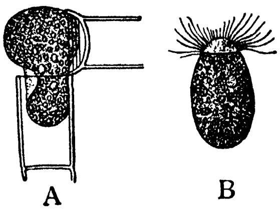

FIG. 74.—Zoospores of *Œdogonium*; A, escaping from the mother-cell; B, free, with the fringe of cilia. Magnified 350. (After Pringsheim.)

b. Sexual

Œdogonium is propagated very freely by the simple method just described, but it also possesses a mode of sexual reproduction involving the fertilisation of a relatively large and stationary ovum by a small and actively moving spermatozoid. The distribution of the sexes varies much in the different species of the genus. Some are monœcious, others diœcious, while in a third set (the most numerous) a more complex arrangement prevails. In monœcious species, the male organs are formed by successive transverse divisions of one of the thallus-cells, the divisions all taking place near the upper end of the mother-cell, so that a row of rather flat cells is produced.These may divide again further, producing a chain of about a dozen cells in some cases, each of which is an antheridium. In every antheridium the contents divide into two, and each mass becomes a spermatozoid. The spermatozoids resemble the zoospores, and are cilated like them (see Fig. 76, *B*). They are, however, much smaller, and relatively poorer in chlorophyll. The spermatozoid contains a single nucleus, which is placed near the end opposite to the cilia. These spermatozoids have much more the character of complete cells than those of the higher Cryptogams. In the latter, as we have already seen, almost the whole body is of nuclear origin, only the cilia and that part of the body to which they are attached being cytoplasmic. In *Œdogonium*, however (and in the lower Cryptogams generally), the greater part of the body is cytoplasmic. The resemblance to the zoospores is a very striking point.

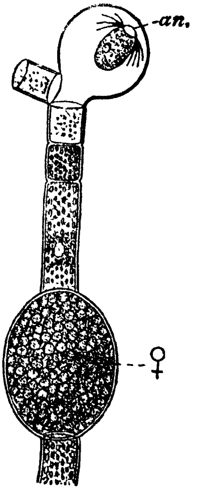

FIG. 75.—Androspore (*an*) of *Œdogonium ciliatum* escaping. At ♀ is an oögonium. Magnified 350. (After Pringsheim.)

The female organ, or *oögonium*, like the antheridium, consists of a single cell (see Figs. 73, 75, and 76), and differs herein from the complex *archegonium* of the Ferns and Mosses. The oögonium at its first formation is nearly similar to the other cells of the filament. A transverse wall is formed in the usual way; the upper of the two daughter-cells is the richer in cytoplasm, and has the larger nucleus; this becomes the oögonium; its lower sister-cell, which is poorer in contents and has a relatively small nucleus, is the supporting-cell, which in some species, however, may grow, undergo further divisions, and give rise to another oögonium. The oögonium swells out, assuming a round or oval outline, and further increases the amount of its protoplasm, which thus encroaches considerably upon the central vacuole. The cell-contents meantime withdraw themselves from the wall, and form a free, rounded protoplasmic body—the ovum (see Fig. 76, A)—in the upper part of which the nucleus is placed. The oögonium now opens, either by the formation of a round hole in the membrane, or by the transverse splitting of the cell-wall near the top, in which case the upper part of the membrane acts as a lid (Figs. 73 and 76, A). The gap is at first closed by a new membrane formed from the adjacent protoplasm of the oögonium, but this partly disappears again, leaving a free passage to the ovum.

Before describing the mode of fertilisation, we will consider the peculiar distribution of the sexes already mentioned, as differing from the ordinary monœcious and diœcious conditions. It is this form which our figures illustrate. The peculiarity consists in the production of dwarf male plants quite different from the ordinary form of the species.

By repeated transverse divisions in parts of the filament a chain of small cells is produced much shorter than the ordinary vegetative cells of the plant. Each of these short cells becomes the mother-cell of a single zoospore of the usual structure, but of a size intermediate between a normal vegetative zoospore and a spermatozoid (Fig. 75, *an*). These small spores (called *androspores*) are most commonly produced from the same filaments which bear the oögonia; more rarely they occur on distinct filaments. Each androspore swims about for a time, and then comes to rest, attaching itself to the female plant either near or actually upon the oögonium (Figs. 73 and 76, A). The androspore surrounds itself with a cell-wall and germinates. The plant which it produces is always of very small size. It may consist of a basal vegetative cell with one or more antheridial cells, or the vegetative part may be absent, and the whole dwarf male be reduced to an antheridium only. In the antheridial cell, or in each of them if more than one be present, two spermatozoids are produced. They escape by a lid-like opening of the antheridium, and make their way to the oögonial aperture (Figs. 73 and 74, A). Like the asexual zoospores, they move by a crown of cilia; they are also able to help themselves along by the contractions of their whole body. The same power of contraction is of service when the oögonial opening is reached, for the entrance may be much narrower than the body of the spermatozoid, which can only pass through by accommodating its form to the size of the passage.

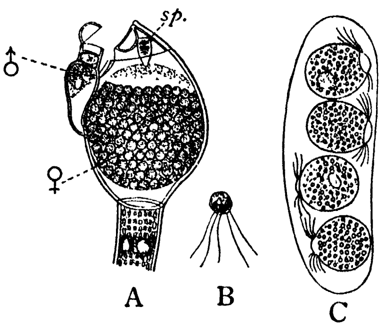

FIG. 76.—A, fertilisation of *Œdogonium ciliatum*; ♂, dwarf male plant from which a spermatozoid has escaped; *sp*, the spermatozoid in contact with the ovum, ♀. Magnified 350. B, a single spermatozoid showing cilia. Magnified 350. C, germination of the oöspore in *Bulbochæte*, showing the contents divided up to form four zoospores. Magnified 250. (After Pringsheim.)

The act of fertilisation now takes place; the spermatozoid comes into contact with the cytoplasm of the ovum, and the two cells unite. The details of fertilisation have been exactly followed in *Œdogonium*; after the cytoplasm of the spermatozoid has united with that of the female cell, the nucleus of the former can still be distinguished. It is much smaller than that of the ovum. The male nucleus passes through the cytoplasm until it reaches the female nucleus, and then the two unite to form a single nucleus.

The fertilised ovum (which is now called the *oöspore*) contracts further, surrounds itself with a cell-wall, and gradually passes into a resting state. The contents undergo great changes; the chlorophyll disappears and is replaced by a brown or red colouring matter, while large quantities of oil appear in the cytoplasm, and at the same time the cell-wall becomes much thickened. The resting stage may only last for a few weeks. It appears that in some at least of the species germination takes place before winter comes on. In the meantime the oöspore has remained enclosed within the oögonial wall.

When germination begins, the inner layers of the cell-wall of the oöspore swell, and burst the hard outer coat; the entire contents surrounded only by a delicate membrane now become free, leaving behind both the outer oöspore-wall and that of the oögonium. In the normal course of development the oöspore does not immediately give rise to a new plant; its contents divide into four cells, each of which rounds itself off and becomes a ciliated zoospore, exactly resembling the zoospores formed in the vegetative cells, except that the contents are at first wholly or partly of a red colour (see Fig. 76, C). These zoospores free themselves from the enclosing membrane, swarm actively for a time and become green, and then come to rest, each giving rise to an ordinary *Œdogonium* plant.

It appears that the filaments of *Œdogonium* are haploid. The oöspore is the only diploid stage. Meiosis occurs at its germination, the four zoospores produced being haploid.

SPIROGYRA

1. STRUCTURE

Our next type is another of the filamentous fresh-water Algæ, but very distinct from that already dealt with. The genus *Spirogyra* contains about one hundred and seventy species, differing much among themselves both in size and in details of structure. We will give a general account of the genus, noting when necessary the points in which the specific differences are of interest.

Spirogyra occurs chiefly in ponds and lakes, that is to say, in still rather than in running water. It is often present in immense quantities, the filaments forming floating masses, sometimes several acres in extent, buoyed up by the bubbles of oxygen which their assimilation has produced. It is characteristic of *Spirogyra* to float, for the filaments of most species are perfectly free, without attachment to any kind of substratum. There is no distinction of apex and base, and all the cells are alike throughout the thread.

In the larger species of *Spirogyra* the cells are, microscopically speaking, of great length (reaching 0·25 mm. in extreme cases). They are therefore very favourable for study.

The cell-wall is stratified into an inner cellulosic layer and an outer mucilaginous one. It is this that makes *Spirogyra* slimy to the touch and it is this that is responsible for the freedom of the filaments from epiphytic algæ which so commonly foul the surface of most filamentous green Algæ. The majority of epiphytes fail to gain a footing on the slippery surface of *Spirogyra*. Within the cell-wall is a lining layer of protoplasm surrounding a central vacuole (Fig. 77).

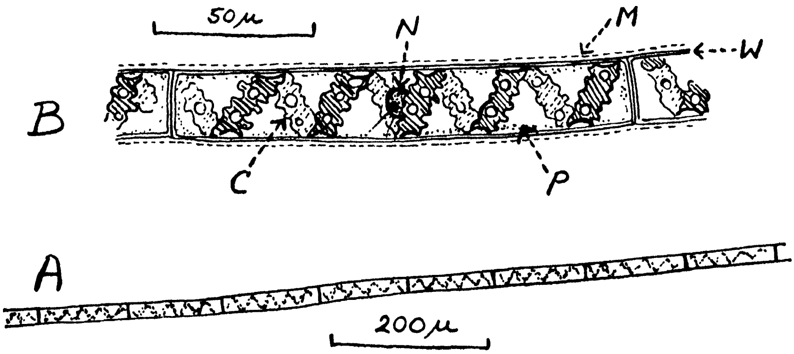

FIG. 77.—*Spirogyra* sp. A, part of unbranched filament. B, single cell: M, mucilage layer; W, cell-wall; P, lining layer of protoplasm; N, nucleus; C, chloroplast containing pyrenoids shown by small circles.

Embedded in the lining layer of protoplasm are the very conspicuous chloroplasts, which here take the form of green spiral bands with toothed edges. They form the most striking feature of the plant under the microscope, and from them the genus derives its name. The chloroplasts vary in number from one to ten in each cell according to the species, but the number is not always constant even in the cells of the same filament. Each chloroplast is studded at intervals with large *pyrenoids*, which can be well seen here, and have a crystalloid form. It is around these protein bodies that much of the starch is formed when assimilation is taking place. Each pyrenoid then becomes surrounded by a coating of minute starch-granules. In every cell there is one large nucleus, usually suspended in the middle of the cell by cytoplasmic fibrils. These fibrils are attached, at the ends remote from the nucleus, to the chloroplast, abutting on it at the points where the pyrenoids are situated. The nucleus contains a large nucleolus.

All the cells are similar, and all take an equal part by growth and transverse division in the development of the plant. *Spirogyra* may therefore be spoken of as *physiologically* a unicellular organism, for all its cells are equivalent, and each appears to be capable of carrying on all the necessary functions for itself. In the ordinary state the plant is *morphologically* multicellular, but occasionally the thread actually breaks up into its separate cells, and we then find that each of these on its own account is capable of independent life, and can start a new plant. In a large number of genera allied to our type, the cells normally lead an isolated existence, separating after each division. This is usually the case in the *Desmids*, a Family of fresh-water microscopic plants of great beauty.

2. Reproduction

Except for the breaking up of a filament into individual or short groups of cells, *Spirogyra* possesses no asexual means of propagation. Its normal reproduction is always sexual and is a form of conjugation, consisting in the union of like cells. Conjugation, in most cases, takes place between two filaments lying side by side. The filaments come into contact with each other throughout their length. The cells of each filament then begin to put forth lateral outgrowths which exactly correspond to each other in position. As these outgrowths elongate the filaments are pushed apart. The walls separating the outgrowths from each other become absorbed, thus leaving an open passage between the opposite cells of the two threads (see Fig. 78).

The contents of the cells in one of the two filaments now contract, receding from the cell-wall, and round themselves off; for a time the cells of the other filament remain unchanged. The contracted cell-contents next begin to insinuate themselves into the connecting passage, and gradually work through it, passing into the opposite cell (Fig. 79). They then unite with the contents of the latter, which in the meantime have themselves somewhat contracted.

In this case the fusion of the nuclei of the two conjugating cells has been observed. The united protoplasmic mass assumes a rounded or oval form, and surrounds itself with a cell-wall, which becomes thickened and cuticularised on its external surface. The chloroplasts of the gamete which moves over to join the other one undergo disorganisation so that the number of chloroplasts proper to the species remains constant from generation to generation.

That there is actually a certain distinction of sex in *Spirogyra* is evident from the fact that all the cells of each conjugating filament usually behave in the same way, either giving up their own protoplasm or receiving that of the fellow-filament. That the difference, however, is not fixed is shown by the fact that conjugation sometimes takes place *monœciously*, *i.e.* between the cells of the same filament. This mode of union is called "*chain-like*" or "*lateral,*" as against the more usual diœcious or "*ladder-like*" method; both processes may occur in the same species. In *monœcious* conjugation two adjoining cells put out very short lateral processes, which arise in contact with each other, on either side of the transverse wall separating the two cells. The processes unite, and the contents of the one cell pass through the side passage and fuse with those of its neighbour. In this case there may be a certain sexual difference among the individual cells, but the filament is obviously bisexual.

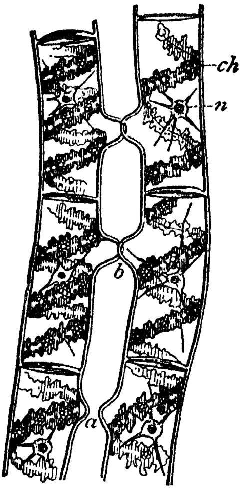

FIG. 78.—*Spirogyra* sp. conjugating. The two parallel filaments are putting out the conjugating outgrowths *a*, which at *b* are in contact; *ch*, spiral chloroplast; *n*, nucleus, with radiating cytoplasmic fibrils. Magnified about 350. (After Sachs.)

In some species of *Zygnema*, a genus very close to *Spirogyra*, conjugation occurs as in *Spirogyra*, but the zygote is formed in the conjugation tube and the process is completely *isogamous*, that is to say there is no distinction of size or behaviour between the fusing gametes.

The contents of the zygospore assume a darker colour, and the starch disappears, giving place to oil, which constitutes the reserve carbonaceous material during the interval of rest. The zygospore can now survive either a period of drought or the cold of winter, as the case may be. On germination the zygospore gives rise directly to a new plant. The outer wall is burst, the protoplasm grows out, clothed only by the inner cellulose wall, the bright green colour of the chlorophyll reappears, and starch is once more formed. During the germination of the zygospore the nucleus divides twice, the two divisions constituting meiosis, but three of the four nuclei thus formed disorganise (Fig. 80). On first germinating, the young plant show as distinction between apex and base, for it remains for a time attached by one end, which

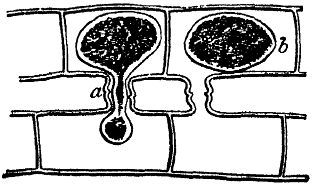

FIG. 79.—Conjugation more advanced. At *a* the protoplasm is in the act of passing over; at *b* the union is complete, one cell having transferred all its contents to the other. Magnified about 350. (After Sachs.)

is pointed and colourless. This distinction is usually soon lost, and the filament floats freely in the water.

As in *Œdogonium* the vegetative filament is haploid, the zygote, produced by the fusion of the two sexual cells, is the only diploid stage, and meiosis occurs at its germination.

PLEUROCOCCUS VULGARIS[1]

Before leaving the Green Algæ we will take two more examples, the very simplest we can find, as illustrations of unicellular structure. *Pleurococcus vulgaris* is in our climate perhaps the most abundant of all plants. Everyone must have noticed how commonly the trunks of trees, palings, and wet walls are covered by a bright green powdery layer, especially on the side away from the sun. In damp winter weather the green coating is most developed. This substance, though it may include many different organisms, is chiefly made up of *Pleurococcus vulgaris*.

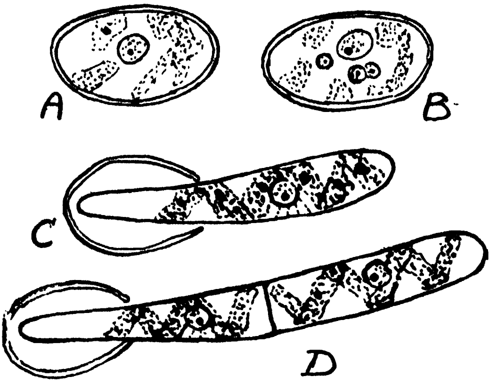

FIG. 80.—*Spirogyra.* Diagram of zygote germination. A, zygote with single diploid fusion nucleus; B, nucleus has undergone meiosis to form four haploid nuclei of which three are degenerating. C, new filament, still consisting of only one cell, bursting out of the zygote wall. D, young filament now consisting of two cells. (Based on figures by Tröndle.)

This Alga, which occurs in prodigious numbers, consists of small rounded cells, sometimes quite separate, sometimes grouped together in little packets of two, four, or eight. When adhering together, the sides in contact are rather flattened. The cells withstand prolonged desiccation.

Each cell has a cellulose wall, and is densely filled with protoplasm, which at first sight appears to be coloured uniformly green. This, however, is not the case, for the chlorophyll is really limited to a definite chloroplast, usually large and with several lobes, occupying the outer part of the cell-contents. The rest of the protoplasm is colourless. About the middle of the cell is a nucleus (Fig. 81). The cells divide freely into two; successive divisions take place in all three directions, and are at right angles to each other. The cells may either round themselves off and separate immediately after each division, or

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[1] Sometimes called *Protococcus viridis.*

may remain grouped together for a few generations. Sooner or later, however, they fall apart. The plant forms small starch-grains in the chloroplasts when exposed to light.

We have in *Pleurococcus* an example of a typically unicellular plant, in which the cells lead a perfectly independent life; each individual cell, however, has the same structure as in higher plants. Evidence has been brought forward to show that *Pleurococcus* may occasionally grow out into short filaments like those of higher green Algæ. The common unicellular condition may be due to reduction from a more advanced type.

Reproduction is by cell-division only and there is no known sexual process.

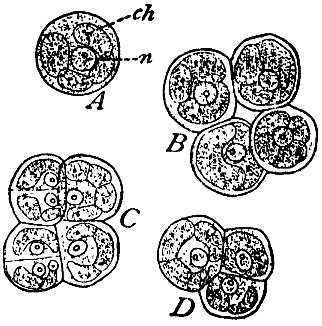

FIG. 81.—*Pleurococcus vulgaris*. *A*, single cell; *n*, nucleus; *ch*, chloroplast. *B*, four cells separating after division. *C*, group of cells remaining in contact. The two to the left have just divided afresh. *D*, tetrahedral group. Magnified 540. (After Strasburger.)

CHLAMYDOMONAS

This type is introduced as a further example of a unicellular Alga, which is of special interest from two points of view. In the first place, unlike any plant hitherto described, it passes its ordinary vegetative life in a state of active movement. Secondly, simple as it is, *Chlamydomonas* has a perfectly definite sexual reproduction, showing important modifications in different species.

Chlamydomonas, of which numerous species have been described, occurs in ponds and quiet places in rivers, but is especially abundant in rain-puddles, often giving a bright green colour to the water. A species of *Chlamydomonas* is one of the forms of Algæ responsible for "red snow" in Alpine and Arctic regions.

The cells are small; about 20 μ[1] (0·02 mm.) is a common length for the full-grown cell, though some are rather larger. In the ordinary condition the form is usually oval, with one end rather more pointed than the other. To this end the two cilia, the organs of motion, are attached (see Fig. 83, A; Fig. 84, G). The cell is surrounded by a delicate cell-wall, often with a papilla at the pointed end. The cilia are continuous with the cytoplasm and pass though minute perforations in the wall. The chlorophyll is contained in a single large chloroplast, occupying most of the cell, and having the form of a cup, open at the top and much thicker at the base than elsewhere. In the lower part of the chloroplast a large pyrenoid (protein body) is embedded; sometimes

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[1] A μ is $\frac{1}{1000}$ of a millimetre.

there are two or more. Both around the pyrenoid and in other parts of the chloroplast starch-grains are formed.

At the pointed end and in the hollow of the chloroplast there is clear cytoplasm, and embedded in this is the nucleus. On one side of the cell, near the ciliated end, there is a red eye-spot. Lastly, in the clear protoplasm near the point, there are two contractile vacuoles, which expand and contract, the two pulsating alternately. This then is the structure of the cell—a highly organised one, as we see.

These cells swim about, through the water, ciliated end foremost, rotating as they go, If we keep them in a saucer near a window, we find that they assemble on the side towards the light. They behave, in fact, just like zoospores, but we cannot call them zoospores, for they are the ordinary vegetative cells of the plant—the first example we have had of a plant which is in active movement through most of its life, like an animal. Yet the structure is altogether that of a plantcell. The presence of a cell-wall indicates that the active cells are something more permanent than zoospores.

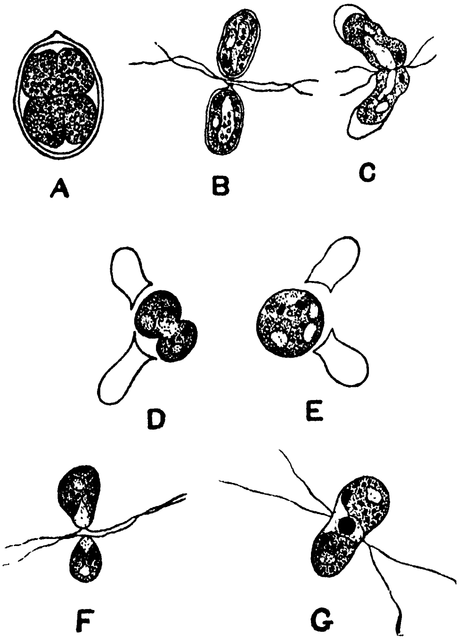

FIG. 82.—A–E, *Chlamydomonas longistigma*, A, vegetative cell dividing into four. B–E, successive stages of conjugation of the walled gametes, which escape from their walls in the process. F, G, *Chlamydomonas pisiformis*. Conjugation of naked gametes. Magnified about 600. (After Dill.)

During their movements the cells feed and grow and ultimately they divide, division taking place during the evening, night, and early morning. While division is going on the cells lose their cilia and rest for a time. The cell most commonly divides into four (Fig. 82, A), sometimes into two only, sometimes into eight. The first division is usually transverse, but in some species it is longitudinal, or the dividing plane is at first longitudinal, the cells then shifting so that it becomes transverse. The second division is at right angles to the first, but the daughter-cells arrange themselves so that their long axes are parallel. Each forms its own pair of cilia and cell-wall, and the cells break out through the common wall. This is the ordinary mode of multiplication, and the remarkable thing about it is that a motile cell gives rise directly to new motile cells without anything more than a temporary rest during division.

But there is sometimes another process, in which the division is repeated several times without the daughter-cells espaping or becoming active, the result being a colony of many cells, commonly grouped in packets of four or eight, and held together by a common mucilaginous investment (Fig. 84, H). This is called the *palmelloid* condition, and in some species these masses attain quite a large size. There is a species growing in springs in the Black Forest, in which they are said to be as big as walnuts. Ultimately the cells acquire cilia and escape, again starting the active condition. Thus the stationary phase, in which *Chlamydomonas* lives like an ordinary plant, is as a rule exceptional, though in some species it may be of long duration.

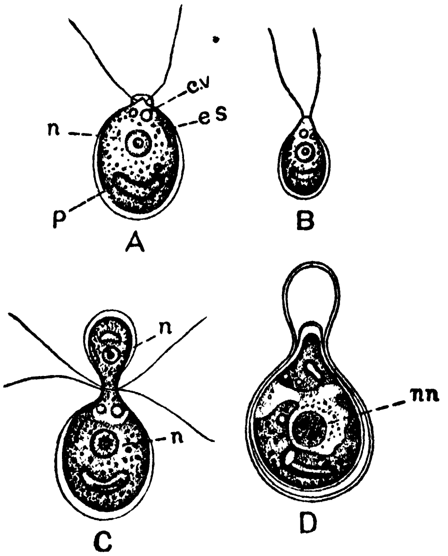

Fig. 83.—*Chlamydomonas braunii.* A, female gamete (closely resembling a large vegetative cell); *n*, nucleus; *p*, pyrenoid; *e.s.*, eye-spot; *c.v.*, contractile vacuoles. B, male gamete. C, early stage of conjugation; *n*, *n*, the nuclei of the two gametes. D, advanced stage of conjugation; *nn*, the united nuclei of the two gametes. Magnified about 500. (After Goroschankin.)

Most interesting of all is the sexual process, which takes place in three different ways, in different species.

The simplest method is isogamy. The sexual cells are formed by the division of an ordinary cell into a larger number of parts than usual, so that the gametes are small compared with the vegetative cells; they are also, as a rule, more slender in form, but otherwise there is little difference. The gametes in the first type do not form a cell-wall. They swim about as usual, and when two, derived from different mother-cells, meet they entangle each other with their cilia, and the pair go waltzing through the water together (Fig. 82, F). Then they come into contact, and begin to fuse, either end to end, or side to side, according to the species. After union has begun the pair still goes on swimming with its four cilia (Fig. 82, G). The corresponding parts of the cells unite, and the two nuclei meet and fuse, retaining for a time the two nucleoli. A cell-wall is formed around the whole, and the resultant body is a resting zygospore.

The second type differs from the first in the fact that the gametes, like the vegetative cells, are provided with cell-walls (Fig. 82, B, C). The meeting takes place as before; for two or three hours the cells keep together, but not in close contact. Then they approach closer, but union is prevented by the cell-walls. Each gamete now contracts a little way from its wall, and then leaves it behind altogether (Fig. 82, D, E), the contents passing out at the narrow end and rounding themselves off. At this stage the cilia are lost. The two protoplasmic cells, as they are set free, gradually fuse, and as in the previous case, a zygospore is the result (cf. Fig. 84, E). This form of conjugation occurs in a British species, *C. ehrenbergii.*

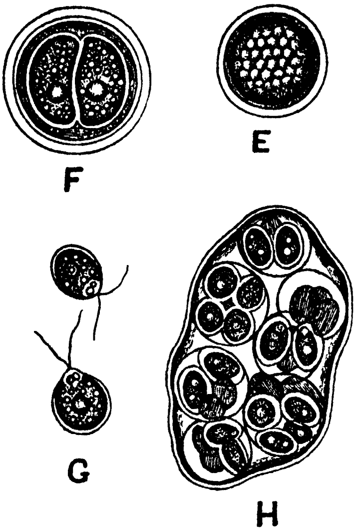

FIG. 84.—*Chlamydomonas braunii.* E, zygospore, containing oil-drops. F, germinating zygospore, divided into two cells. G, vegetative cells produced from a zygospore. H, palmelloid condition consisting of numerous groups of cells within a common wall. E–G, magnified about 400. (After Goroschankin.)

The third type is more remarkable; so far the fusing sexual cells have been of the same size or with only accidental differences between them. In the third type (represented by *C. braunii*[1]) there is a marked and constant distinction between the two. The one is smaller than the smallest vegetative cells, the other is much larger and less motile (Fig. 83, A, B). The structure is like that of the ordinary cells, and each gamete, as in the second type, is surrounded by a cell-wall. A large and a small sexual cell meet by their ciliated ends as usual. The walls at the point of contact break down, so that an open canal is formed. The contents of each cell then contract away from the wall, and those of the small cell pass over through the canal, and unite with those of the large cell—reminding one of the conjugation of *Spirogyra.* Fig. 83, C, shows an early stage of the passage, while D represents a later stage, when union has been accomplished. The two nuclei have now joined into one, but have not yet completely fused—the line of demarcation between the original nuclei is still evident, and the two nucleoli are distinct. The common cell-wall of the united gametes still persists and betrays by its form what has taken place. Then a new and thick cell-wall is developed around the fused contents, and the zygospore is constituted (Fig. 84, E).

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[1] Sometimes called *C. monadina.*

This process appears to be much in advance of that in the other species, as there is a marked distinction between the sexes—we might even speak of ovum and spermatozoid, though the former as well as the latter has the power of active locomotion. At the same time we must remember that the female cell is practically identical with a large vegetative cell, and not, as far as we can see, specially differentiated as an ovum. But however we may regard it, the sexual reproduction of *Chlamydomonas braunii* is certainly on a remarkably high level for a unicellular plant.

The fate of the zygospore is much the same in all three types. It surrounds itself, as we have seen, with a cell-wall of its own which becomes much thickened in the resting stage (Fig. 84, E). A red or red-brown oily pigment forms in the contents and hides the chlorophyll. In this condition the zygospore, like other resting spores, can survive a time of drought or cold. The zygospores may be distributed by wind with dust particles. When conditions are favourable the contents gradually regain their green colour and begin to divide. The first stage of division is shown in Fig. 84, F—division may be into two, four, or more. The resulting cells escape as ciliated individuals not essentially different from the ordinary vegetative cells (see Fig. 84, G) and resume the regular life of the plant. As in *Œdogonium* and *Spirogyra* the vegetative stage is haploid and meiosis occurs at the germination of the zygote.

Chlamydomonas is of special interest because it is close to the boundary between plants and animals. It is plant-like in its photosynthetic nutrition and in the possession of a cell-wall. It resembles animals in its motility. Still nearer the boundary is the flagellate *Dunaliella* which differs from *Chlamydomonas* only in the absence of a wall. A further step in the animal direction is seen in *Hyaliella*, very like a colourless *Dunaliella*, which being devoid of chlorophyll cannot obtain its organic food by photosynthesis and, in fact, lives as a saprophyte by absorbing soluble organic substances. In the plant direction it is easy to see how such a form as *Chlamydomonas* might have given rise to simple filamentous algæ like *Ulothrix*. This common alga, during the course of both asexual and sexual reproduction, produces motile reproductive cells that are essentially like individuals of *Chlamydomonas*, but are without cell-walls.

B. THE BROWN ALGÆ (*Phæophyceæ*)

The Brown Algæ, almost all of which are seaweeds, are probably better known to the ordinary observer than even the green group, owing to the large size which many of them attain, and the extraordinary abundance in which they occur on our coasts. In dimensions and structure they present an even wider range than the Chlorophyceæ, for though no Brown Algæ are quite so small or so simple as *Pleurococcus*, yet many of them much exceed any of the former group in size and complexity. Some, in fact, approach the Flowering Plants in the differentiation of their vegetative organisation. The peculiar colour of their thallus results from the fact that the plastids contain a brown pigment, *fucoxanthin*, as well as most of the substances in ordinary chlorophyll. The brown colour is the expression of this complex pigmentation. Treatment with hot water, which dissolves the fucoxanthin, has the effect of turning brown seaweeds green.

The Phæophyceæ certainly form a natural group, for from the lowest to the highest there are certain points in their organisation which are common to all. The colour coincides roughly with structural features, and affords a useful external mark by which the group can in most cases be recognised. This mark must, however, be used with caution, for some Algæ (the Diatoms) resemble the Phæophyceæ in colour but have otherwise little in common with them.

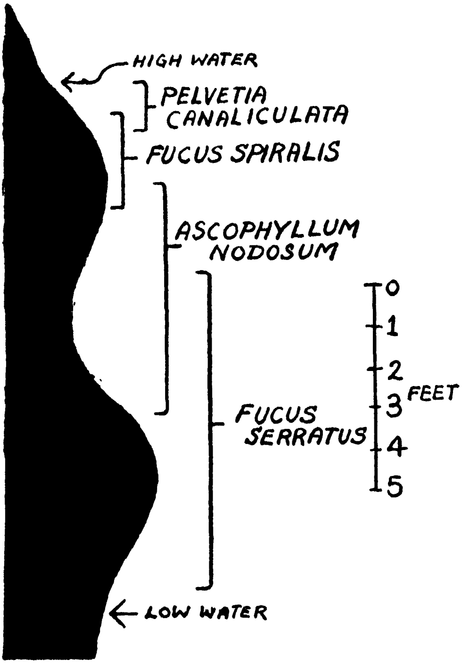

FIG. 85.—Wall of rock (in the intertidal zone at Calf Sound, Isle of Man) showing the zonation of members of Fucaceæ. *Fucus vesiculosus*, which usually occurs at much the same level as *Ascophyllum*, was not present in this particular transect.

FUCUS SERRATUS

Amongst the commonest and most conspicuous seaweeds on the coasts of cold and temperate countries are the *Fucales.* Members of this order are large brown plants growing attached to rocks in the intertidal region, that is to say between high-water mark and low-water mark. If the coast is not too exposed, rocks in this region are covered with seaweeds and the dominant species belong to the *Fucales.* A conspicuous feature of this intertidal vegetation is that each species

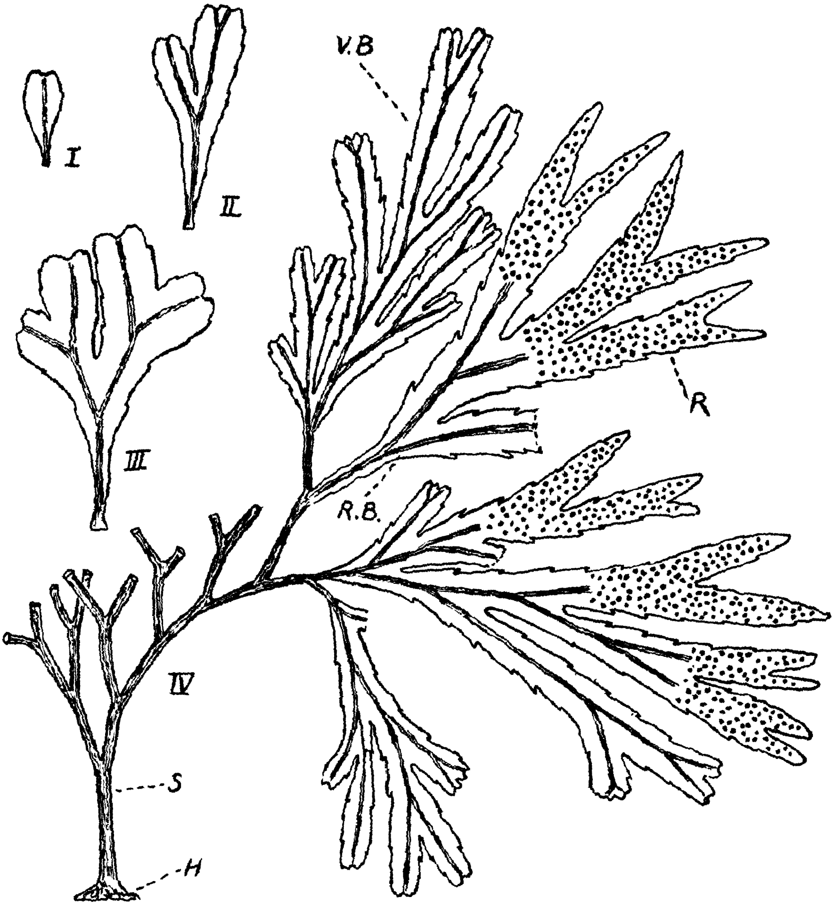

FIG. 86.—*Fucus serratus* I–III young plants of increasing age showing dichotomous branching. IV, part of a large male plant probably just over a year old. H, holdfast; S, sripe; V.B, vegative branch; R.B, reproductive branch; R, receptacle (the dots on it are conceptacles). Half natural size.

has a fairly definite vertical range. Fig. 85 illustrates this zonation at Calf Sound in the Isle of Man. Three species of *Fucus* are involved, of which *F. serratus* is readily distinguished by the toothed or serrate margin of the thallus and by the absence of air-bladders.

1. STRUCTURE

Fucus serratus is usually found in abundance on any rocky coast extending a few feet above and round about the low-water mark. It has a forked flattened thallus (Fig. 86) attached to the rock by a substantial disc-shaped holdfast and may reach a length of about two feet. Branching is dichotomous, or nearly so, resulting from the periodic equal division of the growing-point. The flattened thallus has a conspicuous thickened midrib thinning out to wings on either side. The plant is perennial, usually lasting for four or five years. During this time the midrib in the lower regions of the plant undergoes considerable secondary thickening whilst the wings wear away, so that in older plants definite stalks, almost circular in section, are formed.

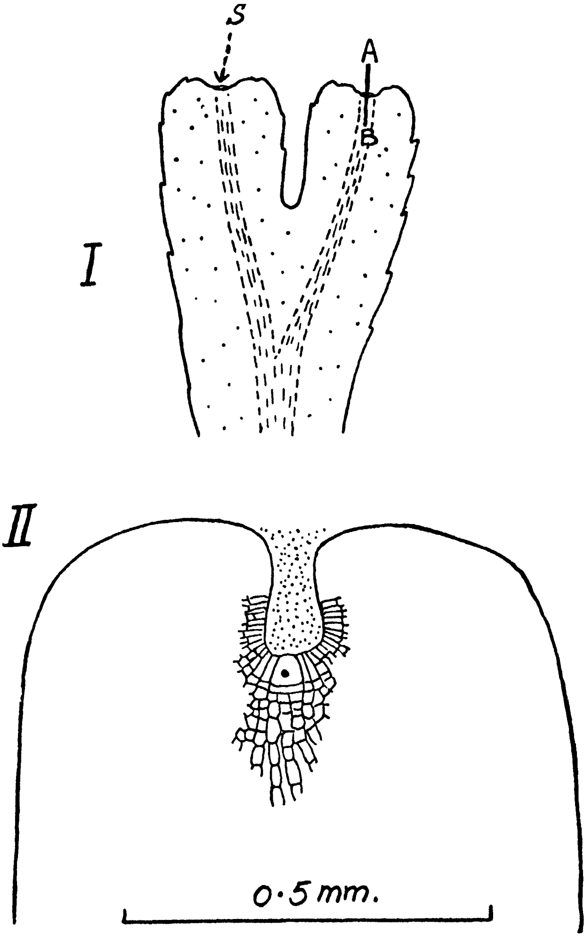

Fig. 87.—*Fucus serratus* I, portion of vegetative branch showing terminal slit (S) where growing-point occurs. The dots on the surface of the wings are sterile conceptacles (Natural size). II, section along line A–B at right angles to the paper showing apical cell, at base of mucilage-filled pit, and some of the surrounding tissue.

Growth is apical, being dominated, as in archegoniate plants, by a pyramidal cell which cuts off new cells on its sides and base. Each apical cell is situated at the bottom of a little pit filled with mucilage

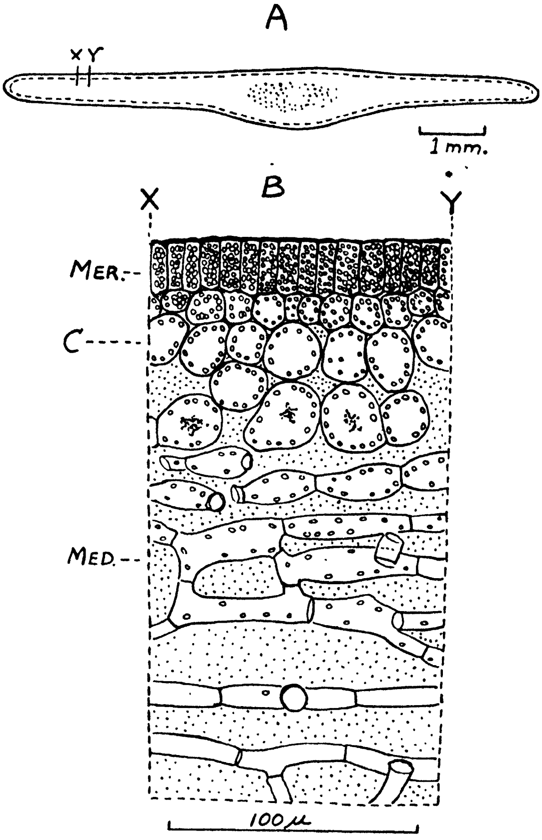

FIG. 88.—*Fucus serratus.* A, transverse section of vegetative branch about 2 cm. behind apex. The interrupted line shows the inner limit of the cortex. The dotted area in the midrib shows the position of fibres. B, part of the tissue (between lines X and Y in A) highly magnified. MER, meristoderm; C, cortex; MED, medulla. The small oval bodies in the cells are chloroplasts.

(Fig. 87). It should be emphasised that the structure of the plant body is truly parenchymatous.

If a transverse section of the thallus is examined in the region of the wing (Fig. 88) it will be seen that the outermost single layer of cells is clearly marked. This is the *meristoderm* and its cells are very rich in small brown plastids. Below this is the *cortex* consisting of larger roundish cells with fewer plastids. Finally, as the middle of the thallus is approached, the cortex passes into the *medulla* which appears to consist of filaments of cells joined up by cross-connections and containing very few plastids. These filaments lie in a mucilaginous

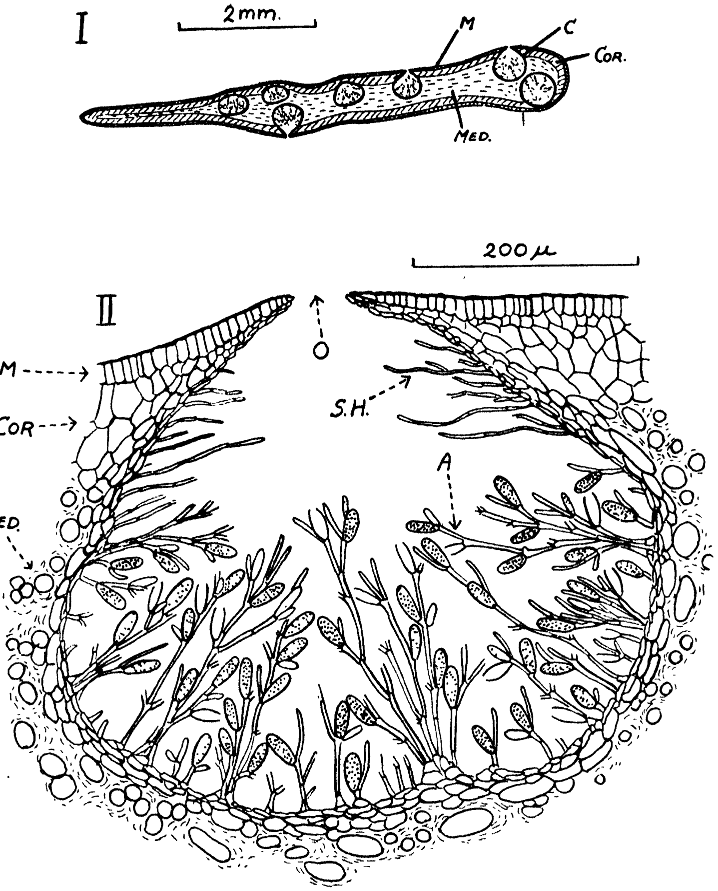

FIG. 89.—*Fucus serratus.* I, transverse section of receptacle of a male plant showing conceptacles (C). M, meristoderm; COR, cortex; MED, medulla. II, Male conceptacle. The section passes through the ostiole. O, ostiole; S.H, sterile hairs; A, branched filament bearing antheridia.

mass (shown stippled in Fig. 88, B) that really represents the outer cell-walls which merge with one another to form a common slime. In spite of its filamentous appearance the medulla is a parenchymatous tissue, but in development chains of cells get pushed apart by the formation of mucillage between them. It is clear that the meristoderm and the outer cortex are the principal photosynthetic regions of the thallus.

The anatomy of the midrib section is somewhat similar, but in addition there are thick-walled fibres following a longitudinal course. These no doubt give mechanical strength and it is to their increase that the main secondary thickening of the midrib is due, although a surface meristem (the meristoderm) also contributes after the fashion of cork-formation in higher plants.

An outstanding feature of the thallus is its great flexibility which allows it to conform with the violent movements of the waves without tearing.

2. REPRODUCTION

In most species of *Fucus*, including *F. serratus*, there are separate male and female plants which look alike. They differ from the gametophytes of most plants in being diploid.

Let us first consider the male plant. Certain of the thallus tips cease to be capable of further extension growth and become modified in connection with reproduction, but others retain their purely vegetative character. The reproductive tips are known as *receptacles* and are covered with little warts (*conceptacles*) (Fig. 86).

In sectional view each conceptacle is seen to be an almost spherical cavity in the thallus filled with slime (mucilage) and opening to the outside by a narrow pore (*ostiole*). From the inside wall of the conceptacle branched filaments bearing antheridia grow into the cavity (Fig. 89). The antheridia are single cells (Fig. 90). At first each contains one diploid nucleus. This undergoes two divisions which constitute meiosis, but no cell-walls are formed. Meiosis is followed by a number of mitotic divisions until sixty-four haploid nuclei are present. Each of these now becomes the centre of a distinct cell, the contents of the antheridium dividing up simultaneously into as many cytoplasmic bodies as there are nuclei present. These bodies become spermatozoids, each of which consists of cytoplasm, a nucleus, and a plastid and bears two lateral cilia of unequal length.

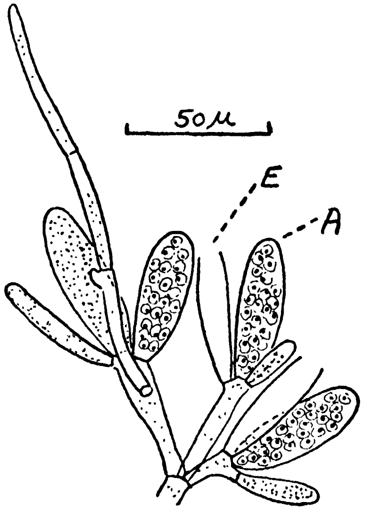

FIG. 90.—*Fucus serratus*. Part of branched system from male conceptacle. A, mature antheridium containing spermatozoids. E, empty antheridium.

The antheridium wall is double, and when the organ is ripe the outer membrane bursts at the top and the contents, still enclosed within the delicate inner cell-wall, are expelled. These packets of spermatozoids are liberated in great numbers into the slime within the conceptacle. Eventually the packets exude through the ostiole and accumulate outside as drops of orange slime. Just what causes the exudation of the mucilage containing the spermatozoid-packets through the ostiole is not clear. It may be the result of slight drying of the whole receptacle when the thallus is exposed at low tide, but that cannot be the whole story as exudation may occur below water.

In the sea-water the spermatozoids escape from their packets. This takes place by the solution of the wall at one end of the packet, so that the sperms are free to swim out. Fig. 91 shows the process in *Pelvetia*, but in *Fucus* it is exactly similar.

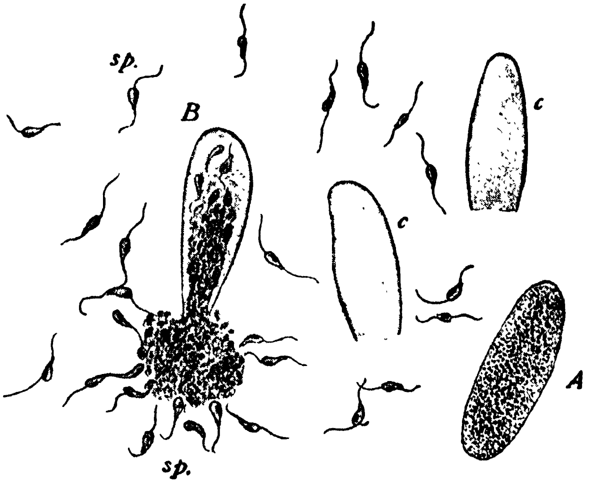

FIG. 91.—Spermatozoids of *Pelvetia*. *A*, unripe antheridium, already freed from outer membrane; *B*, antheridium opening to emit the biciliate spermatozoids (*sp*); *c*, *c*, empty membranes. Magnified about 450. (After Thuret and Bornet.)

Let us now consider the female plants. To look at they are just like the male ones and the sexual organs occur in conceptacles borne on fertile branches or receptacles. The female conceptacle (Fig. 92) as seen in section resembles the male, but instead of antheridia there are conspicuous and more or less spherical oögonia borne singly each on a small stalk cell. As well as oögonia there are numerous simple filamentous outgrowths or paraphyses jutting into the cavity of the conceptacle, and hairs of this kind also line the ostiole and project beyond it. It should be noted that both in the male and female plants *sterile conceptacles* (Fig. 87, I), which are minute pits lined with projecting hairs, are scattered generally over the surface of the thallus, being absent, however, from the midribs and the receptacles.

Each oögonium is a single large cell containing a great many plastids. There is, at first, a single diploid nucleus. This divides twice by meiosis to give four haploid nuclei and each of these undergo a further mitosis so that there are eight haploid nuclei in the protoplasm of the oögonium. Cleavage now occurs to form eight eggs or ova each of which is a naked uninucleate mass of protoplasm. The wall of the oögonium consists of three layers. The outer of these ruptures and the eggs, still surrounded by the two inner layers, are liberated into the fluid mucilage of the conceptacle cavity. Packets of eggs escape through the ostiole in the same manner as do the packets of spermatozoids. In the sea-water the membranes around each group of eight eggs dissolve, the eggs are set free, round off and, being of the same density as the sea-water, remain in suspension (Fig. 93).

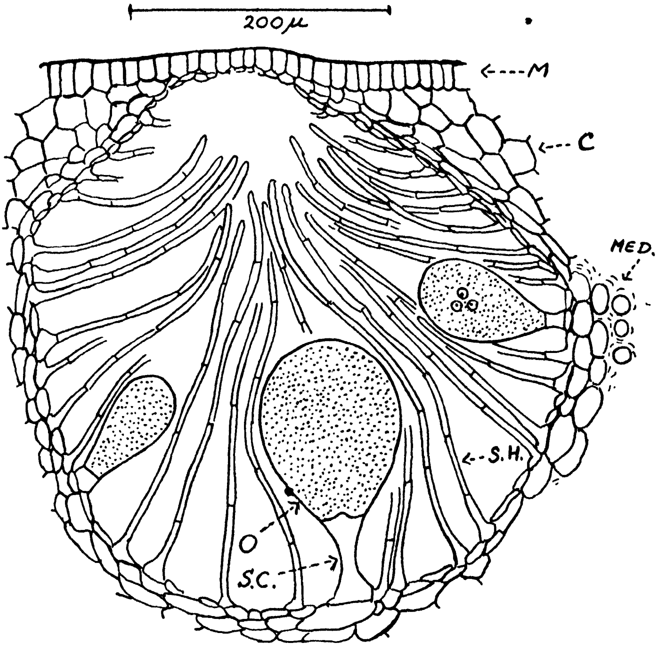

FIG. 92.—*Fucus serratus*. Female conceptacle as seen in T.S. of female receptacle. The section does not quite pass through an ostiole. M, meristoderm; C, cortex; MED, medulla; S.H, sterile hair; O, young oögonium; S.C, stalk-cell.

The spermatozoid swimming about are, apparently, attracted to the ova. If spermatozoids are added to eggs suspended in a few drops of sea-water in a watch glass, they swarm around the eggs and these soon begin to rotate like catherine wheels due to the lashing of the cilia of the attached motile male gametes (Fig. 94). Ultimately only a single spermatozoid succeeds in entering the cytoplasm of the ovum.

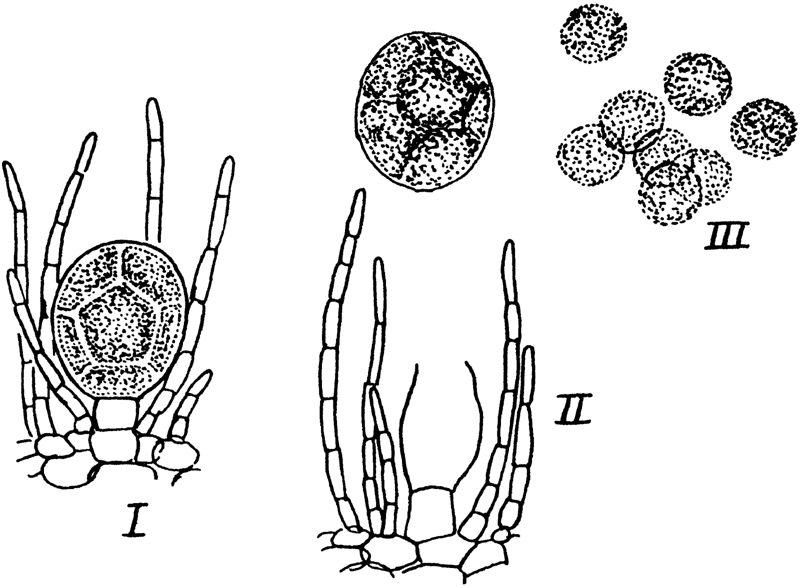

FIG. 93.—*Fucus vesiculosus.* I Oögonium, containing eight eggs attached to the conceptacle wall by a stalk-cell and surrounded by a group of simple filaments. II A similar oögonium at a later stage. The eggs, still surrounded by the inner layers of the oögonium wall, have escaped. III The inner layers of the oögonium wall have dissolved and the naked eggs are separating from one another and are rounding off. (After Sauvageau.)

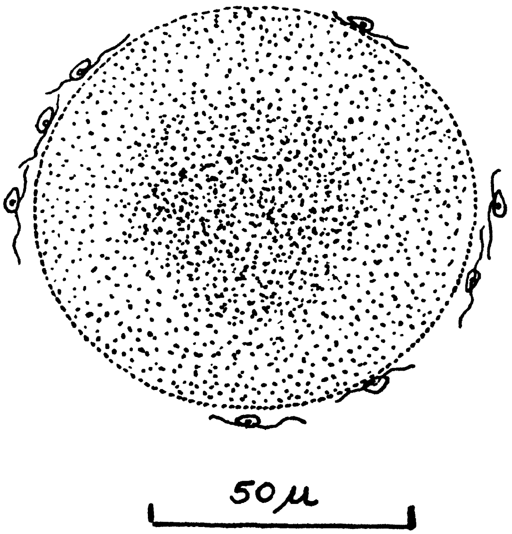

FIG. 94.—*Ascophyllum nodosum.* Antherozoids (sperm) clustering around an egg prior to fertilisation.

The details of fertilisation have been thoroughly worked out and the fusion of the small male nucleus with the large nucleus of the ovum has been observed as shown in Fig. 95 which represents fertilisation in another member of Fucales.

Following fertilisation the ovum surrounds itself with a cell-wall, becomes slightly denser than sea-water and sinks. When it comes in contact with a rocky surface, it becomes firmly stuck and begins immediately to develop into a new *Fucus* plant. The fertilised egg first becomes pear-shaped and divides transversely into two by a cross wall. The more pointed basal cell is destined to give rise to the attachment system and the upper cell to the rest of the plant. Light has an important morphogenic effect at this early stage for the pointed basal cell is formed away from light, the blunter upper cell being towards the light and the first cross-wall at right angles to the rays.

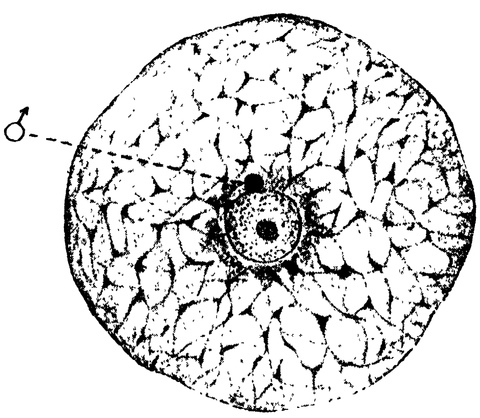

Fig. 95.—Ovum of one of the Fucales (*Ascophyllum nodosum*), seen in section at the moment of ferilisation. ♂, small male nucleus of a spermatozoid, which has traversed the cytoplasm, and is now in contact with the large nucleus of the ovum. The cytoplasm of the ovum shows a distinct foam-like structure. Magnified about 650. (After Farmer.)

Fig. 96 shows early stages in the growth of the young *Fucus* plant. At first cell-divisions occur in all regions of the young plant, but soon an apical cell is differentiated which dominates further development.

We have seen that *Fucus serratus* is a perennial plant, but the receptacles last only for one season. They then rot away, but in plants several years old their stumps can still be recognised.

There are certain features of special interest in *Fucus*. First, it is an alga of massive parenchymatous structure, not formed on the filamentous plan, but built up by cell division occurring in all directions. Secondly, it offers an excellent example of oögamous sexual fusion, with relatively large non-motile ova and very minute motile sperm, occurring outside the parent plant. Thirdly, we have in *Fucus* an example of a gametophyte[1] which is diploid, meiosis occurring at gamete formation. This should be contrasted with *Spirogyra* and *Œdogonium* in which the

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[1] Some have argued that in *Fucus* the thallus is really a sporophyte, that the oögonium is a megasporangium and the antheridium is equivalent to a microsporangium, but this is a very "academic" point of view.

gametophyte is haploid and meiosis takes place on the germination of the zygote. Finally *Fucus* is of interest as an alga that relies on the sexual process both for reproduction and for dispersal. There is no asexual stage.

The Phæophyceæ, of which *Fucus* is a somewhat specialised example, are of interest to students of plant evolution because within this single group there is such a variety of life-cycle. Thus, in *Dictyota*, a dichotomous ribbon-like seaweed, common in low-level rock pools in the south of England, there is an alternation of generations between male and female haploid plants and diploid asexual plants. All three types of plant, male, female, and asexual, are similar in general appearance. Again in the giant kelps (*Laminaria* spp.), which form sub-marine forests at and below low-water mark, there is the same alternation of generations but the haploid gametophytes are microscopic whilst the diploid sporophyte is large and conspicuous. Both the gametophytes and the sporophyte are, however, independent, both structurally and physiologically, and we are strongly reminded of the type of alternation found in ferns.

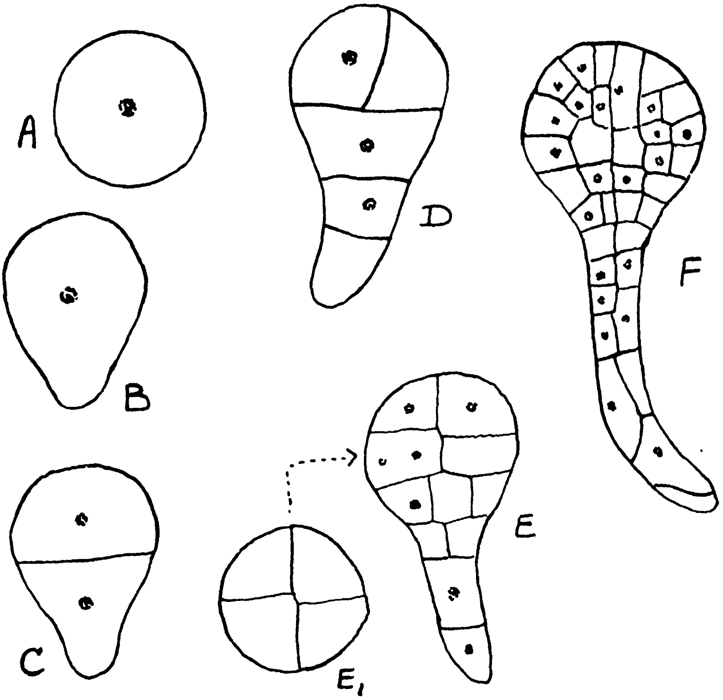

FIG. 96.—*Fucus* sp. Diagram showing successive stages (A to F) in the development of the very young plant from the fertilised egg (A). E_1 shows a transverse section of E at the point indicated by the arrow. At stage F apical growth has not yet been established. Highly magnified. D–F. (After Nienburg.)

OTHER CLASSES OF ALGÆ

Our types of Algæ have been selected from two classes only: Chorophyceæ (Green Algæ) and Phæophyceæ (Brown Algæ). There are, however, a number of other important and interesting classes. Especially worthy of mention are Myxophyceæ, Rhodophyceæ, and Bacillariophyceæ. Myxophyceæ (Blue-green Algæ) constitute a peculiar group of mainly fresh-water algæ of simple structure and apparently without sexuality. Rhodophyceæ (Red Algæ) include some of the most beautiful of the seaweeds and are noted for their elaborate life-cycle and the complexity of the female sexual apparatus. Bacillariophyceæ (Diatoms), essentially unicellular plants with rigid siliceous walls and brown chloroplasts, are exceedingly abundant. Diatoms usually constitute the major element in marine and fresh-water phytoplankton, the microscopic plant-life suspended in water. It is upon the phytoplankton that aquatic animals directly or indirectly depend for their food. It has been said that "all flesh is grass and all fish diatom."

CHAPTER IV

THE FUNGI

THE Fungi are an immense group—by far the largest of all the cryptogamic Classes. Up to the present time about 50,000 species have been described. The whole of this vast mass of most heterogeneous forms is distinguished by one physiological character—the absence of chlorophyll. Hence all Fungi alike are incapable of assimilating their carbonaceous food from the carbon-dioxide of the atmosphere; they must obtain it ready made, as it were, from other sources. So far as carbon-compounds are concerned, Fungi are entirely dependent on *organic* food. This they obtain either directly from other living creatures, on which they prey, or from dead organic substances produced by living organisms. In the former case we call them *parasites*, in the latter *saprophytes.*

Parasitic and saprophytic plants wholly or nearly destitute of chlorophyll occur in other classes of the vegetable kingdom, as members of very diverse families. Thus among flowering plants, for example, we have the Dodder (*Cuscuta*) and the Broomrape (*Orobanche*) as parasites; the Bird's Nest (*Monotropa*) and the Bird's Nest Orchid (*Neottia nidus-avis*) as saprophytes. In all these cases, however, the parasitic or saprophytic forms are near relations of normal chlorophyll-containing plants, and we attach no great systematic importance to the change in their mode of life. The relationships of the Fungi to other groups are, however, entirely obscure. The old view that Fungi have arisen from algal ancestors is now supported by few authorities, and indeed, many students of Fungi consider that they should be classified in a separate kingdom of living organisms.

Many Fungi are of the greatest practical interest, though chiefly in a disagreeable way. Very many of them are destructive parasites, causing the worst diseases of our field and garden crops and of forest trees. We may mention black stem rust, smut, and bunt of wheat, potato blight, and apple scab, to which innumerable others might be added. Others, such as the dry-rot fungus, do harm by injuring timber in buildings; others, again, destroy articles of food and textiles, which are constantly attacked by "mould."

It must not be supposed that Fungi are altogether to be regarded as injurious to the higher creatures. Not to mention, what everybody knows, that several of the larger kinds are exceedingly good to eat, we may point out that the saprophytes, at any rate, do good service by causing decay, and so ridding the world of the useless remains of dead animals and plants.

In recent times some fungi have become of considerable industrial importance. Thus *Penicillium notatum* is used in the production of the antibiotic penicillin and *Aspergillus niger* in the manufacture of citric acid.

Fungi have been more studied from a practical point of view than any other Cryptogams, and a vast mass of knowledge has now been accumulated as to their physiology and mode of life. Our own point of view is chiefly a morphological one, and we have chosen the few types which we have space to describe, in order to illustrate some of the most striking facts in the comparative structure and life-history of certain of the more important groups.

In Fungi the vegetative plant body consists of a system of colourless branched filaments. This system is known as the *mycelium* and each individual branch is called a *hypha*.

A. PHYCOMYCETES

In this group of Fungi the mycelium is without cross-walls in the young condition, although occasional septa often arise in the older hyphæ. To this group belong all those fungi that produce motile zoospores, and because of this feature the Phycomycetes used to be regarded as closely related to the Algæ. However, it seems more likely that the presence of motile zoospores in both groups merely indicates that both are derived from flagellate ancestors. However, not all Phycomycetes produce motile zoospores. Most of the "higher" members of the group reproduce asexually by non-motile spores formed either within sporangia or produced externally. Such external spores are known as *conidia* and the hypha bearing them is called a *conidiophore*. Whether the spores are borne internally in a sporangium or externally on a conidiophore, their number is indefinite.

PYTHIUM DE BARYANUM

Some species of *Pythium* are parasitic on seedlings, and often do great havoc among them, especially if the seed-beds are kept too damp, and not sufficiently exposed to air and light. One of the commonest species, *P. de Baryanum*, can be obtained almost with certainty by growing Cress seedlings in soil under a bell-glass, and giving them an excessive amount of water; but, unfortunately, the parasite appears often enough when it is not wanted. The disease caused by it is well known to gardeners as the "damping off" of seedlings. The stem of the seedling when attacked by the Fungus soon tumbles over on to the ground. This is because the outer tissues of the stem, at the part where it gives way, have been so much damaged by the parasite that the stem has not the strength to stand upright. The fallen plants lose their colour and soon completely rot away.

1. STRUCTURE

In its vegetative condition, *Pythium* consists of long, fine, irregularly branched filaments or *hyphæ*. These hyphæ are not divided into cells. The inside of the hypha is occupied by vacuolated cytoplasm, in which numerous nuclei are embedded. Although the cell-wall of *Pythium* contains cellulose, in most Fungi the wall consists of other substances, one of which is *fungus-cellulose* and another resembles the *chitin* of some animals. The hyphæ, as in Fungi generally, grow at the apex. The vegetative body or thallus of a Fungus is the *mycelium*. The mycelium of *Pythium* penetrates the tissues of its victim or "host," and spends most of its life within them. A hypha can make its way into the stem either by way of a stoma or by boring directly through the outer cell-walls; it goes on growing and branching inside the host plant, where it is not confined to the intercellular spaces, but can enter the cells themselves. Thus the whole plant comes to be infected, and is traversed throughout by the branched mycelium of the parasite, which lives at its expense.

Parasitic Fungi have the power of secreting *enzymes*, which play a very important part in bringing their victims into subjection. The advancing tip of a hypha secretes a toxic enzyme on coming into contact with the host cells, which forthwith kills the protoplasm of the host in the immediate vicinity. The hypha grows into the cells which it has thus killed, more of the enzyme is secreted and kills additional host cells, and a considerable mycelium is established by the growth and branching of the infecting hypha. *Pythium* thus feeds on the nutritive substances in the host cells which it has itself killed, enzymes secreted by the mycelium probably playing an important part in rendering the food materials available to the fungus. The mode of life of *Pythium* represents a very simple and destructive type of parasitism in which the fungus kills its host immediately on coming into contact with it. Having killed its host, *Pythium* lives on the dead remains as a saprophyte.

In this way, then, *Pythium* makes itself thoroughly at home in the body of its victim, infests it in every part, and eventually completely destroys its tissues, converting their materials to its own use. Often the hyphæ leave the host, and grow out upon the soil until they reach other victims, which they then infect. In the meantime the Fungus does not neglect to make provision for future generations. The reproduction takes place in two ways—asexual and sexual. We will first describe the former.

2. REPRODUCTION

a. Asexual

The hyphæ which are to produce the asexual organs of reproduction grow out from the host, and form a number of spherical *sporangia* which are terminal, being seated on the ends of short branches or of the main hyphæ (see Fig. 97, A). The sporangia are beaked at the apex, and, when ripe, the entire protoplasm passes out into the beak, which swells up into a bladder-like sac (see Fig. 97, B). The whole process can only go on when there is water enough to immerse the sporangia. The contents of the sac now divide up into a number of uninucleate masses of protoplasm which become *zoospores*, each bearing two cilia. The zoospores escape and swim away through the water. After some time they come to rest, surround themselves with a delicate wall, and germinate, producing a hypha, which finds its way into a fresh seedling if opportunity offers.

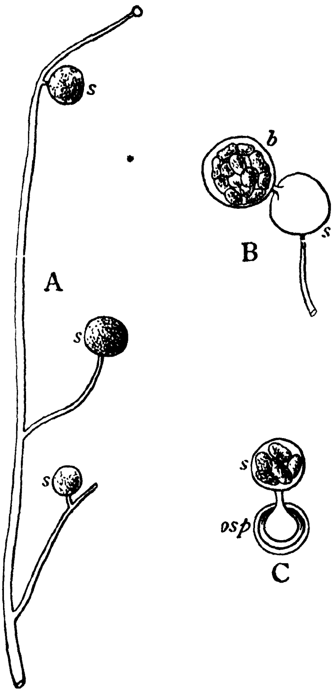

FIG. 97.—*Pythium*. A, branch of the mycelium, bearing three zoosporangia (*s*). Magnified 145. B, zoosporangium (*s*) discharging its contents (*b*), which are still enclosed in the enlarged papilla, but have already divided to form the zoospores. Magnified 145. C-germinating oöspore (*osp*) forming an asexual sporan. gium (*s*). Magnified 300. (After De Bary.)

This mode of reproduction, we see, is altogether that of an Alga. *Pythium*, though a Fungus, is not thoroughly adapted for growth on dry land, for its normal reproductive processes can only go on under water. This is one reason why seedlings attacked by *Pythium* are said to *damp off*, for it is when they are kept too damp that their enemy is best able to attack them; the moisture enables the *Pythium* to spread. This method of propagation by zoospores allows of rapid multiplication under favourable conditions; its success, however, is entirely dependent on the presence of water. It is true that only a little water is necessary, but still *Pythium* is entirely powerless to propagate its kind in this manner, under such conditions as prevail in nature when the weather is at all dry.

The great majority of the Fungi, however, are adapted to the same conditions of life as the ordinary land plants, on which so many of them are parasitic, and this implies that their reproductive bodies are fitted for dissemination through comparatively dry air. In *Pythium* and among its near allies we can trace the steps by which this adaptation to an aërial environment has been attained. In some species of *Pythium*, as, for example, in the species *P. de Baryanum*, which is so common on Cress seedlings, it sometimes happens that the sporangium does not form zoospores at all, but grows out directly into a hypha, thus starting a new plant at once, without the intervention of the active aquatic cells.

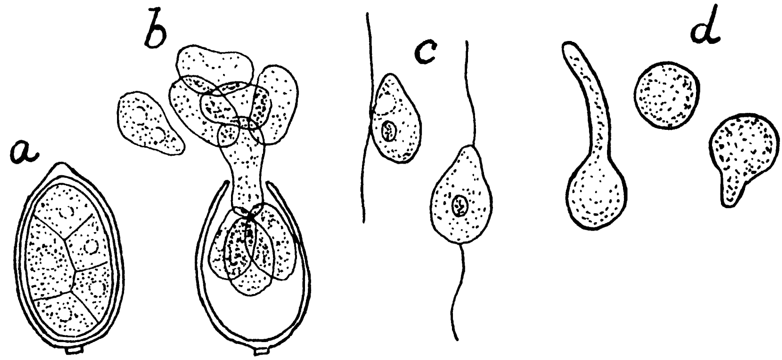

FIG. 98.—*Phytophthora infestans*. Germination of the conidium (sporangium) with the production of zoospores. a, zoospores delimited within sporangium; b, escape of zoospores which have not yet acquired cilia; c, mobile zoospores; d, zoospores have come to rest and two have germinated. X700. (After De Bary.)

The same thing happens regularly in the closely-allied genus *Phytophthora*. Thus in *P. infestans*, which causes Potato Blight, the zoosporangia behave as conidia. They are borne on branched conidiophores which project through the stomata of infected plants and are easily detached and scattered by wind. Germinating in a drop of dew on a healthy leaf, each conidium usually behaves as a zoosporangium and liberates several zoospores (Fig. 98). These come to rest after a brief period of motility, secrete walls and germinate by germ-tubes which enter the leaf by way of stomata. Less often a conidium fails to divide into zoospores and germinates directly by a germ-tube. In *Peronospora*, which is considered below, the conidia can no longer behave as zoosporangia and are capable only of direct germination.

We will now return to *Pythium*. Zoospores afford a rapid means of propagation so long as a plentiful supply of victims, in the shape of young seedlings, is forthcoming. *Pythium* is not, however, altogether limited to a parasitic mode of life for, if host-plants are wanting, it can live for some time as a *saprophyte* on any decaying organic matter which may happen to be at its disposal. Provision, however, has to be made for bad times when food fails altogether, or when there is not enough moisture for active growth to go on. Such contingencies are provided against by the formation of *resting-spores*, which are the result of a sexual process.

b. Sexual

The organs of sexual reproduction (oögonia and antheridia) may be produced either inside the tissues of the host plant, or on hyphæ which have grown out into the air. An oögonium arises as a spherical swelling on a hypha, and may be either terminal, as shown in our Fig. 99, or *intercalary*, *i.e.* produced at some intermediate point in the course of the filament. The young oögonium is cut off from the rest of the hypha by a transverse cell-wall, or by two, if intercalary.

Its protoplasm now separates into two parts—a central granular portion which becomes the ovum, and a peripheral layer, lining the cell-wall, called the *periplasm*. The behaviour of the nuclei has now been made out in several Fungi of this group; in *Pythium*, the oögonium at first contains a large number of nuclei, nearly all of which pass out into the periplasm, leaving behind, in the central mass, a single nucleus, which is the functional female nucleus, and is alone concerned in the act of fertilisation and the subsequent development.

In the meantime the antheridium is formed. It is usually a lateral, club-shaped branch, arising either from the same filament which bears the oögonium (see Fig. 99) or from a different one, and separated from the hypha on which it is borne by a transverse wall. The antheridium directs its growth towards the neighbouring oögonium, to which it closely applies itself.

It may be mentioned here that the mycelium of *Pythium* and its allies, which is non-cellular during its vegetative growth, generally becomes irregularly partitioned up, by a few scattered transverse walls, as the period of reproduction approaches. Previous to this the bulk of the protoplasm has travelled into the more terminal portions of the mycelium, where the reproductive cells are to be produced.

The protoplasmic contents of the antheridium, like those of the oögonium, undergo a differentiation into a central fertile portion and an external layer of periplasm, and here also it is the uninucleate central part which plays an active part in the reproductive process. There is no division into spermatozoids, and in fact these bodies are extremely rare among Fungi. The antheridium sends out a short branch, the *fertilising tube*, which penetrates the wall of the oögonium, and reaches the ovum (Fig. 99). The fertilising tube opens at its end, and now the whole contents of the antheridium (with the exception of the periplasm) pass through the tube, and unite with the protoplasm of the ovum (Fig. 99, *B*). The whole process can be directly followed with ease, under the high power of the microscope, and, indeed, *Pythium* is one of the most favourable plants for the immediate observation of the fertilising act. It is established that the nucleus passes over with the male protoplasm, and unites with that of the ovum.

Following fertilisation, the ovum surrounds itself with a thick cell-wall, the outer layer of which is derived from the periplasm by which it is surrounded. The ovum has now become an *oöspore*; its contents form a quantity of oil, as a reserve of carbonaceous food, and it next passes into a period of rest.

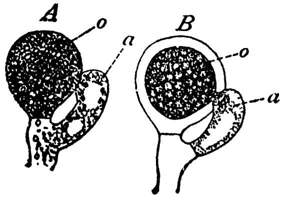

FIG. 99.—Fertilisation of *Pythium*. *A*, early stage; oögonium (*o*) and antheridium (*a*) still immature. *B*, moment of fertilisation. The contents of the antheridium (*a*) are passing through the fertilising rube, to unite with the ovum (*o*). Magnified 800. (After De Bary.)

The germination of the oöspore takes place after a long interval, and only when it is brought into contact with water. The process shows variations, both among different species and among individuals of the same species, comparable to the variations in the behaviour of the asexual sporangium described above. In some cases the outer thick layers of the oöspore membrane are burst, and the contents, surrounded by a delicate cell-wall, grow out into a hypha, thus starting a new mycelium directly. In other cases the process begins in the same way, but the hypha at once forms a sporangium, into which the whole contents pass, dividing up into a number of zoospores (see Fig. 97, *C*). In a third mode of germination, the formation of the hypha is suppressed, and the zoospores are produced in the interior of the oöspore itself. The zoospores swim about like those formed on the vegetative plant, and on coming to rest reproduce the ordinary form of the Fungus.

PERONOSPORA PARASITICA

I. STRUCTURE AND MODE OF LIFE

This fungus is probably closely related to *Pythium de Baryanum*, but its mode of life is entirely different, as it does not immediately destroy its host. The mycelium lives a life together with the host cells, gradually withdrawing food but not killing them. Such a fungus, which can only continue to live in contact with living host cells, is said to be an ***obligate parasite***. ***Peronospora parasitica*** is commonly found on Shepherd's Purse (*Capsella bursa-pastoris*) and other plants belonging to the family Cruciferæ. It attacks the stem, leaves, and inflorescences. In the reproductive stage it protrudes from the host as a delicate whitish down or fluff, and hence it is sometimes called a "downy mildew." The parts of the host invaded by the mycelium are sometimes deformed. This *hyper trophy* is due to the mycelium exercising a stimulus on the growth of the host cells.

The asexual spores of *Peronospora* are conidia (see below), which are blown about by the wind. If they alight on a moist surface they germinate directly by the formation of a hypha, and if this occurs on a suitable host plant the hypha obtains entry into the tissues by growing through a stoma. Having entered the space below the stoma, the hypha advances until it comes into contact with the wall of a host cell. A portion of the hypha then puts out a protuberance which penetrates the wall of the host cell and expands within it to form a branched, sucker-like process, the ***haustorium*** (Fig. 100). Food material passes from the host cell by way of the haustorium back to the hypha in the intercellular space. The hypha continues to grow, it branches, and soon an extensive mycelium is established in the intercellular spaces of the host, new haustoria being formed as growth proceeds. The mycelium of this fungus, like that of *Pythium*, is devoid of cross-septa. As pointed out above, *Peronospora* lives a kind of common life with its host without gravely damaging it. After the fungus has spread considerably in the tissues it begins to reproduce itself.

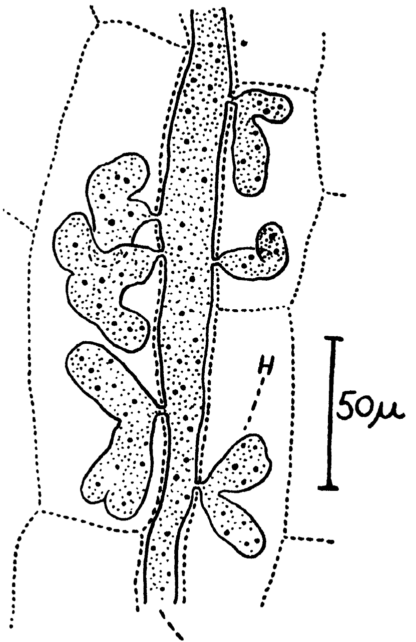

FIG. 100.—*Peronospora parasitica.* Intercellular mycelium (I.M.) with haustoria (H) seen in longitudinal section of Shepherd's Purse stem. The pith cells of the host are shown with dotted lines.

2. REPRODUCTION

a. Asexual

Branches arise from the mycelium near the stomata, through which they grow out. These hyphæ divide dichotomously many times on reaching the air and become *conidiophores*. The tip of each branch of a conidiophore swells up to form a single oval or nearly spherical conidium which ultimately falls off (Fig. 101). It is in consequence of the formation of innumerable conidiophores that the surface of the host appears to be covered with a kind of down when the parasite is in the reproductive stage.

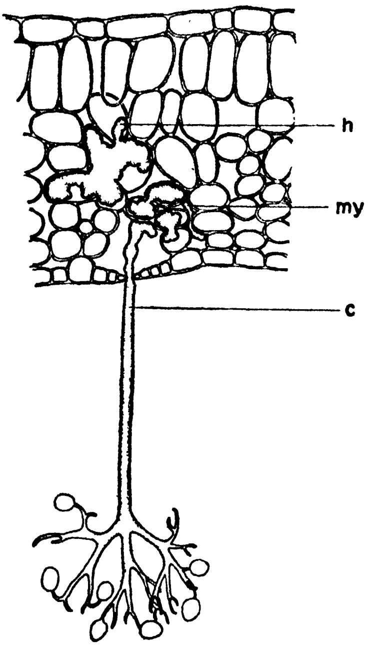

FIG. 101. — *Peronospora parasitica.* Vertical section of leaf of Shepherd's Purse attacked by fungus. *h*, haustorium; *my*, mycelium; *c*, conidiophore. Magnified 160. (R. W. Marsh.)

b. Sexual

After the development of conidiophores and as the host tissues become old, sexual organs, similar to those of *Pythium*, may be formed on the mycelium in the intercellular spaces of the host. The process of fertilisation is the same as that in *Pythium*, but the fusion of the male and female nuclei is delayed until the oöspore wall has been formed. The oöspores, which have a brown exterior, remain embedded in the tissues until these disintegrate, when they pass into the soil. The oöspores remain dormant for a considerable time. When temperature and moisture conditions are suitable they germinate by the formation of a germ tube. The oöspores may be splashed by rain on to the surface of plants just above soil level. In *Peronospora parasitica*, sexual organs are not invariably formed in the host tissues, and the precise conditions which lead to their development are not yet clearly understood.

MUCOR HIEMALIS

Species of *Mucor* are sometimes called pin-moulds because the long straight sporangiophore bearing its terminal sporangium looks somewhat like a pin. They are saprophytes occurring very commonly on freshly deposited horse dung, on damp bread and in the soil. *Mucor hiemalis* is a common soil species.

1. STRUCTURE

The mycelium or vegetative thallus consists of branched hyphæ which spread in all directions through the substratum and resembles the mycelium of *Pythium*. Cross-walls are absent from the young mycelium, but occur to some extent in the old, walling off sections devoid of protoplasm. The hyphæ grow apically and very rapidly, so that if hyphæ on nutrient jelly are watched under the high power of the microscope, a visible increase in length can be observed after five minutes. The growing hyphæ are filled with finely granular protoplasm. If these are stained with nuclear dyes, the protoplasm can be shown to contain numerous very minute nuclei. In the older parts of the mycelium vacuoles occur and also conspicuous droplets of oil. Protoplasmic streaming can often be observed in the larger hyphæ. This process is dependent on evaporation from the aërial parts of the fungus and ceases in a saturated atmosphere.

The mycelium obtains its food from the nutrient substratum, but can take in substances only if they are in true solution. When a mycelium is growing on such a substratum as damp bread, the main food, starch, is not in a soluble state. This is made available, however, by the hyphæ secreting enzymes, such as diastase, which convert the starch to soluble sugar that can then be absorbed.

2. REPRODUCTION

a. Asexual

The usual means of asexual reproduction is by spores formed in sporangia (Fig. 102). The feeding mycelium ramifies in the nutrient substratum, but certain hyphæ grow out into the air to a distance of a centimetre or two. The apex of such an aërial hypha enlarges to form a nearly spherical sac in which dense protoplasm accumulates. This sac is then cut off as a *sporangium* by a highly curved cross-wall which protrudes into the sporangium as a knob-like *columella*. Within the sporangium the contents cleave up into a very large number of equal segments each with several nuclei. These acquire cell-walls and become the spores. The aërial hypha bearing the sporangium is the *sporangiophore*. The sporangium-wall is very thin and is ornamented on its outside by minute crystals of calcium oxalate. When ripe it undergoes liquifaction and water apparently passes into the spore mass through the columella, so that the whole structure is converted into a sporangial drop. When this dries the spores are firmly cemented to the columella and cannot be blown off by wind. It is not at all clear how they are dispersed in nature. Perhaps they are spread by insects or by rain-splash.

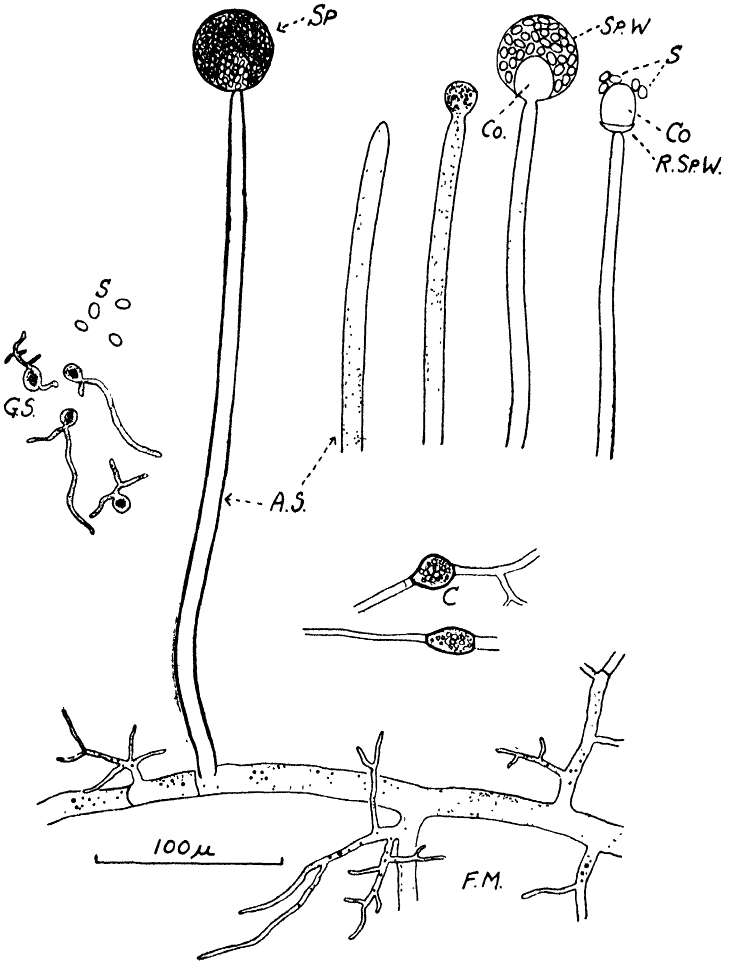

FIG. 102.—*Mucor hiemalis.* Spore germination, mature structure, chlamydospores and stages in sporangiophore development. S, spores; G.S, germinating spores; F.M, feeding mycelium; A.S, aerial sporangiophore; SP, sporangium; Co, columella; SP.W, sporangium wall; R.SP.W, remains of sporangium wall; C, chlamydospores formed in feeding mycelium.

However, in some of the pin-moulds wind dispersal occurs. Thus in *Rhizopus nigricans* Ehr. (= *Mucor stolonifer*), the black bread-mould, the spores exposed on the columella form a dry powdery mass readily blown away. Another type of dispersal is found in *Pilobolus*, species of which develop regularly in a few days if freshly deposited horse-dung is kept in the light under a bell-jar (Fig. 103). The structure of the sporangiophore is in essentials like that of *Mucor*, but it is separated by a cross-wall from the feeding mycelium (Fig. 104). Further, at its base and near its apex the sporangiophore is swollen to form a basal and a sub-sporangial bulb. The mature structure, about a centimetre long, is a highly turgid cell which finally bursts, shooting the sporangium to a distance of one to two metres. Under natural conditions the sporangia are thus scattered over the grass around the dung. Eventually this grass may be eaten by a horse or other herbivore. The spores not only pass uninjured through the alimentary canal of the animal, but encounter conditions there that stimulate their subsequent germination n the dung. Horse dung is an ideal nutrient medium for many fungi, and, indeed, there is a very characteristic flora of beautiful fungi which grow on it. In all these the story of dispersal is essentially the same.

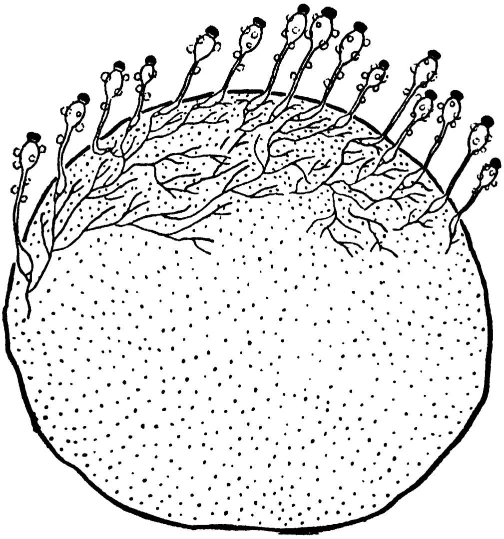

FIG. 103.—*Pilobolus kleinii*. Sectional view of a dung pellet of rabbit showing mycelium bearing sporangiophores. These all point towards the light.

To return to *Mucor* the spores will germinate in water, but they do so more freely and more rapidly in a nutrient solution such as a 2 per cent. solution of malt extract. During the first few hours in the malt solution the spore swells considerably and then puts forth one or two germ-tubes which increase in length by apical growth and soon branch

(Fig. 102). We have already noted that most species of *Mucor* grow quickly. In *M. hiemalis* a spore planted on 2 per cent. malt agar will give rise to a mycelium bearing sporangia in from three to four days at 20° C.

In addition to the production of spores in sporangia, most species of *Mucor* form *chlamydospores* in the old feeding mycelium. These are thick-walled spores formed in an intercalary position (Fig. 102). Under suitable conditions they can give rise to a new mycelium.

Again if certain species are grown in a liquid medium with a plentiful supply of sugar, some of the submerged terminal hyphæ divide by transverse walls into numerous cells which round off and are liberated. These cells or *oidia* can further increase by budding in much the same manner as in yeasts. This behaviour is especially characteristic of *Mucor racemosus* (Fig. 105).

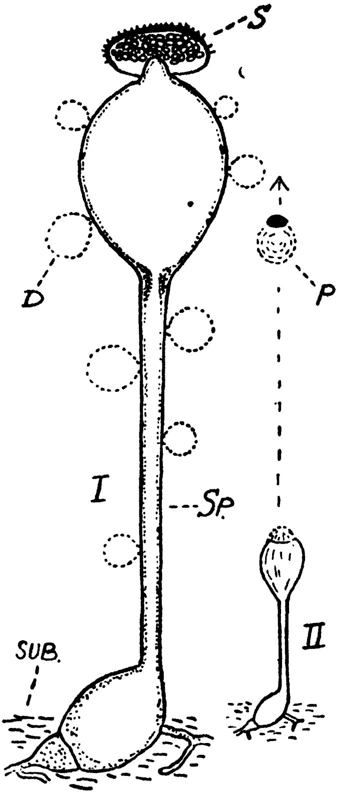

FIG. 104.—*Pilobolus kleinii.* I, Diagram of structure as seen in longitudinal section. II, At moment of discharge drawn in solid view at lower magnification. S, sporangium containing spores; SP, sporangiophore; D, drop of exuded water; SUB, substratum; P, projectile. I X 25., II X 6.

b. Sexual

The sexual process in *Mucor* and its close allies has been studied extensively. Of special significance is the classical work of Blakeslee. In most species he found that cultures derived from single spores never gave rise to *zygospores*. If a large number of single-spore cultures of a species were made from various sources, these could be sorted into two types: (+) and (—). Both types looked alike and both produced sporangia. Where a (+) culture encountered a (+) one nothing happened, and the same was true of the union of two (—) cultures, but when a (+) colony met a (—) colony zygospores were formed.

If a (+) and a (—) spore are placed at opposite sides of a petri dish containing nutrient agar, each gives rise to a mycelium bearing sporangia containing spores of the same sign as the original spore. As they grow the two colonies quickly approach, but apparently before they actually meet, they stimulate one another to form *zygophores* (Fig. 106). These are long aërial hyphæ. The sexual stage occurs where two such zygophores of opposite sign come in contact. Where they touch each stimulates the other to put out little protuberances. These are the *progametangia* (Figs. 106 and 107) and from each a multinucleate *gametangium* is delimited by a cross-wall, the remaining part of the original protuberance being referred to as the *suspensor*. The two gametangia [(+) and (−)] are in contact from their inception. The wall between now dissolves and the protoplasmic contents intermingle. Probably nuclear fusion occurs at this stage between nuclei of opposite sign, but the evidence on this point is not conclusive. The nuclei are so small that even nuclear fusion has not been clearly demonstrated. The other point that in each fusing pair a (+) and a (−) nucleus are involved would probably be impossible to establish by cytological evidence. Again such cytological evidence as we have suggests that nuclear fusion is followed very shortly by meiosis, so that the diploid phase is of very brief duration. The cell formed by the fusion of the two gametangia is referred to as the young *zygospore*. This enlarges and the wall becomes warted and blackened. Further an additional thick wall is deposited within the original one. The mature zygospore contains a considerable reserve of oil. Zygospores are formed in great numbers along the line of union of cultures of opposite sign or mating

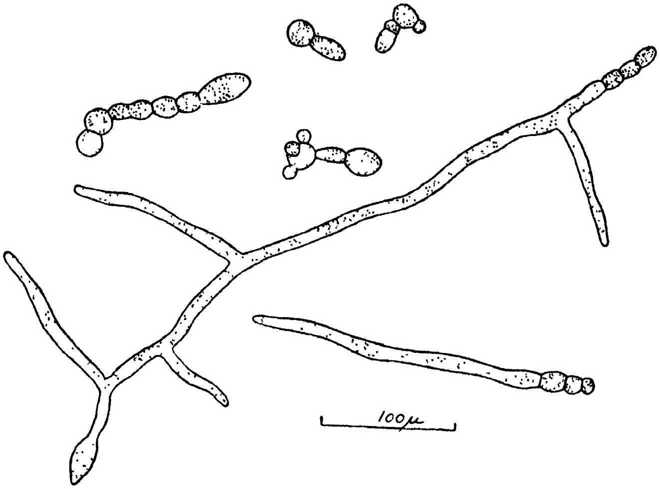

FIG. 105.—*Mucor racemosus*. From culture in 2 per cent. malt solution plus 10 per cent. glucose. The mycelium is giving rise to sprout cells which themselves increase by budding.

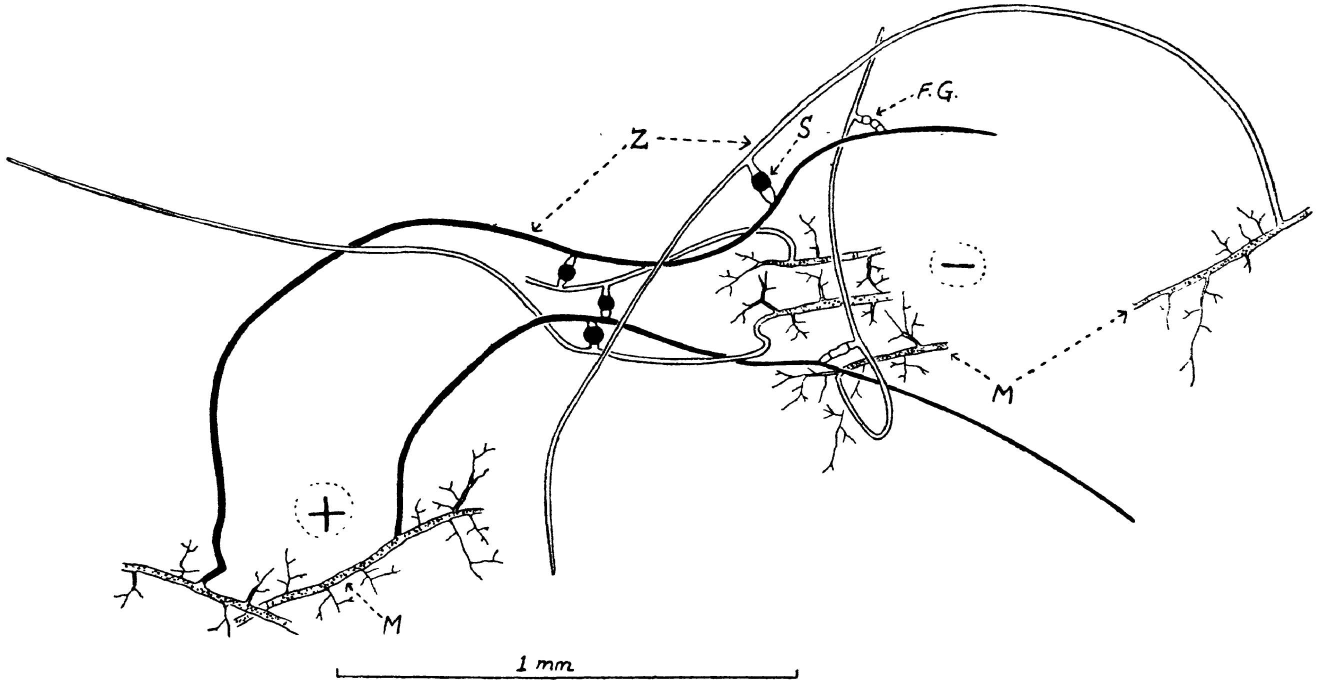

FIG. 106.—*Mucor hiemalis*. Region where a (+) mycelium joins a (−) one on nutrient agar. M, part of the feeding mycelium in the agar; Z, aerial zygophores (the (+) zygophores are shown black and the (−) white), F.G, fusing gametangia; S, zygospore.

type. In the formation of a zygospore there is no consistent difference in the size of the two fusing gametangia, so it is impossible to use the terms "male" and "female" for the two types of culture and, therefore, the non-commital terms (+) and (—) are employed.

The sexual process in *Mucor* is usually referred to as isogamous. However, the two cells that fuse are usually called gametangia. It is difficult to say what should be regarded as the gametes: the multinucleate mass within each gametangium or the individual nuclei.

Species such as *M. hiemalis* with separate (+) and (—) strains are said to be *heterothallic*, but in some members of the Mucorales zygospores are produced on cultures derived from single spores and are thus *homothallic*. An example of this is *Rhizopus sexualis* (Fig. 108) in which the zygospore is formed between branches of one and the same zygophore.

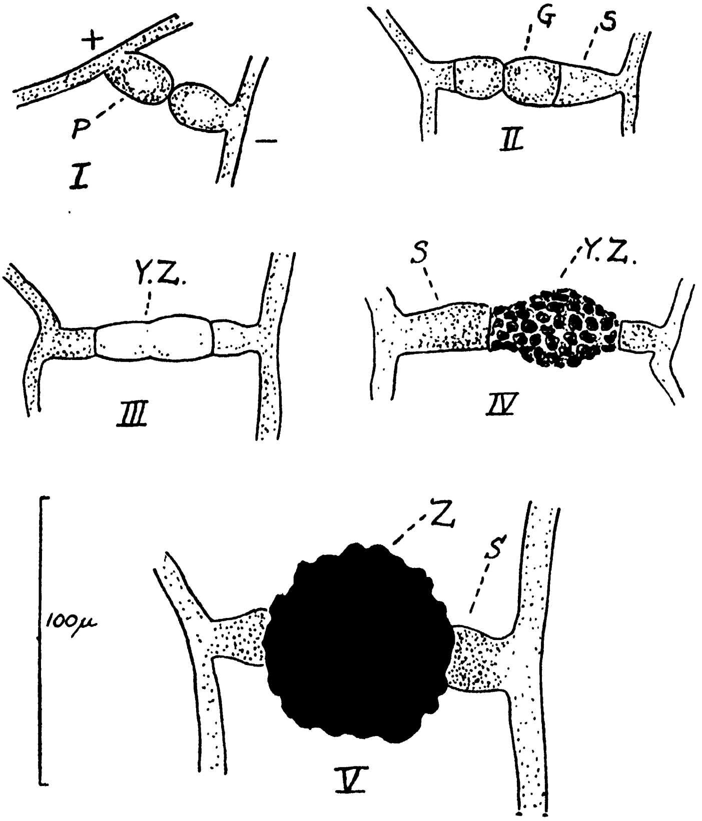

FIG. 107.—*Mucor hiemalis*. I–IV. Stages in zygospore formation P, progametangium; G, gametangium; S, suspensor; Y.Z, young zygospore; Z, mature zygospore.

The zygospore is a resting spore in the sense that it can germinate only after a period of rest varying from a few weeks to several months. However, zygospores do not seem to be very long-lived and after a year or two are no longer viable. On the other hand spores from the sporangia of some species (*e.g. Rhizopus nigricans*), if kept dry, may retain their power to germinate for over ten years.

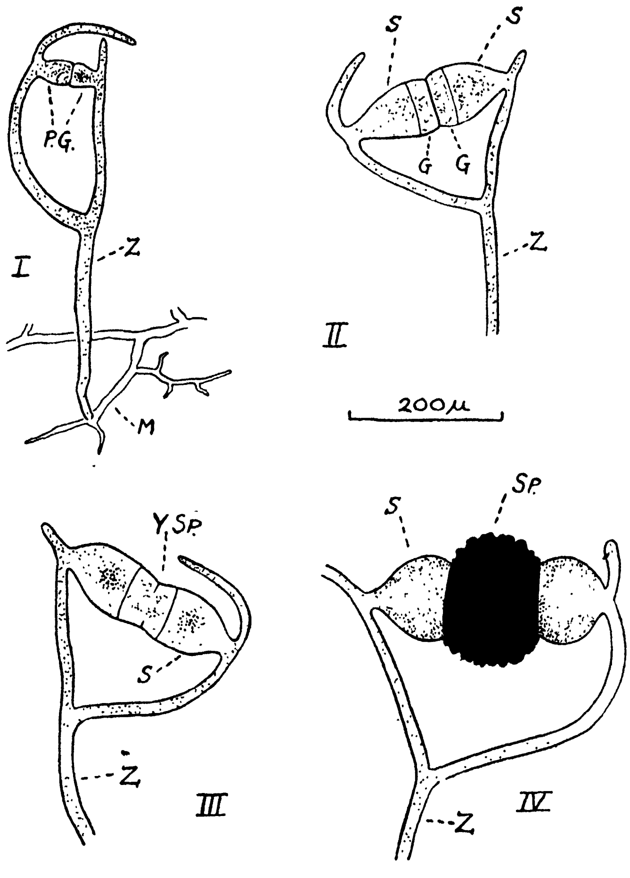

FIG. 108.—*Mucor* (*Rhizopus*) *sexualis*. I, II, III, IV stages in zygospore formation. M, feeding mycelium; Z, aerial zygophore; P.G, progametangium; S, suspensor; G, gametangium; Y.SP, young zygospore; SP, mature zygospore.

On germination the zygospore puts forth a germ-tube which usually develops directly into a sporangiophore bearing a single terminal sporangium (Fig. 109). Structurally this *germ-sporangium* is just like other sporangia. Analysis shows that in *Mucor* the spores in the germ sporangium are either all (+) or all (—). However, a different state of affairs exists in *Phycomyces*, a genus closely related to *Mucor*. In *Phycomyces blakesleeanus* the germ-sporangium contains (+) spores, (—) spores, and also a few spores which give somewhat abnormal homothallic cultures.

B. ASCOMYCETES

In this large group of Fungi the mycelium is septate and reproduction is typically by *ascospores* contained within a special kind of sporangium known as an *ascus*. This normally contains eight ascospores and has a characteristic development (Fig. 110). It starts as a cell with two haploid nuclei. These fuse to form a diploid nucleus and the two divisions of meiosis follow so that four haploid nuclei are present. These undergo a further division, this time mitosis, so that eight nuclei are present, no cell walls being produced during the three divisions. Around each nucleus a spore is organised. In most Ascomycetes the ascus contains eight spores. Usually it is an elongated turgid cell and in very many species it bursts when mature, discharging the ascospores to a distance of a few centimetres.

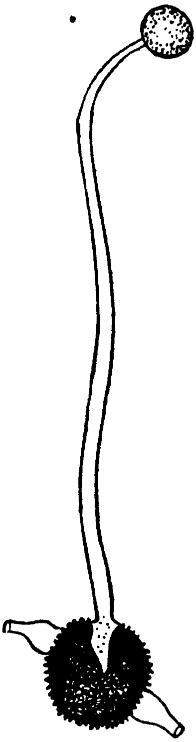

FIG. 109.—*Mucor* sp. Zygospore germinating to produce a germ sporangium. The two suspensors are still attached to the zygospore. (After Biefeld.)

ALEURIA VESICULOSA

Aleuria vesiculosa may be selected as a rather typical member of Ascomycetes. It is found quite commonly on well-manured ground. The branched septate feeding mycelium ramifies in the soil and lives at the expense of organic material there. The fruit bodies, formed at the surface either singly or in small groups, are cup-like structures several centimetres in diameter. Each cup or *apothecium* (Fig. 111) is composed entirely of interwoven hyphæ and lining the cup is the spore-producing layer or *hymenium*. In vertical section of the apothecium the structure of the hymenium can be seen. It is composed of numerous elongated and very closely packed elements. Some of these are asci in various stages of development and the remainder are straight septate packing hyphæ or *paraphyses*. The mature ascus is a long tubular cell bounded by a much stretched elastic cell-wall and lined with a thin layer of protoplasm. Within this is a large central vacuole in which eight oval ascospores are suspended near the apex of the ascus. The ripe ascus is a turgid living cell which finally bursts. When this happens a small apical lid hinges back, the stretched wall of

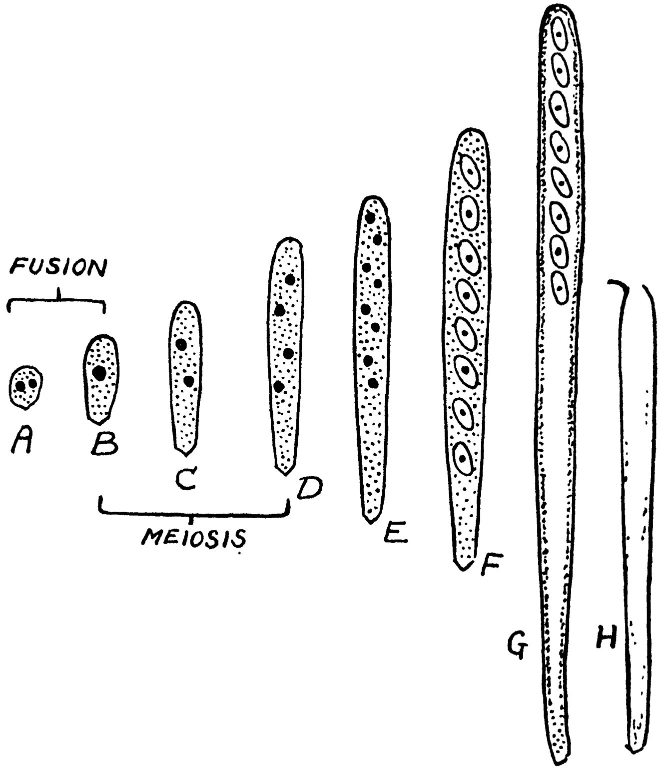

FIG. 110.—*Aleuria.* Diagram of ascus development. A, binucleate ascus-initial cell. B, young ascus with diploid fusion nucleus; D, after meiosis the young ascus contains four haploid nuclei; E, a further mitosis has occurred and there are eight haploid nuclei present; F, ascospores have been formed leaving epiplasm around them; G, the ascus is mature, the epiplasm is reduced to a thin lining layer of protoplasm and the spores are suspended in a large central vacuole. H, the ascus has burst, by an apical hinged lid, and its contents have been discharged.

the ascus contracts and its contents, including the eight ascospores, are squirted into the air to a height of two or three centimetres. In *Aleuria* the phenomenon of *puffing* occurs. During a period of quiescence thousands of asci ripen and attain a condition of unstable equilibrium, so that a slight shock, as when the apothecium is touched or breathed upon, causes them all to discharge simultaneously, sending a smoke-like cloud of spores into the air that drifts away in the breeze.

Both the asci and paraphyses are responsive to light and bend in the direction of the strongest light. The result is that instead of being arranged at right-angles to the surface of the hymenium, the asci and paraphyses curve so that their upper parts are parallel to the light rays entering the apothecium from above. This feature is clearly of biological importance since when the asci burst the spores tend to be shot out of the apothecium and there is no wastage due to discharge of the sticky spores from one wall of the cup on to the opposite hymenial surface.

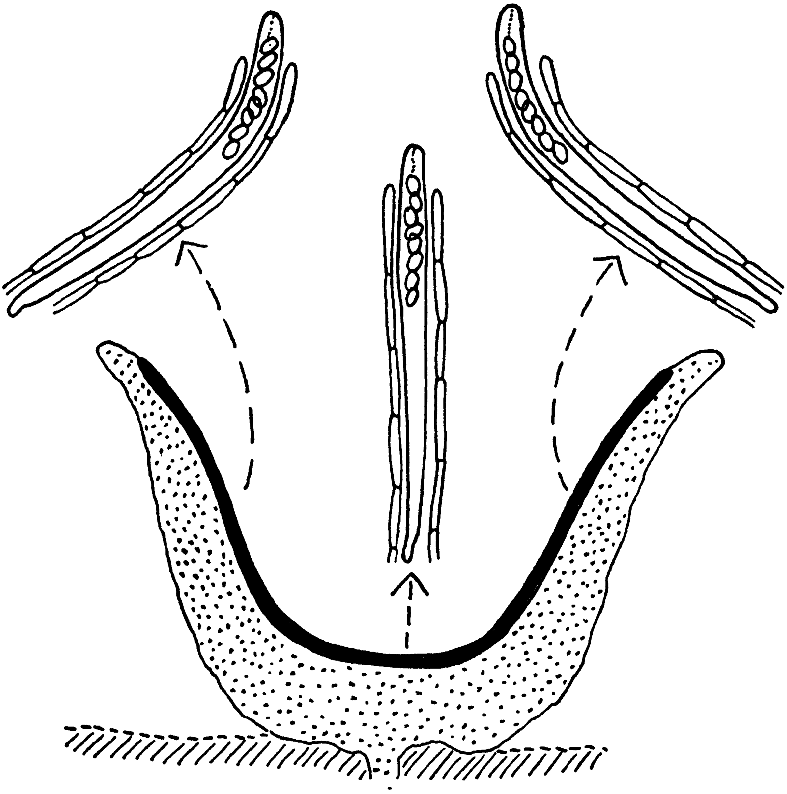

FIG. 111.—*Aleuria vesiculosa.* Apothecium in vertical section. Hymenium shown black. An ascus and two paraphyses are shown from three indicated positions. Based on figures by Buller (1934). Apothecium X 4. Ascus X 146.

The spores are dispersed by the wind and under suitable conditions germinate to produce a new mycelium.

The apothecium is only one of the types of fruit-body produced in the Ascomycetes. In some the asci are contained within a flask-like structure or *perithecium* which opens to the outside by a narrow canal.

In others (*e.g. Sphærotheca*) the asci occur within a closed structure or *cleistothecium*. Whatever the form of the fruit-body, some kind of sexual process is usually involved in its inception, although often the sexua organs themselves are much reduced or absent.

SPHÆROTHECA HUMULI

1. STRUCTURE

The species of *Sphærotheca* and its nearer allies (forming the family *Erysiphaceæ*, so named after its largest genus *Erysiphe*) are all obligate parasites. One species (*S. humuli*) is exceedingly common on Hops, and produces a very serious disease, the mildew, which causes great loss to the hop-growing industry. Another species (*S. pannosa*) is equally abundant on the shoots of Roses. All these Fungi are remarkable for being *external* parasites, that is to say, their much-branched mycelium forms a web on the surface of the leaves and other organs of the host plant. The presence of the parasite is quite evident to the naked eye owing to the white to greyish-brown colour of its mycelium which obscures the natural green of the leaf. The mycelium is white when young and greyish brown when old. The popular name "mildew" (equivalent to mealy dew) refers to this appearance, the leaves looking as if they had been powdered with flour. It must have been to Fungi of this kind that the name mildew was originally applied, though now it is extended in popular usage to other diseases of plants, presenting quite different symptoms.

The mycelium which spreads over the leaf, when examined microscopically, is found to give rise at intervals on both surfaces to short outgrowths that penetrate into the interior of the cells of the epidermis, forming suckers or haustoria, which absorb the organic substances in the cells attacked, and thus supply the whole Fungus with its food, at the expense of the living tissue of the host (Fig. 112). The mycelium, as in all the higher Fungi, is multicellular, consisting of branched chains of cells, each of which has a single nucleus. The mycelium, as already mentioned, forms a dense web on the surface of the leaf; its hyphæ cross and touch each other at many places.

2. REPRODUCTION

Our plant reproduces by conidia (see Figs. 112 and 113), the formation of which precedes that of cleistothecia. The conidia are produced on vertical hyphæ (called the *conidiophores*) which produce the conidia at the free end. A whole chain of conidia is formed in basipetal order, the oldest thus being at the top. They are detached and scattered by the wind, germinating immediately under suitable conditions and readily infecting hop leaves and "cones." They produce mycelium like that from which they sprang, and constitute a ready means of propagation during the summer. When conidia are being produced abundantly, the mildew assumes a powdery appearance, hence such a fungus as *Sphærotheca* is sometimes called a "powdery" mildew. In general, the conidia of these mildews do not survive the winter. The ascus stage arises in late summer when the conidial stage is dying down.

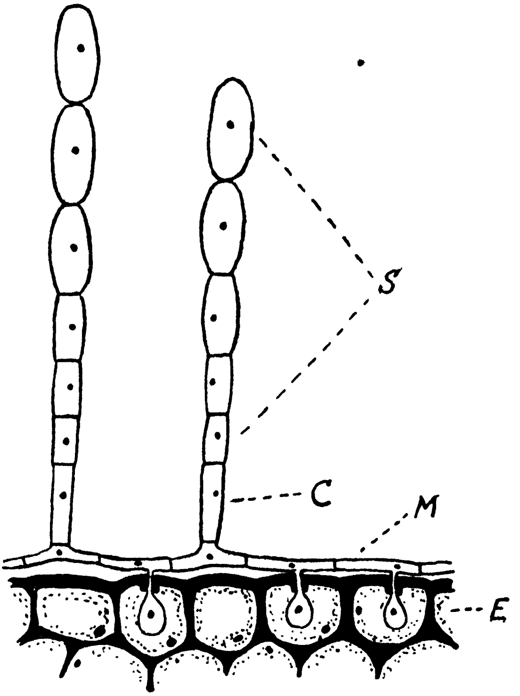

Fig. 112.—*Sphærotheca* sp. Diagram showing the surface mycelium (M) with haustoria in the epidermal cells (E) of the host and producing a chain of conidia (S) from each conidiophore (C).

It is at the points where two hyphæ cross or come into contact that the cleistothecia originate. Each of the adjoining hyphæ sends out an upright branch; the one enlarges and becomes club-shaped, and is cut off by a transverse wall; the other remains more slender, comes into close contact with the former, and grows up with it, soon overtopping it and bending over its apex (Fig. 113, A). Two transverse walls are formed in this second branch, one near its base, and the other higher up.

Of these two organs the former, *i.e.* the club-shaped branch, bears the name of the *ascogonium*, for it is from it that the ascus ultimately arises. It corresponds to the oögonium of the lower Fungi. Investigations have proved that the second organ is really an *antheridium*. Fusion takes place between the ascogonium and the terminal cell of the antheridial branch, the cell-walls between them disappearing. Then the nucleus of the antheridium passes over through the opening and lies beside the nucleus of the ascogonium.

As regards the subsequent development of the ascogonium, the main facts are clear. After two or three transverse divisions one of the cells of the row (in normal cases the last but one) thus formed increases in size, and becomes the ascus. The young ascus contains two nuclei, which fuse into one. Meiosis then occurs followed by a mitosis so that there are eight haploid nuclei, around each of which a cell is formed. These eight cells are the *ascospores*. In the meantime the vegetative cell next below the female organ has sent out several branches, which grow up around the ascogonium, completely enveloping it in a double layer of densely crowded hyphæ (Fig. 113, B and C). From the inner cells of the envelope thus formed, short branches filled with very dense protoplasm grow inwards and apply themselves closely to the ascus, probably supplying it with food. The outer cells of the envelope become thick-walled, and form a dense protective layer, completely enclosing the ascus. The ascus-fruit bears the name of the *cleistothecium*; some of its superficial cells grow out into long hairs (see Fig. 113, D). The ripe cleistothecia are visible to the naked eye, as little black dots in the mycelium on the surface of the diseased leaf.

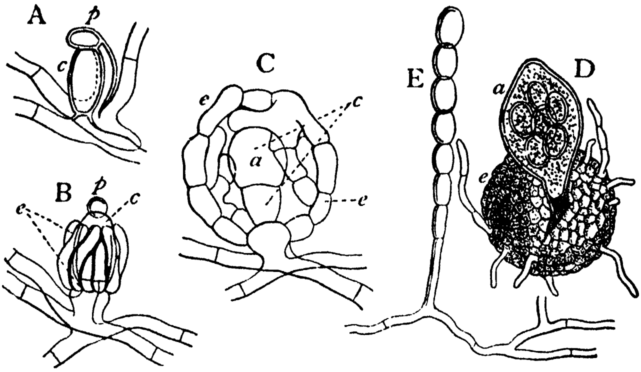

FIG. 113.—A–C, *Sphærotheca humuli*. A, early stage in formation of fruit; *p*, antheridium; *c*, ascogonium. B, more advanced; *p*, antheridium; *c*, ascogonium; *e*, enveloping hyphæ. C, ripening fruit in section; *c*, ascogonium, from which the young ascus (*a*) is now developed; *e*, *e*, enveloping hyphæ, forming perithecium. D. and E, *S. pannosa*; D, ripe cleistothecium (*e*) bursting to set free the ascus (*a*), in which only six out of the eight ascospores are shown. E, chain of conidia, borne on a vertical branch of the mycelium. A–C magnified 450; D and E less magnified. (After De Bary and Tulasne.)

The hard cleistothecium serves to protect the ascus during the winter, for the fruits remain inactive until the following spring on the dead leaves or on the soil to which they may have fallen. When germination takes place, the ascus absorbs water, swells up, and bursts the cleistothecium (Fig. 113, D), whereupon its own membrane dehisces at the top, and the ascospores are violently shot forth into the air. On germination on a suitable host they at once reproduce the ordinary mycelium of the Fungus. In most of the allies of *Sphærotheca* each cleistothecium contains several asci (the product of a single ascogonium), instead of one only.

PENICILLIUM

Damp leather, decaying fruit, and old moist bread often become covered with a blue mould. This is the spore-bearing stage of mould fungi belonging to the genus *Penicillium* of which there are very many species. The spores are regularly present in the air, and if petri dishes containing sterilised nutrient jelly (*e.g.* malt agar) are exposed to the air for a few minutes and then incubated at 20° C. for several days, colonies of *Penicillium* almost always develop.

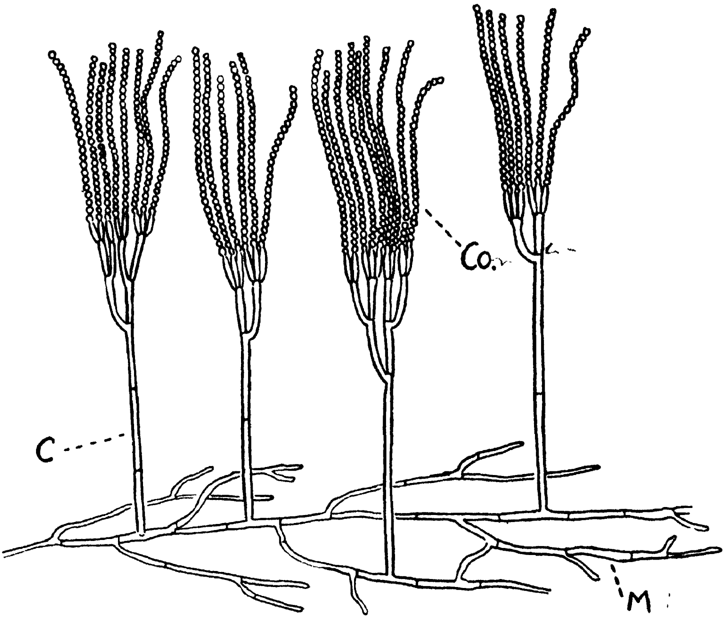

FIG. 114.—*Penicillium* sp. M, feeding mycelium; C, conidiophore; Co, conidia. × 300.

Penicillium, like *Sphærotheca*, is a member of the Ascomycetes, but the ascus-bearing stage is rarely developed and in many species is quite unknown.

The mycelium is branched and septate and ramifies in the nutrient substratum. From this mycelium erect aërial spore-bearing structures (*conidiophores*) arise (Fig. 114). These are unbranched near the base, but branch repeatedly towards their free end. From the terminal cells chains of minute spherical spores (*conidia*) are produced.

A single spore-producing cell is known as a *phialide*. From the end of this a conidium is produced somewhat as a bulb is blown at the end of a piece of glass tubing. When this is fully grown, it becomes divided from its phialide, and then another conidium is formed. So a chain of conidia is formed which grows longer and longer and may finally consist of dozens of spores. The conidia are dry and powdery and are easily blown away by wind.

The readiness with which *Penicillium* develops on damp organic substrata, the enormous spore-production and the ease with which the conidia are dispersed by air currents explains the omnipresence of this mould.

Penicillium is an interesting genus from many points of view. Although most species are *saprophytes*, a few may behave as unspecialised parasites. Thus *P. italicum* causes a soft-rot of citrus fruits in storage and is very frequently seen on oranges and lemons. Other species are used in the ripening of special cheeses (*e.g. P. roqueforti* and *P. camemberti*). However, the species of greatest human importance is *P. notatum*. Fleming in 1929 discovered that this fungus growing on nutrient jelly inhibited the development of certain bacteria in a broad zone around it. The specific substance involved is the antibiotic penicillin, which has the remarkable property of checking the development of many pathogenic bacteria whilst at the same time being harmless to man and other animals. Penicillin is a by-product of metabolism that is produced in the medium in which the mould is growing.

XANTHORIA PARIETINA (A LICHEN)

A very large group of Ascomycetes have their ascus-fruits in the form of an open cup, or even a flat, shield-like disc (*apothecium*). These constitute the Discomycetes. The inside of the cup or the free surface of the disc is coated by the *hymenium*, a name applied in descriptions of the higher Fungi to the layer of spore-producing cells. In the case of Discomycetes the hymenium is made up of a large number of vertical asci, with sterile hairs—the paraphyses—between them.

This particular fungus is a true Discomycetous Fungus, like *Aleuria*, as regards its fructification, but it belongs to a set of plants which are so different in habit and mode of life from all other Fungi, that they are sometimes treated as a distinct class of the Vegetable Kingdom. These are the *Lichens*, plants with a definite and often conspicuous thallus, freely exposed to the air and light, very different from the merely filamentous mycelium of ordinary Fungi, which is usually immersed in the substratum. Some Lichens grow on the bark of trees, some on rocks, walls, or roofs, and others on the ground.

1. STRUCTURE AND MODE OF LIFE

Our example, *Xanthoria parietina*, is extremely common (especially near the sea) on rocks, old walls, and roofs in the country, where it forms a conspicuous and most beautiful object, owing to its brilliant orange colour. The smoky atmosphere of towns, however, is very deleterious to Lichens. We see at once, from the habitat of the plant, that its mode of nutrition must be totally different from that of a typical Fungus. So far from requiring any organic matter, living or dead, on which to feed, *Xanthoria* grows on the most barren and unpromising substratum conceivable. Many Lichens, in fact, thrive for years and even centuries under conditions of drought and apparent starvation, which would be absolutely intolerable to any other plants whatsoever. A Lichen, considered as a whole, is neither a parasite nor a saprophyte; it requires nothing but water and a little mineral food, and can provide itself with carbon from the carbon dioxide of the air, like an ordinary green plant. Lichens therefore can live only in the light, which is not the case with Fungi. We will now proceed to describe the structure of *Xanthoria*, and find out the explanation of its remarkable mode of life.

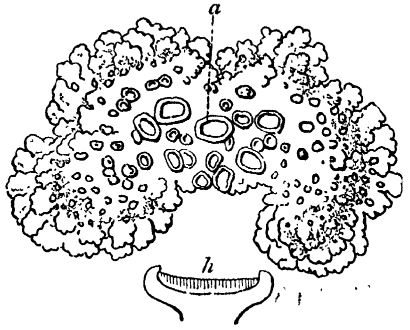

FIG. 115.—*Xanthoria parietina*; thallus seen from above. *a*, apothecia, of which the ripest are near the middle. Natural size. *h*, section of apothecium, showing the hymenium. Magnified about 5. (After Lauder Lindsay.)

Xanthoria parietina is described as a foliaceous Lichen because its thallus has a flat, much lobed, leaf-like form (Fig. 115). New lobes of the thallus arise from just below the tip or growing portion of an older lobe, and grow outwards and upwards. The under surface, which is almost white, is attached to the substratum by means of tufts of hyphæ (rhizines) which perform the functions of absorption and anchorage.

The anatomical structure of the thallus is shown in vertical longitudinal section in Fig. 116. Towards the upper surface is a dense layer of hyphæ forming closely packed cells at right angles to the surface, with some dead cells on the exterior bearing yellow grains of ***parietin*** on their outer walls. This tissue is termed ***pseudoparenchymatous*** because it is formed from closely interwoven hyphæ, and not as in parenchyma.

The orange colour is due to crystalline granules of parietin deposited outside the cells, both on the free surface of the thallus and between the hyphæ. The amount of parietin present varies with the light intensity. Such organic pigments as parietin are common in Lichens, and from some of these organisms *litmus* (used in testing for acids and alkalies) is obtained.

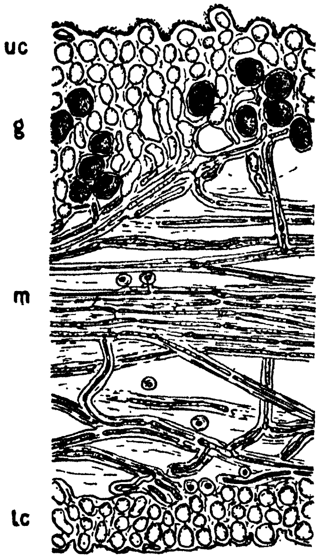

FIG. 116.—*Xanthoria parietina.* Vertical longitudinal section of mature thallus. *u.c*, upper cortex; *g*, gonidia; *m*, medulla; *l.c*, lower cortex. Magnified 300. (O. V. Darbishire.)

Underneath the dense upper cortex comes the *medulla*, a broad zone of hyphæ with large air spaces between them in certain regions. In the centre of the medulla the hyphæ run longitudinally through the thallus, forming anastomosing strands, but in other parts of the medulla scattered hyphæ run in all directions.

Below the medulla is the lower cortical layer, resembling that on the upper surface and arising from which are the rhizines. The latter develop as contiguous outgrowths from the cortical hyphæ. The extremities of the rhizines broaden out and form flat discs, which secrete mucilage and attach themselves firmly to the substratum.

In the lower part of the upper cortex, and forming a more or less definite layer, are groups of large green cells embedded amongst the hyphæ. The green cells of Lichens bear the name of *gonidia*, and the part of the thallus containing them may be distinguished as the gonidial layer. The gonidia of *Xanthoria* each contain a large, more or less lobed chloroplast with a central pyrenoid, and a nucleus. The gonidia reproduce themselves by divisions of the protoplast into a considerable number of separate cells (Fig. 117), which becomes free when the wall of the mother-cell breaks down. Small suckers or haustoria penetrate the gonidia from the surrounding hyphæ and absorb food from them.

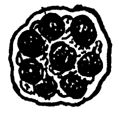

FIG. 117.—*Xanthoria parietina.* Gonidium showing mode of division. Magnified 600. (O.V.Darbishire.)

Now the most important question as to the thallus of a Lichen concerns the nature of the green cells, or gonidia. They play an essential part in the economy of the plant, for, like other chlorophyll-containing cells, they are able to assimilate carbon from the carbon dioxide of the air or from the carbon dioxide produced by the respiration of the Fungus.

For a long time, in fact down to about the year 1868, the gonidia were regarded as forming, like the hyphæ, a constituent part of the thallus. So long as that view remained undisturbed, the Lichens were rightly ranked as a distinct Class, equivalent to the Algæ or the Fungi, and in some respects intermediate between them. It is now proved conclusively that the gonidia do not belong to the same plant with the hyphæ, but that they are distinct organisms, referable to definite genera of the Algæ. Hence a Lichen is in reality a *compound organism*, made up of two totally different plants, an Alga and a Fungus, living in the closest association.

The evidence on which this striking conclusion is based is of various kinds. In the first place, the so-called "gonidia" of Lichens are always found to agree exactly with certain species of the lower Algæ, which are also well known in a free and independent condition. Thus in our type *Xanthoria parietina*, the algal constituent is *Cystococcus humicola*, a unicellular form nearly related to *Pleurococcus*. Further, the "gonidia" have been isolated from the Lichen-thallus, and are then able to lead a perfectly independent life, growing and multiplying on their own account, just like their fellows which have never been in bondage.

Some lichens have been synthesised by building up a new plant out of the Fungus and its appropriate Alga. This has been observed in the case of our type, and Fig. 118 represents the process. The ascospores of the *Xanthoria* have been sown among the cells of the Alga, *Cystococcus*. The spore on germination sends out a hypha, which at once begins to branch, and its finer ramifications attach themselves closely to the algal cells (Fig. 118, A). As growth proceeds, more and more of the algal colony becomes involved in the web of hyphæ arising from the fungal spore, and one after another the *Cystococcus* cells are seized upon by the suckers of the Fungus (Fig. 118, B). Soon the filaments of the Fungus, well fed at the expense of the Alga, are strong enough to build up a thallus. In the middle of Fig. 118 the hyphæ are seen uniting to form a network. If the ascospores of *X. parietina* are sown alone on a nutritive medium the Fungus grows to the extent of forming a rudimentary cortex, but no parietin is produced. If, however, such a culture is then brought into contact with the gonidia, parietin is formed. This indicates the great influence which the gonidia have upon the Fungus.

Observations such as these have removed all doubt as to the compound nature of the organisms called Lichens. What, then, is the real relation between the Alga and the Fungus of which the Lichen is built up? It might be supposed that the case is one simply of parasitism, the Alga playing the part of a mere victim to the Fungus. This does not, however, seem to be the real condition of affairs. The Alga is not, on the whole, injured when the Fungus annexes it. A few of the algal cells may be exhausted and die, but the great majority live and go on multiplying within the Lichen, quite as happily as if living at liberty in the open air. It seems that there are advantages on both sides; the Alga, by the aid of its green chloroplasts, undertakes the whole duty of the assimilation of carbon, thus providing the Fungus with the organic food which it is unable to manufacture for itself. On the other hand, the rhizines of the fungal partner supply water and mineral food, probably in a more effectual way than the Alga could obtain them for itself. At the same time the tissues of the Fungus shelter the Alga and protect it from the weather, and especially from the effects of drought and intense light. It is probable that many unicellular Algæ, when enclosed in the thallus of a Lichen, are able to exist, perhaps for centuries, in places, as, for example, on the surface of exposed rocks, where they could not possibly carry on their life if left to themselves.

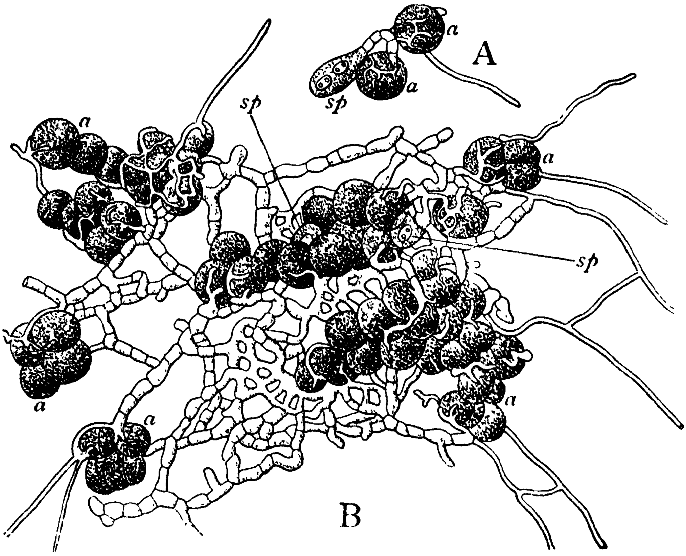

Fig. 118.—*Xanthoria parietina*; building up of the Lichen out of the Alga and Fungus. A, germinating ascospore (*sp*); the hyphæ have seized upon two cells (*a*, *a*) of *Cystococcus humicola*. B, more advanced stage; *sp*, *sp*, ascospores which have produced a web of hyphæ, enveloping the *Cystococcus* cells (*a*, *a*) in every direction. Magnified about 400. (After Bonnier.)

Such a relation between two organisms which live in common, and perform certain functions each to the good of the other, is known by the name of *symbiosis*, or *commensalism*, the former word simply calling attention to their living in union, while the latter term means that they share the same table, implying that they mutually help each other to food.

2. REPRODUCTION

The Lichens being, as we have seen, compound organisms, might be described either under the heading "Algæ" or "Fungi." It is usual, however, to take them with the latter class, because the organs of fructification, on which classification is chiefly based, belong entirely to the fungal partner. The captive Algæ go on increasing by division, but rarely produce any characteristic reproductive organs, so long as they form part of the Lichen. Nearly all Lichen-Fungi are Ascomycetes, and the majority belong to the group Discomycetes, in which the hymenium is exposed when mature. So far as the fructification is concerned, there is no essential difference between Lichens and other Fungi of the same group, which lead an ordinary parasitic or saprophytic existence.

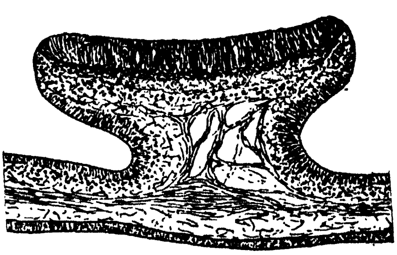

FIG. 119. — *Xanthoria parietina.* Vertical section through a young apothecium. Magnified 50. (O. V. Darbishire.)

The ascus-fruits of *Xanthoria parietina* are conspicuous to the naked eye as flat discs on the upper surface of the thallus, generally of a rather deeper orange colour than the rest of the plant (see Fig. 115). These open fruits of the Discomycetes bear the name of *apothecia.* In the mature condition there is a rim of sterile tissue at the edge of the apothecium, the whole disc within this rim being covered by the hymenium. Below the hymenium is a dense mass of closely interwoven hyphæ forming the *hypothecium.* The hymenium itself consists of elements of two kinds—the asci and the paraphyses. The asci, of which a great number are present in each fruit, are stout, club-shaped cells set vertically to the surface of the apothecium, each ascus when ripe containing eight ascospores. The paraphyses are sterile hairs rising to a greater height than the asci, both being closely packed together, so that the hymenium has a smooth, continuous surface (see Figs. 115 and 119).

At an earlier stage of development the apothecium is closed, and consists of a mass of hyphæ surrounded by a cortical layer. The paraphyses which arise from the hypothecium are the first elements of the hymenium to be developed. The asci, which in many cases have been observed to arise from the branches of distinct hyphæ, differing from those which produce the paraphyses, are developed relatively late. They grow up among the paraphyses, insinuating themselves between them until they attain nearly the same height. At the same time the envelope of the fruit is opened at the apex, and the edges gradually pushed back as the apothecium expands.

The development of the apothecium may go on for a very long time, even for years in some cases, new asci arising towards the exterior margin. Each ascus at a certain stage of development contains a single nucleus (the product of a fusion), which subsequently undergoes repeated division, into two, four, and eight. When the full number is attained, a cell is formed around each nucleus, and these cells become the eight ascospores (Fig. 120).

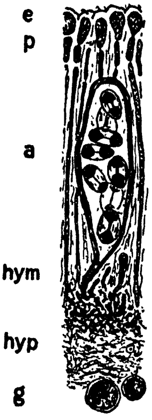

FIG. 120.—*Xanthoria parietina*. Vertical section through a mature ascus, etc. *e*, epithecium; *p*, paraphyses; *a*, ascus with ascospores; *hym*, hymenium; *hyp*, hypothecium; *g*, gonidia. Magnified 300. (O. V. Darbishire.)

The ascospores of *Xanthoria*, we have seen, can only complete their germination under natural conditions and form a new Lichen-thallus if they come into contact with the cells of *Cystococcus*, with which they can enter into partnership. The same applies to all Lichens, each containing a particular Alga.

SACCHAROMYCES

Saccharomyces, or Yeast, is a very simple type of fungus which belongs to the Ascomycetes, although its relationships to other members of the group are somewhat obscure. The genus *Saccharomyces* is a large one, but the species are only distinguishable from one another with great difficulty.

Yeasts occur naturally in the sugary exudate so often present on the surface of fruits, *e.g.* grapes and apples, and on other plant tissues. Some forms have been "domesticated," notably those used in the manufacture of beer and in bread-making. Yeast cells are small and are readily carried about by wind. When seen in mass, yeast cells are usually white or brownish white, but some species are pink or otherwise coloured.

If a small portion of Baker's Yeast (*Saccharomyces cerevisecæ*) is mounted in water and examined under the microscope, it will be seen to consist of innumerable hyaline, spherical or oval cells, about 5–10 μ in diameter (Fig. 121, A). In the middle of each cell is a vacuole and to one side of this a granule which is visible only after staining. The interpretation of these structures has been much disputed. Some consider that the granule is the nucleus, others that the vacuole corresponds to most of the nucleus and that the granule is merely the nucleolus. The rest of the cell is filled with cytoplasm containing granules of reserve food, including glycogen, a substance allied to starch which is commonly found in Fungi.

If yeast cells are kept in a nutritive solution they reproduce themselves rapidly by a peculiar process known as *budding*. In this, a cell gives rise to a small protuberance or bud, which gradually grows until the bud is nearly as large as the mother-cell (Fig. 121, A.). The bud then becomes separated from the mother-cell, and the process may be repeated indefinitely. Sometimes, however, the first bud proliferates again before abstriction from the mother-cell, and the second or third buds may behave similarly, so that considerable colonies of cells loosely joined together may be seen. Sooner or later, however, the colonies break asunder into their constituent cells. At the commencement of budding, the nucleus divides into two, one of the daughter nuclei passing into the bud. In most yeasts hyphæ are never formed, but in some of them the cells may either grow out into short hyphæ, or produce buds.

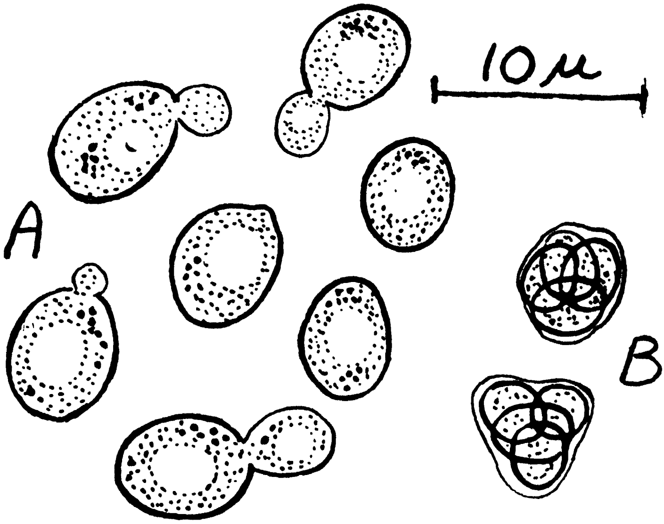

FIG. 121.—*Saccharomyces cerevisecæ* (Yeast). A, vegetative cells some of which are budding. B, two cells in which endospores (ascospores) have formed.

In many yeasts "budding" is the only form of reproduction. In some, however, spores are formed under certain conditions. In the laboratory spore-formation can be induced by various means such as sudden starvation following a period of growth in a rich food solution. In the process of spore formation the protoplasm divides, usually into four portions, each of which becomes surrounded with a wall (Fig. 121, B).

In the past twenty years much has been learned concerning the life-cycles of yeasts, the pioneer in this subject being the Danish botanist, Winge. It has been established that most yeasts are diploid, meiosis occurring in the ascus so that the ascospores, usually four in number, are haploid. If a single ascospore is isolated from an ascus and planted on a nutrient medium, it buds to give rise to a colony of small haplophase cells. Most strains of yeast seem to be more or less heterothallic, two spores in the ascus being of one mating type (+) and two of the other (—). Union occurs between a (+) and a (—) haplophase cell and from the fusion-cell there buds off a relatively large diplophase cell which continues to bud and eventually gives a diplophase colony (Fig. 122). Any diplophase cell may become an ascus under appropriate conditions. Sometimes union occurs between two haplophase cells of the same mating type to initiate the diplophase and this is of regular occurrence in some strains of *Saccharomyces*.

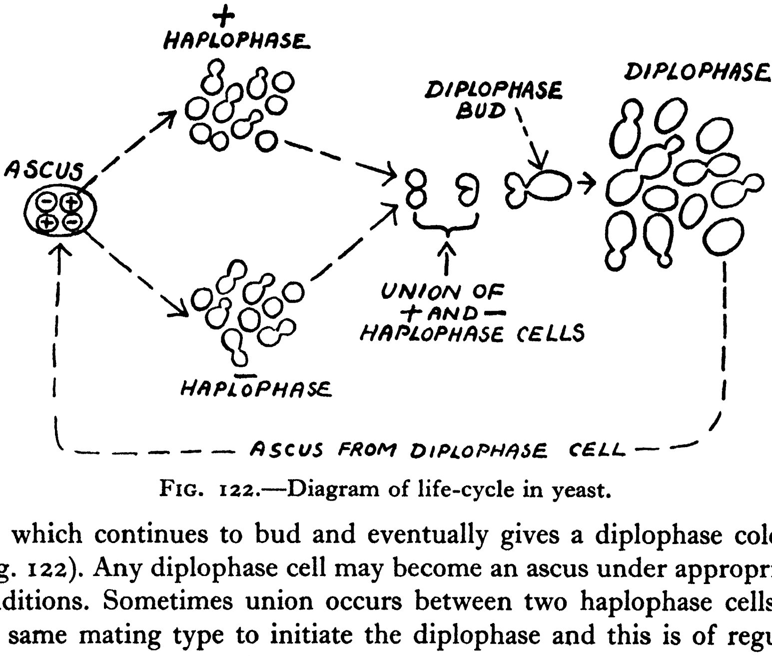

FIG. 122.—Diagram of life-cycle in yeast.

Yeasts grow best in a solution of glucose containing in addition the necessary mineral salts. When supplied with free oxygen, yeast respires partly in the usual way, but it also liberates carbon dioxide as the result of the decomposition of glucose without oxygen, alcohol being formed at the same time as follows:

$$C_6H_{12}O_6 \rightarrow 2CO_2 + 2C_2H_5OH.$$

As with normal respiration this process results in the liberation of energy which is utilised for carrying out other vital activities. In the absence of oxygen, yeast can decompose glucose into carbon dioxide and alcohol. When the alcohol reaches a certain concentration, the yeast ceases to grow. The giving off of large quantities of carbon dioxide by yeast in the complete or partial absence of free oxygen is known as *fermentation*, and the alcoholic fermentation of sugar by yeast is the best known process of this kind. Many other micro-organisms, especially certain bacteria, ferment organic compounds, and gases, other than carbon dioxide, and substances, other than alcohol, are often produced in these fermentation processes.

It has been shown that the decomposition of glucose into carbon dioxide and alcohol by yeast is due to the enzyme, *zymase*, contained in its cells. By pounding up yeast cells the zymase can be extracted from the protoplasm, and it will then decompose glucose precisely as the living yeast does. Zymase is not, however, a single enzyme. The breakdown of glucose to carbon dioxide and alcohol is not achieved in a single step. There are in fact about half a dozen stages each catalysed by its own particular enzyme. The name zymase is applied to this whole collection of enzymes. The yeast cell contains many other enzymes besides zymase. If yeast is grown in a solution of cane sugar (sucrose) the enzyme *invertase* first transforms the sucrose into fructose and glucose before the latter is decomposed by zymase. The metabolism of yeast is extremely complicated, and only an outline of it has been presented. In particular it should be borne in mind that small quantities of several other substances besides alcohol are formed during the growth of yeast, these depending upon the particular kind of yeast and upon the constitution of the nutritive medium.

In brewing beer, wort, an aqueous infusion of germinated barley grains (malt) is fermented by yeast. Sometimes the yeast is added in the form of a pure culture of a known variety in order to prevent adverse developments in the beer, which may be caused by the inclusion of wild yeasts. When the barley grains germinate, the enzyme *diastase* in them converts the starch into sugar, so that there is a large quantity of this substance in the wort for the growth of the yeast. Hops are added to the wort during brewing to flavour the beer and to prevent the development of harmful bacteria which might convert the alcohol into acetic acid. In making cider, the juice is extracted from apples by pressure and is fermented by yeasts present on the surface of the fruits or in the air. Wine is similarly made by the spontaneous fermentation of grape juice. Yeast also plays an important part in bread-making, causing it to "rise" and thereby increasing its palatability. In making bread a special kind of yeast, called Baker's Yeast, is used. This is produced on a large scale by the fermentation industries, and is pressed together into blocks for convenient handling. The baker incorporates some of this yeast with the dough, which is kept warm for some hours to promote the rapid growth of the yeast. There are small quantities of sugar in the dough produced by the action of diastase on the starch in the flour. The yeast ferments the sugar, and the bubbles of carbon dioxide cause the dough to rise and the bread to become porous. When the dough is baked, the bubbles of carbon dioxide burst and the gas is dissipated as well as the alcohol formed during the fermentation.

C. BASIDIOMYCETES

This big group includes most of the larger fungi such as toadstools, bracket fungi, puff-balls as well as certain important obligate parasites, especially rusts and smuts. The mycelium is branched and septate. Reproduction is typically by *basidiospores* which are borne externally on a special structure called a *basidium.* This begins as a cell with two haploid nuclei. These proceed to fuse, but fusion is immediately followed by meiosis so that four haploid nuclei are present. Up to this point the development of the basidium is in agreement with that of the ascus. Now, however, the basidium produces four fine tubular projections (*sterigmata*) each of which swells at its end to form a basidiospore rather as a glass bulb is blown at the end of a piece of glass tubing. Into each of these spores a nucleus passes by way of the sterigma, leaving the basidium devoid of nuclei. In the majority of Basidiomycetes the mature spore is violently discharged from its sterigma to a distance of 0·1–0·5 mm.

THE MUSHROOM (*Psalliota campestris*)

The Mushroom, which to most people is the best known of all Fungi, represents a group of great extent, including more than ten thousand species. The Mushroom and its near allies (most of which are commonly called "Toadstools") are among the most highly organised of the Fungi. Gill-bearing fungi including "Toadstools" and Mushrooms are conveniently referred to as agarics. What is known in ordinary language as the Mushroom is simply the fructification, for the mycelium is very inconspicuous, and remains hidden in the soil. The "mushroom spawn" of gardeners, from which the Fungus is often grown, consists of blocks of richly manured soil permeated with the mycelium or a pure culture of the organism on a nutritive medium.

The vegetative structure is simple enough, the mycelium consisting of long, branched, multicellular hyphæ, which traverse the soil in every direction. The individual hyphæ are usually not isolated, but woven together into strands. Fusions of the cells are very common, and take place both between neighbouring cells of the same hyphæ and between those of adjacent hyphæ. Each cell of the mycelium contains numerous small nuclei in its cytoplasm. This is, however, an unusual feature in agarics, in most of which each cell of the mycelium contains two nuclei.

The matured fructification consists of a thick stalk (*stipe*) swollen at the base, supporting a hat-like expansion (*pileus*), on the under-side of which are an immense number of radiating *gills* or *lamellæ*, pink when young, but purplish black when mature. If we pull up a Mushroom entire we can see, hanging on to the base of the stalk, remains of the strands of mycelium from which it arose. In Fig. 123, *A*, is shown a large piece of the mycelium made up of the thick branched bundles of hyphæ, and bearing a number of young fructifications.

The fruit-body itself, like every other fungal organ, is entirely built up of hyphæ. In the stalk these filaments are closely packed towards the outside, forming an apparently parenchymatous cortex. Towards the middle they are more loosely arranged, so that the separate strands are easily distinguished, and large air-spaces are left between them. The multinucleate cells of which the hyphæ are composed communicate with each other by means of pits, one of which is present in the middle of each transverse wall.

On the stalk of a ripe Mushroom, rather more than half-way up, is a membranous ring, formed of the remains of a veil, which at an earlier stage covered in the lower surface of the pileus, as shown in Fig. 123, *E* and *F*.

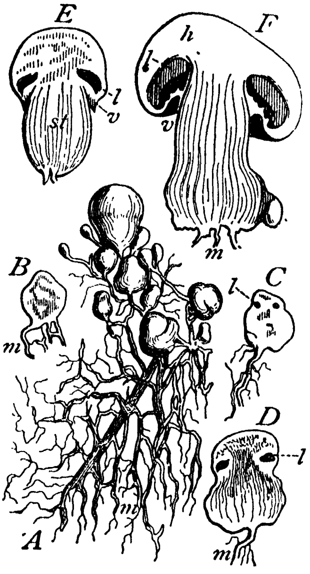

FIG. 123.—Development of a Mushroom. *A*, mycelium (*m*) giving rise to a number of young fructifications. *B*, very young mushroom in section; *m*, mycelium. *C*, slightly older; *l*, the gills just appearing. *D*, still older; *l*, gills; *m*, mycelium. *E*, older again; *l*, gills; *v*, veil; *st*, stipe. *F*, nearly ripe; *h*, pileus; other letters as before. Reduced. (After Sachs.)

The tissue of the pileus is like that of the stalk, but rather denser. The gills on the under-surface are formed by an extension of the hyphæ of the pileus. If we cut a tangential section of the pileus, we see the gills or lamellæ in transverse section, and can make out their structure (see Fig. 124). The middle part of each lamella is formed of hyphæ coming down from the pileus, and following on the whole a longitudinal course, their lateral branches, however, diverging towards the two surfaces. This central tissue of the lamellà is called the *trama* (Fig. 124, *B*, *C*, *t*). Towards the free surfaces the cells of the diverging hyphæ are shorter and more closely packed, forming the *sub-hymenial layer* (*sh*), and beyond this again we come to the hymenium itself, which is thus composed of the terminal cells of the same hyhpæ which constitute the trama and sub-hymenial layer (Fig. 124). In this last part of their course the filaments have diverged from their original direction to such an extent that they now stand at right angles to the surface of the lamella.

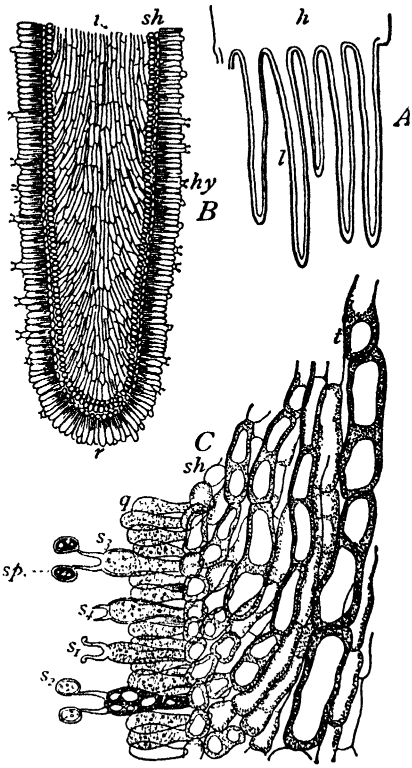

FIG. 124.—Gills of Mushroom (cultivated variety). *A*, part of tangential section of pileus (*h*), showing gills (*l*). Slightly magnified. *B*, single gill in section; *t*, trama; *sh*, sub-hymenial layer; *hy*, hymenium; *r*, lower edge of gill. Magnified about 80. *C*, part of *B* enlarged; *t*, cells of trama; *sh*, sub-hymenial layer; *q*, paraphyses and very young basidia; s_1-s_4, stages in development of basidia; *sp*, basidiospores. Magnified 230. (After Sachs.)

The hymenium consists of a palisade-like layer of club-shaped cells rich in protoplasm. A few of these are somewhat more slender than the rest, and remain sterile, bearing the name of *paraphyses.* The others are of stouter build at maturity, and are the spore-producing elements, here called *basidia.* Each basidium gives rise at its free end to four minute peg-like outgrowths (the *sterigmata*), each of which enlarges at the tip to form a *basidiospore* (see Fig. 124, *C*, *s*). The cultivated variety of Mushroom, recognised by some as a distinct species, has only two spores on each basidium, in contrast to the wild Mushroom and most other agarics in which the number is regularly four. The young spores are white then pink, but when ripe are purplish black. The basidium at an early stage possesses a single nucleus formed by the fusion of the two nuclei which it originally contained. The fused nucleus of the basidium divides into four by meiosis, and the daughter-nuclei pass into the basidiospores, one into each. In the cultivated variety two nuclei pass into each spore. If the surface of a young gill is examined it will be seen to be faintly mottled in an irregular manner, some areas being pink and others nearly white. This is due to the fact that the basidia do not develop simultaneously on all parts of the gills. In the pink zones the basidia are nearly ready to shed their spores, whereas in the paler zones the basidia are only ust beginning to form their spores. At maturity the spores are violently shot forth from the sterigmata. After spore discharge the basidia collapse, and this part of the gill again becomes pale in colour. Subsequently, the same area once more becomes pink owing to the development of another crop of basidia. At a later stage the whole of he gills become brownish or purplish black on account of a darkening of the cells in the matrix of the gills. The wave-like ripening of the basidia can be seen by examining the surface of a young gill under he microscope.

At maturity the four spores of the basidium are violently discharged

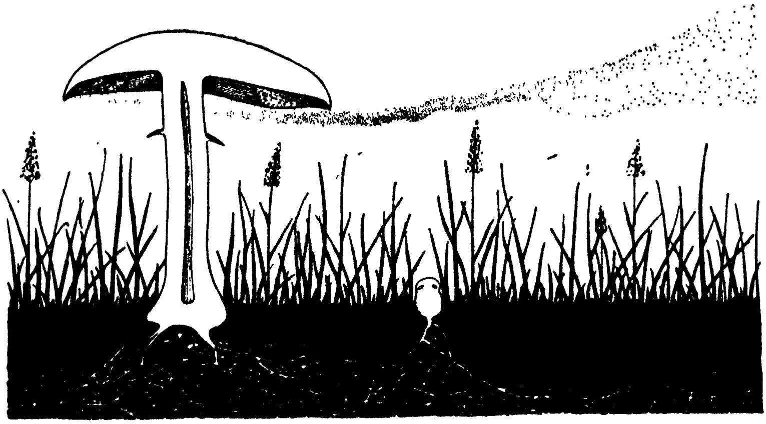

Fig. 125.—*Psalliota arvensis* (Horse mushroom). The mycelium in the soil is giving rise to sporophores: one is in the button-stage, the other is fully expanded and liberating spores which are being carried away by the wind (After Buller, 1909). Reduced.

o a distance of a tenth of a millimetre. To Buller we owe most of our knowledge of the fruit-body of an agaric as an apparatus essentially concerned with the production and efficient liberation of spores. For successful spore liberation the gills must be vertical, for if they were not the discharged sticky spores would either fall back on to the gill surface from which they came or on to the opposite gill and become permanently stuck. The stipe is negatively geotropic and so gives a rough vertical orientation to the gills that hang from the under-side of the cap. Further, by its great rigidity the stipe prevents the fruit-body from swaying in the breeze. Moreover, the stipe has another mportance in providing a space between the pileus and the ground so that the falling spores have a reasonable chance of being carried away by currents of air (Fig. 125). As well as the rough vertical adjustment of the gills by the geotropism of the stipe, there is also a fine adjustment. Each individual gill is positively geotropic and if the fruit-body is slightly disturbed so that the gills no longer are quite vertical, each undergoes growth adjustments until it is again in the vertical plane.

Near its junction with its sterigma each basidiospore has a small projection or hilum. Just before a spore is to be discharged, a droplet of fluid appears at the hilum and grows to a definite size. Then the spore is shot away carrying the drop with it, the actual mechanism of discharge being still not fully understood. Soon after the discharge of one spore of a basidium, another is shot off and so on until all four have gone. Soon afterwards the basidium withers away. The process, in a common toadstool, is illustrated in Fig. 126. It is essentially the same in all agarics.

The fruit-body of an agaric looks like an umbrella and may be said to have an umbrella's function to some extent, for the spore-bearing hymenium is protected from rain. Water destroys the hymenium at least temporarily and this protection is of real biological importance. This state of affairs may be contrasted with that in the Discomycetes (*e.g. Aleuria*) in which the hymenium of asci and paraphyses is unharmed by a film of water.

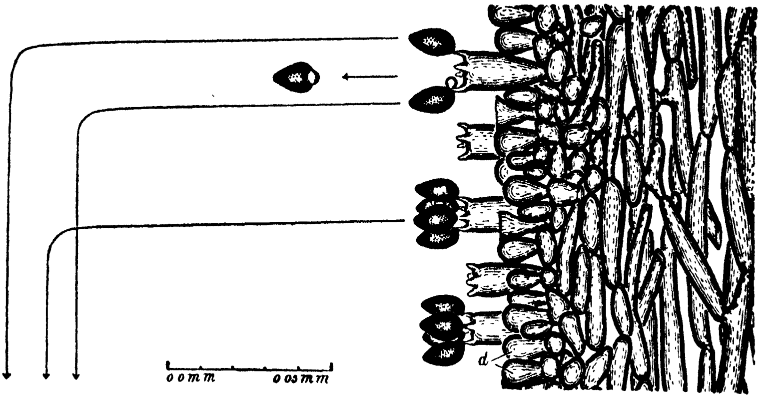

Fig. 126.—*Panæolus campanulatus*. Part of gill seen in longitudinal section showing spore discharge. Solid lines represent trajectories of discharged spores. (After Buller.)

An immense number of spores are produced from the gills of a Mushroom. Some idea of their multitude may be obtained by cutting off the pileus of a Mushroom and laying it, gills downward, on a sheet of white paper. If it be removed after a few hours an exact print of the gills will be found on the paper, in the form of a fine powdery deposit of spores which have fallen from them.

Until recently, nothing satisfactory was known as to the germination of the spores of the Mushroom. Of late years, however, Mushrooms have been successfully raised from spores; the entire development, up to the formation of ripe fructifications, takes from six to seven months. As a rule they are raised from the mycelium or "spawn."

The Mushroom is a saprophyte growing in pastures and in richly manured soil, but some of its near relations are parasitic on trees to which they do great damage. Some Toadstools are poisonous and even fatal to human beings if eaten, hence great care should be taken in the selection of mushroom-like Fungi for food.

CHAPTER V

THE BACTERIA

THE Bacteria are an extensive group of organisms of the most minute size, and, so far as we know them, of the most simple structure. Most Bacteria are unicellular. In their mode of life they bear a general resemblance to Fungi, for, though sometimes pigmented, they are destitute of chlorophyll, and as a rule adapted either to a parasitic or saprophytic existence, obtaining their carbon supplies usually from organic sources. A few coloured Bacteria can, however, photosynthesise their own organic food in a manner analagous to photosynthesis in green plants, but the pigments involved are different. Bacteria are, as we shall see, quite different from any known Fungi in structure and development, and constitute a wholly distinct class of organisms. Like the Fungi the Bacteria should probably be assigned to a separate Kingdom.

Both as parasites and as saprophytes, the Bacteria play an enormously important part in the world. Parasitic Bacteria are now known to be the cause of very many of the infectious diseases of man and animals, *e.g.* tuberculosis and cholera, and in many cases the actual species to which the different diseases are due have been strictly determined. Other Bacteria cause important plant diseases although Fungi are much more important in this connection. As saprophytes, Bacteria are the great agents of decay of all kinds, owing to the fact that they set up rapid and profound chemical transformations in the organic substances on which they feed. Thus when milk turns sour, or when wine is converted into vinegar, or protein substances, such as meat, undergo putrefaction, the change is in each case due to the action of a definite species of the Bacteria. On the same power of initiating far-reaching decompositions in the bodies which they inhabit, depends the fatal efficiency of the parasitic Bacteria in producing disease. The whole subject of the fermentations set up by these organisms is of the greatest possible practical importance in relation both to medicine, as regards the parasite forms, and to innumerable branches of industry, as regards the saprophytes. A new science, Bacteriology, has grown up on these subjects, which lie beyond the province of the present Introduction.

BACILLUS SUBTILIS

This is one of the commonest and best-known forms of Bacteria. It occurs constantly in hay, and can be obtained with certainty by soaking or boiling hay in water. In the latter case the appearance of the *Bacillus* depends on the extraordinary resistance to heat shown by its spores, which can stand an hour's boiling with impunity. After a little time the whole of the liquid simply swarms with the cells of the *Bacillus*, which in its active vegetative condition is a strictly unicellular organism, the isolated cells having the shape of short rods rather more than $\frac{1}{1000}$th of a millimetre ($1\ \mu$) in diameter and from $\frac{5}{1000}$ to $\frac{8}{1000}$ mm. (5–$8\ \mu$) in length. The cells are thus far more minute than those of any plant we have hitherto considered. The excessive smallness of the cells has placed great difficulties in the way of their investigation, and the cell-structure of Bacteria is still very little understood. So far as we know at present, however, this structure appears to be very simple. There is a definite membrane which, however, does not consist of cellulose, but seems to be chiefly of a protein nature. The cells move actively, and their movements are now known to be due to flagella (cilia) and are probably attached to the protoplasm and penetrate the wall (see Fig. 127, *a*, *d*). Not all Bacteria are truly motile. Many lack flagella, but, nevertheless, show rapid dancing movement when observed in water. This is because, on account of their small size, they are buffeted about by the moving water molecules. This movement, known as Brownian Movement, is also shown by minute inanimate particles when mounted in a liquid.

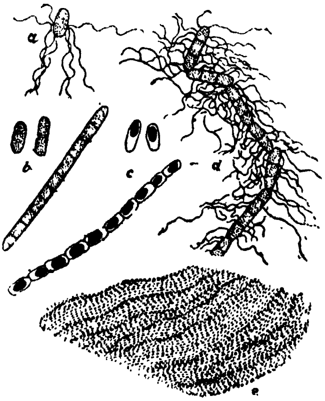

FIG. 127.—*Bacillus subtilis*. *a*, *d*, ciliated motile cell and filament; *b*, non-motile cells and filament; *e*, zoogloea, during spore-formation; *c*, cells and filament with endospores, from the zoogloea. *a*-*d*, × 1050. *e*, × 175. (After A. Fischer.)

The whole interior of the cell is occupied by protoplasm. This is differentiated into a central nucleus surrounded by cytoplasm.

For some time *B. subtilis* continues in the actively swarming condition, multiplying abundantly by the repeated transverse division of the cells. It should be emphasised that reproduction of bacteria is mainly by cell-division. A cell elongates and divides in the middle to form two daughter-cells. This process can be completed under favourable conditions in twenty minutes. The result is that at the end of an hour a single individual may have given rise to eight bacteria; at the end of two hours the number may be sixty-four; at the end of four hours over 4000; at the end of eight hours over 16,000,000. In a confined space such increase clearly cannot go on indefinitely and it soon becomes limited by shortage of food or, more usually, by accumulation of toxic by-products. However, the rapid rate of increase of bacteria is one of their outstanding features.

After some days the individuals begin to seek the surface of the liquid, where they pass into a resting condition. At this stage the cells remain connected together in long filaments, and their outer cell-walls become very gelatinous. This is called the *zooglœa* condition, and is easily recognised by the gelatinous iridescent film which the colonies of the organism form on the surface.

Lastly, the spores begin to form. This takes place when the *Bacillus* has entered the filamentous condition (see Fig. 127). The spores are *endospores*, one spore being produced in the interior of each cell. A new wall appears round a portion of the contents. The young spore absorbs the remaining protoplasm, and it becomes elliptical in form, and increases sufficiently in bulk for its walls to touch those of the mother-cell. In the meantime it has completely used up the surrounding protoplasm, and now lies within an empty membrane. The endospore itself acquires a resistant cell-wall, and is extraordinarily tenacious of life. These spores can bear being completely dried up without injury; they are little affected by poisons, and survive a very high temperature, withstanding even an hour's boiling in the case of the hay *Bacillus*. Hence spore-forming Bacteria are extremely difficult to extirpate, so that in order to make sure of effectually "sterilising" any substance (*i.e.* destroying any living things which it contains) it is often necessary to expose it to a temperature considerably above the boiling-point of water, or, if that be impracticable, at least to continue boiling for some hours. Aqueous solutions are normally sterilised in a pressure cooker (autoclave) at 125° C. for 20 minutes or by boiling for some minutes on three successive days.

The spores germinate when brought into a suitable food-solution at an appropriate temperature. The outer membrane splits across, and the entire contents escape as an ordinary bacterial cell, which at once begins to move about by means of flagella (see Fig. 127, *a*).

Fig. 128 shows very completely the stages in the formation and germination of the spores in another *Bacillus*, called *B. megatherium*, because for one of the Bacteria it is quite a monster, though its cells are only about $\frac{1}{400}$th of a millimetre ($2{\cdot}5\ \mu$) in diameter. This species was originally found in boiled cabbages, and was afterwards cultivated by its discoverer in solutions of glucose, to which a little extract of meat had been added. The formation of endospores characterises one great group of Bacteria, and distinguishes them from similar unicellular organisms. Many other Bacteria, however, are devoid of spores.

Bacillus subtilis, like most other living things, requires plenty of atmospheric oxygen in order to flourish. Some of the other Bacteria, owever, have the remarkable peculiarity that they thrive best in the *bsence* of free oxygen. This is the case, for example, with *Clostridium utyricum*, the organism to which the formation of butyric acid by the ermentation of sugar is due.

It may be mentioned here that numerous experiments have proved hat bright light has a very unfavourable effect on Bacteria, completely topping their growth and multiplication in many cases, and even, hen intense enough, killing the cells outright. It is the rays towards he violet end of the spectrum and he ultra-violet rays which exercise he greatest retarding effect on the rowth of these organisms. The ction of light in checking the inrease of these agents of decomosition and disease is evidently a act of great practical importance.

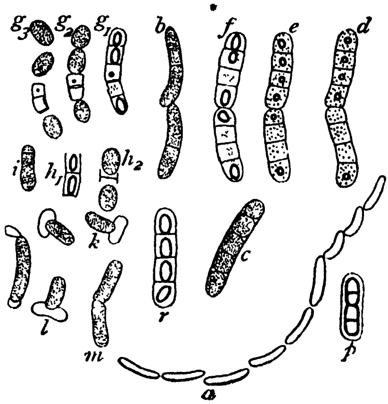

FIG. 128.—*Bacillus megatherium*. *a*, chain of vegetative rods, each consisting of two or more cells, but septa not shown. Magnified 250. *p*, four-celled rod, after treatment with alcoholic solution of iodine; *b*, vegetative rods; *c-f*, rods, showing the formation of endospores; *r*, four-celled rod with ripe spores; g_1-g_3 and h_1, h_2, spores swelling before germination; the mother cell-walls disappear; *k-m*, germination of spores. All figures except *a* magnified 600. (After De Bary.)

Plants of the Pea and Bean kind, nlike ordinary green plants, are ble, by the help of certain bacterial ompanions, to obtain their nitroenous food from the free nitrogen f the atmosphere. The plants in uestion, including most if not ll of our native Leguminosæ, inariably have swellings or tubercles n their roots. These tubercles are nhabited by a symbiotic bacterium, he entrance of which into the oot is the cause of the first fornation of the tubercle. It has been roved conclusively that it is only vhen this organism is present in he soil that the tubercles develop on the roots, and only when the ubercles are formed that free nitrogen can be assimilated. If the plants re grown in sterilised soil, *i.e.* soil which has been heated sufficiently o kill all living things contained in it, then no tubercles develop, and o nitrogen is absorbed from the air. When the tubercles are present, owever, nitrogen is assimilated, and the plant can thrive even if itrogenous compounds be quite absent from the soil. A very important esult of this fact is that leguminous crops actually enrich the soil in itrogen. Clover is often grown before wheat in the farm rotation of rops. The remains of the clover on being ploughed into the soil enrich t in nitrogen for the growth of the wheat.

The subject is mentioned here because the organism to which this assimilation of gaseous nitrogen is due is a bacterium named *Rhizobium leguminosarum*. Moreover, the relation of this organism to its leguminous host seems to be one of symbiosis, or mutual service rather than of one-sided parasitism, for the bacterium obtains its supplies of carbon from the green plant and, as it were, in return provides its host with nitrogenous food.

R. leguminosarum is only one of many kinds of Bacteria that play an essential part in the circulation of nitrogen in Nature. Many Bacteria convert proteins and other organic nitrogenous substances such as urea into ammonium compounds, which other soil Bacteria (the nitrifying Bacteria) change first into nitrites and then into nitrates. These nitrifying Bacteria have the remarkable property of assimilating carbon dioxide, although devoid of chlorophyll. This is done with the aid of the energy liberated in the process of oxidation that leads to the formation of nitrites and nitrates. Still other soil Bacteria utilise atmospheric nitrogen in their own metabolism, and in this way add to the reserve of nitrogen in the soil available to higher plants. It is not too much to say that green plants are ultimately dependent on Bacteria for their nitrogen, for, in general, green plants absorb nitrogen from the soil in the form of nitrates or sometimes ammonium compounds. Without these Bacteria, green plants would cease to exist.

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