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FLOWERLESS PLANTS

PART II. OF AN INTRODUCTION TO STRUCTURAL BOTANY

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"STUDIES IN FOSSIL BOTANY" "THE EVOLUTION OF PLANTS"
"EXTINCT PLANTS AND PROBLEMS OF EVOLUTION" ETC.

AND

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ELEVENTH EDITION
WITH 131 ILLUSTRATIONS
AND A GLOSSARY

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PREFACE TO THE ELEVENTH EDITION

THE present edition has again been thoroughly revised in the light of recent research. In addition, and at the request of several botanical teachers, an account of *Lycopodium Selago* has been included as an Appendix.

I am grateful to Professor F. E. Fritsch, Professor T. G. Hill, Dr. P. W. Richards and Dr. W. J. Dowson for many valuable suggestions. To the last-named I am also indebted for Figs. 120–123.

F. T. BROOKS.

BOTANY SCHOOL
CAMBRIDGE
November 1942

PREFACE TO THE TENTH EDITION

HAVING assisted in the revision of the last edition of *Structural Botany*, Part I., Dr. D. H. Scott requested me to re-edit *Structural Botany*, Part II.

In consultation with him it was decided to introduce certain new types in the present edition, namely, *Peronospora parasitica*, *Saccharomyces*, and *Euglena viridis*, and to exclude *Cladothrix dichotoma*.

Since the Ninth Edition of this book was prepared, a good deal of research has been done in connection with some of the types of Algæ and Fungi described therein,

notably on *Ulothrix zonata*, on the life-history of *Ectocarpus siliculosus*, on the function of the spermatia of *Puccinia graminis*, and on the organisation of the hymenium of the Mushroom. As far as possible the results of these recent investigations have been incorporated; further information about the general biology of Fungi and Bacteria has also been included.

In preparing this new edition I have been greatly assisted by botanical friends. Professor F. E. Fritsch and Dr. Margery Knight have spent much time and trouble in giving me the benefit of their wide knowledge of the Algæ. Professor O. V. Darbishire has made valuable suggestions concerning the structure and mode of life of the Lichen, *Xanthoria parietina*, and he has most generously provided Figs. 99, 99*, 101, 101*, and 102. To all these and to my colleague, Mr. G. E. Briggs, I offer my best thanks for help freely rendered. I am also indebted to Mr. R. W. Marsh for Figs, 95*, 104*, and 117.

For the alterations which have been made in the present edition I am wholly responsible. I have tried—imperfectly, I fear—to retain the style of the original author.

F. T. BROOKS

BOTANY SCHOOL
CAMBRIDGE
April 1932

NOTES ON RECENT EDITIONS

THE chief alterations in the Seventh Edition were the introduction of a new type, *Chlamydomonas*, and the addition of a Glossary. A new figure was also added to illustrate further the spermatozoids of *Cycas*. I was indebted to Professor Dame Helen Gwynne-Vaughan, Professor F. E. Fritsch, and Professor G. S. West for kind advice and help on various points.

In the Eighth Edition, parts of the concluding chapter were modified in so far as the sketch of the relationships between the main groups was affected by remarkable discoveries (especially those of Drs. Kidston and Lang) in the older Devonian Flora. An account of these results will be found in the third edition of *Studies in Fossil Botany*.

In the Ninth Edition the wording was altered at several places, often in order to indicate a change of view as to the affinities of the plants discussed. Greater caution in questions of descent has proved necessary. In particular, the once popular belief in the origin of the Fungi from Algæ has been given up, chiefly on the ground of arguments adduced by Mr. F. T. Brooks in his Presidential Address to the British Mycological Society, 1923.

D. H. SCOTT.

AUTHOR'S PREFACE

OWING to the immense variety of organisation among the Cryptogams, it has been necessary to describe a much larger number of types in the present volume than in Part I. While it was possible to give some idea of the main outlines of structure in Flowering Plants by the full description of three representatives, it has seemed desirable to select no less than twenty-three types for the illustration of Cryptogams, and even then many important groups have been left out. The increased number of types has involved a curtness of treatment, in most cases, which only the relative simplicity of many of the forms has rendered possible.

It is hoped, however, that the essential morphological points have been brought out, and that a certain continuity has been maintained throughout the book, so that the study of the selected examples may serve to give a connected idea—however elementary—of the great groups of plants. In order to afford a general view of the whole field, the concluding summary has been added.

When theoretical points are touched on, the great aim has been to avoid dogmatism, and, so far as space permitted, to put the reader in possession of the evidence as a whole. This applies especially to the question of

alternation of generations, as to the nature of which such different views are held.

As regards the fundamental homologies between Cryptogams and Phanerogams, an attempt has been made to demonstrate, and not merely to state them. Unless the student be taught to follow the reasoning by which such conclusions are arrived at, morphology loses at once its interest and its educational value.

It may be well to state again explicitly that the use of this book requires to be accompanied from the first commencement onwards—(1) by the study of living plants in the field, without which all botanical teaching is dull and barren ; and (2) by practical work in the laboratory.

The author is indebted to the Trustees of the British Museum for permission to make use of the cuts, reproduced in Figs. 112–116, from Mr. Arthur Lister's Monograph of the Mycetozoa. As in Part I., the figures signed R. S. have been drawn from nature by Mrs. D. H. Scott. Figs. 5 and 44 are the work of Mr. W. C. Worsdell. The source of all figures not original is acknowledged in the descriptions. Special thanks are due to Professor J. Bretland Farmer for his kind help in connection with the Liverworts and the Fucaceæ.

D. H. SCOTT.

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ecological mortality is often greatly reduced, and both curves differ only slightly. In some cases, as in that of the honey-bee, practically no mortality occurs before the bee has left the hive as field-bee. The analysis of the factors causing the difference between the curves of the physiological and the ecological life-tables is one of the main tasks of animal ecology.

A small series of life-tables based on breedings or, in the case of man, on comprehensive census work will be produced below. It should be kept in mind, however, that breedings, if carefully carried out, offer sub-optimal conditions to the animal, and are therefore apt to lower the death-rate by providing protection from enemies, diseases, and accidents, by providing suitable food, sufficient in quantity and quality, and by maintaining a comfortable temperature and humidity. We can, therefore, learn relatively little from these life-tables. But by varying certain factors separately, we may study the influence of the individual major factors on longevity.

We shall begin with Pearl's work on *Drosophila*, as it analyses the influence of a series of external factors on longevity (Fig. 1). First we compare the vitality of wild *Drosophila* and some mutants of the second chromosome, with characters which have never before been connected with other than morphological changes of minor importance.[27]

This result with mutants of a highly homozygotic strain of wild *Drosophila* gives a clear idea as to the amount of constitutional variation in longevity to be expected in any heterozygotic insect population. In different strains of wild *Drosophila* adult longevity at constant conditions varied from 26 to 54 days.[28,29]

The influence of temperature[7] is illustrated by the following figures, representing adult longevity of *Drosophila* females, under different conditions:

Temperature during adult life	*Mean duration of life of flies reared at*	
	18° C.	*28° C.*
18° C.	70·61	65·25 days
25° C.	40·96	35·75 „
28° C.	30·67	28·52 „

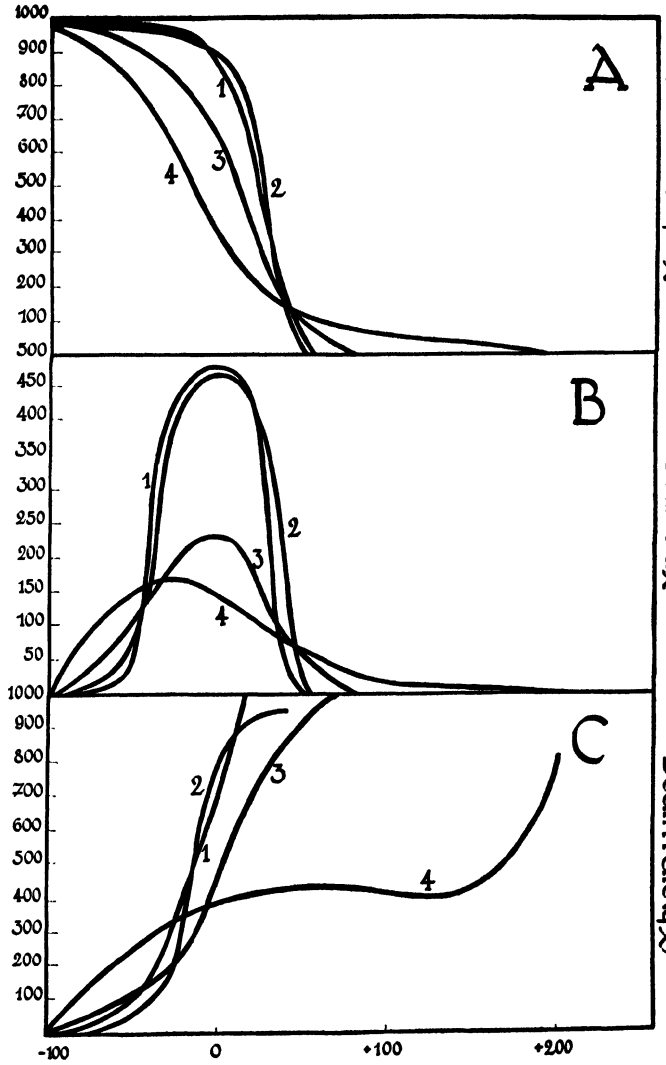


FIG. 1. Life-table curves of *Drosophila*. A. Survivorship (*lx*); B. Death curve (*dx*); C. Death rate (*qx*). The abscissa shows longevity, the mean longevity being assumed as O, all other ages being expressed as + or — percentage deviation from this mean. 1. Starved wild *Drosophila*; 2. Vestigial starved *Drosophila*; 3. Wild *Drosophila*; 4. Vestigial *Drosophila*. (After Pearl.)

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FLOWERLESS PLANTS

BEING PART II. OF

AN INTRODUCTION TO STRUCTURAL BOTANY

CHAPTER I

THE VASCULAR CRYPTOGAMS OR PTERIDOPHYTA

TYPE IV

SELAGINELLA KRAUSSIANA

Selaginella, from which our first type of Cryptogams is taken, 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 spinosa*,[1] grows in our own country, on boggy moors, or in mountainous districts. Some of the tropical species are universally grown in hothouses. Both *Selaginella* and the allied genus *Lycopodium* belong to the Class *Lycopodiales* or Club Mosses. *L. Selago* is described in the Appendix (p. 316).

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

[1] Also known as *S. spinulosa* or *S. selaginoides*.

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 therefore pass rapidly over this part of its organisation, and give most of our attention to those reproductive processes which illustrate the relation between Cryptogams and Phanerogams. 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 a creeping stem, which, however, rises a little above the surface of the ground. 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

[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.

is not the case 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.

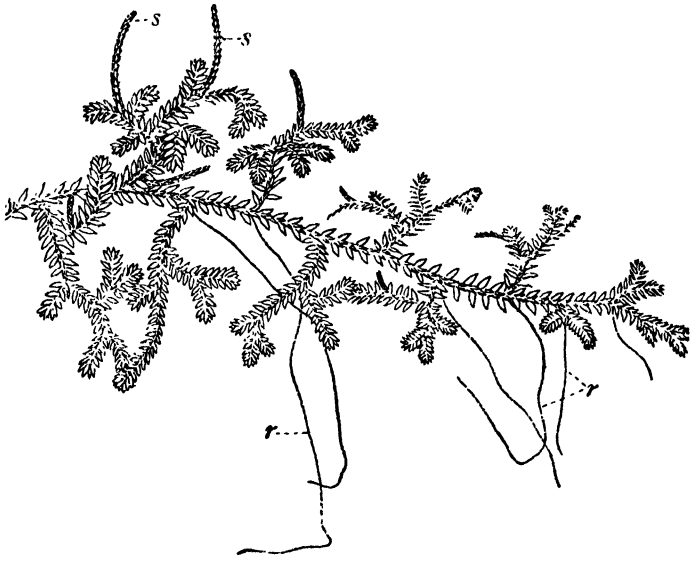


FIG. 1.—*Selaginella Kraussiana*; general view. *r*, rhizophores; *s*, spikes or cones. (Reduced.)

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*).[1]

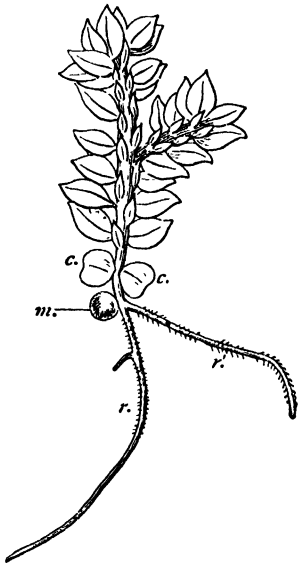


FIG. 2.—*Selaginella Kraussiana*; young plant. *m*, megaspore still in connection with plant; *c*, two cotyledons; *r*, main root; *r'*, first lateral root. Note the two kinds of leaves. Magnified 6 diameters. (R. S.)

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

[1] See *Studies in Fossil Botany*, 3rd ed.

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.

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*).

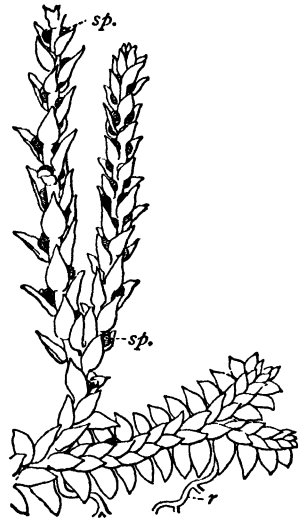


FIG. 3.—*Selaginella helvetica*, showing procumbent stem and two fertile spikes. *r*, rhizophore; *sp*, sporangia. Slightly magnified. (After Dodel-Port.)

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. spinosa*) 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 reproductive organs of a *Selaginella* plant are the *sporangia*, containing the spores. Each sporangium is a stalked sac, reaching a diameter of about a millimetre ($\frac{1}{25}$ inch), and is borne in the axil of one of the leaves of the cone (see Figs. 4 and 5).

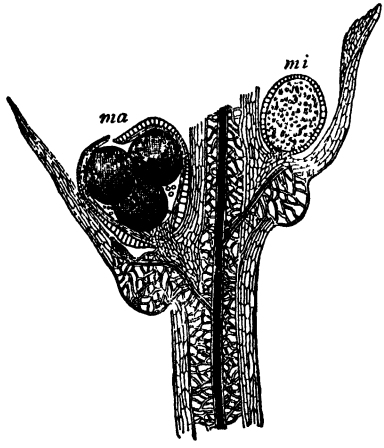


Fig. 4.—*Selaginella helvetica*; part of longitudinal section through spike, showing two sporophylls. *ma*, megasporangium dehiscing; three out of four megaspores visible; note abortive mother-cells; *mi*, microsporangium with numerous microspores. Magnified about 15 diameters. (After Dodel-Port.)

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 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,

[1] The word *spore* is applied to any single cell which becomes isolated from the parent plant for reproductive purposes; cf. Part I. Ch. I. III c.

varies in different species. The development and structure of the sporangia will be further described below.

II. *INTERNAL CHARACTERS OF THE VEGETATIVE ORGANS*

Among the Flowerless Plants we find a very great variety in characters which in the Phanerogams remain fairly constant throughout whole Classes.

This holds good especially for the internal structure. A description of the anatomy of the Wallflower was sufficient to give a fair general idea of the chief anatomical features of the Dicotyledons generally, and so it was with our other types of flowering plants. With the Cryptogams the case is quite different. Not only is the anatomy of *Selaginella* peculiar to that one genus among plants now living, but the variation of structure among the species is so great that a general description, even of the genus as a whole, is impossible. In an elementary book, we cannot enter into all these variations; we can only give a short description of two or three forms, which may serve to give some idea of the peculiarities of the genus and of the range of variation among its species.



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

a. The Stem

In each of our types of Flowering Plants we found that the stem was traversed by one central cylinder,

consisting of the vascular bundles and conjunctive tissue (see Part I. Ch. I. II B a, Ch. II. II a, Ch. IV. II a). We learnt further that the bundles of the stem are directly continuous with those of the leaves. These facts hold good, with certain exceptions, for the Phanerogams generally.

In the Selaginellas the arrangement is totally different. The number of cylinders or *steles* varies from one up to five or more, not only in different species, but sometimes even in different parts of the same plant. The conjunctive tissue is very little developed, and pith is almost always absent, the whole interior of the cylinder being occupied by a solid strand of wood. Consequently it is generally impossible to distinguish the limits of the individual vascular bundles in the stele, or, to be more accurate, the stele in the stem is not differentiated into distinct bundles. Lastly, the vascular system of the stem is not built up entirely of leaf-trace bundles. The greater part of the xylem and phloëm can be traced continuously through the whole stem, and only certain portions of the vascular tissue are directly connected with the bundles of the leaves.

It will be convenient to begin with a short description of the anatomy of our native species, *S. spinosa*, 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 structure quite different from

anything which we have previously met with in a stem. There is no pith ; the whole interior of the cylinder is occupied by solid wood, which consists 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

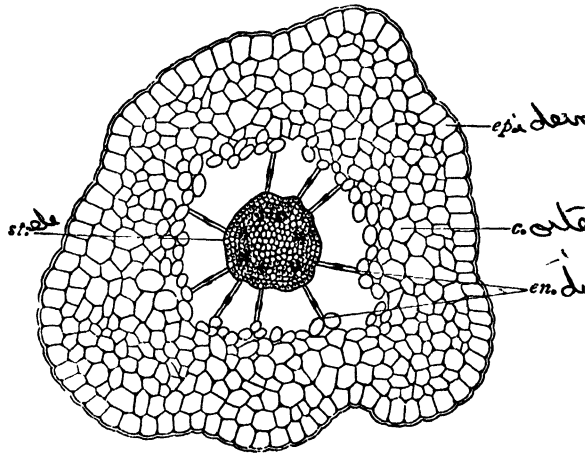


FIG. 6.—*Selaginella spinosa* ; transverse section of stem. *ep*, epidermis ; *en*, trabeculæ representing endodermis ; *c*, external cortex ; *st*, stele ; the seven dark groups are protoxylem. Magnified about 35 diameters. (After Harvey Gibson.)

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 [1] for the stems of the Selaginellas and their allies.

[1] In the trailing part of the stem of *S. spinosa* it appears that the protoxylem is central. See also p. 13.

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 cuticularised band; these cells represent the endodermis.

We see, then, that we have a vascular structure in this plant which differs from anything which we have seen before in stems, as shown by (1) the centripetal xylem; (2) the absence of pith; (3) the want of separation between the vascular bundles. 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. spinosa*, though on a much larger scale. This was the case, for example, in stems such as that of which the stump is shown in Part I., Fig. 5.

From each angle of the stele in *S. spinosa*, 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. spinosa*, have only a single vascular cylinder, or, in other words, are *monostelic*; but most commonly the single stele has a simpler structure.

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, as is usually the case. The other tracheids usually have long transverse pits, and are hence called scalariform (see Fig. 23, p. 45), 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.

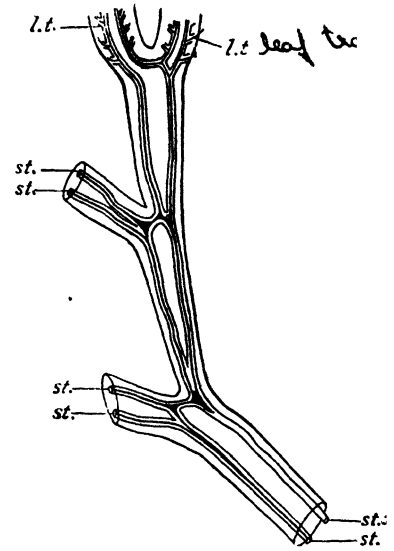


FIG. 7.—*Selaginella Kraussiana* ; diagrammatic transparent view of stem. *st*, the two steles, anastomosing at base of branches ; *l.t*, leaf-trace bundles, only shown in upper part. (After Harvey Gibson.)

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.

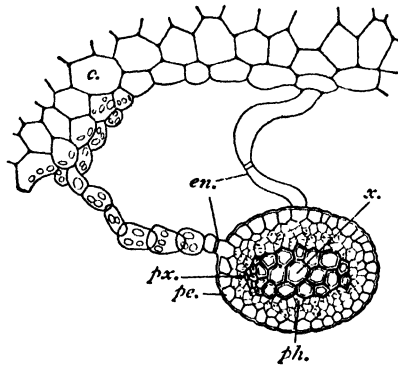


FIG. 8.—*Selaginella Kraussiana* ; part of transverse section of stem showing one stele. *x*, the wood ; *px*, protoxylem ; *ph*, phloëm ; *pe*, pericycle ; *en*, endodermal cells forming the whole or part of trabeculæ ; *c*, inner layers of cortex. Magnified about 100 diameters. (After Harvey Gibson.)

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 chlorophyll bodies 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 (p. 4 ; Figs. 10 and 16, pp. 17 and 28).

This is the simplest type of leaf that we have yet met with.

c. The Rhizophores and the Roots

These organs are generally similar to one another in structure; the rhizophores in fact may be regarded as roots which have not yet begun to form 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.

d. Growing-Points and Mode of Branching

a. The Stem

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.

The *branches* arise laterally by the growth of a group

of cells just below the apex; the main axis and its lateral branch, however, often develop so equally that the stem appears to be forked. The branching of *Selaginella* may be described as an apparent bifurcation or *dichotomy*. True dichotomy only exists when the growing-point itself is equally divided. The branches of *Selaginella*, unlike those of Flowering Plants, are not axillary.

The development of the leaves proceeds in the same way as in the Phanerogams (see Part I. Ch. I. II B e, Ch. II. II d, Ch. IV. II d *a*).

β. Rhizophores and Roots

In those species which have special rhizophores, the latter may either grow by means of an apical cell, or may have a small-celled meristem more like that of the higher plants. As soon as the rhizophore reaches the ground, roots begin to grow out at its end. The growing-points of these roots arise *endogenously, i.e.* from the interior of the tissue at the end of the rhizophore. The roots themselves, which grow by means of an apical cell, differ from most other roots in their manner of branching. The rootlets arise quite close to the growing-point, where they are only covered by the root-cap of the parent root, so that they are not really endogenous in origin like other roots, which arise beneath the cortex. This is a very rare case, and does not hold good for most other Vascular Cryptogams.

We have found great differences between *Selaginella* and the Flowering Plants, even as regards the vegetative organs. The structure of both stem and root, the apical growth, and the mode of branching are all quite distinct from anything we met with in our Phanerogamic types. These differences, however, are unimportant

compared with those which we shall find in the reproductive organs and life-history. We will now go on to describe the reproductive processes. We shall find that they at first seem quite distinct from those in Flowering Plants, but a careful comparison will enable us to see that there is, after all, a close relation between the two methods of reproduction. Among the flowerless plants *Selaginella* is one of those which in its course of development approaches most nearly to the Phanerogams. It is this fact which makes it of special interest to the student of botany.

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 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* (see Part I. Ch. I. III c, Ch. IV. III a), 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.

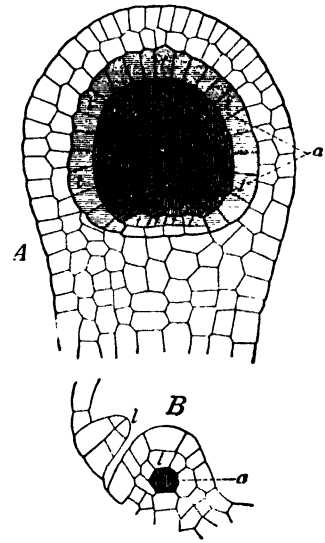


FIG. 9.—*Selaginella spinosa*. *A*, young microsporangium in longitudinal section; *t*, tapetum; *a* (darkly shaded), mass of sporogenous cells derived from archesporium. *B*, very young megasporangium; *t*, tapetum; *a*, archesporium; *l*, ligule of sporophyll. Magnified about 300 diameters. (After 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 (compare Fig. 9, *A*, with one of the four pollen-sacs shown in Fig. 39, A, in Part I. Ch. I. III c. It is also evident that in the youngest stages there is a considerable resemblance to an ovule at its first origin (cf. Fig. 9, *B*, with Fig. 44, 1 or 2, in Part I. Ch. I. III d).

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*. Each of the spore mother-cells, lying free within the cavity of the sporangium, next divides into four, the division taking place exactly in the same way as in the pollen mother-cells of Dicotyledons (see Part I. Fig. 39, B, Ch. I. III c). 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.

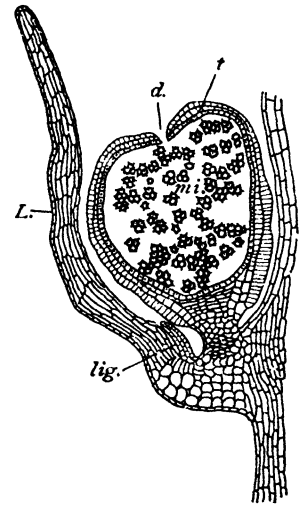


FIG. 10.—*Selaginella spinosa*; microsporangium in radial section. *L*, sporophyll; *lig*, ligule of sporophyll; *mi*, microspores still grouped in tetrads inside the sporangium; *t*, persistent tapetum; *d*, place of dehiscence. Magnified about 40 diameters. (R. S.)

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*.

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 division; all the rest remain undivided and are abortive (see Fig. 4).

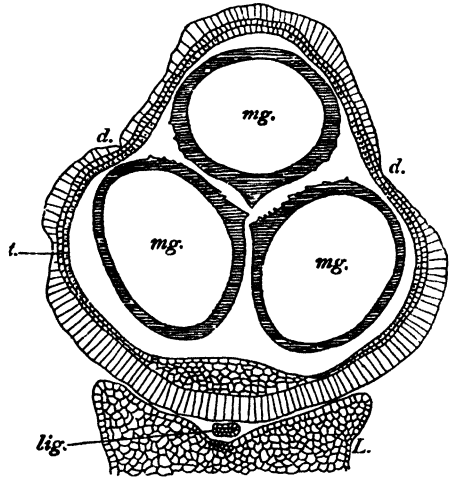


FIG. 11.—*Selaginella spinosa*; megasporangium from same cone in tangential section (transverse to sporophyll); *mg*, megaspores, three out of the four are visible; *t*, persistent tapetum; *d*, line of dehiscence; *lig*, ligule; *L*, sporophyll. Magnified about 40 diameters. (R. S.)

The one favoured mother-cell divides into four tetrahedrally arranged 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. The wall of the mother-cell breaks down.

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 Flowering 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 change 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*). Subsequently the external cells become disorganised, their contents contributing to the nutrition of the central group. The prothallus-cell, however, persists all through. The round central cells are alone concerned in the further development.

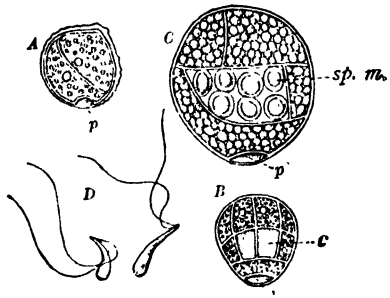


FIG. 12.—*Selaginella*; germinating microspores. *A*, young stage; *p*, prothallus-cell; first wall formed in antheridium. *B*, more advanced stage; *c*, central cells which will form spermatozoids. *C*, mature stage; *sp. m*, spermatozoid mother-cells, surrounded by cells of wall of antheridium. *D*,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

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*. 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.

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, exactly like some water-animalcule.

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. Its motion, in fact, is just like that of a rifle bullet through the air, or that of the screw of a steamer through the water.

We must remember that the spermatozoids are of a very minute size; the body is about 0·0125 mm. ($\frac{1}{2000}$ of an inch) 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 (see Part I. Ch. II. III e, Ch. IV. III c). 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 (see p. 311), is conveyed passively to its destination by the growth of the pollen-tube.

It may seem strange to us at first to find a cell belonging to a plant swimming actively about, as if it were an animal. When the first examples of such moving vegetable cells were observed, about the year 1830, the discoverer was so much astonished that he thought he had caught the plant at the very moment of its turning into an animal! Now, we know better. Actively moving cells are produced by most cryptogamic plants; sometimes they are male cells, as in *Selaginella*; sometimes they are sexless spores (see below, p. 144). Movement, in fact, is not specially characteristic of animals as distinguished from plants, for all protoplasm is capable of spontaneous motion. We have seen this already in the case of *Elodea* (Part I. Ch. I. II A e), only there the movements go on within a closed cell-wall. Wherever movement is of advantage to the plant, we find that its protoplasm can show itself just as active as that of animal cells. In plants, however, owing to their different mode of nutrition, the necessity for locomotion arises less often.

We cannot follow the fate of the spermatozoids to the end, until we have seen how the megaspores germinate. Before we go on to this, however, we will carry the comparison between a microspore and a pollen-grain rather further than we have done hitherto.

If we refer back to the account given in Part I. Ch. IV. III a, Ch. IV. III c, of the maturation and germination of the pollen-grain in the Spruce Fir, we shall recall the fact that several cell-divisions take place before the generative cells are formed. In like manner we have found several cell-divisions in the microspore of *Selaginella* before the spermatozoid mother-cells are formed.

The little prothallus-cell, which is first cut off, probably corresponds to the first two cells cut off in the pollen-grain of *Picea* (see Part I. Fig. 111, cells marked 2 and 3).

In neither case do these cells take any part in the further development. The succeeding divisions are more numerous in *Selaginella* than in our gymnospermous type. The whole resulting group, including both enveloping and central cells, constitutes an *antheridium*, the characteristic male organ of the Cryptogams. In the higher Cryptogams, this organ always consists of an enveloping layer of cells enclosing the central group from which the spermatozoids are derived. In the Gymnosperms the antheridium is only represented by the " stalk-cell " and the two generative cells (see Part I. Fig. 111, 4 and 5, Ch. IV. 111 a). The whole is enclosed in the undifferentiated vegetative cell, which forms the bulk of the pollen-grain. In *Selaginella* the vegetative cell ceases to exist; it is all used up in forming the antheridium, while in Gymnosperms it persists in order to produce the pollen-tube.

We see, then, that microspores and pollen-grains, which agree exactly in their mode of origin, agree also up to a certain point in their mode of germination. The differences between them are connected with the different means by which fertilisation is effected.

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 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 cases this process is com-

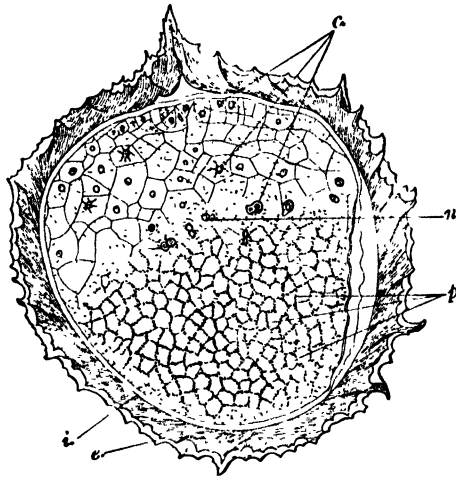


FIG. 13.—*Selaginella Martensii*; germinating megaspore. *c*, cellular tissue of prothallus, only complete in upper part of spore; *n*, free nuclei; *p*, undivided protoplasm of spore forming a network; *i*, inner, *e*, outer, layer of cell-wall of spore. Magnified 335 diameters. (After Heinsen.)

pleted even before the megaspores are set free from the sporangium, while in other cases 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 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, p. 66, Fig. 35). We see, then, that the development is just like that in *Picea*, except that in *Selaginella* we find two canal-cells instead of one. 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).

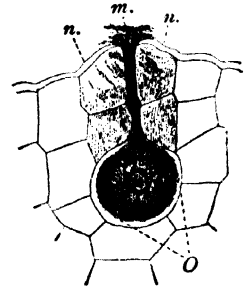


FIG. 14.—*Selaginella*; archegonium ready for fertilisation. *O*, ovum; *n*, cells of neck; *m*, mucilage in canal. Magnified about 500 diameters. (After Pfeffer.)

The first archegonium is sometimes formed before the megaspore is shed.[1] After the dehiscence of the megasporangium, which takes place violently by a longitudinal slit, the megaspores are shed on the ground. The growth of the prothallus continues, the coats of

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

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).

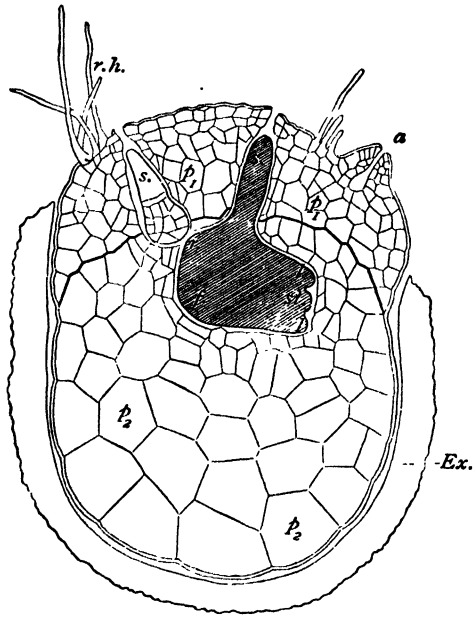


FIG. 15.—*Selaginella Martensii*; longitudinal section through old prothallus showing two embryos. p_1 and p_2, prothallus; *a*, unfertilised archegonium; *r.h*, rhizoids; *s*, suspensors of embryos; larger embryo shaded, no cells shown; *r*, root; *f*, foot; *st*, stem; *l*, *l*, cotyledons; *Ex*, wall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

Other archegonia are formed around the first one, and a few root-hairs (*rhizoids*) grow out from the prothallus. The mode of development of the prothallus bears a striking resemblance to that of the " endosperm " of the Spruce Fir or other Gymnosperms, so that we are

justified in calling both by the one name of prothallus (see Part I. Ch. IV. III b). The archegonia are formed in the same way in both. The prothallus of *Picea* is developed within the embryo-sac, that of *Selaginella* within the megaspore.

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. 68). 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 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 really important distinction, then, between the fertilisation of a Cryptogam, such as *Selaginella*, and that of an ordinary Flowering Plant, consists in the mode in which the male cell is conveyed to the ovum. In the Cryptogams, the journey is accomplished by the active locomotion of the male cell itself; the spermatozoid moves by means of its cilia, and this can only take place under water. In most Phanerogams the generative cell is carried from the pollen-grain to the ovum by the growth of the pollen-tube; the final result, the union

of the nuclei of the two cells, and, no doubt, of certain portions of their cytoplasm also, is the same in both Sub-kingdoms. It is now ascertained that spermatozoids are formed in certain Gymnosperms. (See p. 311.)

After fertilisation the ovum 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 sus-

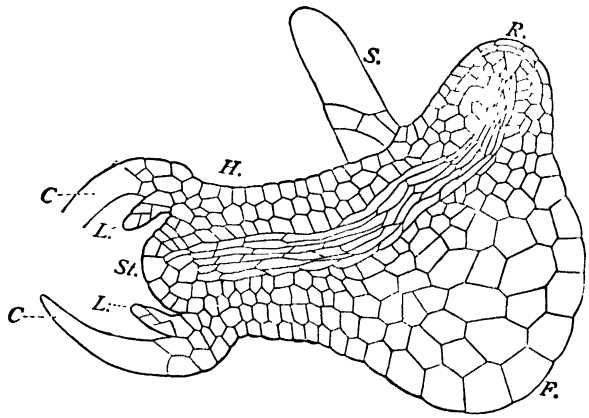


FIG. 16.—*Selaginella*; advanced embryo in longitudinal section. *S*, suspensor; *R*, root; *F*, foot; *C*, cotyledons (cell-walls omitted); *L*, ligules; *St.* apex of stem; *H*, hypocotyl. Magnified 165 diameters. (After Pfeffer.)

pensor, 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 apex of the stem lies at the end opposite the suspensor, but not quite in the middle; the two cotyledons lie on either

side of it. One side of the hypocotyl grows out into a temporary organ, the *foot*, which grows so rapidly as to force the apex of the stem to one side (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.

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.

In possessing a suspensor, *Selaginella* resembles the Gymnosperms and most other Flowering Plants. The position of the organs of the embryo, however, is different. Although the embryo is dicotyledonous, like that of many Gymnosperms as well as of the Dicotyledons, properly so called, the apex of the stem is displaced towards one side, and the first root, though it arises near the suspensor, is not in a line with it (cf. Part I. Figs. 114, *F*, and 115, Ch. IV. III d). The peculiarities of the embryo are connected with the presence of the absorbing organ called the foot, which in *Selaginella* and most of the higher Cryptogams performs the function of absorbing food from the prothallus, while in most Flowering Plants the corresponding function is discharged by the cotyledon or cotyledons.

Comparison between Selaginella and the Gymnosperms

At first sight the differences between even the highest Flowerless Plants, such as *Selaginella*, and the Flowering 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 *gymnospermous* Flowering Plant, we shall find it quite possible to trace the corresponding stages in their life-history; and, having accomplished this for the lower Flowering Plants 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. The relations between Gymnosperms and Angiosperms have already been briefly discussed in Part I. Chap. IV.

As regards the male organs, the comparison has been drawn above (p. 17). We need only recapitulate the results here. We found that the development and structure of the microsporangium of *Selaginella* agreed very closely with that of a pollen-sac in the Flowering Plants. The microspores produced in the former are developed precisely in the same way, and have just the same 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.

Two Japanese botanists were the first to make the brilliant discovery that in some of the Gymnosperms the generative cells become converted into actively moving spermatozoids comparable to those of the Ferns (see p. 311). 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 pollen-tube of the Gymnosperm is not represented in *Selaginella*, for in the latter the whole contents of the microspore are used up to form the prothallus-cell and antheridium. The comparison of the development gives us then the following chief results :

Selaginella.	*Gymnosperm.*
1. Spermatozoids	= Generative cells.
2. Prothallus and antheridium	= Cell-group in pollen-grain
3. Microspore	= Pollen-grain.
4. Microsporangium	= Pollen-sac.

The student, however, must clearly understand that it is quite useless to learn up the names of the equivalent organs, unless he thoroughly grasps the developmental facts on which their comparison is based.

We will now compare the female organs in the two Classes. It is best to start with the ovum, which is beyond question the same thing in both. The ovum in *Selaginella* is produced in an archegonium, which is almost exactly like that of a Gymnosperm, such as *Picea*, and which develops in just the same way. The archegonia of *Selaginella* are formed from superficial cells of the prothallus, exactly as those of the Fir are formed from superficial cells of the " endosperm." The development, moreover, of the prothallus itself is just like that of the " endosperm." In both cases free nuclear division first takes place, then cell-formation begins, and the tissue thus formed goes on growing until it has filled all the

available space. We can have no doubt, then, that the female prothallus of *Selaginella* corresponds to the " endosperm " of the Fir, which we may, if we like, call by the same name. The only 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 *Picea* arises is the *embryo-sac*. We therefore arrive at a new term in the comparison ; the megaspore is the equivalent of the embryo-sac.

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. It is interesting, however, to know that in some Gymnosperms the membrane of the embryo-sac likewise becomes cuticularised. It has also been found that in some plants of this class (Cycadales) the development of the " endosperm " is only completed while the seeds are lying on the ground, and in a few cases the " endosperm " has been observed to burst through the embryo-sac and seed-coats and to become green, just like the prothallus of *Selaginella*.

A more serious difficulty is that there are four megaspores in *Selaginella*, and only one embryo-sac in the

Fir, though there are Gymnosperms which have more than one, as *Gnetum*. In most Gymnosperms the 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. The similarity of their development has already been pointed out (see p. 15). 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 further, and to find the equivalent in the Cryptogam of the carpels and stamens of the Flowering Plant, we meet with some difficulty. In *Selaginella* neither kind of sporangium is

borne actually on a leaf, but in its axil. Similar cases, however, are known among Flowering Plants. We may regard the leaves, in the axils of which the sporangia of *Selaginella* are situated, as representing stamens or carpels, according as the adjoining sporangium is a micro- or megasporangium. There is, however, no differentiation between carpels and stamens in *Selaginella* or in any Cryptogam. We may compare the whole spike of *Selaginella* to a hermaphrodite [1] flower with no perianth, and with stamens and carpels resembling each other. In some Gymnosperms also, as in certain members of the group Cycadales,[2] the stamens and carpels are just alike in their vegetative parts.

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 the 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*. To go back to our old illustration in the introduction to Part I. (Fig. 2), the tuber of a potato is *homologous* with a branch of the stem, but *analogous* with a fleshy root such as that of a carrot. In our comparison between

[1] Flowers are called *hermaphrodite* when, as in those of the Wallflower and the Lily, the stamens and carpels are both contained in the same flower.

[2] As the Cycadales have been referred to more than once, it may be worth while to mention that they are a group of Gymnosperms, of great geological antiquity, now represented by a few tropical genera, with a palm-like habit. They all have pinnate leaves of great size. The student will find a magnificent collection of living Cycads in the Palm-house at Kew.

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 Flowering 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 (see p. 311).

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 among other ancient groups including the Pteridosperms, Palæozoic Seed-plants resembling Ferns. Some primitive seeds, however, may have only developed an embryo when germination set in, as sometimes happens in Cycads at the present day.

The genus *Lycopodium* is described in the Appendix (p. 316).

TYPE V

The Male Fern (*Aspidium*[1] *Filix-mas*, L.)

The Ferns or *Filicales* are a vast group, enormously outnumbering all the other Vascular Cryptogams. The Class in the widest sense includes about 150 genera and over 6000 species. In our own native Flora seventeen genera and about forty species are represented. The Ferns are the only Class of Pteridophyta which has successfully held its own down to the present day, while the other groups are represented by comparatively few surviving forms.

It need hardly be said that among this immense group of plants every possible variety of habit is to be found, while in structure the differences are scarcely less great. In size, we find every gradation, from the Tree Ferns of the tropics and New Zealand, which may reach 60 feet in height, down to minute Filmy Ferns hardly larger than Mosses. The main outlines of the life-history are, however, with few exceptions, fairly uniform throughout.

[1] Also known as *Dryopteris*, *Nephrodium* or *Lastræa F.-m.*

The particular Fern which we have chosen as a type serves well to illustrate the chief points in the development and morphology, but we cannot expect any single representative to give a fair conception of the Class as a whole.

I. *EXTERNAL CHARACTERS*

A. Vegetative Organs

The Male Fern, one of the commonest British Ferns, grows abundantly in woods and hedgerows. The short, stout stem grows obliquely upwards, and rises but little above the surface of the ground. Such a stem is often called a rhizome. It often reaches a length of about eight inches and a diameter of about one inch ; but it appears much thicker than it really is, because it is completely covered with the bases of the old leaves.

The stem at first has the form of a cone with the thin end downwards ; for it grows thicker for a time towards the top, till a constant diameter is attained (Fig. 17). This is commonly the case in plants which have no secondary growth in thickness, and in which, therefore, the increase in bulk must depend entirely on gradual strengthening of the growing-point. In this respect, though in no other, Ferns resemble the Monocotyledons (see Part I. Ch. II. 11, Summary).

The leaves, often called *Fronds*, are of very large size, one to three feet long, and much subdivided (see Figs. 17 and 18).

This is the first example of a *compound leaf* we have had. A compound leaf is one in which the lamina or blade is completely subdivided, so that its several parts, called *leaflets*, resemble distinct leaves. The leaves of the Male Fern are *pinnate*, that is, the main stalk, or *rachis*, bears two rows of leaflets, or *pinnæ*, one row on

each side (see Fig. 18). The pinnæ are often subdivided themselves in the same way, and then the whole leaf is

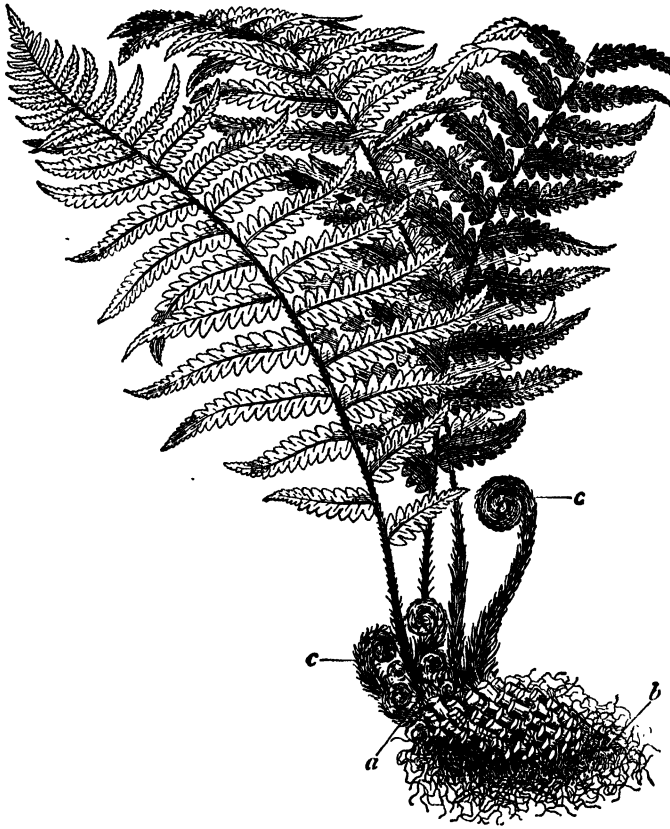


FIG. 17.—General view of the Male Fern. *a*, apex; *b*, base of stem, which is covered with the remains of old leaves, and bears numerous adventitious roots; *c*, *c*, young leaves, showing circinate vernation. Greatly reduced.

said to be *bi-pinnate*. In the specimen figured, the pinnæ are deeply lobed, but not completely subdivided. Each lobe, like that shown singly in Fig. 18, B, may

be called a *segment*. The segment is traversed by a main vein, springing from the midrib, and giving rise to lateral veins, which fork, and end near the edge of the leaf. This type of venation is a common one in Ferns (see Fig. 18, B).

The petiole and rachis, and sometimes also the larger veins of the leaflets, are clothed with brown chaffy hairs, the *paleæ* or *ramenta*, which are characteristic of the Class (see Fig. 18).

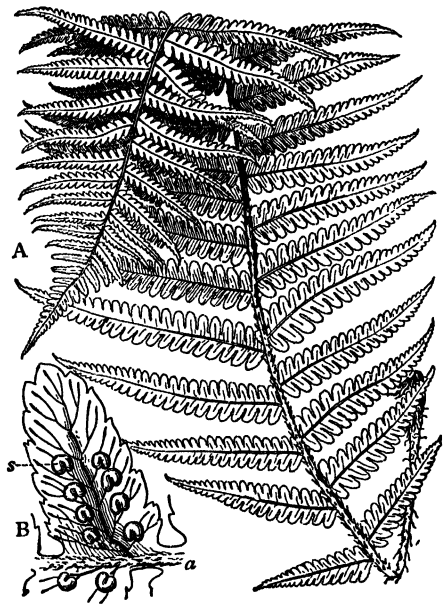


FIG. 18.—A, leaf of Male Fern (much reduced). B, part of a fertile pinna seen from below; *a*, midrib; *s*, sorus. Magnified. (After Luerssen.)

The leaves develop very slowly, arising in the bud two years before they unfold. The growth of the leaf goes on at the apex like that of the stem. Thus the leaf-stalk is the first part to be formed, and is generally the only part developed in the first year of growth. The blade is formed later, and this also grows from the base upwards. The blade of the young leaf is rolled up in such a way that the rachis or midrib forms a spiral like a watch-spring, the apex of the leaf being at the centre of the spiral (see Fig. 17, *c*). Everyone who has ever watched a Fern coming up in spring must have noticed the form of

the young leaves. The curvature is due to the greater growth of the under-side of the leaf, which is external in the bud. 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.

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.

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. 17).

B. Reproductive Organs

The ordinary Fern plant, such as we have described, is purely asexual. Like *Selaginella*, it bears, at this

stage, 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. In this respect such Ferns are on a lower level, as regards the physiological division of labour, than any plants which we have yet considered.

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. 18, 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, so that the reproduction of the plant is extremely well provided for.

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. 31, p. 61). The prothallus is a flat, green, heart-shaped body, sometimes as much as half an inch in diameter, attached to the soil by the root-hairs or 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.

II. *INTERNAL STRUCTURE OF THE SPOROPHYTE*

A. The Vegetative Organs

1. The Stem or Rhizome

a. The Vascular System

In all the plants with which we have had to do so far (except some of the Selaginellas), the vascular system of the stem evidently constitutes a single cylinder, or *stele*. 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 the case with the majority of Ferns, but a few retain a protostelic structure throughout life.

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

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. 21).



FIG. 19.—Longitudinal section of small stem of Male Fern. *a*, apex ; *l*, *l*, bases of leaves ; *st*, stem ; *g*, leaf gap. Natural size. (After Sachs.)

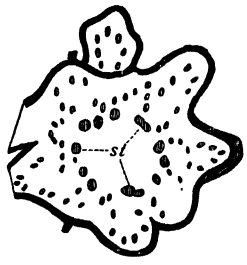


FIG. 21.—Transverse section of stem of Male Fern, showing the bases of leaves. *st*, principal strands of the stem. (After De Bary.)

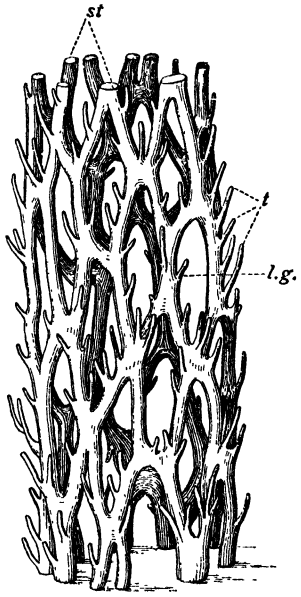


FIG. 20.—Stelar system of the Male Fern dissected out. *st*, principal strands of the stem ; *l.g.* leaf gap corresponding to the insertion of a leaf ; *t*, strands passing out into the leaf. Magnified. (After Reinke.)

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. 20. 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. 19, 20). As the leaf-bases of the Male Fern cover the surface of the

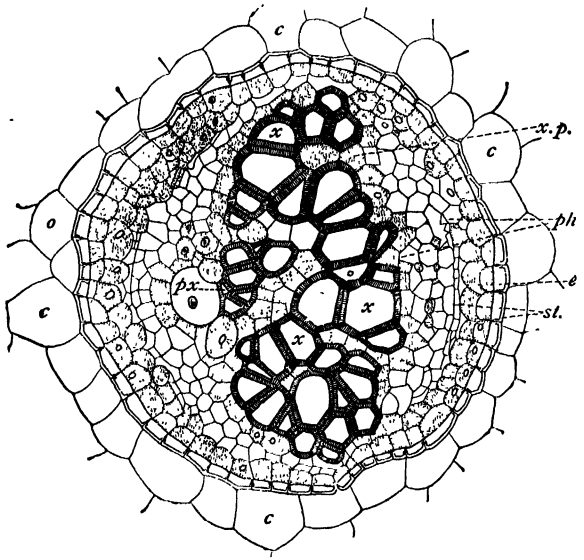


FIG. 22.—Transverse section of small strand or bundle from petiole of Male Fern. *c*, *c*, cortical cells; *e*, endodermis; *st*, starch sheath, made up of inner endodermis and pericycle; *ph*, phloëm; *x*, *x*, xylem; *p.x*, protoxylem; *x.p*, xylem-parenchyma. Magnified 200 diameters. (R. S.)

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. 21).

Every strand of the stele consists of a central mass of wood surrounded by a ring of phloëm (see Fig. 22).

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 tracheæ and parenchyma; the tracheæ of Ferns are generally of the kind called *scalariform*, or ladder-like, from the peculiar structure of their walls, shown in Fig. 23. 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. It was stated a few years ago that the elongated elements of the wood, commonly called tracheids, are everywhere in open communication with each other, the closing membranes of the pits being absorbed, but the most recent investigations confirm the older view, that in Ferns, with very rare exceptions, the water-conducting elements remain permanently closed, and are not of the nature of vessels.

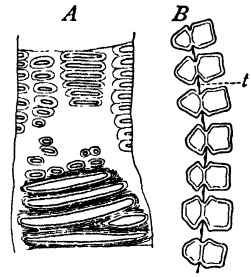


Fig. 23. — Portions of scalariform tracheæ. *A*, part of wall in surface view. Magnified 187 diameters. *B*, part of wall in section, showing bordered pits, *t*, torus on closing membrane. Magnified 375 diameters. (After De Bary.)

In the strand figured (see Fig. 22) 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 paren-

chyma. The former have their sieve-plates on the lateral as well as on the oblique terminal walls. They are not unlike those which we observed in *Pinus*.

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 (see Part I. Ch. I. II B c) 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. They serve to give mechanical stiffness to the stem. 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.

2. The Leaf

As we have seen, each leaf, at least in the mature plant, receives several vascular strands from the stem (see Figs. 19, 20, and 21). The structure of the petiole is simple enough. The strands (see Fig. 22), as seen in transverse section, are arranged in a horshoe, 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. 18, 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 very generally the case in Ferns.

If we now endeavour to sum up what we have learnt of the vascular system of the Male Fern, we see that its most striking peculiarity consists in the dictyostely of the stem, where each strand of wood and phloëm resembles an entire central cylinder rather than a single vascular bundle. As we follow the leaf-traces outwards, however, we find that the strands assume more and more the character of simple vascular bundles, until in the lamina they have the same collateral structure as in the leaves of flowering plants. It is evident that no sharp line can be drawn between an individual strand of a dictyostele and a bundle.

Returning to the lamina of the leaf, we find that its structure 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 chlorophyll granules (see Fig. 28, *A*).

The epidermis of the lower surface alone bears the stomata, which are very numerous (see Fig. 24).

The stomata are characteristic: each pair of guard-cells is half surrounded by a subsidiary cell, shaped like a horseshoe. The subsidiary cell and guard-cells are ultimately derived from a single mother-cell, which is cut out from one of the epidermal cells by a curved wall.

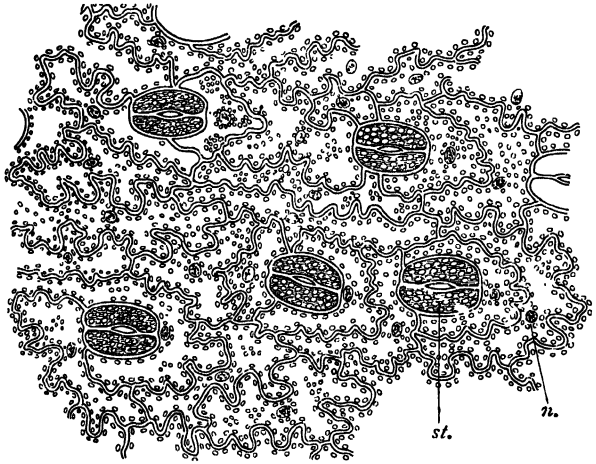


FIG. 24.—Part of epidermis from the under-side of leaf of Male Fern. Note the undulating cell-walls and numerous chlorophyll-granules. *n*, nucleus of epidermal cell; *st*, stoma. Magnified 105. (R. S.)

The cells of the epidermis on both surfaces of the leaf have undulating cell-walls fitting closely together. The cells contain chlorophyll, as is generally the case in the epidermis of Ferns, though 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.

The structure of the root in Ferns is, with one or two exceptions, essentially similar to that of the root in flowering plants. In the Male Fern and in many other Ferns the vascular cylinder of the root is diarch (see Fig. 25). The first-formed elements of the wood, protoxylem, lie at the two ends of the xylemplate, exactly as in the Wallflower (see Part I. Ch. I. II B c), and the development of the wood advances from these two points in centripetal direction to the middle of the cylinder.

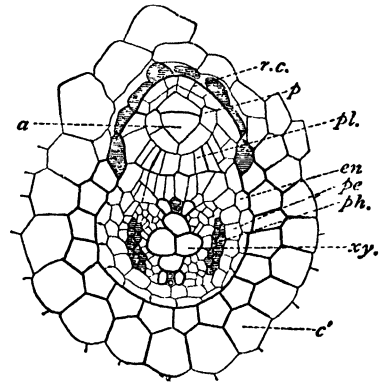


FIG. 25.—Transverse section of central part of young root of a Fern, showing origin of rootlet. *xy*, diarch xylem ; *ph*, phloëm ; *pe*, pericycle ; *en*, endodermis ; *c'*, cortical cells ; *a*, apical cell of rootlet ; *r.c*, root-cap ; *p*, cortex of rootlet ; *pl*, stele of rootlet. Magnified about 150 diameters. (After Van Tieghem.)

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 cuticularised 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. We see that, except for minute details, such a root resembles a young root of the Wallflower (see Part I. Ch. I. II B c), but in the case of the Ferns there is no secondary growth of thickness. When we come to consider the development, we shall find considerable differences from any of the previous types.

4. The Growing-points

a. 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. 26, which is taken from a simpler Fern-stem, but illustrates the essential features).

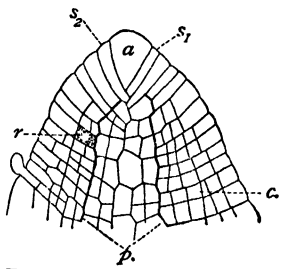


FIG. 26.—Apex of stem of a Fern (stolon of *Nephrolepis*) in longitudinal section. *a*, apical cell; s_1, s_2, segments; *c*, cortex; *p*, stele; *r*, cell from which a root will arise. Magnified 80 diameters. (After Van Tieghem.)

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 upwards (assuming the stem to be erect). 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. 26). By the growth and repeated subdivision of the three rows of segments all the tissues of the stem are produced. The stem figured has a simple monostele; here the first tangential walls formed in the segments mark the limit between the central cylinder and the cortex. In a dictyostelic stem, such as that of the Male Fern, the strands are not marked out until after more numerous divisions have taken place. It is probable that each leaf owes its origin to the outgrowth of cells derived from a single segment.

B. 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. 27) 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.

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. 25). The young root, as it makes its way through the tissues of the parent organ, is at first enveloped in a digestive sac, derived from an inner layer

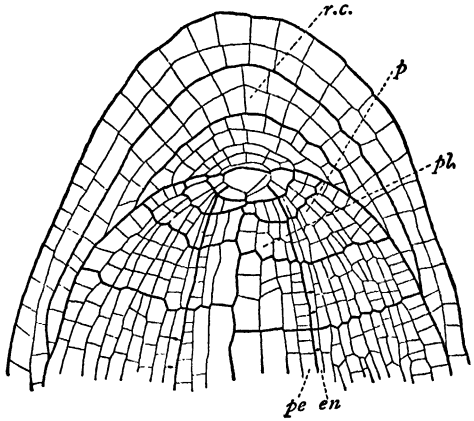


FIG. 27.—Apex of root of a Fern in longitudinal section, showing triangular apical cell. *pl*, stele; *pe*, pericycle; *en*, endodermis; *p*, cortex; *r.c.* root-cap. The dark lines mark out the cell-groups, each formed from a single segment. Magnified 120 diameters. (After Van Tieghem.)

of the cortex, and serving to absorb the tissues which have to be penetrated.

In the Ferns, the pericycle has nothing to do with the development of the rootlet, beyond forming a pedicel by which it is connected with the vascular tissues of the main root.

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. 26, 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, over the lateral veins of a segment or pinnule (see Fig. 18, B).

Beneath each sorus is a prominent mass of tissue, which we may call the *placenta* (see Fig. 28, *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. 28, *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. 28, *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 ring or *annulus* (see Fig. 28, *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; this is the place where the capsule ultimately opens (see Fig. 28, *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 function of the annulus is to cause 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 pollen-sacs and ovules of Flowering Plants, and the two kinds of sporangia in *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. 28, *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

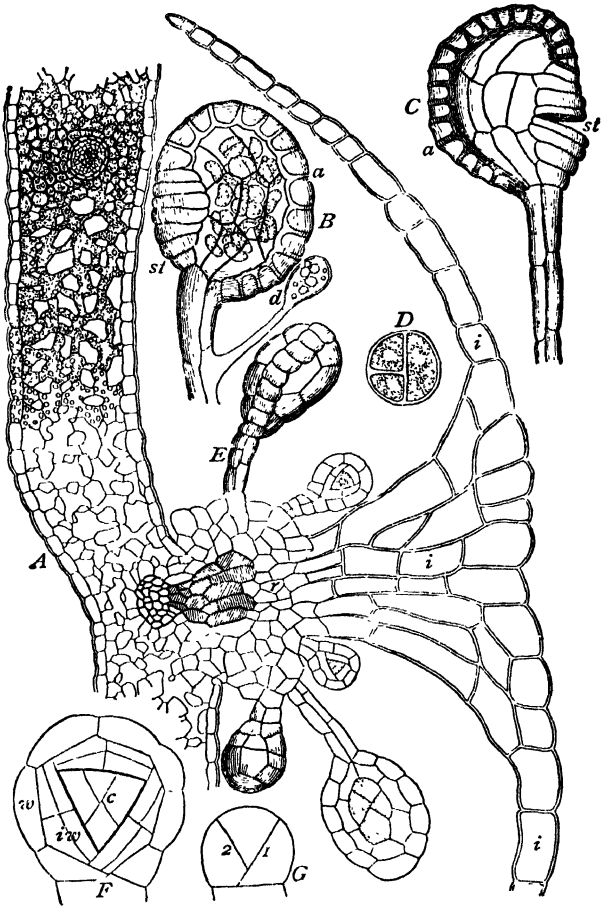


FIG. 28.—*A*, transverse section of portion of lamina of Male Fern passing through a sorus ; *i*, indusium. Magnified 80 diameters. *B*, single sporangium in side view ; *a*, annulus ; *st*, cells which dehisce ; *d*, glandular hair. *C*, sporangium dehiscing at *st* ; *a*, annulus. *B* and *C* magnified 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.)

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 central 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. 28, *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. 28, *F*, *c*). We see, then, that in this case the archesporium begins as a single cell. It undergoes several cell-divisions (see Fig. 28, *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 as to form four cells, each of which has at first the shape of a quadrant of a sphere (see Fig. 28, *D*). These four daughter-cells

are the spores. 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 much thickened, and consists of two layers, the outer of which is strongly cuticularised, and assumes a dark-brown colour. The walls of the mother-cells break down. We have now seen how the myriads of microscopic dust-like spores which we find on the back of a Fern-frond are produced.

It is the annulus which causes the sporangium to open ; dehiscence takes place when the wall of the ripe sporangium has begun to dry up. The cells of the annulus lose water, and consequently contract, the thin outer walls of the cells becoming concave instead of convex (see Fig. 28, *C*). The water in the annulus cells is in a state of tension. The whole annulus tends to straighten, and this finally causes the rupture of the sporangium at the broad, thin-walled cells at the end of the annulus (see Fig. 28, *C*, *st*). The annulus not only straightens, but bends back on itself in the opposite direction. This primary movement takes place quite slowly. The annulus cells continue to lose water : their thin outer walls are drawn in yet more, and the annulus bends back still further. This goes on until the tension in the water is so great that the water comes away from the walls of the cells and a gas bubble appears in each cell. This causes a sudden release of the tension, and the walls of the cells and the annulus as a whole recover with a violent jerk. It is this secondary movement that causes the ejection of the spores, which may then be carried to a great distance by the wind.

On the island of Krakatoa (Malay Archipelago), the vegetation of which was completely destroyed by the volcanic eruption of 1883, and which lies about eleven

miles from the nearest land, Ferns were among the very first plants to reappear after the catastrophe.

It is a very general rule that the dehiscence of sporangia is so contrived as to take place in dry weather; the advantage of this to the plant is obvious. When the air is dry the spores form a powdery dust, which is easily scattered by the wind, whereas in wet weather they hang together in damp clusters, and could never be properly disseminated.

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 arrangement 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 glass, and to 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. Fern spores which contain no chlorophyll when ripe keep their power of germination for a long time. In a few kinds, such as the Royal Fern, *Osmunda*, the spores are green, and will only germinate if sown at once. 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. 29), each cell of which may produce a rhizoid. In most Ferns the rhizoids of the prothallus remain unicellular ; in a few they become multicellular.

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. 30). 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.

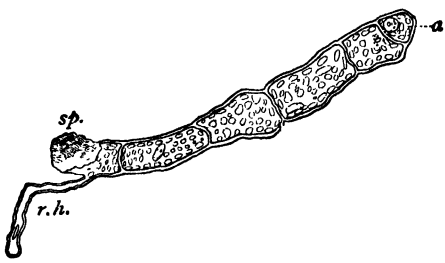


FIG. 29.—Very young prothallus of an *Aspidium*. *sp*. membrane of spore ; *r.h*, first rhizoid ; *a*, apical cell. Magnified 210. (R. S.)

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.

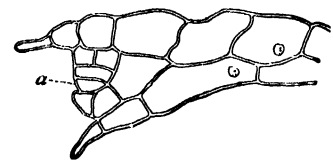


FIG. 30.—Apex of young prothallus of *Aspidium*, older than in Fig. 29, seen in surface view. *a*, apical cell. Magnified 210. (R. S.)

A normal full-grown prothallus seen from below is shown in Fig. 31. 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. In ordinary cases the prothallus is monœcious, bearing both kinds of sexual organs; but this is not always so. Male prothalli are not uncommon,

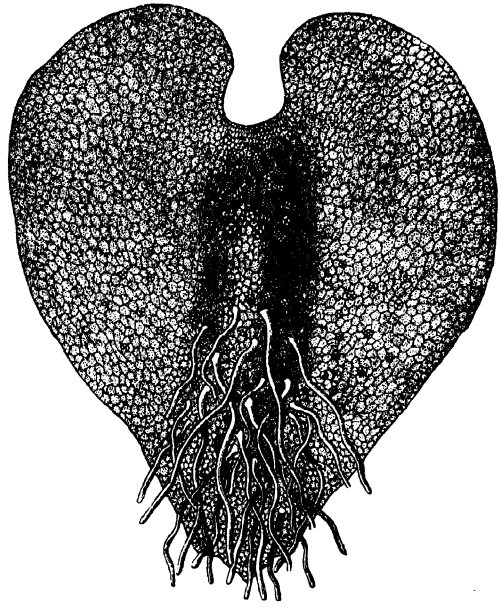


FIG. 31.—Full-grown prothallus seen from below, showing archegonia towards the apex, antheridia and rhizoids towards the base. Magnified about 25 diameters. (After Luerssen.)

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. 32, but still smaller ones occur.

Specimens with archegonia only are rarer, and are of

the ordinary form. These variations are interesting, because they show how the distinction of sex among the individual prothalli, which has become fixed in *Selaginella* and other heterosporous forms, appears occasionally as a more or less casual phenomenon even in the homosporous Ferns. Small and ill-nourished prothalli suffice for the production of antheridia, which quickly fulfil their function and make no great demands on the food supply. On the other hand, archegonia are useless unless provision be made for the nutrition of the embryo after fertilisation; and so we find female organs on full-grown and well-nourished prothalli only. In the heterosporous Cryptogams provision is made beforehand, in the spore, for the more abundant nutrition of the female prothallus.

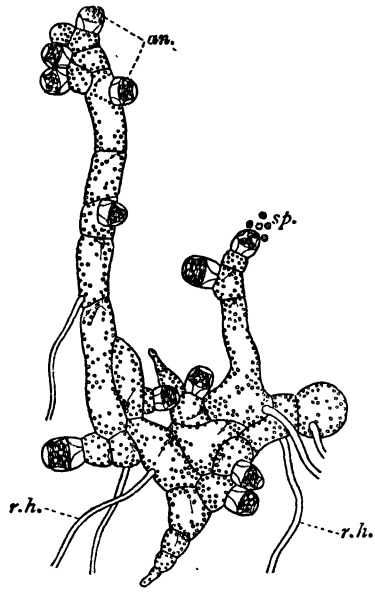


FIG. 32.—Young male prothallus of Male Fern. *an*, antheridia; *sp*, spermatozoids escaping; *r.h*, rhizoids. Magnified about 70 diameters. (After Kny.)

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. 33, A.

The central cell divides up repeatedly, and gives rise to the spermatozoid mother-cells, the number of which in

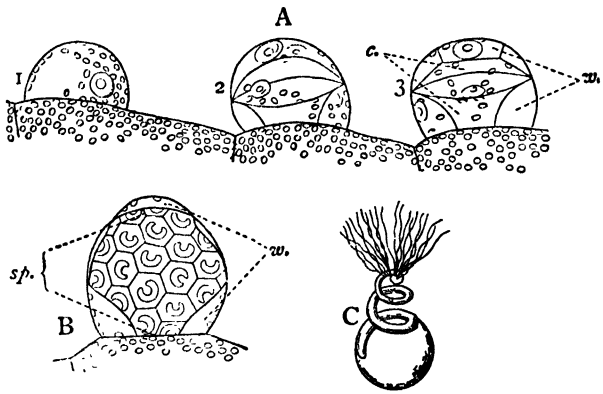


FIG. 33.—Antheridia of Male Fern. A, 1, 2, and 3, antheridia three successive stages seated on prothallus; *c*, central cell; *w*, wall. B, older antheridium; *sp*, mass of spermatozoid mother-cells; *w*, wall. C, a single spermatozoid. Magnified, A and B about 300, C about 700 diameters. (After Kny.)

each antheridium averages about twenty (see Fig. 33, 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. 33, C).

The development has been very exactly followed; it is known that the greater part of the body of the spermato-

zoid is formed from the *nucleus* of the mother-cell ; the cilia, however, and the part of the body to which they are attached, are derived from the cytoplasm. In Fig. 33, B the young spermatozoids are shown enclosed in their mother-cells.

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. 34).

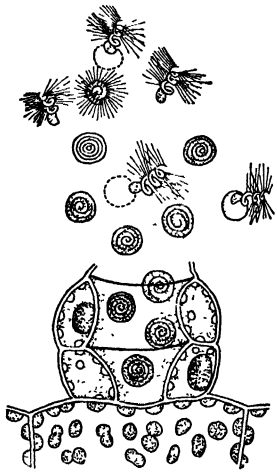


FIG. 34.—Ripe antheridium, showing spermatozoids escaping. Magnified 350 diameters. (After Luerssen.)

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. 33, C, and 34). 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. 35). The neck is the only part which projects beyond the surface of the cushion.

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. 35, 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. 35, 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. 35 and 36).

We see that the archegonia are really quite similar to

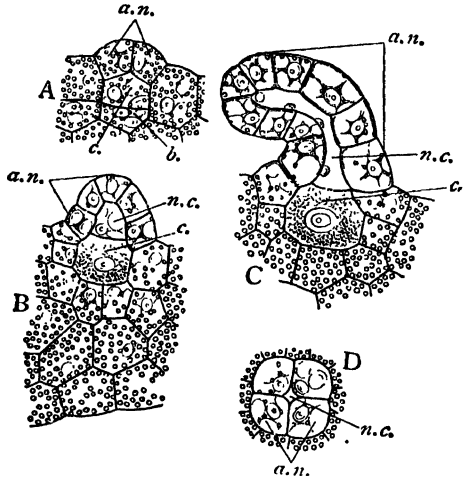


FIG. 35.—Development of archegonium of Male Fern. A, very young ; *a.n*, neck of archegonium ; *c*, central cell ; *b*, basal cell. B, rather older ; *n.c*, neck canal. C, nearly ripe ; *n.c*, canal cells disorganised. A, B, C, in longitudinal section. D, neck seen from above. Magnified about 250 diameters. (After Kny.)

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. 36).

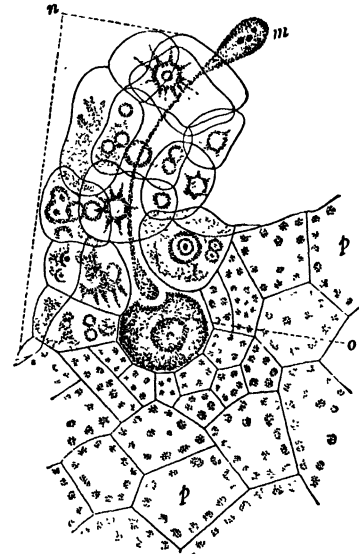


FIG. 36.—Archegonium ready for fertilisation. *o*, ovum; *n*. neck; *m*, mucilage extruded from canal; *p*, cells of prothallus. Magnified 350. (After Strasburger.)

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. This is a remarkable illustration of the great fact that the protoplasm of plants and animals is essentially the same, and that the living matter of a plant may show properties usually regarded as belonging especially to animals, whenever such properties are needed.

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 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. 37, *f*).

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.

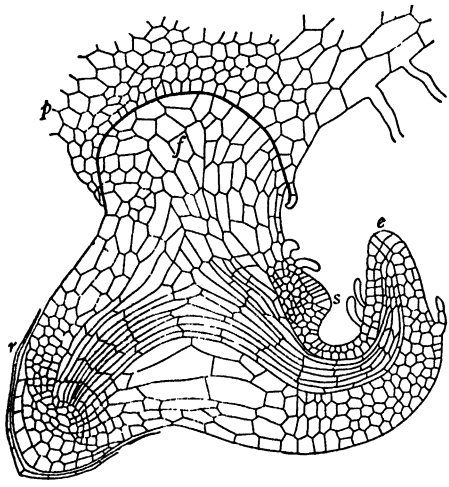


FIG. 37.—Embryo of a Fern (*Pteris*) in median section. *s*, apex of stem; *e*, first leaf; *r*, root; *f*, foot by which embryo is attached to prothallus; *p*, prothallus. Magnified 150. (After Hofmeister.)

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

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

In the Ferns, for the first time, the occurrence of a distinct alternation of generations becomes 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 ordinary 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 arise, though it had been recognised in the animal kingdom long before.

Of course the same phenomenon really occurs in *Selaginella* and even in Flowering Plants, but in all these it is much less conspicuous, because, as we ascend the scale, the sexual generation becomes more and more dependent on the asexual, so that at last the former is reduced to a mere insignificant appendage of the latter, and can scarcely be distinguished from it.

We have just seen that, even in such Ferns as our type, when the prothalli happen to be diœcious, the male specimens often remain rudimentary. In *Selaginella*, where the difference of sex is fixed, this has gone much further ; the male prothallus is reduced to one little cell, and is so insignificant as to be scarcely recognisable. The female prothallus, which has much more work to do, is much less reduced, but remains almost shut up in the coats of the megaspore, and so does not obviously suggest an independent individual. When we come to the more ancient Flowering Plants—the Gymnosperms —we find the male prothallus at an equally low level

with that of *Selaginella*, but much modified, in accordance with changes in the method of fertilisation. The fact that the pollen-grains are set free and germinate, clearly indicates that they mark the beginning of a new generation, while the production of active spermatozoids in some Gymnosperms links them directly with the Cryptogams. The female prothallus, though not less bulky than that of *Selaginella*, remains for ever shut up in the megaspore, which itself never gets free from the sporangium; so on the female side all trace of an independent existence of the prothallus has been lost, and, except for minute developmental research, we should never have suspected the presence of a gametophyte at all.

In the Angiosperms matters are still worse for the sexual generation. On the male side, indeed, there is no great change, except that the homologue of the antheridium is harder to recognise, but in the embryo-sac the prothallus is scarcely to be traced; the endosperm, which has sometimes been considered to represent the prothallus, is an after-product of fertilisation and differs from a prothallus in origin. In fact, the sexual generation in Angiosperms has become so thoroughly incorporated with the asexual, that it seems almost an affectation here to talk of alternating generations at all, and certainly the existence of such an alternation would never have been discovered except by the comparison with Cryptogams. The clue afforded by the life-history of the Ferns has thus enabled botanists to follow accurately the true course of development in the higher plants, which otherwise we should never have understood.

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* and *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 specimens.

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.

In apogamy, which has been sometimes observed in our type, the Male Fern, and in many other species, the vegetative tissue of the prothallus grows out into the various organs (leaf, stem, and root) of the new Fern-plant, the origin of which cannot often be traced to any single cell, or even necessarily to any definite initial group. At the same time vascular elements appear in the tissue of the prothallus. Archegonia may be absent altogether, or, if present, may have nothing to do with the production of the new plant, which may arise entirely as a vegetative outgrowth on the prothallus. Every stage of transition between prothallus and plant may be found. In a Fern, nearly related to our type, and in at least one other species, sporangia are sometimes produced on the prothallus itself, among the archegonia and antheridia. Recent investigations have shown that a fusion of nuclei — a kind of false fertilisation — may take place in the prothallus-cells concerned in the apogamous development.

In the converse case, that of apospory, which has been observed in several native Ferns, especially garden varieties, either an abortive sporangium grows out into a prothallus, without first forming spores; or else the sporangia are altogether undeveloped, and the prothallus arises simply as a vegetative growth from the tissues of the leaf itself. In both these cases the sexual generation is formed from the asexual directly, without the intervention of spores. Frequently apospory and apogamy occur together in the same plant, in which case there is no nuclear fusion.

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.

TYPE VI

THE FIELD 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, a Club Moss 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. 38). 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 (as in our type, shown in Fig. 38) 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

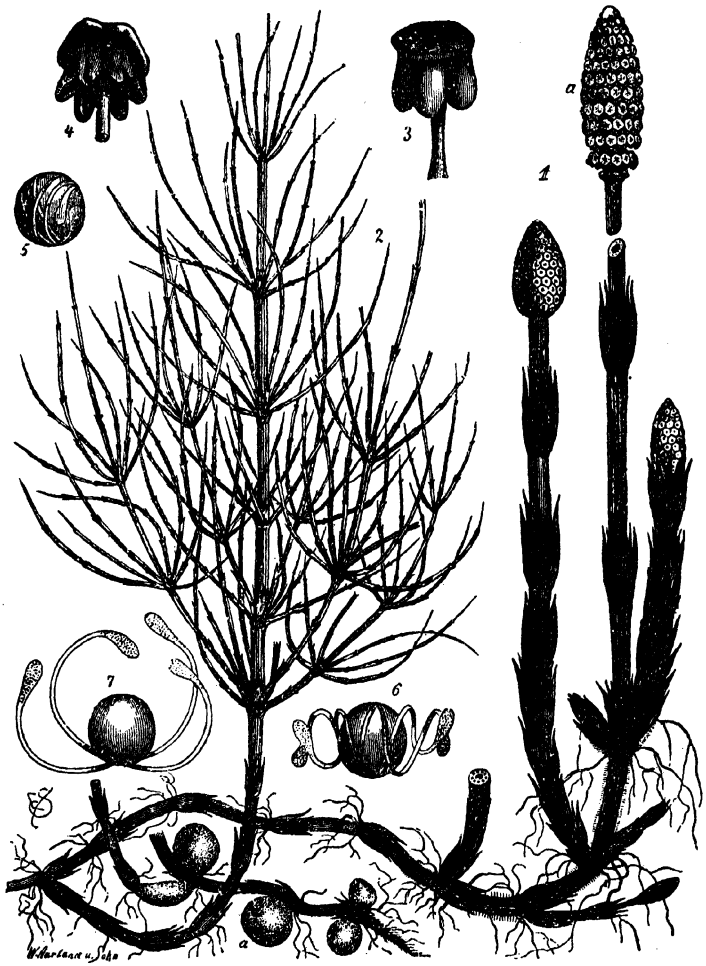


FIG. 38.—*Equisetum arvense.* 1 and 2, general view of plant, showing underground rhizome, bearing roots, with fertile and sterile aërial stems. 1, Fertile stems ; *a*, ripe cone. 2, much branched sterile stem ; *a* (on rhizome), tubers. 3, single peltate scale from cone, showing sporangia. 4, similar 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.)

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 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 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. 38, 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 only represented 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. 38, 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. 38, 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. 38, 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 aërial 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 flowers of some Coniferæ, such as the Yew, are found to bear a certain resemblance to it when closely examined. The cone is terminal either on the main fertile shoot (as in *E. arvense*) or on a branch (as in *E. limosum*). 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. 38, 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 sporangium-bearers. In each whorl there are a considerable number of sporangiophores—about twenty in many cases. Each sporangiophore has a short cylindrical stalk, and expands at the end into a flat disc, to the under-side of which the sporangia are attached—five to ten on each scale. 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, so as to fill up all the room that is left between the peltate scales. 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. 38, 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. 39).

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

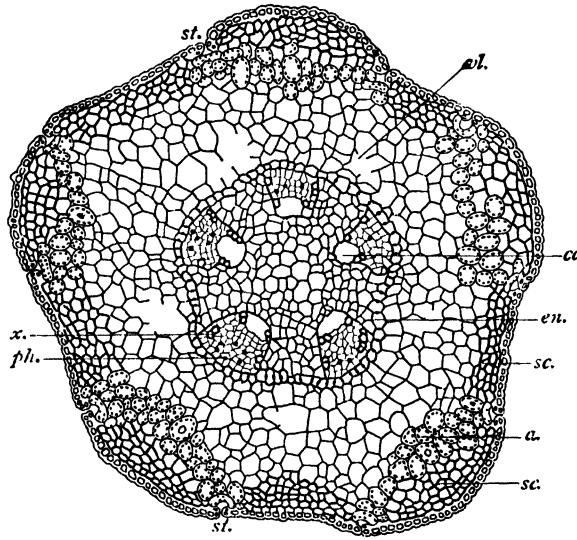


FIG. 39.—*Equisetum arvense* ; transverse section of a branch of sterile stem. *x*, xylem ; *ph*, phloëm ; *ca*, carinal cavity ; *en*, endodermis ; *sc*, sclerenchyma ; *a*, assimilating tissue ; *vl*, vallecular cavities (imperfectly formed) ; *st*, stomata. Magnified 45 diameters. (R. S.)

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 aërial stems; but in the finer aërial branches (see Fig. 39) 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 and the central cavity usually contain water, while the vallecular cavities are always full of air. 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* (see Fig. 40).

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 in these cases the appearance of the transverse section may be very different from that of a main stem or larger branch (see Fig. 40).

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. 39). Here a few tracheids have become thickened (in an annular or spiral

manner) at a 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 tracheæ (see Fig. 39). 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.

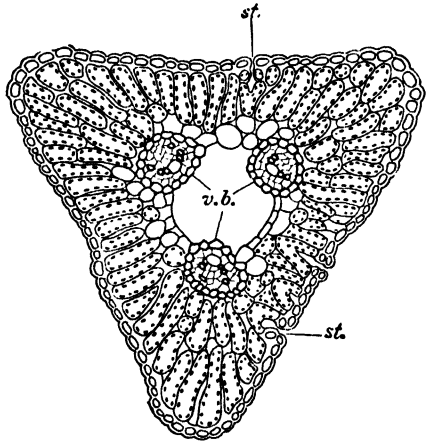


FIG. 40.—*Equisetum limosum*; transverse section of an ultimate branch of the aërial stem. *v.b*, the three vascular bundles, each with its own endodermis ; *st*, the depressed stomata. The pith is hollow, but there are no vallecular cavities. Almost the whole cortex is assimilating palisade-tissue. Magnified 100 diameters. (R. S.)

The phloëm lies between the limbs of the V (see Fig. 39, *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 cuticularised bands on its radial walls) which marks the beginning of the cortex (Fig. 39). 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.

The cortex, however, at least in the aërial 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 functions of assimilation and transpiration belong (see Fig. 39). 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 compromise is made between these two competing interests. Each prominent ridge of the stem is occupied by a strand of sclerenchyma, and there are an equal number of additional strands placed at the bottom of the furrows (see Fig. 39, *sc*). The assimilat-

ing tissue occurs in curved bands, each of which lies behind one of the sclerenchymatous ridges, and reaches the surface on either side of it, between the mechanical tissue of the ridge and that of the furrow (see Fig. 39, *a*). The epidermis has stomata at those places only where the chlorophyll-tissue reaches the surface, so they are placed where they are most needed for transpiration and the passage of gases. We notice also that the bands of chlorophyll-tissue lie directly opposite the vascular bundles, so that they are well situated both for receiving the water and mineral substances from the latter, and also for transferring to them in return the products of assimilation. In the very minute ultimate branches, such as that of which a transverse section is shown in Fig. 40, things are simplified. Here there is little need for mechanical strength, as the weight of the branch is trifling, and so we find the whole cortex utilised for assimilation; the vallecular spaces also are absent. Functionally these little twigs do duty as leaves.

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

The description of the structure of the stem, which we have just given, refers more especially to the sterile shoots growing above ground. Both the underground rhizomes and the fertile shoots are somewhat modified in structure. In the former the epidermis is destitute of stomata, and the cortex of chlorophyll-tissue, while mechanical tissues are little needed and little developed;

thus the whole differentiation of the outer tissues is much reduced.

In *E. arvense* the pith of the rhizome is solid, and this is often the case in the smaller aërial branches also, as shown in our Fig. 39. The tubers consist simply of parenchyma crowded with starch, and traversed by a few reduced vascular bundles ; each tuber corresponds to a single internode.

The fertile stem being a transitory organ, with no other function than to bear the cone, has a simplified structure, and is destitute at once of stomata, chlorophyll, and sclerenchyma. Throughout all parts of the shoot, however, the vascular system maintains the same structure, and this tissue-system is the most constant and characteristic feature in the anatomy.

b. The Leaves

The leaves of *Equisetum* are of little importance as organs for gaseous interchange, and probably serve chiefly as a protection to the lateral buds which arise beneath them. However, they no doubt take a certain part in assimilation and transpiration, as is shown by their structure. These functions are of course limited to the leaves of aërial shoots, and in the case of species like *E. arvense*, to those of the sterile stems.

The vascular bundles of the leaf-sheaths are of simple collateral structure, and do not have carinal canals. Each bundle is surrounded by its own endodermis, whether this is the case in the stem or not. As in the stem, the bundles correspond in position to the ridges of the sheath ; outside each bundle lies a strand of sclerenchyma. A narrow band of chlorophyll-containing tissue lies between the sclerenchyma and the vascular 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.

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. 38). 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. 41, which was drawn from the main root, will serve to represent either.

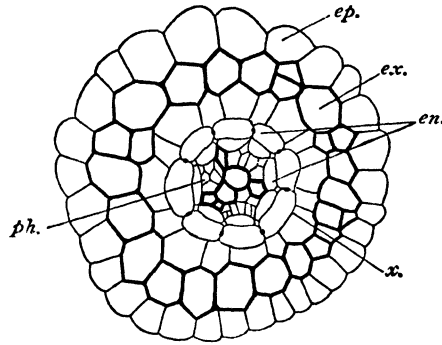


FIG. 41.—*Equisetum* ; transverse section of main root. *x*, triarch xylem ; *ph*, phloëm (three groups) ; *en*, double endodermis ; *ex*, thick-walled exodermis ; *ep*, epidermis. Magnified about 100 diameters. (After Buchtien.)

The young parts of the root bear numerous root-hairs. They have a wide cortex, enclosing a small and simple central cylinder, the structure of which is usually either triarch or tetrarch.

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. 41, *en*). This double endodermis is a character quite peculiar to the roots of *Equisetum*. 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. 42), 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. There is here no trace of the distinct layers giving rise to epidermis, cortex, and stele, such as are sometimes to be

recognised in Flowering Plants. 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

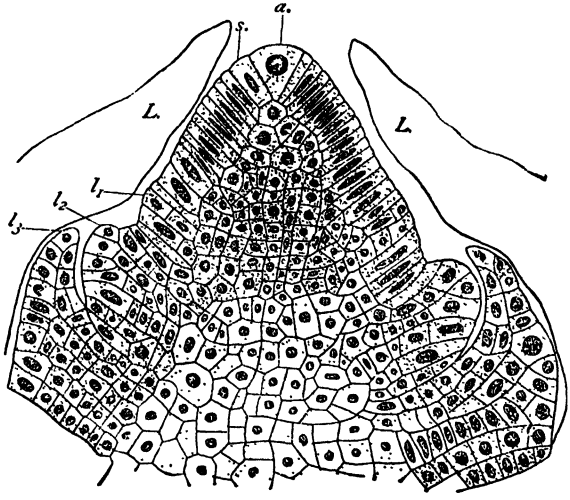


FIG. 42.—*Equisetum arvense* ; longitudinal median section of the apex of the stem. *a*, apical cell; *s*, segment cut off from it; l_1, l_2, l_3, youngest leaves, in order of age. *I*, outline of older leaves. Magnified 180 diameters. (R. S.)

them. The epidermis is also differentiated late, for there is no distinct dermatogen near the apex.

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. 42, 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, though this is not the case. The branches are

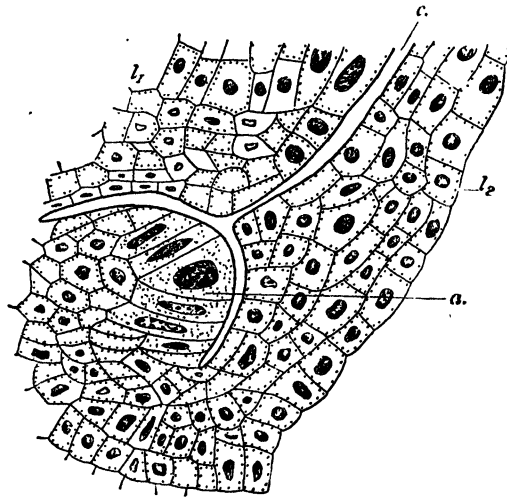


FIG. 43.—*Equisetum arvense*; part of a radial section of stem, just below the apex, to show exogenous origin of branch, *a*, apical cell of branch; l_1, cortex of stem; l_2, base of leaf below branch; *c*, crevice between them, about to close up. Magnified 360 diameters. (R. S.)

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. 43).

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, which of course is not the case really. 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. 27 (p. 52).

The roots of *Equisetum* branch freely ; the origin of

the branches, as in other roots, is deep-seated or endogenous. In this case 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, and in doing so is helped by the presence of a digestive sac (see Part I. Ch. II. II d), formed from the outer endodermal layer, which thus constitutes a temporary covering to the young root.

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 (see p. 79). 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 cells

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. 44 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

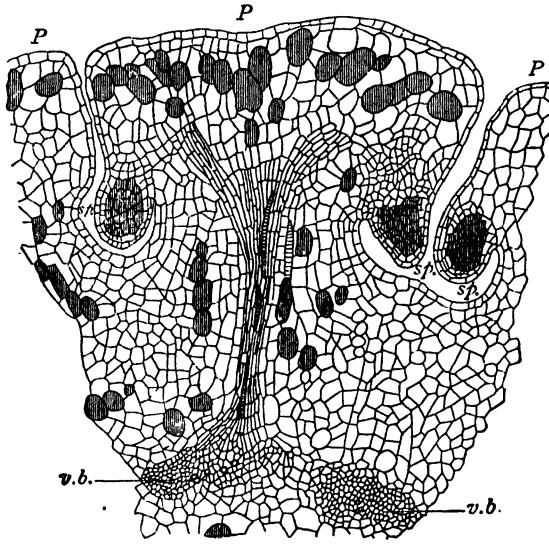


FIG. 44.—*Equisetum maximum* ; part of transverse section of young cone, showing one complete peltate scale, and parts of two others (*P*). *sp*, sporangia ; the shaded part is the archesporium ; *v.b*, vascular bundles ; the scattered shaded cells are tannin sacs. Magnified 50 diameters. (W. C. W.)

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.

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. Finally, the four daughter-cells are arranged in a tetrahedron. This rule of the division of the spore mother-cells into four is wonderfully constant, and holds good throughout the whole of the Mosses and Vascular Cryptogams, as well as in the anthers of Flowering Plants.

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 a structure 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 p. 76, Fig. 38, 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. 38, 7). If it is damp they coil themselves up again (Fig. 38, 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. 38, 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. 44 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 chlorophyll-granules. 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.

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

1. The Prothallus

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 *Aspidium*. The spore begins by dividing into two unequal cells, and usually the smaller of these grows out into the first rhizoid, while the larger gives rise to the green part of the prothallus. The latter usually divides up so as to form at once a flat plate of

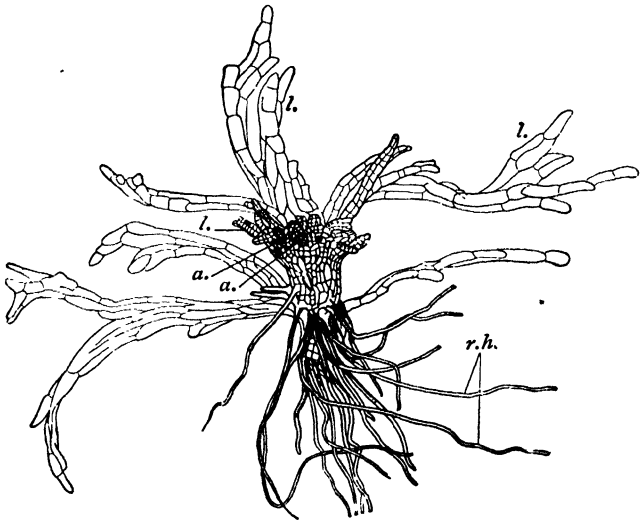


FIG. 45.—*Equisetum maximum*; large female prothallus, seen from below. *l*, *l*, lobes; *a*, *a*, archegonia; *r.h*, rhizoids. Magnified about 30 diameters. After Buchtien.)

tissue; a distinct apical cell is not always to be found. The development is very variable, but generally the prothallus puts out filamentous branches, and forms a kind of cushion with a midrib in the middle, while the sides remain one cell thick. The male prothalli often have no definite growing-point. They remain, on the whole, decidedly smaller than the females, and begin to form antheridia very early. Sometimes antheridia are

formed at the ends of branches, while in other cases they arise from the thickened cushion. Fig. 45 represents a very large and complicated female prothallus; the male individuals are much smaller and less branched. The large female prothalli possess a distinct growing-point, which produces a series of lobes on the lower side of the prothallus. Between these lobes the archegonia are placed.

2. The Sexual Organs

a. The Antheridia

The antheridium of an *Equisetum* is a very simple structure (see Fig. 46). It arises from a single cell, which divides into two by a wall parallel to the free external surface. The outer of these two cells simply forms the cover; the inner, after very numerous divisions, gives rise to all the spermatozoid mother-cells. The cover-cell divides up two or three times, by walls at right angles to the surface, usually forming a triangular cell in the middle of the cover, through which dehiscence takes place.

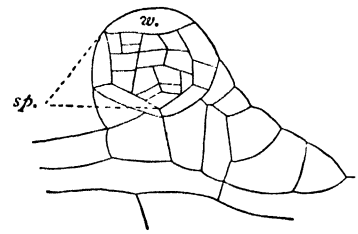


FIG. 46.—*Equisetum maximum*; young antheridium. *w*, wall; *sp*, tissue from which spermatozoids will be formed. Magnified about 200 diameters. (After Buchtien.)

In each of the very numerous cells in the interior of the antheridium a single spermatozoid is produced. Its spirally coiled body is derived almost entirely from the nucleus of the mother-cell, while the cilia themselves, and just that part of the body to which they are attached, are formed from the cytoplasm. The spermatozoids are almost exactly like those of Ferns, and go spinning

through the water in the same way. In fact there are some Ferns in which the antheridia as well as the spermatozoids agree in every respect with those of the Horsetails.

b. The Archegonia

The first archegonia arise on the cushion-like part of the prothallus ; as fresh lobes go on forming, additional archegonia are developed at the base of each lobe (Fig. 45, *a*). The archegonia at first point downwards as in the Ferns, but subsequently get turned upwards by the growth of the lobes. The development of the individual archegonium is almost exactly like that in some Ferns. Usually no basal-cell is formed ; the mother-cell of the archegonium divides at once into central cell and neck. The central cell cuts off two canal-cells at the top, and in the meantime the neck goes on growing. Here also there are four rows of neck-cells, each row consisting of three or four cells. The four cells at the top are very long, and bend far back, leaving a wide opening between them when the organ is ripe (see Fig. 47).

It is remarkable that while the Horsetail plant bears no resemblance whatever to a Fern plant, the prothallus and sexual organs are so much alike in both. It is true that they differ a good deal from those of the Male Fern, but other Ferns come very near the Horsetails as regards their sexual generation.

The conditions of life of the sexual prothallus are, as a rule, simple and uniform compared with those to which the asexual plant is exposed, so that the former has less need for varied structural adaptations. Consequently we often find that at this stage there is much in common between Classes which, so far as their sporophytes are concerned, have lost all traces of relationship.

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 further 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 and provided with plenty of food (say in the shape of a food-solution such as that described in Part I. Ch. III. 1) will generally become females. This is interesting, for here we see the beginning of sexual differentiation of the prothallus, which has become quite a fixed thing in other groups of Cryptogams. It is now a well-established fact that some of the relations of the Horsetails, which lived in the very ancient coal period, were heterosporous. Evidently our living Equiseta come from some of the less specialised members of the stock.

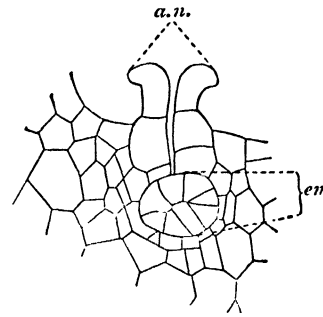


FIG. 47.—*Equisetum maximum*; fertilised archegonium. *a.n*, neck of archegonium; *em*, young embryo, showing first divisions. Magnified about 150 diameters. (After Buchtien.)

3. 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 other sex. 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.

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. 47 shows a very young embryo enclosed in the venter of the archegonium, when only a few divisions have taken place. In Fig. 48 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.

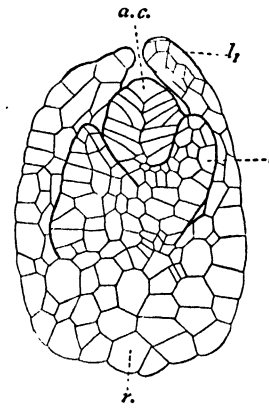


FIG. 48.—*Equisetum maximum*; embryo in median longitudinal section. *a.c*, apical cell of stem; l_1, leaf of first whorl; l_2, leaf of second whorl; *r*, position of root. Magnified about 200 diameters. (After Buchtien.)

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 dicœcious, 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 both 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 (in the widest sense), 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, represented by some of the oldest fossiliferous strata. *Selaginella* serves as well as any other type to enable us to form an idea how Cryptogamic and Phanerogamic modes of reproduction are related.

In finishing our account of the Vascular Cryptogams or Pteridophyta, we have also come to the last of our series of vascular plants. So far, the same general system of anatomical structure has prevailed all through ; henceforth we shall leave it behind altogether, and find ourselves among plants with a much simpler, or at least a totally different, internal organisation.

CHAPTER II

THE BRYOPHYTA

THE step which we are about to take, in passing on to our next type, carries us across one of the widest gaps in the Vegetable Kingdom. So far, the *plant*, in the ordinary sense of the word, has in all cases been represented by the sporophyte generation. We have always found that the stage of the life-cycle, lying between fertilisation and spore-production, is that in which the chief vegetative development is attained. The other stage, namely, that which succeeds spore-production and precedes fertilisation, has up to this point appeared as a comparatively insignificant organism, hardly recognisable as a distinct generation in the Phanerogams or *Selaginella*, though maintaining a more independent position in the Ferns and Horsetails. Henceforth we shall find the relative proportions of the two generations reversed, the chief vegetative growth taking place in the sexual stage, corresponding to the prothallus of the higher plants, while the sporophyte develops as a fruit rather than as a plant, and serves for little more than the mere production of spores.

The sub-kingdom, then, 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 mosslike 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 much simpler 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 simpler Liverworts for our first type of the Bryophyta, because its gametophyte generation is so much like the prothallus of a Fern, a fact which helps us at once to grasp the true homologies between plants otherwise so different.

A. THE LIVERWORTS (HEPATICÆ)

TYPE VII

PELLIA EPIPHYLLA

1. THE THALLUS

Pellia epiphylla 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. 49).

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. 50). 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.

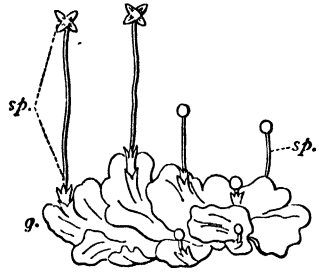


FIG. 49.—General view of a plant of *Pellia epiphylla*. *g*, the lobed thallus, constituting the gametophyte generation; *sp*, the sporophyte generation. The sporogonia to the left have opened; those to the right are younger and still closed. Half natural size. (After Cooke)

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 bye, *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 spread 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.

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. Chlorophyll-granules occur chiefly in the more superficial cells. They are most 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 root-hairs, or rhizoids, are unicellular; the cell-walls of the older rhizoids have a brownish colour, but give cellulose reactions.

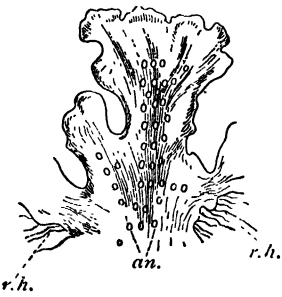


FIG. 50.—Part of the thallus of *Pellia*, seen from above. *an*, the numerous antheridia; *r.h*, *r.h*, the rhizoids. Slightly magnified. (R. S.)

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

Pellia epiphylla is monœcious, the thallus 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. 50).

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. 52). 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. 51). 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. 52). 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. 51 and 52).

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.

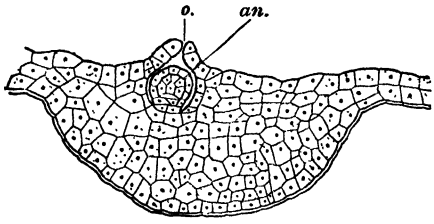


FIG. 51.—Transverse section through the midrib of the thallus of *Pellia*, showing a young antheridium. *an*, antheridium ; *o*, opening of the sheath surrounding the antheridium. Magnified 80. (R. S.)

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

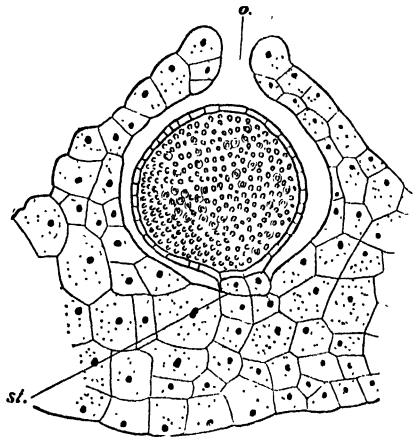


FIG. 52.—Part of a similar section showing a nearly ripe antheridium. *st*, stalk of antheridium ; *o*, opening of sheath Magnified 80. (R. S.)

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. 53). 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 outgrowth 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. 53.—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. 54). 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. 54). 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

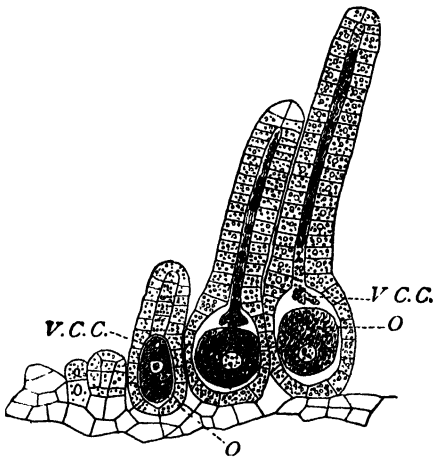


FIG. 54.—Archegonia of a Liverwort (*Marchantia*). The youngest stages are shown on the left. In the more mature archegonia, the venter, neck, and canal are clearly shown. *O*, ovum; *V.C.C*, ventral canal-cells. Magnified about 200.

bottom (see Fig. 54). 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.

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. 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 (see Part I. Ch. III), 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, so far as the details have been worked out, 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. 49). 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 it 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. 49). 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. 49, on right). Shortly afterwards the dehiscence of the capsule takes place, by four longitudinal fissures, splitting the walls into four valves, which straighten themselves out, forming a horizontal cross on the top of the seta (see Fig. 49, 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

After fertilisation, the ovum first divides by a transverse wall, but of the two cells thus produced the lower takes no part in the further development. Capsule and seta are both entirely derived from the upper cell, which next divides by a vertical and then by a transverse wall, the latter marking the boundary between capsule and seta. Cell-walls parallel to the external surface now appear in both parts. In the young capsule these divisions separate the external layer from the archesporium which constitutes the whole of the internal group. Innumerable cell-divisions take place, keeping pace with the growth both in seta and capsule, until a stage is reached like that shown in longitudinal section in Fig. 55. The seta at its lower end develops a conical foot, with a flange projecting upwards, firmly fixing the seta in the thallus, with which, however, there is never any real continuity of tissue.

The seta itself consists throughout of very uniform short-celled parenchyma. The capsule has a wall three or more cells in thickness; from the internal mass of

cells the sporogenous tissue is produced, but the whole of this is not used up to form the mother-cells of spores. A certain number of the cells grow in length, while remaining narrow, and ultimately form long tubular structures with a double spiral thickening. These curious elements — very characteristic of the Liverworts — are called the *elaters*. When young, the elaters no doubt serve to convey food-substances from the seta to the developing spores. At a later stage they play a part in the dissemination of the spores, as we shall see further on. In *Pellia* the elaters radiate from the base of the capsule, where they are attached to a mass of shorter cells, likewise spirally thickened. They extend from this part, upwards and outwards, passing between the mother-cells, which chiefly occupy the outer and upper part of the capsule (Fig. 55). Young elaters, with the spiral bands just beginning to form, are shown in Fig. 56, and nearly mature ones are represented in Fig. 57 among the spores.

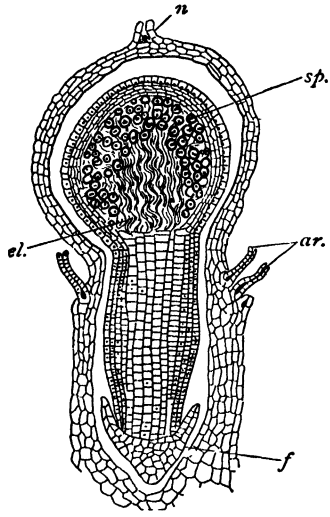


FIG. 55.—Sporophyte of *Pellia*, in longitudinal section. It is enclosed within the calyptra. *n*, neck of archegonium, in which the fruit was formed; *ar*, abortive archegonia; *f*, foot of sporophyte; *sp*, spore mother-cells; *el*, elaters. Magnified 40. (R. S.)

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. 56, *sp*). The lobes are connected in the middle by a quite narrow neck, in which the nucleus, which remains for a long time undivided, is situated. Eventually the nucleus of the mother-cell divides into 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. We must not, however, suppose that this peculiar form of mother-cell is general in all Liverworts, though it is very common among them.

The venter of the archegonium enlarges very rapidly

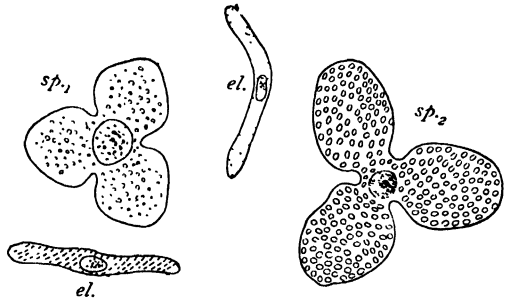


FIG. 56.—Elaters and spore mother-cells of *Pellia*. *sp.*$_1$ and *sp.*$_2$, spore mother-cells about to divide; *el*, *el*, young elaters with indications of spiral thickenings. Magnified 360. (R. S.)

to keep pace with the growth of the fruit inside, which it completely envelops for a long time; in *Pellia*, however, this envelope (called the *calyptra*) is not entirely formed from the venter of the archegonium, but the neighbouring thallus-tissue also takes part in its growth, so that we see abortive, unfertilised archegonia carried up on the sides of the calyptra (see Fig. 55, *ar*), while at the top, the neck of the fertilised archegonium itself can still be recognised (Fig. 55, *n*). The cells of the thallus surrounding the foot become especially crowded with starch, and thus provide food for the developing fruit.

The whole structure of the fruit 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.

The spores of *Pellia* present a peculiarity which is quite exceptional among Liverworts, for they become multicellular while still enclosed in the capsule. In Fig. 57 the oval spores are shown at various stages of cell-division; when ripe they consist of several tiers of cells. They contain chlorophyll, and continue their germination, under favourable conditions, as soon as shed. A wedge-shaped cell, such as is shown in Fig. 57 in the lower spore on the left, becomes the growing-point of the new plant, while one or both ends grow out into the first root-hairs. The elaters may entangle the spores together so that they are blown away gradually and only by relatively strong gusts of wind. The elaters show feeble hygroscopic movements. The development of the sporophyte of *Pellia* occupies a full year; when the

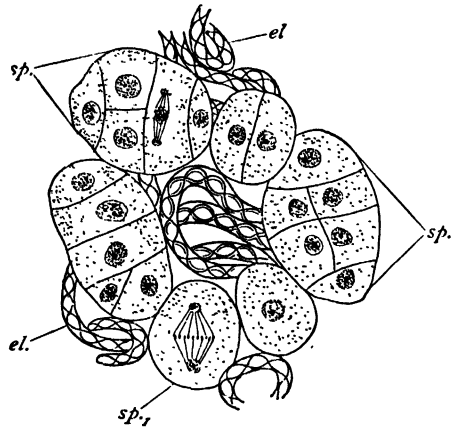


FIG. 57.—Spores and elaters from an almost ripe capsule of *Pellia*. Each spore (*sp.*) is dividing into several cells. At *sp.*$_1$, a stage of division is shown. *el*, *el*, elaters. Magnified 360. (R. S.)

spores are shed new archegonia are already ripe for fertilisation.

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 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 a plant at all, but merely into a sporogonium, 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

TYPE VIII

FUNARIA HYGROMETRICA

The true Mosses, the general appearance of which will be familiar to everyone, are more highly organised plants

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.

b. Sexual

Œdogonium is propagated very freely by the simple method just described, but it also possesses a mode of sexual reproduction essentially similar to that of the higher Cryptogams, in so far as it consists in 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 ciliated like them (see Fig. 69, 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 (p. 110), 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 point of the greatest importance.

The female organ, or *oögonium*, like the antheridium, consists of a single cell (see Figs. 66, 68, and 69), 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. 69, 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. 66 and

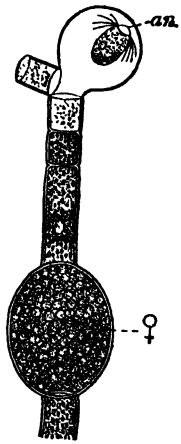


FIG. 68.—Androspore (*an*) of *Œdogonium ciliatum* escaping. At ♀ is an oögonium. Magnified 350. (After Pringsheim.)

69, 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.

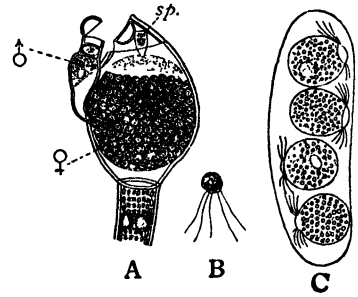


FIG. 69.—A, fertilisation of *Œdogonium ciliatum*; ♂, dwarf male plant from which a spermatozoid has escaped; *sp*, the spermatozoid in contact with the ovum, ♀. Magnified 350. B, a single spermatozoid showing cilia. Magnified 350. C, germination of the oöspore in *Bulbochæte*, showing the contents divided up to form four zoospores. Magnified 250. (After Pringsheim.)

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. 68, *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. 66 and 69, 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. 66 and 69, 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.

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. Thus even in so simple an Alga as this, we see that fertilisation is in essentials precisely the same process as in the highest Phanerogams, such as the Lily.

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. 69, 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 in many cases the plants remain through the winter in the state of young filaments of three or four cells. In a few exceptional cases the oöspore grows out directly into a filament, and the contents of an unfertilised oögonium sometimes behave in the same way. In other cases again the contents divide as usual, but each of the cells germinates directly within the oöspore, without passing through the swarming stage. All these cases, however, are exceptions; the regular process is the production from the oöspore of the four zoospores, each of which gives rise to a new plant.

We have now completed the life-history of this remarkable Alga. In what way can we compare it with that of

the higher Cryptogams? One thing is evident; we have here no such clear and regular alternation of generations as we have hitherto found. We cannot draw any sharp distinction between the asexual and sexual individuals, for in most cases the male and female plants themselves give rise also to the asexual zoospores. On the other hand, we may regard the germinating oöspore, producing four asexual reproductive cells, as representing an extremely simple sporophytic generation. The oöspore, however, is in some cases capable of direct germination into a new plant, which is as if the fertilised ovum of a Moss were to grow out directly into a Moss-plant without forming a spore-fruit. It is evident that the well-marked alternation of generations by which all the higher plants are characterised does not occur in many Algæ such as *Œdogonium*, though we can perhaps trace some indication of an analogous process in a rudimentary form.[1]

It has been well pointed out that the great development of the sporophytic generation in the higher Cryptogams may be viewed as an adaptation to life on land. The sexual plant, owing to its mode of fertilisation, is always dependent on the presence of water; the formation of spores suitable for dissemination through the air is advantageously handed over to a distinct generation. The asexual reproduction by locomotive spores is evidently adapted to aquatic life, and is extremely common among Algæ and some of the lower Fungi.

As regards the mode of fertilisation, we still find in *Œdogonium* (which in this respect is one of the highest Algæ) that it takes place within the female organ (*oögonium*), while there is a sharp differentiation of the sexual cells—on the one hand the large stationary ovum on the other the small active spermatozoid. The sper-

[1] In certain Green Algæ, *e.g. Cladophora*, *Ulva*, *Enteromorpha*, etc., distinct sexual and asexual plants occur.

matozoid, however, is here much more like an ordinary cell, *i.e.* less specially adapted to its function, than in the higher Cryptogams. At the same time, the unmistakable resemblance between a spermatozoid and an asexual zoospore is very striking.

It is particularly interesting that in *Œdogonium* we have in the androspores of some species a form of cell exactly intermediate between the ordinary zoospores and the spermatozoids. This formation of androspores giving rise to dwarf-males is quite a peculiar case, and only occurs in some species of *Œdogonium* and in the allied genus *Bulbochæte*, which chiefly differs from *Œdogonium* in having branched instead of simple filaments. Its significance is not perfectly understood; possibly by dividing the period of locomotion into two stages (first, the swarming androspore, and secondly, the swarming spermatozoid) the chance of the male cell reaching an oögonium at the right time may be increased.

TYPE X

ULOTHRIX ZONATA

1. STRUCTURE

We will next consider another fresh-water Alga, not at all unlike *Œdogonium* in general habit, but representing a very different and much lower type of reproduction. *Ulothrix zonata* is an extremely common Alga, of the filamentous or confervoid kind,[1] growing by preference

[1] Simple filamentous Algæ are often spoken of as *confervoid*, because all such forms were in the days of Linnæus included in the old genus *Conferva*, which since that time has been subdivided again and again, as the important distinctions among the species originally referred to it came to be better understood.

in running streams, or in water which is constantly renewed, as in brooks, open watercourses, or in open-air tanks with a constant supply.

The thread which constitutes the Alga is very slender, not usually exceeding about 0·04 millimetre (two-thousandths of an inch) in diameter. The filament consists of a single row of cells, often very numerous, amounting to a thousand or more in a single thread. The threads are usually attached at one end to the stones or other things in the water, but they can live equally well detached, floating in tangled masses on the surface.

The cells of *Ulothrix* are somewhat similar in structure to those of our last type. Within the cell-wall is the cytoplasmic layer, or primordial utricle, in which the nucleus is embedded. The chloroplast has the form of a broad transverse band, in which pyrenoids are contained. When, as is often the case, the cells remain short, the chloroplast may occupy almost the whole length of the cell, but when the latter grows longer the green band forms a girdle around its middle part. In the interior of the cell is a large vacuole containing only cell-sap. When the filament is attached by one end, the root-cell is nearly or quite colourless; sometimes this organ of attachment is branched, though the rest of the thread always remains simple. The thallus grows throughout its length, and has no special growing-point. The cells divide by transverse walls to keep pace with the growth.

2. Reproduction

The reproductive cells of *Ulothrix* are active zoospores and gametes. The zoospores are of two kinds, the chief distinction consisting in the number of the cilia, of which

there are four in the one kind and usually two in the other. Both vary much in size, but on the average the quadriciliate is decidedly larger than the biciliate form. We will first consider the former. The macrozoospores arise from ordinary cells of the filament; each mother-cell may produce one, two, four, or eight of these bodies from its contents. In the first case the whole protoplasm (with the exception of a thin external layer) is used up to form the single zoospore; if two are to be produced, a transverse cell-division first takes place, and each half of the contents constitutes a zoospore; if the number be four, a longitudinal division succeeds the transverse one; and if eight are to be formed, another division again, at right angles to the other two, completes the partition of the contents.

In any case the resulting zoospores are pear-shaped, contain each one nucleus, and have the chloroplast in the broader part of the cell, while the pointed end is made up of clear cytoplasm. In each zoospore there are two " pulsating vacuoles " which alternately contract and expand about every ten or fifteen seconds; in this respect these vegetable cells precisely resemble some of the unicellular animals. At the point are the four long cilia by which the locomotion is brought about. The mother cell-wall breaks down at one side, and the zoospores escape. Their movements are very active, and they have formed the subject of some of the best observations on the locomotion of vegetable cells. Relatively to their own length their speed is great. A zoospore will travel through twice or three times its own length in a second, while a fast ship requires from ten to fifteen seconds to traverse its own length; on the other hand, zoospores are so small that their *actual* speed is slow (about a metre in an hour). Considering the distance they are required to travel, we may say that their locomotion is very active.

Under the microscope their size and speed are magnified together, so that we are enabled to realise the true relation between their movements and their dimensions.

We saw some time back (pp. 68 and 130) that the spermatozoids of the higher Cryptogams are sensitive to certain chemical substances when dissolved in the water. Zoospores of Algæ are also sensitive, though in different ways; in this case they react especially to the influence of light. In darkness these zoospores wander aimlessly about in all directions, and do not come to rest until they are exhausted and die. In darkness therefore they cannot reproduce the plant; but as they are normally set free in the morning, and come to rest before evening, this difficulty does not arise in Nature. Light, however, shining from one side, at once exercises a directive effect on the movements of the zoospores. If the light be of moderate intensity, they swim towards its source; if the brightness be excessive, they hasten with equal decision in the opposite direction. As the swarming period nears its end, the zoospores tend more and more to avoid the light, and so are brought into contact with dark solid objects in the water, on which they can come to rest and germinate. Hence the reaction to light is of service to the plant, for the zoospores are thus induced to disperse themselves in the open water where their own assimilation can go on, while at the same time seeking shelter from too intense sunlight, which is dangerous to unprotected protoplasm. Finally, their changing sensitiveness ultimately brings them to rest in a position where germination can take place.

The zoospores of *Ulothrix* and of many other Algæ are provided with a red pigment-spot at one side of the clear protoplasm; this has been called the *eye-spot*, a fanciful name, though it is probable that the red pigment may really have something to do with the action of light

on the zoospore. These comparatively large, four-ciliated zoospores of *Ulothrix* swim about for some hours, and when they come to rest attach themselves by the colourless end, surround themselves with a wall, and grow out at once into a new *Ulothrix* filament, like the parent.

In other cells, it may be of the same or of different filaments, swarm-cells of a somewhat different kind are formed. These often have two cilia instead of four, but in other respects are like the former kind, though smaller. These microzoospores are produced to the number of 8, 16, 32, or even more, in a mother-cell, by successive bipartition, just as in the former case. Except in size and sometimes in ciliation there is no visible difference between the two kinds. On germination the microzoospores grow out into new filaments

In addition to these two kinds of zoospores biciliate sexual cells (gametes) are formed. These look extremely like microzoospores but are somewhat smaller. In some species of *Ulothrix* the gametes are formed under different environmental conditions from those which favour the development of microzoospores. When the gametes escape from their mother-cells they swim off through the water just like the zoospores. If, however, as often happens, one of them meets with another gamete just set free from another cell of the same or of a different thread, an extraordinary process takes place. When two gametes from different mother-cells happen to touch one another they at first become entangled by their cilia, and the pair go on spinning through the water together. They gradually become more closely united ; their bodies come into contact laterally, and soon begin to fuse. The fusion starts at the pointed colourless ends, and after these parts are quite joined up the opposite ends remain for a time separate. Soon however, in fact within a very few minutes, fusion is

complete ; the two cells have become one, and now constitute a single four-ciliated spore (see Fig. 70). Its origin from two cells can long be recognised by the two eye-spots and the two chlorophyll bodies.

The movements do not last long after fusion is complete. The spore resulting from this union withdraws its four cilia and comes to rest, attaching itself like a zoospore by the colourless end. In most cases the two cells which unite are of about the same size ; sometimes it happens that a smaller cell unites with a larger (Fig. 70, C), for of course the size of the gametes varies somewhat according to the number produced in a mother-cell, and the dimensions of the latter.

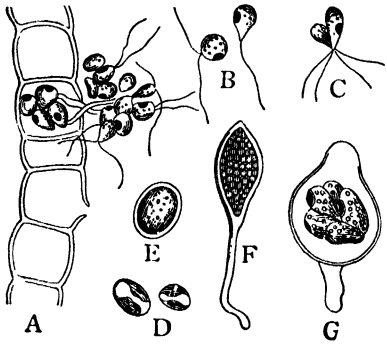


FIG. 70.—*Ulothrix zonata*. A, part of a filament ; most cells are already empty ; from one the biciliate gametes are escaping. B, gametes ; C, two in the act of conjugating ; D, two young zygospores, immediately after conjugation ; E, ripe zygospore ; F, unicellular plant grown from zygospore ; G, similar plant producing cells, which are about to escape. Magnified 482. (After Dodel-Port.)

Apart from such accidental differences, we have here a union of *perfectly similar cells*, whereas in all the plants described above there was a sharp distinction between the male and female cells. We have in fact reached in *Ulothrix* the lowest and simplest stage of sexual reproduction in plants. The process in this rudimentary form requires a special name ; *fertilisation* is the union of *unlike* cells, *e.g.* that of an ovum with a spermatozoid, or with a generative cell from the pollen-tube ; the sexual fusion of *similar* cells is termed *conjugation*, and

the result of such a union is called a *zygospore*, to distinguish it from the *oöspore*, which is the product of fertilisation.[1] Every possible intermediate stage between the two processes is, however, known in various Algæ, so we need not hesitate to regard conjugation as really a primitive form of sexual reproduction. One point of importance must be noticed : only gametes from different mother-cells will conjugate, not those from the same. Hence we see that in this very simple plant *self-conjugation* is avoided, just as *self-fertilisation* is so often avoided among the higher plants.

We will now see what becomes of the zygospore. It soon acquires a cell-wall, and may put out a colourless rhizoid (of variable length) by which it is attached to the substratum. The germinating zygospore goes on growing slowly for some weeks, but never attains any great length, and always remains unicellular (see Fig. 70, F). Its contents become denser and of a dark-green colour, while the cell-wall is much thickened, and now the little plant enters on a stage of rest.

After some time the plantlets produced from the zygospores wake up, but they never grow into *Ulothrix* filaments. Their contents divide up into a number of cells, usually from three up to about fourteen (Fig. 70, G). These cells are generally liberated in a non-motile condition and germinate to form new *Ulothrix* filaments.

Ulothrix, though so simple an organism, has been considered as presenting certain analogies with the life-history of the higher Cryptogams. The resting cells, resulting from the act of conjugation, may be regarded as a dwarf form of plant, limited entirely to reproductive

[1] The sexual union of similar gametes is often termed *isogamy*, and that of unlike gametes *heterogamy*. In the latter the process is spoken of as *oögamy* when the female gamete is non-motile. The cell formed from the union of two gametes, whether like or unlike, is often called the *zygote*.

functions, and as, in an extremely rudimentary form, so far comparable to the sporophytic generation of the Bryophytes.

Occasionally *Ulothrix* reproduces itself in a manner which is a modification of the process of zoospore formation. Cells of the filaments divide up in all directions into colonies of rounded cells which become surrounded with mucilaginous membranes, the walls of the mother-cells also becoming mucilaginous. This may go on repeatedly, so that large groups of cells embedded in mucilage may be formed. This has been called the *Palmella* condition, because the plant when in this state somewhat resembles another genus, *Palmella*. The *Palmella* state of *Ulothrix* is chiefly found when the plant is left by the receding water on the damp parts of the pool or stream in which it grows. Rarely, too, the cells of the filament may round themselves off, acquire thick walls, and pass into a resting condition. Ultimately these cells reproduce the normal filaments, either by direct germination or by forming zoospores in their interior which escape and ultimately grow into new plants. The thick-walled resting cells are a means of protection against death by drought.

The great scientific interest of *Ulothrix* depends on the variety in its methods of propagation, and especially on the fact that we can here study sexual reproduction in its most primitive form.

TYPE XI

SPIROGYRA

1. STRUCTURE

Our next type is another of the filamentous fresh-water Algæ, but very distinct from those 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. = one-hundredth of an inch, in extreme cases). They are therefore very favourable for study. Within the stratified cell-wall is the primordial utricle, in which protoplasmic circulation can be well observed in vigorous plants. Imbedded in this 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 (see Figs. 71 and 72) 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 freshwater microscopic plants of great beauty.

In *Spirogyra* the division of the cell coincides with that of the nucleus, which takes place by a complicated process (much like that in the higher plants) resulting in the formation of two exactly similar daughter-nuclei. While this is going on, a transverse septum gradually grows in from the cell wall, first appearing as a mere ring, and gradually advancing towards the middle, until a complete disc of cellulose is formed across the cell, dividing its contents into two parts and separating the newly-formed daughter-nuclei (see Fig. 71). The growth of the cell-wall is entirely due to additions from the cytoplasm. This mode of cell-division by ingrowth from the wall is common among the lower plants, while in the rest of the Vegetable Kingdom the new wall is as a rule formed simultaneously over its whole area.

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. As we shall see, however, it is quite different from the mode of conjugation in *Ulothrix*, for in *Spirogyra* and its allies it is the ordinary vegetative cells which unite. Conjugation, in most cases, takes place between two filaments lying side

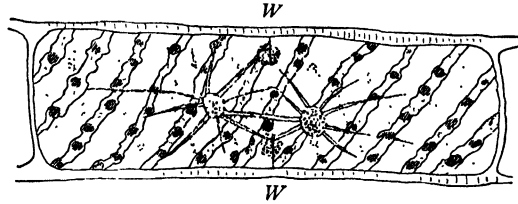


Fig. 71.—Cell of *Spirogyra nitida* during division. There are several spiral chloroplasts, with numerous pyrenoids. The two daughter-nuclei have already separated; at *W*—*W* the new cell-wall is growing in between them. Cytoplasm concentrated at the growing edge of the cell-wall. Magnified about 200. (R. S.)

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. 72).

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. 73). 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.

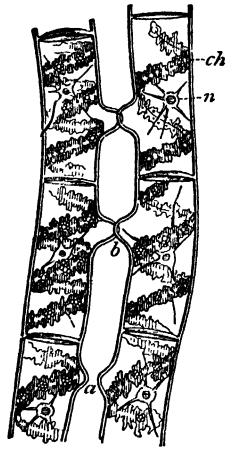


FIG. 72. — *Spirogyra longata* conjugating. The two parallel filaments are putting out the conjugating outgrowths *a*, which at *b* are in contact; *ch*, spiral chloroplast; *n*, nucleus, with radiating cytoplasmic fibrils. Magnified about 350. (After Sachs.)

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.

In most of the allies of *Spirogyra* (*e.g.* in the Desmids) there is no trace of any difference of sex, for the cell-contents meet and fuse midway between the parent cells, each of which thus takes an equal part in the process.

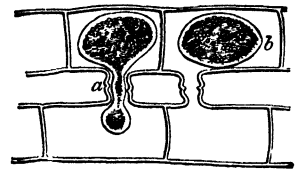


FIG. 73.—Conjugation more advanced. At *a* the protoplasm is in the act of passing over; at *b* the union is complete, one cell having transferred all its contents to the other. Magnified about 350. (After Sachs.)

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, unlike that of *Ulothrix* and its allies, 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, but three of the four nuclei thus formed disorganise. On first germinating, the young plant shows a distinction between apex and base, for it remains for a time attached by one end, which is pointed and colourless. This distinction is usually soon lost, and the filament floats freely in the water. In a few cases, where

conjugation fails to take place, the single cells have been observed to form resting-spores asexually, and in one or two species this is the rule.

The life-history of *Spirogyra*, which represents a considerable Order of fresh-water Algæ, is, as we see, extremely simple; there is not the slightest indication of any alternation of generations. All individuals alike are capable of conjugation, and are therefore sexual. The name Conjugatæ is applied to this Order, for it was among them that the union of similar cells to form a zygospore was first observed. In this group it is always the ordinary vegetative cells which unite, so the process is essentially different from the union of actively moving cells such as takes place in *Ulothrix*. The Conjugatæ appear to be an isolated group, showing no near relation to any of the higher forms, whereas from the motile conjugation of *Ulothrix* we can trace a series of steps leading on to the well-marked fertilisation of Algæ like *Œdogonium*. In *Spirogyra*, however, we have really the type of all sexual reproduction, which consists essentially in the fusion of two distinct cells, accompanied by the union of their nuclei. The structural differences between male and female, so generally found in the higher plants, are of only secondary importance, and must be regarded as special adaptations to secure this union with the least expenditure of material and energy. In one word, we may regard conjugation as the primitive form of fertilisation.

TYPE XII

VAUCHERIA

We now come to a group of plants, which in their general structure differ more profoundly from all our

previous types than any of the latter differ from one another. So far, all the plants we have considered have been cellular, protoplasmic continuity depending on minute connecting fibrils : in *Vaucheria* the protoplasm is not partitioned by cell-walls at all, but is perfectly uninterrupted throughout the whole plant. A large number of Green Algæ—including the extensive Order Siphonales—are distinguished by this non-cellular structure. Peculiar as these plants are in their internal organisation, they are none the less capable of attaining on their own lines a high development. Many of them are of large size, and some possess organs analogous to the stem, leaf, and root of higher plants.

Vaucheria is one of the simplest of the non-cellular Algæ in its vegetative organs, but as regards its reproduction is more highly differentiated than any other genus of this type at present known. Some few species of *Vaucheria* are marine, but most are either fresh-water or terrestrial plants. Some of them are among the very commonest of Algæ, occurring everywhere in ponds and ditches, or on damp earth, as, for instance, on the soil of neglected flowerpots, where they form a tangled green web, and are often troublesome weeds, especially to Fern cultivators. Their threads are rather coarse, darkish-green, and branched. When submerged, they often form dense masses of large size, becoming conspicuous objects in the water.

1. Structure

In the vegetative condition a *Vaucheria* consists of a cylindrical green filament, repeatedly branched at irregular intervals, and often attached by a colourless branched rhizoid (see Fig. 75, *B*). The contents are uniform throughout the green part of the plant. The filament is bounded externally by a cellulose membrane, but inter-

nally there is nowhere the least trace of cell-walls, as long as the plant remains in its normal vegetative condition ; the cell-contents are continuous throughout its entire length (which may amount to many inches), and extend without a break into the branches.

The cytoplasm forms a thick layer lining the external wall, and contains an immense number of roundish chlorophyll-granules, the abundance of which accounts for the deep-green colour of the threads. Imbedded in the cytoplasm, just inside the layer of chlorophyll-granules, there are innumerable minute nuclei, which increase by division as the plant grows. This feature is very characteristic of the non-cellular Algæ and some allied forms, which always have numerous nuclei scattered in their cytoplasm. We see, then, that *Vaucheria* possesses the essentials of cell-structure—cytoplasm and nuclei—though not partitioned into distinct cells. The growth of the stem and its branches is apical ; at the extreme growing end of each filament the protoplasm is colourless and transparent. *Vaucheria* does not form starch ; the product of its assimilation is deposited in the form of a fatty oil.

2. Reproduction

Vaucheria produces reproductive cells of two kinds—asexual and sexual. The asexual reproduction affords a rapid means of propagation, and goes on chiefly when the plant is growing in abundance of water, and generally under conditions that suit it.

The protoplasm accumulates and becomes denser at the end of a branch, which assumes a club-like form. The enlarged end is then separated from the rest of the filament by a transverse septum, for *Vaucheria* forms cell-walls in connection with its reproductive organs, though not elsewhere, except in case of injury. The cell thus

formed may be called the *zoosporangium*. The entire contents of the zoosporangium constitute a single zoospore of relatively large size, clothed over its whole surface with numerous short paired cilia (see Fig. 74).

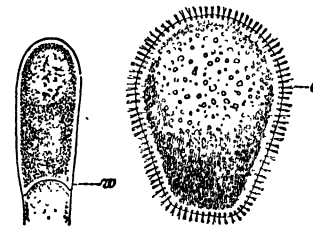


FIG. 74.—Zoospore of *Vaucheria sessilis*. To the left is shown the end of a filament just cut off, by the wall (*w*), to form a zoosporangium. Magnified 25. To the right is a zoospore covered with the numerous cilia (*c*). Magnified 95. (After Strasburger.)

The sporangium opens at the apex ; the expulsion of the zoospore is helped by the expansion of mucilage contained in the cell, but depends to a great extent on its own movements. The opening is much narrower than the zoospore, which has to push its way through, and to change its form in the process (see Fig. 75, *A*). Sometimes the front part, which tries to rotate as it becomes free, gets twisted

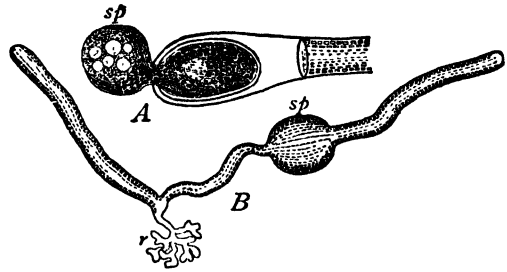


FIG. 75.—Zoospore and its germination in *Vaucheria sessilis*. *A*, zoospore (*sp*) in the act of escaping from the sporangium. Magnified about 30. *B*, germinating zoospore (*sp*), which has formed two green filaments and a rhizoid (*r*). Magnified about 20. (After Sachs.)

off from the rest of the cell, and then two zoospores are formed instead of one.

The zoospore contains a great number of chloroplasts

and nuclei. In this case the nuclei lie near the outside, in a clear zone of cytoplasm. The numerous cilia are in pairs, each pair corresponding to a nucleus. Evidently the whole of this great zoospore corresponds to a multitude of small zoospores, not separated from each other. In most allied Algæ we find that numerous zoospores, usually with two cilia each, are formed in the sporangium.

The escape of the zoospores of *Vaucheria* generally takes place in the morning. They swim about rather lazily for a quarter of an hour or so, and are so big that their movements can be followed with the naked eye. Then they come to rest, and immediately withdraw their cilia and surround themselves with a membrane. The zoospore germinates at once, sending out a filament which attaches itself to the substratum by a colourless rhizoid and soon begins to branch (see Fig. 75, *B*).

This mode of reproduction may go on indefinitely, from generation to generation, as long as weather and water remain favourable. Sometimes, however, *Vaucheria* proceeds to form reproductive bodies of another kind, especially in bright light and perhaps also when drought threatens. This plant, so simple in its vegetative structure, possesses more sharply differentiated antheridia and oögonia than any of the Algæ already described. Both organs arise as lateral outgrowths. In some species they are seated directly on the main filament; in others a short special branch forms a pedicel on which the sexual organs are borne, as shown in Fig. 76, where the oögonium is terminal on the pedicel, while the antheridium is seated laterally below it. Diœcious forms also occur rarely.

The antheridium at its first origin resembles a young vegetative branch. It contains abundant cytoplasm with chloroplasts and very numerous nuclei. As it

approaches maturity, it usually becomes curved like a horn (Fig. 76). The terminal part is cut off from the rest by a transverse wall, and forms the true antheridium. The nuclei assemble in the interior of the cell, leaving

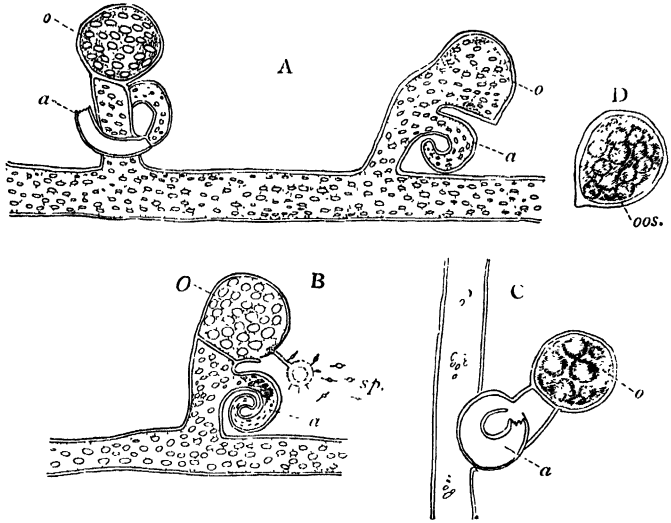


FIG. 76.—Fertilisation of *Vaucheria terrestris*. A, part of filament bearing two reproductive branches; *a*, antherid um; *o*, oogonium. On the right an early stage is shown. On the left the antheridium is already empty, and the oögonium fertilised. B, right-hand group of Fig. A later on, showing fertilisation. The minute spermatozoids (*sp*) are caught in the drop of mucilage expelled from the oögonium. Antheridium of same branch not yet open. C, some time after fertilisation. The antheridium and filament are empty, and the oöspore is ripening. D, ripe oöspore, containing oil-drops. Magnified 110. (R. S.)

the chloroplasts and part of the cytoplasm in contact with the wall. The more internal portion of the contents now breaks up into the minute yellowish spermatozoids, each of which consists of one of the nuclei, together with an extremely small quantity of cytoplasm, and is provided with two cilia. They begin to swarm within the

antheridium, which now opens at the apex, and expels the spermatozoids, together with a portion of the unused cytoplasm, some of which, however, remains behind.

In the meantime the development of the oögonium has been going on. Arising, like the antheridium, as a lateral outgrowth (or as in the species figured, at the end of the pedicel), it soon assumes a globular form. The protoplasm of the oögonium contains a large quantity of oil, as well as chloroplasts, and at first a very large number of nuclei. After a time a sort of papilla or beak is formed (Fig. 76, A) on one side. A remarkable change now takes place in the contents. A portion of the cytoplasm may wander back into the filament, carrying with it all the nuclei except one, so that the oögonium becomes a uninucleate cell. Alternatively, all the nuclei except one become disorganised in the oögonium. It is now cut off by a transverse wall from the filament. The contents rearrange themselves so that the portion towards the papilla becomes clear and free from chloroplasts, forming the *receptive spot*. The now solitary nucleus (which has grown rather larger than before) with associated cytoplasm lies towards the middle of the cell, connected by a strand of cytoplasm with the clear receptive spot. The wall of the oögonium opens at the papilla, and at the same moment a portion of the colourless cytoplasm is expelled. It is probably due to the pressure of the cytoplasmic mass that the wall is opened; sometimes the extruded part of the contents remains in connection with the cytoplasm within the oögonium. From this point onwards we may speak of the contents of the oögonium as the *ovum*.

Fertilisation now takes place. The minute spermatozoids swarm in at the oögonial aperture, but do not necessarily select the particular oögonium near which they were formed. In Fig. 76, B, for example, an

antheridium is shown which has not yet discharged its spermatozoids, although the adjoining oögonium is actually being fertilised. Numerous spermatozoids may enter an oögonium, but only one fuses with the ovum, which it penetrates at the receptive spot where the cytoplasm is clear. The nucleus of the spermatozoid has been traced through the cytoplasm of the ovum, until it reaches the sole remaining nucleus, with which it unites. It appears then that in *Vaucheria*, in spite of the remarkable peculiarities of its organisation, fertilisation is precisely the same process as in the higher plants.

The fertilised ovum surrounds itself with a cell-wall of some thickness, and passes into a resting-stage (see Fig. 76, D) during which a period of drought can be endured with safety. Then germination takes place; the oöspore gives rise directly to a new *Vaucheria* plant, which may soon begin to form the asexual zoospores.

We see that there is in this plant no indication of a regular alternation of generations. Sexual and asexual reproduction may both occur in the same individual, and it depends on the external conditions whether the one or the other takes place.

The sexually produced resting-spore is itself a provision against drought, but the plant can also protect itself against this danger in a more rough-and-ready fashion. If the water sinks and the filaments are left stranded on the mud, it sometimes happens that they divide up into a number of portions, each of which surrounds itself with a thick wall. This is so different from the normal form of the plant that specimens of *Vaucheria* in this condition used to be placed in a different genus. We see then that Siphonaceous filaments *can* separate into distinct cells when necessary, though this does not happen in the normal course of their vegetative life.

The Vaucheriaceæ stand quite alone among the Siphonales in the perfection of their reproductive arrangements. In other cases, where any sexual process has been observed, it takes the form of the fusion of motile cells. The *Vaucherias* therefore, though among the simplest of these Algæ in vegetative respects, appear to rank highest as regards sexual reproduction.

TYPE XIII

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*.

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 thin 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, occupy-

[1] Sometimes called *Protococcus viridis*.

ing the outer part of the cell-contents. The rest of the protoplasm is colourless. About the middle of the cell is a nucleus, containing a nucleolus (Fig. 77). 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 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.

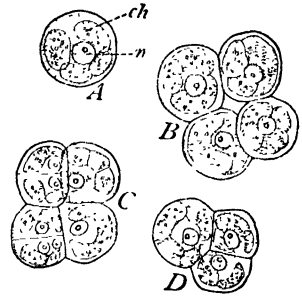


FIG. 77.—*Pleurococcus vulgaris*. *A*, single cell; *n*, nucleus; *ch*, chloroplast. *B*, four cells separating after division. *C*, group of cells remaining in contact. The two to the left have just divided afresh. *D*, tetrahedral group. Magnified 540. (After Strasburger.)

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.

TYPE XIV

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. 77**, A; Fig. 77***, 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 through 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 imbedded; sometimes 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 imbedded 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 alter-

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

nately. 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 plant-cell. The presence of a cell-wall indicates that the active cells are something more permanent than zoospores.

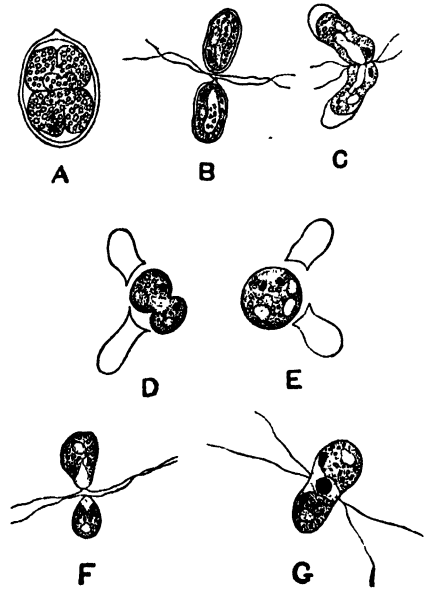


FIG. 77*.—A–E, *Chlamydomonas longistigma*, A, vegetative cell dividing into four. B–E, successive stages of conjugation of the walled gametes, which escape from their walls in the process. F, G, *Chlamydomonas pisiformis*. Conjugation of naked gametes. Magnified about 600. (After Dill.)

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. 77*, 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 escaping 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. 77***, 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.

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

The simplest method is like the conjugation of *Ulothrix*. 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 meet they entangle each other with their

cilia, and the pair go waltzing through the water together (Fig. 77*, 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. 77*, 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. There is a British species, *C. Debaryana*, which belongs to this type.

The second type differs from the first in the fact that the gametes, like the vegetative cells, are provided with cell-walls (Fig. 77*, 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 away from its wall, and then leaves it behind altogether (Fig. 77*, 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. 77***, E). This form of conjugation occurs in the British species, *C. Ehrenbergii*.

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. 77**, 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

[1] Sometimes called *C. monadina*.

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. 77**, 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. 77***, E).

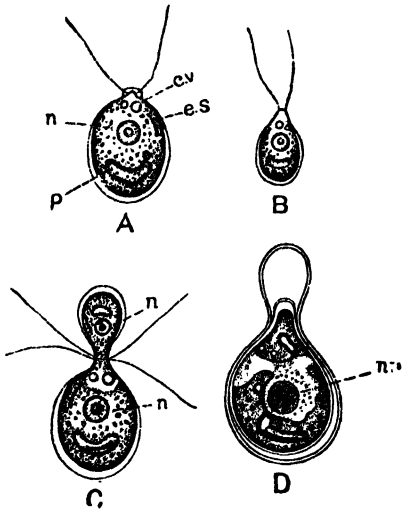


FIG. 77**.—*Chlamydomonas Braunii*. A, female gamete (closely resembling a large vegetative cell); *n*, nucleus; *p*, pyrenoid; *e.s.*, eye-spot; *c.v.*, contractile vacuoles. B, male gamete. C, early stage of conjugation; *n*, *n*, the nuclei of the two gametes. D, advanced stage of conjugation; *nn*, the united nuclei of the two gametes. Magnified about 500. (After Goroschankin.)

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. 77***, 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, like 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. 77***, 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. 77***, G) and resume the regular life of the plant.

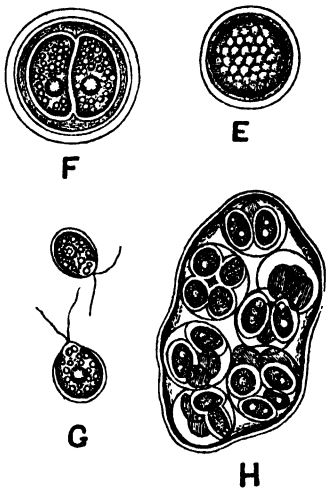


FIG. 77***.—*Chlamydomonas Braunii*. E, zygospore, containing oil-drops. F, germinating zygospore, divided into two cells. G, vegetative cells produced from a zygospore. H, palmelloid condition consisting of numerous groups of cells within a common wall. E–G, magnified about 500; H, magnified about 400. (After Goroschankin.)

There is another unicellular Alga (*Sphærella* or *Hæma-*

tococcus lacustris), commonly found in water-butts and puddles, which is nearly related to *Chlamydomonas*, but differs from it, among other characters, in the fact that the inner part of the cell-wall is transformed into a wide mucilaginous layer which is traversed by radiating branched strands of cytoplasm. In this plant a red pigment is often present, in addition to the chlorophyll, even during the actively moving stage. The vegetative cells frequently occur in a resting condition, in which the cell-wall becomes thickened and in which the contents appear to be wholly red. Such resting cells are termed *cysts*. Sexual reproduction is by the fusion of similar gametes, without cell-walls, as in the first type of *Chlamydomonas*. In this genus the resting stage is more lasting than in *Chlamydomonas*.

These plants are important, because, on the one hand, they represent some of the simplest known types of green plants which, with many others, are sometimes classed as unicellular animals under the name of Flagellata, while on the other hand they are nearly related to more highly organised groups of plants (see pp. 300–301). Some of their nearer allies spend their lives associated in definite and complex colonies of regular form, as in the beautiful *Volvox globator*. In another direction it is probable that plants of the *Chlamydomonas* group may have given rise to some of the lines of the filamentous Algæ, such, for example, as *Ulothrix*. The actively moving stage, which in *Chlamydomonas* is the normal vegetative condition, tends in the higher Algæ to be more and more restricted to reproductive cells.

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 (as well as other methods of killing) 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 in itself is not a character of much importance, but it 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 nothing in common with them.

Many of the Phæophyceæ are reproduced by motile cells (zoospores and gametes), one Order of which is the *Ectocarpales*. A second Order only forms sexually produced oöspores ; this is the *Fucales*. We will take one example of each, for space will not allow us to do more, though really a large number of types would be necessary if our object were to gain any adequate idea of the diversity of the brown seaweeds.

TYPE XV

ECTOCARPUS SILICULOSUS

1. STRUCTURE

The genus *Ectocarpus*, various species of which are extremely common on our shores, includes some of the simplest forms of the Phæophyceæ. The thallus is filamentous, and repeatedly branched. It consists of two parts; a creeping primary portion by which the plant is attached to the substratum (usually one of the larger seaweeds), and a tuft of branched threads, arising from the creeping part and waving freely in the water, often reaching a length of several inches. Throughout the plant the filaments usually remain one cell thick, though occasionally longitudinal divisions occur. Each cell contains a single nucleus and a varying number of plastids, to the pigments contained in which the brown colour of the whole plant is due.

The mode of growth of the free filaments is peculiar. Instead of having an apical growing-point, each branch grows chiefly near its base. In this part short meristematic cells are found, which increase by transverse division, while the more apical part of the branch consists of long, full-grown cells, which have ceased to divide (see Fig. 78). These *intercalary* growing-points, as they are called, are characteristic of this group of plants, though not by any means constant among them.

2. REPRODUCTION

The reproductive organs are of two kinds, which are distinguished as *unilocular* and *plurilocular* sporangia. They are usually borne simultaneously or consecutively

on the same plant, but they sometimes occur on separate plants. Both kinds of sporangia arise as lateral branches, either stalked or sessile.

The unilocular sporangia are simply ovoid or ellipsoid cells, borne at the sides of the branches (Fig. 79). They become densely filled with protoplasm, and their contents divide up into a large number of small motile cells. Each motile cell contains a nucleus, two brown plastids and an eye-spot, and bears two cilia, which are inserted at the side, not at one end of the cell. The sporangium dehisces at the apex, the contents are shot out in a gelatinous mass, and after a short interval the motile cells disentangle their cilia and swim away. During their movements one cilium points forward in the direction of movement, and the other trails behind. In the great majority of the Phæophyceæ the motile cells have two cilia each, which are always inserted laterally, a point which distinguishes them from the corresponding bodies in the Green Algæ. These motile cells, which are all of the same size, behave

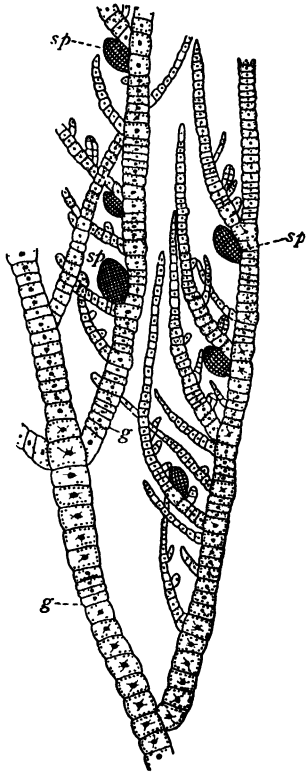


FIG. 78.—General view of part of the thallus of *Ectocarpus*, showing several branches. *sp*, *sp*, plurilocular sporangia, borne laterally on the branches; *g*, *g*, intercalary growing-points, where cell-division is going on. Magnified 56. (R. S.)

as zoospores, *i.e.* each cell on coming to rest surrounds itself with a wall and germinates to produce a new plant that bears plurilocular sporangia only. In British waters, however, the motile cells from the unilocular sporangia may behave as gametes and fuse in pairs, the products of fusion germinating forthwith into new plants that bear both unilocular and plurilocular sporangia.

The *plurilocular* sporangia, unlike the *unilocular* sporangia, are multicellular structures. In British waters they are much more abundant than the *unilocular* sporangia. The *plurilocular* sporangium is divided by numerous cell-walls, longitudinal as well as transverse, into many small compartments (Figs. 78 and 80, A). In each compartment a single motile cell is formed which does not differ obviously from the motile cells in the unilocular organ except that it may be somewhat smaller. The motile cells usually escape from the plurilocular sporangium by an opening at the end, the walls between the different compartments being absorbed, so that the swarming cells pass out, one after the other, through the same aperture.

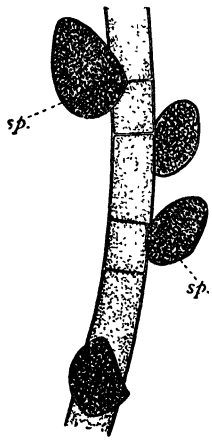


FIG. 79.—Unilocular sporangia (*sp.*) borne laterally on a filament of *Ectocarpus ovatus*. Magnified 300. (After Reinke.)

In plants arising from zoospores and bearing only plurilocular sporangia the motile cells from the latter, all of equal size, behave as gametes and fuse in pairs. After fusion the zygospore develops forthwith into a new plant which often bears both unilocular and plurilocular sporangia, the motile cells from both behaving as zoospores. In British waters, however, the motile cells

from plurilocular sporangia appear usually to behave as zoospores.

It is clear, therefore, that the life-cycle of *E. siliculosus* varies according to locality. Thus, in the Mediterranean some plants bear only plurilocular sporangia, which produce gametes, while other plants have both unilocular and plurilocular sporangia, both of which form zoospores. In British waters, however, as far as is known at present, there is only one kind of plant, which bears both unilocular and plurilocular sporangia, the first producing gametes and the latter zoospores. The difference in behaviour of the same species growing in widely separated localities is of great interest, and is an indication of the

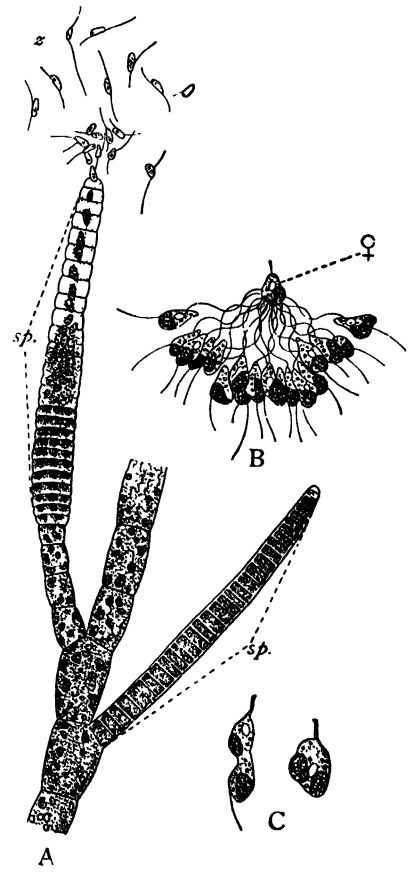


FIG. 80.—*Ectocarpus siliculosus*. A, part of a branch, bearing two plurilocular sporangia (*sp.*), from one of which the gametes (*z*) are escaping. Magnified 330. B, female cell (♀) which has come to rest, with numerous male cells swarming around it. C, two stages of conjugation. B and C magnified 790. (A after Thuret B and C after Berthold.)

plasticity of the developmental phases of some of the lower organisms.

In *Ectocarpus siliculosus* there seems occasionally to be a certain functional difference between the sexes, though in appearance the gametes are all alike. Furthermore, the fusing gametes come from different plants. Certain of the gametes come to rest before the others, and withdraw their cilia. Such a cell, which we may regard as a female, exercises an attraction on the others which are swimming about. They swarm round it in great numbers (Fig. 80, B), and eventually one of the swarmers begins to fuse with the stationary cell. We see that this process is a step in advance of the conjugation of *Ulothrix*, for in *Ectocarpus* one cell is at rest and the other active at the moment of fusion. We may look upon this as the first approach towards the differentiation of stationary ovum and motile spermatozoid.[1]

TYPE XVI

Pelvetia canaliculata

Among the commonest and most conspicuous seaweeds on the coasts of cold and temperate countries are the members of the Order *Fucales*. The species chosen for our type is distinguished from all others on our shores by the position in which it grows, which is always close to high-water mark of the spring tides. The plants are thus only under water for a comparatively short time, not more than a quarter of the day during the spring tides. During the neap tides *Pelvetia canaliculata* is often not covered by the sea, and it may be only splashed by spray. This seaweed is able to bear a state of comparative drought without injury.

[1] In another species, *Ectocarpus secundus*, there is a marked difference in size between the male and female cells.

1. Structure

Pelvetia canaliculata is usually found in abundance on any rocky shore, forming a well-defined band, just below the highest level reached by the spring tides. The plants are only a few inches high (smaller than most of their relatives), and have a forked, flattened thallus

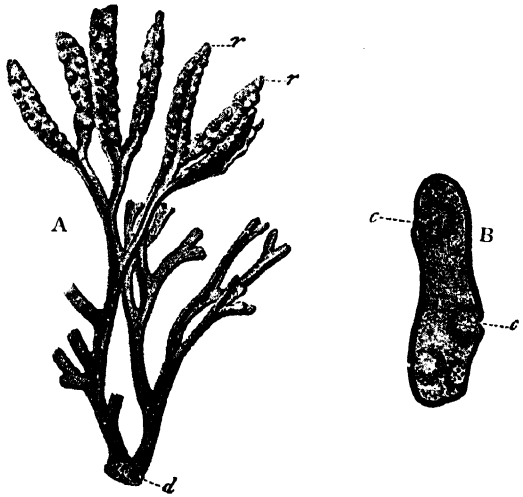


Fig. 81.—*Pelvetia canaliculata.* A, small fertile plant; *d*, attaching disc; *r*, *r*, receptacles, each of which bears a number of wart-like conceptacles. ½ of natural size. B, transverse section of a receptacle, passing through several conceptacles (*c*). Magnified about 4. (After Thuret and Bornet.)

attached to the rocks by a rounded disc (see Fig. 81, A). The thallus shows a conspicuous groove or furrow along one side, to which the species owes its name. In addition to the regular dichotomous branches, adventitious shoots may arise on any part of the thallus.

When the plant is in fructification, which happens chiefly in the late summer and autumn, the ends of

some of the branches become enlarged and studded with wart-like projections, each of which has a minute pore at the top (see Fig. 81, A, *r*). The swollen ends of the branches are called the *receptacles*; the wart-like bodies mark the position of the *conceptacles*, which are cavities in the tissue, containing the organs of reproduction (see Figs. 81, B, and 82).

Pelvetia, though one of the simplest of the Fucales, is a very highly organised plant compared with the

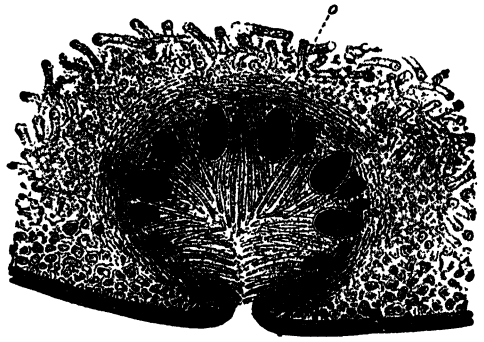


FIG. 82.—Conceptacle of *Pelvetia*, in median section. *o*, one of the oögonia, each of which contains two ova. Surrounding tissues of thallus also shown. Magnified about 10 (After Thuret and Bornet.)

Algæ already considered, and shows a rather complex anatomical structure, which we will now very briefly describe.

The external layer of tissue consists of small cells with abundant plastids, giving their contents a dull brown colour. This superficial layer is no doubt the chief assimilating tissue. Within this we come to large parenchymatous cells, less deeply coloured, and as we approach the middle of the thallus the cells become elongated (cf. Fig. 82). In the lower part of the plant the

elongation of the central cells is so extreme that they form a tangled web of branched filaments. The elongated cells appear to serve the purpose of conducting food-substances, and it is sometimes claimed that the extremities of these cells are perforated, somewhat like the sieve-plates of vascular plants. The filaments of the basal disc and lower parts of the thallus are generally thick-walled. Their function is to strengthen the plant mechanically, and it will be found that the lower portion of the thallus, where these filaments are most abundant, offers the greatest resistance to tearing.

Although it is thus possible to distinguish several systems of tissue in mature parts of the thallus, it must not be supposed that the different layers remain permanently distinct one from another. As a matter of fact the cells of one system constantly give rise to those of another. For example, the outermost assimilating cells divide tangentially, and the inner daughter-cells, thus cut off, contribute to the more internal cortical parenchyma, which appears to discharge the function of storing the assimilated food. Again, the cells of the inner cortex grow in length and may give rise to filaments, thus adding to the bulk of the central tissue. The elements which conduct food materials may subsequently undergo further elongation, thicken their walls, and assume the part of mechanical elements.

In the older parts of the thallus the assimilating layer dies away, and is replaced by a secondary tissue answering the same purpose, produced by the repeated divisions of the underlying cortical cells. Thus we see that the various kinds of tissue, which appear so distinct when fully developed, can be derived the one from the other. Owing to the cell-formation in the superficial and other layers, and to the growth of new filaments

which insinuate themselves among the old, a constant increase in the thickness of the thallus goes on.

True starch is not formed as the result of assimilation ; it is represented by another carbohydrate occurring in granules, but not capable of being stained by iodine.

The growth in length of the thallus takes place with the aid of a definite apical cell, by the division of which all the tissues originate. Such a cell is situated at the apex of each branch, and lies at the bottom of a slit-like depression, which can be detected on examining the tip of the branch with a lens. When branching is to take place, the apical cell simply divides into two by a wall down the middle ; so here we have a true instance of dichotomy, the two branches being on exactly equal terms from their first origin.

Adventitious shoots arise chiefly as the result of accidental injuries. The internal cells lying beneath the wound are stimulated to renewed growth and division, and give rise to a new thallus which may become an independent plant. Thus the Alga ensures itself against permanent loss in consequence of violence, for the damaged parts are replaced by fresh and vigorous shoots. The formation of these new growths, if they become separated from the old plant, affords a simple but effective means of vegetative propagation. The regular reproduction, however, of *Pelvetia*, in common with all other Fucales, is exclusively by the sexual method.

2. Reproduction

As we have seen, each *receptacle* or enlarged end of a branch contains numerous *conceptacles* or cavities in which the reproductive organs are placed. When ripe, the conceptacle is an approximately spherical hollow, communicating with the exterior by a narrow pore (see

Figs. 81, B, and 82). It arises as a depression on the surface of the thallus, the part which is to form the bottom of the hollow becoming arched over by the greater growth of the surrounding tissue. The formation of the cavity is, however, in some cases at any rate, helped by the breaking down of a central cell, so as to leave a gap in the tissue.

In *Pelvetia* the conceptacle contains organs of three kinds: (1) sterile hairs or *paraphyses* arising all over the wall of the conceptacle, with their free ends converging towards the pore (see Fig. 82); (2) branched filaments, on the lower parts of which the *antheridia* are borne; (3) the sessile *oögonia*, which are placed chiefly in the lower half of the conceptacle (see Fig. 82). This species is therefore hermaphrodite, for the organs of both the sexes occur in the same conceptacle. In most other Fucales the plants are diœcious, all the conceptacles of each individual containing organs of the same sex.

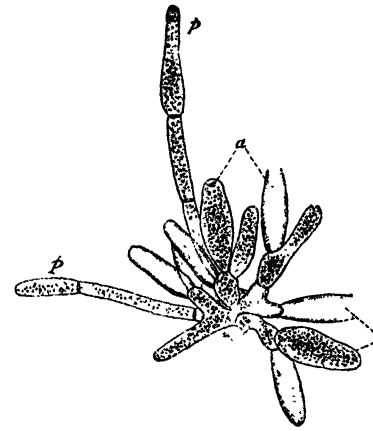


FIG. 83.—Antheridia of *Pelvetia*. *p*,*p*, hairs; *a*, *a*, antheridia, some of which are already emptied. Magnified about 260. (After Thuret and Bornet.)

The antheridia arise as single cells, borne laterally in small numbers near the base of the branched filaments (see Fig. 83, *a*). At first the antheridium, like other cells in Fucales, contains a single nucleus. This undergoes repeated division into two until the total number of sixty-four nuclei is reached. Each of these nuclei

now becomes the centre of a distinct cell, the contents of the antheridium dividing up simultaneously into as many cytoplasmic bodies as nuclei are present. These bodies become *spermatozoids*, each of which consists of cytoplasm, a nucleus, and a plastid ; the latter, however, contains but little colouring matter. The spermatozoids are of oval shape, and bear two lateral cilia of unequal

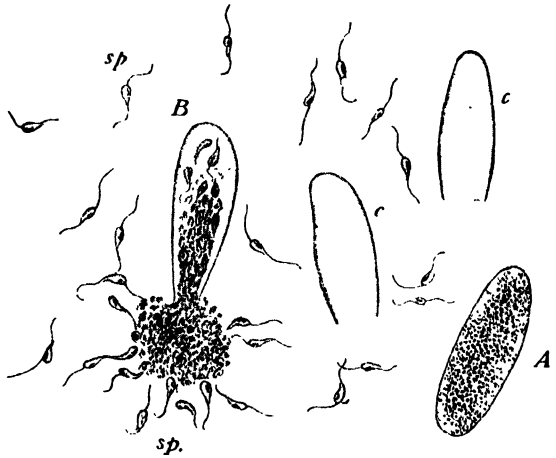


FIG. 84.—Spermatozoids of *Pelvetia*. *A*, unripe antheridium, already freed from outer membrane ; *B*, antheridium opening to emit the biciliate spermatozoids (*sp*) ; *c*, *c*, empty membranes. Magnified about 450. (After Thuret and Bornet.)

length (see Fig. 84, *sp*). The antheridial wall is double, and when the organ is ripe the outer membrane bursts at the top, and the whole contents, which may be already developed into spermatozoids, but are still enclosed within the delicate inner cell-wall, are expelled.

The oögonia are single cells, of large size, seated on the tissue at the base of the conceptacle (Figs. 82 and 85) ; they contain a great many plastids, and turn a very

dark colour as they become ripe. In each oögonium there is at first a single nucleus, which divides successively into two, four, and eight. The cell contents, however, divide into two cells only (see Fig. 85) by a transverse wall. Each of the two daughter-cells has one central nucleus; the remaining six nuclei are expelled from the ova, together with a little cytoplasm. The bodies seen close to the transverse septum in Fig. 86, A, are some of these rejected nuclei. In *Fucus* itself all the eight nuclei are utilised, for the oögonium there divides into eight cells; in another genus (*Ascophyllum*) four cells are formed and four nuclei rejected, while in other genera no division of the cell contents takes place, and of the eight nuclei formed in the oögonium only one serves as the functional nucleus of the ovum.[1]

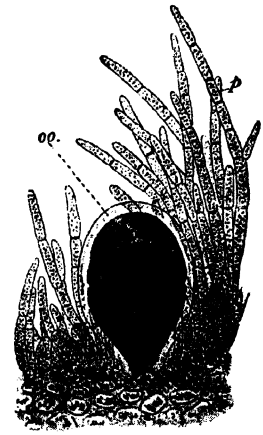


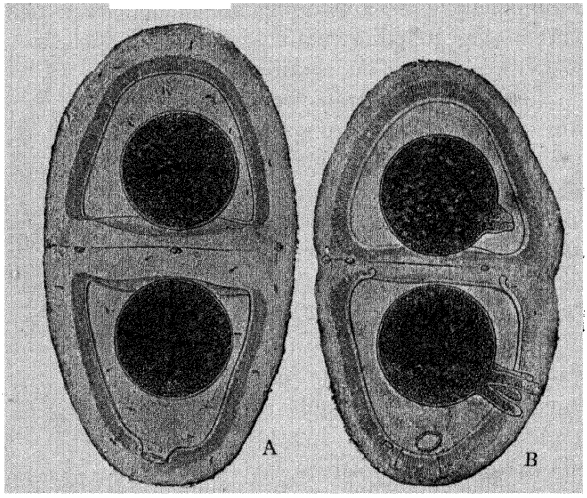
FIG. 85.—Oögonium (*oo*) of *Pelvetia*, already divided to form the two ova. *p*, paraphyses. To the left of the oögonium some antheridia are also shown. Magnified about 110. (After Thuret and Bornet.)

In *Pelvetia*, then, the oögonium forms two ova which are surrounded by a thick and very gelatinous cell-wall showing three distinct layers (see Fig. 86). When ripe, the outer layer of the oögonial wall gives way, and the two ova, surrounded by the thick mucilaginous inner layer of the cell-wall, are set free.

The expulsion of the spermatozoids and ova from the

[1] The fact that a number of nuclei are always formed suggests that the oögonium of the Fucales may have been originally a structure of the nature of a sporangium.

conceptacles generally takes place in *Pelvetia* when the tide has gone down and left the plants exposed to the air, though it may also go on under water. The cavity of the conceptacle is full of mucilage secreted by the hairs which line it. The surrounding tissue presses on the



FIGS. 86, A and B.—A, oöspores of *Pelvetia* beginning to divide immediately after fertilisation. They are still enclosed in the gelatinous inner wall of the oögonium. The small bodies in the gelatinous mass are spermatozoids; the larger bodies near the septum are the rejected nuclei of the oögonium. B, later stage. The oöspores are dividing to form many cells, and are sending out rhizoids. Magnified about 120. (After Thuret and Bornet.)

full conceptacle and forces out the mucilaginous contents through the pore; mixed with this extruded mucilage are the spermatozoids and ova. If we hang up *Pelvetia*, or some other Fucaceous seaweed, freshly taken from the water, we can see the little slimy drops appearing at the pores of the conceptacles; and these drops, if examined

under the microscope, are found to contain spermatozoids or ova or both, according to the diœcious or hermaphrodite character of the species. In *Pelvetia* we should find both organs in the same drop. The spermatozoids are expelled while still enclosed in the inner antheridial membrane; the ova are in pairs, held together by the inner oögonial wall. There are many packets of spermatozoids and many pairs of ova sent out from each conceptacle. As the spray dashes up over the plants with the returning tide, their reproductive cells are washed down from the receptacles, sometimes on to the rocks, sometimes only on to the lower part of the plant itself, where they often come to rest in the groove of the thallus.

It is a constant rule among the Fucales that fertilisation takes place outside the parent plant, after the sexual cells have been set free. The remaining antheridial membrane bursts after expulsion from the conceptacle, and the spermatozoids are at liberty to swim off by means of their cilia (Fig. 84, *B*). In this species, however, the ova remain enclosed within the soft mucilaginous membrane derived from the oögonial wall. In most Fucales this is not the case; the ova are set free as bare masses of protoplasm; the peculiar state of things in *Pelvetia* probably has to do with the long exposure to the air; the mucilaginous envelope protects the protoplasm within from danger of drought.

The spermatozoids during their movements come across the pairs of ova, and swarm around them in large numbers. Some of them make their way into the mucilage, and penetrate to the cytoplasm, which it seems is generally approached at the side, where the two ova are in contact. It has been shown that ultimately only a single spermatozoid succeeds in entering the cytoplasm, and making its way to the nucleus of the ovum. The details of the process have now been thoroughly worked

out, and the fusion of the small male nucleus with the large nucleus of the ovum observed, as shown in Fig. 87, which represents the act of fertilisation in another member of the Fucales. The proof of sexuality has also been afforded by experiment. If the ova are kept apart from the spermatozoids (as can be easily done in the case of the diœcious species) they soon perish, making perhaps some slight attempt at germination, which comes to nothing. If, however, the spermatozoids have access, fertilisation occurs and the result is quite different. The ovum now surrounds itself with a cell-wall of its own, and after a few hours begins to divide. The direction of the first cell-wall formed across the fertilised ovum is said to be determined by light, and to be always at right angles to the incident rays. Other cell-walls follow, and soon the oöspore (which here does not pass through a resting-stage) is converted into a little mass of tissue, but without at first changing its external form. After eight or ten days, several rhizoids begin to grow out at the end away from the light (see Fig. 86, B). They burst through the oögonial wall, which has lasted all this time, and attach the embryo to the rock or whatever else it may be lying

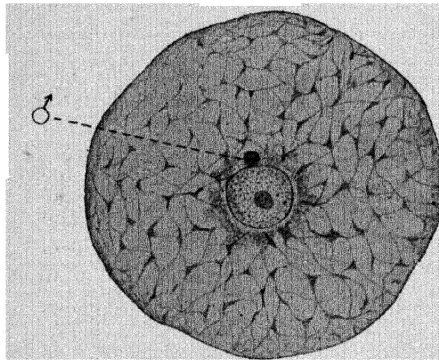


FIG. 87.—Ovum of one of the Fucales (*Ascophyllum nodosum*), seen in section at the moment of fertilisation. ♂, small male nucleus of a spermatozoid, which has traversed the cytoplasm, and is now in contact with the large nucleus of the ovum. The cytoplasm of the ovum shows a distinct foam-like structure. Magnified about 650. (After Farmer.)

upon. The upper part of the embryo now elongates and becomes first cylindrical and then flattened at the free end; a depression soon arises at its apex, in which a definite apical cell appears, and now we have in all essentials a new *Pelvetia* plant fairly started in the world.

In these Algæ the result of fertilisation is a plant just like the parent. There is no kind of asexual reproduction, and therefore no possibility of any real alternation of generations.

We see, then, that in the Order Fucales we have the simplest possible life-history combined with a very perfect form of sexual reproduction. The plants are altogether very highly organised, as shown not only by the elaboration of their reproductive arrangements, but by their whole structure. Some members of the Order bear perfectly distinct and well-formed leaves, and rival the flowering plants in the perfection of their external morphology. This is the case notably in the genus *Sargassum*, of which everybody has heard, from the fact that the plant forms prodigious floating masses in the mid-Atlantic, giving its name to the well-known Sargasso Sea, which is many thousands of square miles in extent. In anatomical complexity also we have seen that even *Pelvetia* approaches the level of the vascular plants. It is well to realise at once that Algæ may attain a very high organisation. On their own independent lines some of them have reached a degree of differentiation not much inferior to that of the higher land plants, with which, however, they have no direct relationship.

C. THE RED ALGÆ (*Rhodophyceæ*)

The great majority of the Red Algæ are seaweeds, though some genera are limited to fresh-water streams.

The marine Rhodophyceæ, though they do not reach the great dimensions of some of the brown seaweeds, are well known to every observer, owing to their beauty of colour and form, and are always especially favourite objects with collectors at the seaside. Most of them flourish rather low down on the shore, especially frequenting the sides of deep rock-pools, while many are only found growing below low-water mark.

In the majority of the Rhodophyceæ a red (phycoerythrin) and a blue (phycocyanin) pigment, soluble in fresh water, accompany and usually disguise the green colour of the plastids. The chlorophyll itself is similar to, if not absolutely identical with, that of the higher plants. The shade of colour, produced by the combination of these pigments, varies much in different species, and in different conditions of the same plant. Sometimes a bright rose colour is the result, sometimes a rich purple, sometimes a reddish brown, while in a few cases so little red colouring matter is developed that the green pigment becomes externally visible.

All the plants which have any good claim to rank as Rhodophyceæ agree closely in their minute organisation, methods of reproduction, and life-history; so that the whole group is a manifestly natural one, though in the degree of complexity of the thallus, and in the elaboration of the reproductive processes, there is a great range of variation. The Rhodophyceæ stand almost completely isolated in the vegetable kingdom as at present known to us. They form a perfectly well-characterised group, which attains a remarkably high development on its own lines, especially as regards the process of sexual reproduction. We shall only be able to describe one representative, and that one of the simpler members of the group as regards vegetative structure.

TYPE XVII

CALLITHAMNION CORYMBOSUM

1. STRUCTURE

The form of the thallus among Red Algæ is subject to very great variations; in some the thallus is finely, in others more coarsely filamentous; in some, again, it is of stouter build and cylindrical form, while in others the whole plant assumes a flattened leaf-like shape, or consists of a short axis, bearing leaf-like appendages.

The type which we have chosen is one of the simplest, the whole plant consisting of a repeatedly branched filament, the main axis of which is comparatively thick, the successive branches becoming more and more slender, while the ultimate ramifications terminate at the tips in delicate hairs (see Figs. 88 and 89). The filament is at first only one cell in thickness throughout. In the lower part of the thallus, however, a peculiar kind of secondary cortex is formed, as the plant grows older; the basal cell of a lateral branch gives rise to delicate filaments, which grow in a downward direction, attach themselves closely to the membrane of the main axis, and eventually form a complete coating over it. This mode of forming a cortex by means of adherent branches is by no means uncommon among filamentous Algæ, both of the red and brown divisions.

Each cell of the thallus contains, in addition to the colourless cytoplasm, a number of plastids (the bearers of the combined pigments) and, at least when young, a single nucleus. The cells communicate with each other by pits in their transverse walls; the pit-membrane is covered on either side with a pad of callus like that in sieve-tubes (see Part I. Ch. I. II *B a*, *a*). Fine strands

of cytoplasm extend through the callus and pit-membrane, thus connecting the contents of the adjacent cells. We see, then, that the protoplasm is continuous in these Algæ, as well as in higher plants.

The growth of the thallus goes on entirely at the apex of the various branches ; each branch terminates in an apical cell, which divides by transverse walls to form the successive segments composing the filament. When a fresh branch is to be formed, an oblique wall is produced in a segment which has just been cut off from the apical cell. By the oblique wall two unequal cells are separated, the smaller of which grows out and becomes the apical cell of the new branch. When a branch terminates in a long colourless hair, its growth is at an end ; these branches therefore are of limited length, and in this respect resemble leaves, while other branches retain their apical cell, and are thus capable of indefinite growth. Hence the thallus of a *Callithamnion* comes to have a regular conformation like that of many higher plants, depending on the relative position of its unlimited and limited branches.

2. Reproduction

a. Asexual

The reproduction of *Callithamnion* and of most Rhodophyceæ is of two kinds, asexual and sexual. The asexual reproductive cells are called *tetraspores*, because they are almost always produced four together in one sporangium. In this case the tetrasporangia occur on very short lateral branches (see Fig. 88, A), the end cell of which swells up and becomes filled with exceptionally abundant protoplasm and plastids, assuming a very dense red colour. The contents then divide up into four spores,

arranged in this particular plant in a tetrahedron (see Fig. 88, A).

The membrane of the sporangium ruptures, and the

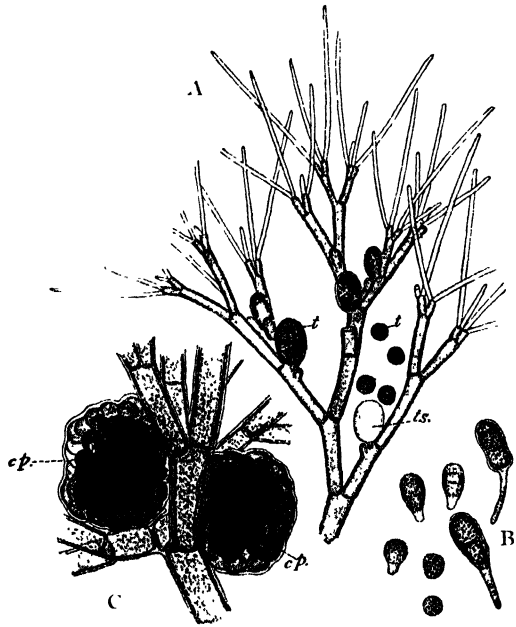


FIG. 88.—*Callithamnion corymbosum.* A, part of an asexual plant, bearing tetrasporangia; the branches terminate in long colourless hairs; *t* (on left), tetrasporangium containing the tetrahedrally arranged spores; *ts*, empty sporangium, from which the tetraspores (*t*) are just discharged. B, germinating tetraspores. C, part of a female plant, bearing two cystocarps (*cp*), both of which are the product of a single procarp. Magnified about 80. (After Thuret and Bornet.)

tetraspores are set free; when they escape they are without any cell-wall, each spore containing a single nucleus. These spores have no cilia, and usually appear to be quite incapable of any spontaneous movements;

no doubt they are disseminated by currents in the water. When a tetraspore comes to rest it forms a cell-wall and germinates, sending out a rhizoid at one end and dividing up at the other to form a filament, as shown in Fig. 88, B. This mode of propagation is almost universal among red seaweeds, but the position of the tetrasporangia and the arrangement of the tetraspores in each vary greatly. The tetraspores form sexual plants, either male or female.

Many Rhodophyceæ are diœcious, and as the tetraspores also are produced on distinct plants, we commonly have three forms of each species,—asexual, male, and female. Sometimes, however, as has occasionally been observed in our type, all these organs occur on the same individual.

b. Sexual

If we examine a male plant we find that the antheridia occur in dense clusters on some of the thallus-cells—usually just below the point where a branch is given off (see Fig. 89). Each cluster is really a little system of densely crowded and very short branches, all springing from the same point. Each terminal cell of all these crowded branchlets becomes an antheridium, and there are so many of these that they form a continuous mass, quite hiding the short branches on which they are borne. It is often easy to recognise the clusters of antheridia in red seaweeds with the naked eye, for they have no pigment, and so appear as white patches on the red thallus. Every terminal cell of the cluster, then, is an antheridium. Its contents round themselves off, becoming free from the cell-wall, which splits open at the end, often detaching a little lid. Then the cell-contents, which have a single nucleus, escape through the opening; they have only a cytoplasmic membrane at first, but no cell-wall. Thus each antheridium produces a single male cell, which in this case is called a *spermatium*. It has no

cilia (in fact cilia are altogether unknown among red seaweeds), but is borne passively along by the movement

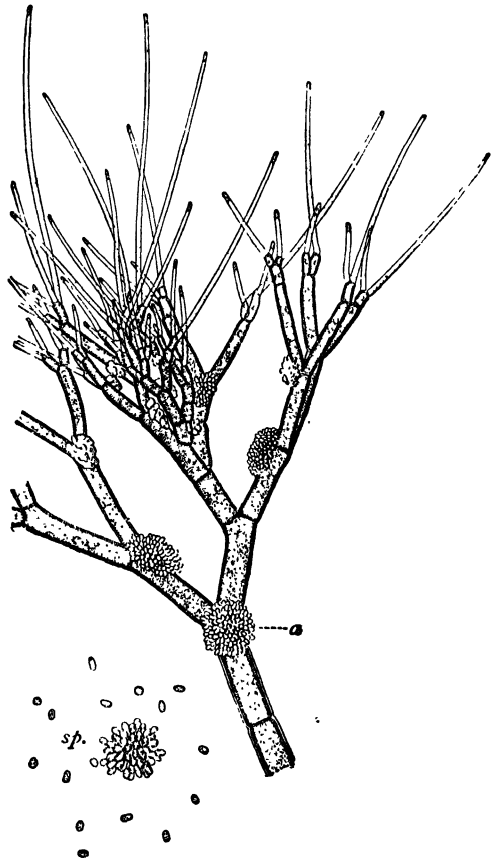


FIG. 89.—*Callithamnion corymbosum*; part of a male plant bearing the clusters of antheridia (*a*). Magnified about 150. *sp*, detached group of antheridia surrounded by free spermatia. Magnified about 240. (After Thuret and Bornet.)

of the sea. Often, after an antheridium has discharged its contents, the cell next below grows up into the empty

cavity, and thus forms a new antheridium inside the membrane of the old one. The spermatia are excessively minute, not more than $\frac{1}{200}$ millimetre in diameter.

We see, then, that the production of the male cells is a fairly simple process; the female structures, however, are much more complicated, and unlike anything we have met with, so far, in any of our types. The whole apparatus destined to form the fruit constitutes a special branch borne laterally on an ordinary cell of the thallus (see Fig. 90). The fertile branch, which is called the *procarp*, consists in *Callithamnion* of six cells, of which four form a curved central filament, while the other two are situated laterally, one on each side. The four-celled central filament arises from one of the two lateral cells. The uppermost cell of the central filament (see Fig. 90, *a*) is called the *carpogonium*, and is prolonged into a slender hair of relatively great length; this is the *trichogyne* (Fig. 90, *t*), or receptive organ. The three cells next the carpogonium remain small, and with the carpogonium form the carpogonial branch; the two lateral cells are the *auxiliary mother-cells*, from which later are produced the *auxiliary cells* which contribute in a very important way to the formation of the fruit. The description of Fig. 90 should be carefully studied, to render the complicated arrangement intelligible. The carpogonium has a single nucleus; the trichogyne which forms the upward prolongation of the same cell has, in this case, no nucleus of its own, but contains a strand of cytoplasm continuous with that of the lower part of the cell; the outer layers of its membrane are gelatinous.

In this condition the procarp is ready for fertilisation. The long trichogyne is specially adapted for receiving the spermatia. The young fruit is generally placed in a sheltered part of the thallus (as, for example, in this case.

among the densely crowded branches of the bushy stem), where its future development is most secure. In such a position, however, it is not readily accessible to the male cells, and consequently we always find in connection with it the hair-like trichogyne, which projects far out towards the exterior, and thus reaches the exposed part of the thallus to which the spermatia are likely to be conveyed by the chance currents of the surrounding water.

When a spermatium happens to reach the trichogyne it adheres to its gelatinous cell-wall, and is thus held fast (see Fig. 90, *s*). In the meantime the spermatium has formed a membrane round its protoplasm. At the point of contact between spermatium and trichogyne the cell-walls are absorbed, and so the contents of the male cell are enabled to enter the receptive organ. All the parts concerned are very minute, but the details of fertilisation have now been completely followed in certain instances. This was first accomplished in *Nemalion*, a genus rather simpler in its arrangements than our type. The nucleus of the spermatium travels down the trichogyne and fuses with that of the carpogonium. So far, therefore, as the act of fertilisation is

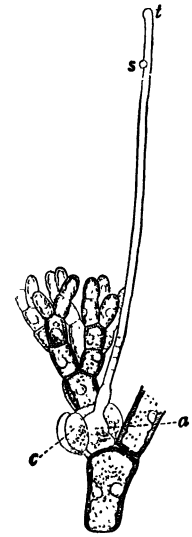


FIG. 90. — *Callithamnion corymbosum*; part of a branch of a female plant bearing a procarp. *t*, apex of the long trichogyne; *s*, a spermatium adhering to it; *a*, basal part of carpogonium; *c*, a cell of the carpogonial branch. The two cells showing to the extreme right and left are the auxiliary mother-cells, which later cut off the auxiliary cells. Magnified 250. (After Thuret and Bornet.)

concerned, the Rhodophyceæ do not differ from other sexual organisms.

The result of fertilisation, however, is not the formation of a single oöspore, but the development of a whole fruit. The fertilised carpogonium is cut off from the trichogyne by a plug of cell-wall, and each auxiliary mother-cell divides unequally by a transverse wall, the upper larger portion constituting the auxiliary cell. The carpogonium divides into a row of four cells and the two end-cells come into close contact with the auxiliary cells on either side; there is an actual union of the contents of the carpogonial cells with the respective auxiliary cells, but the nuclei do not fuse. Each auxiliary cell now divides by a transverse wall (see Fig. 91, *c*); the upper of the two cells in each case becomes a placenta which gives rise to the spores. *Callithamnion* is different from most of the simpler red seaweeds in so far as it regularly forms *two* fruits from each procarp. Each placenta grows out into a dense tuft of threads, so that two groups of cells arise, one on each side of the filament (Fig. 88, C). The groups are built up of a system of short crowded branches, those of each cluster all springing ultimately from the placenta. The whole fruit is enclosed in a gelatinous envelope, and nearly all the cells of the group give rise each to a *spore*, called for

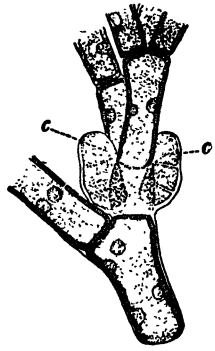


FIG. 91.—*Callithamnion corymbosum*; part of a branch of a female plant, showing the earliest stage of development of the cystocarps (*c*, *c*) after fertilisation. They arise by the growth and division of the two auxiliary cells. The lower cell, formed by the division of the auxiliary mother-cell, can be seen at the base of each group. Magnified 250. (After Thuret and Bornet.)

distinction a *carpospore*, as it forms part of the sexually produced fruit, or *cystocarp*. When ripe, the envelope of the fruit bursts and the spores are set free from their membranes. They are large, uninucleate, deeply pigmented cells, destitute at the time of their escape of any cell-wall. The carpospore nucleus is derived from the product of fertilisation in the carpogonium and not from the nuclei of the auxiliary cells.

The main points in the development are : (1) fertilisation by means of a special receptive organ, or trichogyne ; (2) union of the cytoplasm of the fertilised cell with that of neighbouring cells ; (3) the formation, as the result of this union, of two complex fruits, producing a great number of spores.

Callithamnion occupies an advanced position among the Rhodophyceæ as regards the complexity of its spore-formation. The trichogyne is common to all Rhodophyceæ, but some few members of the group (*e.g. Nemalion* and the fresh-water genus *Batrachospermum*) are simpler, in that the carpogonium directly gives rise to the spores, without any preliminary cell-fusion. In many red seaweeds, moreover, the fertilised carpogonium grows out into a number of threads which undergo repeated cell-fusions with auxiliary cells which in such cases occur on more or less distant branches, with the result that a number of fruits may be formed in consequence of a single act of fertilisation ; these fruits often arise at a considerable distance from the directly fertilised cell.

In some respects the process of sexual reproduction in the Rhodophyceæ is more complex than in any other plants. It offers the advantage that a single spermatium, if it once reaches a trichogyne, may ensure the production of a very large number of spores. In many cases a further complication is due to the fact that a multicellular

envelope grows up around the spores. To the frequent presence of such an envelope, the sexually produced fruit owes its special name of cystocarp.

In so far as the result of fertilisation is the production, not of an oöspore, but of an entire fruit, there is a certain analogy between Rhodophyceæ and Bryophyta ; but in the former the fruit is always in organic connection with the sexual plant, and can therefore scarcely be regarded as a new generation, though it has sometimes been spoken of as the ' sporophyte,' whereas in the Mosses the sporogonium always remains distinct from the gametophyte, though dependent upon it. It is improbable that the Rhodophyceæ have any direct relation with the Mosses, or with any of the higher plants. At the same time it is quite likely that the tetraspores of the Red Seaweeds may really be homologous with the spore-tetrads universally present in the Archegoniate series.

The carpospores germinate in precisely the same way as the asexual tetraspores, but give rise to plants bearing tetraspores. Red seaweeds are difficult to cultivate successfully, and our knowledge of their life-history is still limited ; there is undoubtedly a regular alternation of asexual (tetrasporic) and sexual individuals in many species, although this is not invariably the case.

D. THE CYANOPHYCEÆ

TYPE XVIII

Nostoc

There remains to be considered a group of rather obscure plants of simple structure, which resemble the Algæ in their habit and mode of life, and are therefore best described in this place, though their real relationships are open to doubt. Of the Cyanophyceæ some are

terrestrial, some aquatic, occurring both in fresh water and in the sea. Many of the Cyanophyceæ are bluish-green in colour, hence these organisms are sometimes called the Blue-green Algæ. The representative of the group which we have chosen—a species of *Nostoc* (see Fig. 92)—is filamentous. The threads are associated in colonies held together by the soft gelatinous outer walls of the cells and by mucilage secreted by the cells. Such colonies often form conspicuous masses of bluish-green or yellowish jelly on poor ground, especially in wet weather. Within the mass the filaments wind about in every direction. The cells of which they are made up are rounded, so as to give the whole thread a beaded appearance.

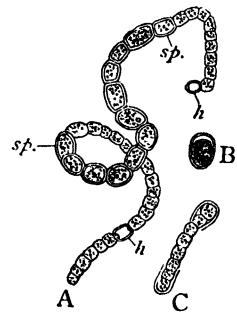


FIG. 92.—*Nostoc Linckii*. A, part of a filament; *h*, *h*, heterocysts; *sp.*, *sp.*, spores. B, isolated spore beginning to germinate. C, young filament formed from a spore, the burst cell-wall of which is shown at the ends. Magnified 470. (After Bornet.)

The ordinary vegetative cell has a thin inner cell-wall, which is alone visible in Fig. 92, A, the confluent gelatinous layers scarcely showing under the microscope owing to their transparency. The interior of each cell is full of protoplasm, which is coloured in its peripheral part. No definite plastids have been found to exist in Cyanophyceæ, nor has the presence of a nucleus been finally determined, though in certain cases a colourless central body certainly exists, which resembles a nucleus in that it contains a chromatin-like substance. In the protoplasm are numerous granules.

Many species float on the surface of water, where they sometimes appear rather suddenly in vast quantities

in ponds and lakes, covering many acres with a bluish-green scum. In these floating species *gas-vacuoles* are present in the cells, that is to say, little cavities in the protoplasm containing a gas, the nature of which has not been determined. The function of these gas-vacuoles is obscure, but they make the plant lighter and perhaps assist it to float.

The apparent simplicity of the histological structure, due to the want of well-defined nuclei and plastids, is the chief reason why the Cyanophyceæ are often separated from the Algæ. The colouring matter contains a blue pigment (phycocyanin), a red pigment (phycoerythrin) but different from the phycoerythrin of the Rhodophyceæ, and some of the constituents of ordinary chlorophyll. The tint varies greatly in different forms, but we never find the pure green of chlorophyll. In *Nostoc* the filament is interrupted at intervals by larger cells with better defined cellulose walls; they usually appear almost devoid of contents and colourless, but their function is at present entirely obscure. These cells are called the *heterocysts* (Fig. 92, A, *h*), and are characteristic of *Nostoc* and its nearer relations. Sometimes the filaments break across at the heterocysts, and the short rows of living cells between them become isolated. These detached filaments (called the *hormogonia*) are capable of creeping movements, though *how* they move is quite unknown. They escape from the gelatinous mass, and start new colonies for themselves.

This is one mode of propagation. Another is by means of resting-spores, formed directly from some of the vegetative cells, which grow larger than the rest, accumulate more abundant protoplasm, and surround themselves with a thick cell-wall (Fig. 92, A, *sp.*). The spores (Fig. 92, B) can pass through a resting-stage, and endure drought; when water is supplied they

germinate, forming new filaments (Fig. 92, C). The vegetative phase can also withstand desiccation as in dry weather the jelly-like masses shrivel and become hard.

Such is the simple history of *Nostoc*. Neither in this genus nor in any of the Blue-green Algæ has any kind of sexual reproduction been observed. The plants of this class must rank, according to our present knowledge, as among the lowest members of the vegetable kingdom, the only others which are equally simple being the Bacteria (to be subsequently described).

The Cyanophyceæ are not infrequently among the first colonisers of newly exposed rock and soil surfaces. It is perhaps significant that certain species have recently been shown to possess the power of fixing atmospheric nitrogen, which they use in their own metabolism. This is an exceptional property which they share with certain Bacteria (see pp. 282, 283).

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. Among Fungi, on the

other hand, there is a real analogy, if not relationship, throughout the entire class (if we leave a few doubtful cases out of consideration)—so that here the common physiological character coincides with a common type of structure. We must not, however, suppose that all Thallophyta which lead the life of parasites or saprophytes are necessarily Fungi. Towards the close of this book we shall have to consider two such groups which cannot be classed under this head.

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 the 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, which are constantly attacked by "mould." Hence, 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.

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 for food, 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. Masses of dead material would otherwise accumulate to such an extent

as to interfere seriously with the life of succeeding generations. Fungi and other saprophytes (notably the Bacteria) bring about the decomposition of dead organic matter, use the products for their own nutrition, and ultimately convert its substance into simple inorganic bodies (such as ammonia and carbon-dioxide), thus rendering it available for the nutrition of green plants, and, through them, for the support of other organisms.

We will begin our illustrations of the Fungi with two examples of a simple type, representing a group which is of special scientific interest, from its evident analogy with certain of the Algæ.

TYPE XIX

PYTHIUM DE BARYANUM AND PERONOSPORA PARASITICA

A. PYTHIUM DE BARYANUM.

We have chosen as our first type of Fungi a genus which much reminds us of the Algæ, showing an unmistakable analogy with *Vaucheria*. 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*; the latter name is given to the filaments of Fungi in general. These hyphæ are *non-cellular*, just like the filaments of a *Vaucheria*. The inside of the hypha is occupied by vacuolated cytoplasm, in which numerous nuclei are embedded. Unlike *Vaucheria*, however, *Pythium* has no chlorophyll and no plastids. Neither is starch formed, either in this genus or in any other Fungus. *Glycogen* is the common food reserve in Fungi. 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.

In the First Part of this book (Ch. III. 11) we learnt that there are chemical bodies in plants called *enzymes* which

have the power of changing the constitution of other organic substances, converting solids into liquids, and indigestible substances into such as are available for nutrition. The example we specially mentioned was *diastase*, which converts starch into sugar, but numerous other *enzymes* also occur in plants. Now 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 an enzyme or a toxin 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 poisonous substance 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, the *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 into the open air. They there form a number of spherical *sporangia* which are terminal, being seated on the ends of short branches or of the main hyphæ (see Fig. 93, 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. 93, 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 membraneless cells 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.

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 an enormously 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. Evidently this allows of propagation taking place, even though there should not be water enough to float the zoospores. The same thing happens in the closely-allied genus *Phytophthora*, to which the Fungus causing Potato Blight (*P. infestans*) belongs. Here, and also in the allied genera, *Plasmopara*, *Bremia*, and *Peronospora*, the sporangia always become detached from the hypha which bears them, before germination

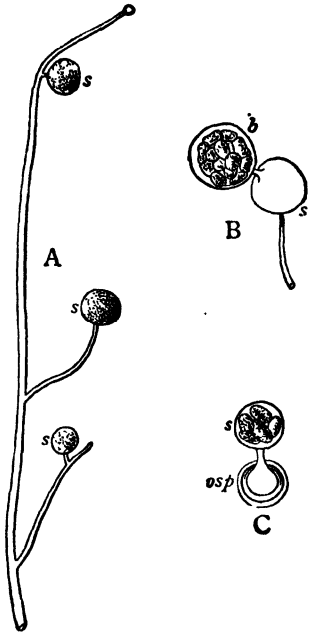


FIG. 93.—*Pythium*. A, branch of the mycelium, bearing three zoosporangia (*s*). Magnified 145. B, zoosporangium (*s*) discharging its contents (*b*), which are still enclosed in the enlarged papilla, but have already divided to form the zoospores. Magnified 145. C, germinating oöspore (*osp*) forming an asexual sporangium (*s*). Magnified 300. (After De Bary.)

(whether by the development of zoospores, or by the direct formation of a hypha) takes place. The illustrations in Fig. 94 are taken from different species of these genera.

In *Pl. nivea* (parasitic on Umbelliferæ) the contents of the sporangium divide up at once into a number of

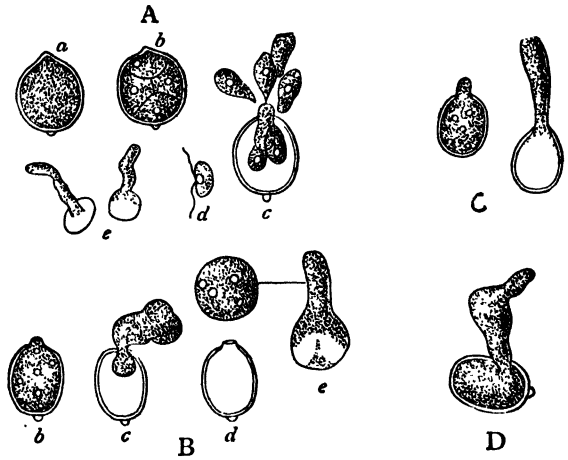


FIG. 94. — Germination of the sporangia in *Plasmopara*, *Bremia* and *Peronospora*. A, *Pl. nivea*; *a*, *b*, *c*, stages in the formation of zoospores; *d*, free biciliate zoospore; *e*, zoospores germinating. B, *Pl. densa*; *b*, commencement of germination; *c*, expulsion of undivided contents; *d*, empty sporangium; *e*, first formation of a hypha from the contents. C, *B. Lactucæ*; direct germination through the apical papilla. D, *Per. Radii*; direct germination, hypha formed laterally. Magnified 400. (After De Bary.)

biciliate zoospores, which escape by the opening of the terminal papilla (Fig. 94, A). In *Pl. densa* (Fig. 94, B), growing on Scrophulariaceæ, the protoplasm of the sporangium is expelled entire through the apical opening without dividing into zoospores; it surrounds itself with a new cell-wall, and germinates directly, to form the

mycelium of the next generation. In *B. Lactucæ* (Fig. 94, C) (which infests Lettuces and their allies) a further step is taken ; the contents do not escape at all, but the sporangium simply puts out a hypha which arises at the apex. Lastly, in *Per. Radii* (occurring on flower-heads of certain Compositæ), with which the majority of species of *Peronospora* agree, the apical opening has ceased to be functional, and the hypha grows out laterally (Fig. 94, D). In these latter instances the sporangium has, in fact, become a *spore*. Such asexual spores of Fungi, germinating directly, bear the name of *conidia*.

We will now return to our type *Pythium*. Zoospores and conidia 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. 95, 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. 95) 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.

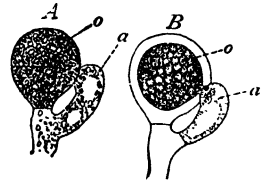


FIG. 95. — Fertilisation of *Pythium*. *A*, early stage; oögonium (*o*) and antheridium (*a*) still immature. *B*, moment of fertilisation. The contents of the antheridium (*a*) are passing through the fertilising tube, to unite with the ovum (*o*). Magnified 800. (After De Bary.)

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 transverse walls may serve the purpose of keeping it where it is wanted.

The protoplasmic contents of the antheridium, like those of the oögonium, undergo a severance into a central fertile portion and an external layer of periplasm.

and here also it is the former alone 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,—another point in which the adaptation to a terrestrial habit of life has involved the disappearance of motile reproductive cells. The antheridium sends out a short branch, the *fertilising tube*, which penetrates the wall of the oögonium, and reaches the ovum (Fig. 95). 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. 95, *B*). The whole process can be directly followed with ease, under a 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 now established that only a single nucleus passes over with the male protoplasm, and unites with that of the ovum.

As the result of 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.

The germination of the oöspore takes place after a long interval, and only when it is brought into contact with water. The process shows very remarkable 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. 93, *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.

These are differences to which considerable systematic importance would be attached in other groups of plants; here the different modes of germination are not even constant for the species, but appear to depend partly on the nutrition, direct germination often taking place when food is abundant, while under less favourable conditions zoospores are formed at once, thus allowing additional chances of a suitable habitat being reached.

Pythium and its allies are more like Algæ than most other Fungi; in fact they were once themselves placed in the former class, and it is evidently with non-cellular Algæ of the type of *Vaucheria* that they have the closest analogies. In histological structure the two genera are almost identical, if we leave out of account the chlorophyll-bodies, which *Pythium* has no need of in its parasitic or saprophytic mode of life. There are great differences, however, between the zoospores of *Pythium* and those of *Vaucheria*. In the reproductive processes there are various deviations from the aquatic type, the most important being the suppression of the spermatozoids, and the gradual replacement (only just indicated in *Pythium*, but more marked among its allies) of zoosporangia by directly germinating conidia. As we advance towards the higher Fungi we shall find the alga-like characters dropping more and more out of sight.

B. PERONOSPORA PARASITICA

1. Structure and Mode of Life

This fungus is closely related to *Pythium de Baryanum*, but its mode of life is entirely different, as it does not 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 inflorescence. 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 *hypertrophy* 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. 95*). 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.

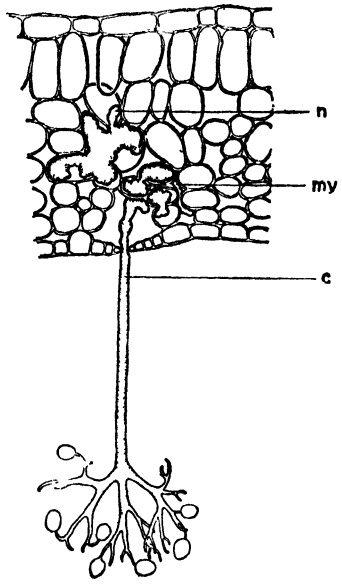


FIG. 95*. — *Peronospora parasitica.* Vertical section of leaf of Shepherd's Purse attacked by fungus. *h*, haustorium; *my*, mycelium; *c*, conidiophore. Magnified 160. (R. W. Marsh.)

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. 95*). 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.

b. Sexual

After the development of conidiophores and as the host tissues become senile, sexual organs, similar to those

of *Pythium*, may be formed on the mycelium in 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.

TYPE XX

Pilobolus crystallinus

Among the Algæ we found in some of our types (as, for example, in *Œdogonium* and *Vaucheria*) a well-marked process of *fertilisation*, in which the cells taking part in the formation of the oöspore showed a distinct difference of sex. In others, however, namely, in *Ulothrix* and *Spirogyra*, union was found to take place between two essentially similar cells, each having an equal share in the act of *conjugation*, with the resulting formation of a zygospore. Both these modes of sexual reproduction are represented also among the Fungi. *Pythium* and *Peronospora* afforded examples of fertilisation; the group to which they belong bears the name of the *Oömycetes*. We are now about to describe a form in which the sexual act is one of *conjugation*; the Fungi in which this process prevails are called the *Zygomycetes*.

A large proportion, though by no means all, of the

Oömycetes are parasites on living plants or animals. Among the Zygomycetes parasitism, though it occurs, is rare; the majority are of saprophytic habit, and to this group many of the commonest "moulds" belong.

We have chosen as our type a little Fungus which is often found growing on the dung of herbivorous animals. In spite of its disagreeable habitat, *Pilobolus*, and especially the species *P. crystallinus*, is a decidedly pretty object. The part of the plant which alone rises above the surface of the substratum and so meets the eye, consists of the stalks bearing the asexual sporangia. Each of these stalks is about a quarter of an inch high, and swells up near the top into a neat little crystalline globule, surmounted by a kind of black cap, which is the sporangium itself (see Fig. 96, A). These facts will enable us to recognise the plant. We will now consider its structure more in detail.

1. Structure

The mycelium or vegetative thallus of *Pilobolus* and its allies is made up of repeatedly branched hyphæ, which spread in all directions through the substratum. Histologically these hyphæ have the same structure as in the Oömycetes; they are without transverse walls, at least in the vegetative condition, and their protoplasm contains very numerous small nuclei, the whole plant being a non-cellular but multinucleate organism. Thus this order betrays an unmistakable analogy with Algæ of the non-cellular type, and therefore Oömycetes and Zygomycetes are grouped together in one class, under the name of *Phycomycetes* or alga-like Fungi. The group to which *Pilobolus* belongs has, however, departed much further from the aquatic habit than the Oömycetes have, for the plants are thoroughly adapted to a terrestrial mode of life, and the power of forming zoospores is altogether lost.

2. Reproduction

a. Asexual

The most abundant means of propagation is by asexual spores formed in sporangia. For the purpose of spore-formation certain of the hyphæ grow out into the air, and assume an upright position. The apex of the aerial hypha enlarges to form a nearly spherical sac, into which most of the protoplasm travels from below. This sac is cut off from the stalk by a transverse cell-wall, and becomes the sporangium (see Fig. 96). Its contents divide up ultimately into a large number of round cells, each of which surrounds itself with a cell-wall and becomes a spore (see Fig. 96, E). A hypha which bears a sporangium is called a *sporangiophore*. We see, than, that in this family the sporangium, insetad of forming zoospores, as in the last group, gives rise to motionless spores with cell-walls. This is the typical method of asexual spore-formation in these moulds. We will now consider the special adaptations which are characteristic of our type *Pilobolus*.[1]

The upper end of the stalk just below the sporangium swells up into a bladder much larger than the sporangium itself, and a second bladder is often formed in the lower part of the hypha (Fig. 96, B). The lower of these two bladders is separated by a transverse wall from the rest of the mycelium; the upper is bounded above by the wall which marks off the sporangium. The whole stalk between the two transverse walls constitutes a water-reservoir, in which a high hydrostatic pressure is set up, so that drops of liquid often exude through the membrane (Fig. 96, A, *st*). Owing to this pressure, the wall bounding the sporangium becomes bulged into its cavity, forming what is here called the *columella*

[1] In the natural substratum sporangia arise and are discharged daily for several days in succession.

(Fig. 96, E, *c*). The wall of the sporangium itself is not uniform throughout; the upper part is thickened and

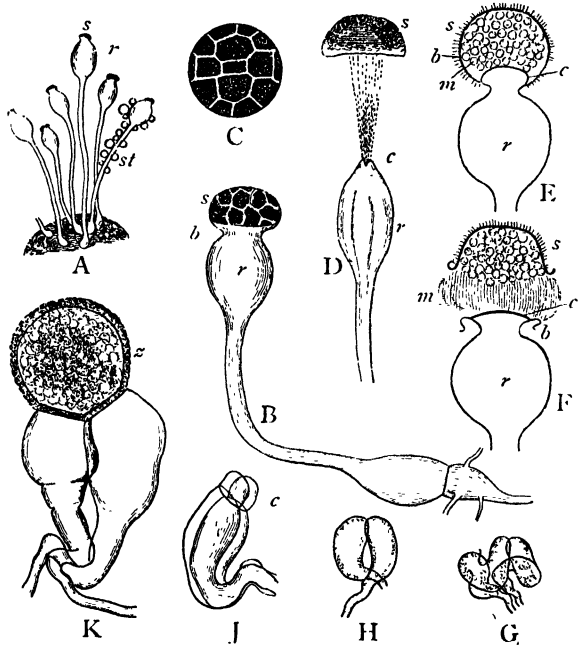


FIG 96.—*Pilobolus*. A, group of sporangiophores; *st*, stalk; *r*, reservoir; *s*, sporangium. Magnified 5. B, hypha and sporangiophore; *r*, reservoir; *s*, *b*, sporangium. Magnified 15. C, sporangium in surface-view. Magnified 15. D, sporangium (*s*) thrown off by bursting of reservoir (*r*); *c*, columella. Magnified 15. E, reservoir (*r*) and sporangium (*s*) seen in section; *b*, thin part of wall; *m*, mucilaginous layer; *c*, columella. F, the same, when the mucilage swells. Magnified about 25. G and H, mycelial branches preparing for conjugation. Magnified 120. J, later stage; *c*, the conjugating cells. Magnified 120. K, after conjugation; *z*, the zygospore. Magnified 120. (After Zopf and Van Tieghem.)

cuticularised, and bristles with crystals of calcium oxalate, while the lower part adjoining the columella remains thin. Inside the lower part of the sporangium

is a mucilaginous layer derived from its protoplasm; when the sporangium is wetted, this mucilage takes up water and swells, bursting the delicate cell-wall, and so freeing the upper portion of the sporangium which contains the spores (Fig. 96, F). The pressure on the upper surface of the columella is thus removed, and no longer balances that of the liquid in the reservoir below; consequently the columella bursts, and a jet of cell sap is ejected from the reservoir, driving the sporangium and spores violently before it (Fig. 96, D). The sporangium may thus be hurled to a great distance, amounting it is said to more than a yard in some cases. Hence the name of the plant, which means "a thrower of missiles." The sporangium, with the wall outwards, sticks to any object which it happens to hit, owing to the mucilage which still clings to it. The sporangiophores are positively phototropic, *i.e.* they bend towards the source of light; the sensitive region is the base of the sub-sporangial swelling, where there is an accumulation of orange pigment. Thus the sporangia tend to be directed towards open spaces, and in nature they are often shot forth on to grass surrounding the dung. The spores are eaten with the grass by herbivorous animals and become disseminated with the dung. Passage of the spores through the body of the animal facilitates germination. When the spores from the sporangium germinate they reproduce the ordinary form of the *Pilobolus* plant.

Other modes of propagation are occasionally observed. If the mycelium grows in a liquid containing plenty of organic food, the hyphæ divide up by transverse walls into numerous cells, which may increase in number by budding, each cell putting out a short branch, which becomes separated from the parent. This is called the *oidial* condition. When food is scanty, some of the cells

produced by transverse division of the mycelium may acquire thick walls, and pass into a resting condition. These thick-walled cells are called *chlamydospores*, and, like the oidia, germinate and form new mycelia when conditions are favourable.

b. Sexual

More important for us is the sexual reproduction, which in *Pilobolus* and many of its relatives takes place but rarely, though in some other members of the group it is a frequent means of propagation. Sexual organs may be formed in *Pilobolus* when some cause hinders the development of the sporangia. It has been found that conjugation may be induced by infecting the aërial hyphæ with a parasitic Fungus (which happens to be a relative, for several members of the group prey upon other members). The parasite hinders the formation of the asexual spores, and the plant is thus led to adopt the other method of propagation, which results in the formation of resting-spores capable of waiting until the bad times are over.

When conjugation is about to take place, two neighbouring hyphæ of the mycelium enlarge, and become club-shaped (Fig. 96, G and H). The swollen portions grow upright, and lay themselves together side by side, accumulating at the same time a large quantity of protoplasm in their interior. The ends of the conjugating hyphæ are next cut off by cell-walls (Fig. 96, J). The terminal parts thus separated, which are the richest in protoplasm, come into close contact, and the cell-walls separating them are absorbed. The protoplasm of the cells now runs together into one mass, the numerous nuclei uniting with one another in pairs, and the two cells completely fuse into a single *zygospore*, which rests upon the two enlarged hyphæ, called the suspensors

(Fig. 99, K, *z*). The zygospore grows to a relatively great size, surrounds itself with a very tough and thick cell-wall, and forms a quantity of oil in its contents. We see that the process is one of perfectly typical conjugation, the two cells concerned taking an exactly equal part in the production of the zygospore. It has recently been shown that in many of the Mucorales (to which *Pilobolus* belongs) there is a physiological differentiation of sex, definite sexual " strains " existing, which will alone conjugate with one another, while hyphæ of the same strain will not fuse sexually among themselves. A fungus which exists in the form of two strains sexually differentiated physiologically from one another is said to be *heterothallic*, in contrast to *homothallic*. *P. crystallinus* is now known to be heterothallic.

After a long period of rest, the zygospore, if moistened and kept at a suitable temperature, germinates. The germination is best known in an allied genus, *Mucor*. The zygospore puts forth a germ-tube which may grow out at once into a new mycelium, especially if food material is abundant, but more frequently the germ-tube proceeds without delay to form an asexual sporangium, the spores in which ensure speedy dispersal.

The Zygomycetes, so far as their sexual reproduction is concerned, stand on a lower level than the last group. On the other hand, they are more fully adapted to a terrestrial mode of life than the Oömycetes. We saw in the case of *Pythium* and its allies how a transition can be traced from the sporangium to a single conidium, germinating directly. A somewhat similar gradation is to be followed among the immediate relations of *Pilobolus*. Some of these produce, in addition to the typical large sporangia, very small sporangioles, containing very few spores, or even only one. In other species sporangioles only are known, and these become detached bodily from

the supporting hypha, and behave like single conidia. Thus in the Zygomycetes, as in the Oömycetes, a succession of steps leads from the typical sporangium to the simple conidium—one of the most characteristic forms of reproductive cell in the Fungi.

TYPE XXI

Sphærotheca Humuli

We now come to the higher Fungi, an immense group of plants, which have become completely adapted to every conceivable variety of parasitic and saprophytic life, and no longer show any clear trace of analogy with the Algæ. While differing among themselves in every other respect, they agree in possessing a septate, multicellular mycelium, with apical growth of the hyphæ of which it is built up.

Our present type is one of the simplest representatives of the great family of the *Ascomycetes*, which are characterised by possessing spore-forming bodies, somewhat like sporangia, of very definite size and form (called *asci*), in the interior of which a definite and usually small number of spores are produced, the number being regularly some multiple of two, usually eight. In this respect, as in many others, they differ from the Phycomycetes, where, as we have seen, the number of spores formed in a sporangium is quite indefinite, and often very large. The whole problem of the real relation of the Ascomycetes to the simpler families of Fungi is still unsolved.

We will proceed at once to the description of our type, which will serve to give us an elementary idea of the main facts in the structure and development of this important and difficult group of plants.

1. Structure

The species of *Sphærotheca* and its nearer allies (forming the family *Erysiphaceæ*, so named after its largest genus *Erysiphe*) are all 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. The mycelium, as in all the higher Fungi, is multicellular, consisting of branched chains of cells, each of which has a single nucleus, though in some allied Fungi the cells are multinucleate. 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

It is at the points where two hyphæ cross or come into contact that the fruits originate. Each of the adjoining hyphæ sends out an upright branch; the one

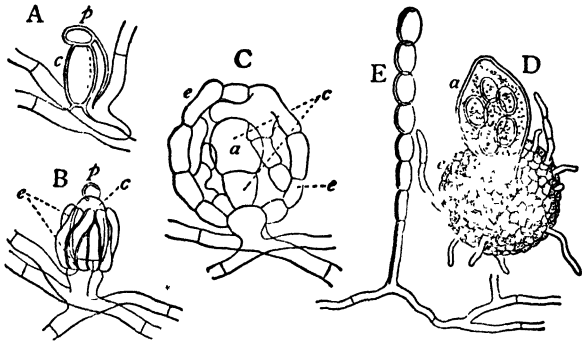


Fig. 97.—A–C, *Sphærotheca Humuli*. A, early stage in formation of fruit; *p*, antheridium; *c*, ascogonium. B, more advanced; *p*, antheridium; *c*, ascogonium; *e*, enveloping hyphæ. C, ripening fruit in section; *c*, ascogonium, from which the young ascus (*a*) is now developed; *e*, *e*, enveloping hyphæ, forming perithecium. D and E, *S. pannosa*; D, ripe perithecium (*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.)

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 97, 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*, and that a true act of fertilisation takes place. According to the investigations referred to, 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 unites with the nucleus of the ascogonium. In the case of *Sphærotheca* and some of its allies these facts are now well established, so it is evident that, in many Ascomycetes at any rate, the development of the ascus-fruit is preceded by a sexual process quite comparable to that of the Oömycetes (cf. p. 222). In other Ascomycetes reduced forms of sexual fusion occur, comparable to those observed in apogamous Fern-prothalli (see p. 74).

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) increases in size, and becomes the ascus. It contains two nuclei, which fuse into one and then divide repeatedly, giving rise to eight daughter-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. 97, 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 *peri-*

thecium; some of its superficial cells grow out into long hairs (see Fig. 97, D). The ripe perithecia are visible to the naked eye, as little black dots in the mycelium on the surface of the diseased leaf.

The hard perithecium 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 perithecium (Fig. 97, 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 perithecium contains several asci (the product of a single ascogonium), instead of one only.

Our plant has another means of reproduction, by conidia (see Fig. 97, E), the formation of which precedes that of perithecia. 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, while, as we have seen, the ascus-fruits are specially adapted for the winter rest. 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. In some allies of *Sphærotheca*, as in the Vine mildew, the conidial fructification was for many years the only one known.

Sphærotheca represents the course of development of an Ascomycete in almost its simplest form. It is not always the case that the ascogonium produces merely a single ascus ; in many Ascomycetes a very large number are formed ; in certain cases it has not been found possible to refer the origin of the asci to any definite ascogonium. There is always a fusion of nuclei in the young asci. In *Sphærotheca Humuli* two nuclear fusions occur in the life-cycle, and this is true of other Ascomycetes. In some of these Fungi, however, the only nuclear fusion which occurs is that in the young asci.

The formation of a completely closed fruit around the ascus or asci is characteristic of the Family (Erysiphaceæ) to which *Sphærotheca* immediately belongs. In the majority of the Ascomycetes, the fruit is more or less open, either having a small pore at the apex, or taking the form of a widely open cup or disc. Our next type will afford an example of the form of fruit last mentioned.

TYPE XXII

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.

The particular plant we have chosen to represent this group is a true Discomycetous Fungus 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 not 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 only live 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.

Xanthoria parietina is described as a foliaceous Lichen

because its thallus has a flat, much lobed, leaf-like form (Fig. 98). 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 rhizoids, arranged in dense tufts, which perform the functions of roots.

The anatomical structure of the thallus is shown in vertical longitudinal section in Fig. 99. 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 *plectenchymatous* 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.

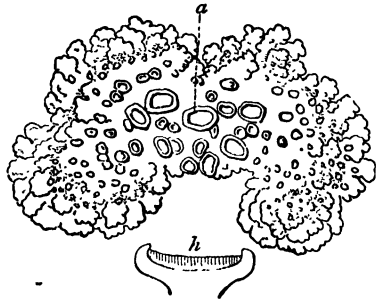


FIG. 98.—*Xanthoria parietina*; thallus seen from above. *a*, apothecia, of which the ripest are near the middle. Natural size. *h*, section of apothecium, showing the hymenium. Magnified about 5. (After Lauder Lindsay.)

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 rhizoids. The latter develop as contiguous outgrowths from the cortical hyphæ. The extremities of the rhizoids broaden out and form flat discs, which secrete mucilage and attach themselves firmly to the substratum.



FIG. 99.—*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.)

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 the division of the protoplast into a considerable number of separate cells (Fig. 99*), which become 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.

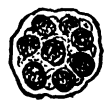


FIG. 99*.—*Xanthoria parietina*. Gonidium showing mode of division. Magnified 600. (O. V. Darbishire.)

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. It is possible also that the gonidia may obtain some of their carbon from certain organic compounds arising from the metabolism 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. Of late years, however, evidence has accumulated, which proves conclusively that the gonidia do not belong to the same plant with the hyphæ, but that they are distinct organisms, identical with definite genera and species 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, and mutually dependent one on the other for certain essential services.

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*,[1] 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

[1] Sometimes called *Trebouxia humicola*.

on their own account, just like their fellows which have never been in bondage. More recently it has been found possible to raise the fungal constituent of a Lichen by growing its spores in a food solution, which, as Algæ are absent, must of course contain organic food substances. In this way a small thallus can be produced, but it *never contains any gonidia*. Thus the fungal as well as the algal constituent can, under suitable conditions, live by itself.

Most conclusive of all, however, is the actual *synthesis* of a Lichen, that is, the building up of a new plant out of the Fungus and its appropriate Alga. This has been observed in the case of our type, and Fig. 100 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. 100, 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. 100, 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. 100 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 devouring Fungus, just as a Cress seedling is preyed upon by *Pythium* or a Hop plant by *Sphærotheca*. This does not, however, seem to be the real condition of affairs. The Alga is not, on the whole, injured when the Fungus

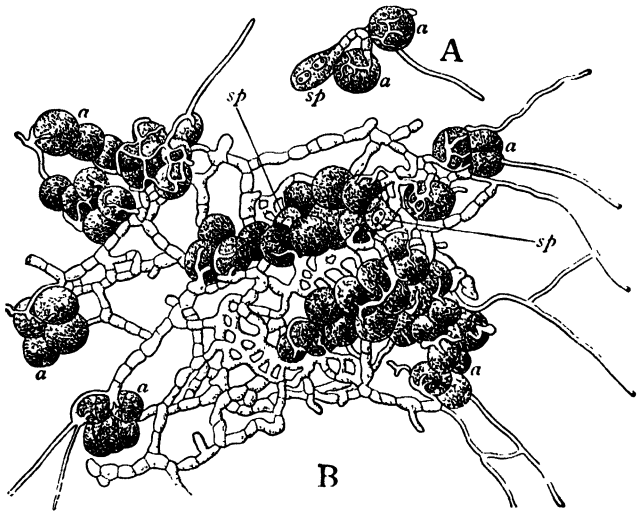


FIG. 100.—*Xanthoria parietina*; building up of the Lichen out of the Alga and Fungus. A, germinating ascospore (*sp*); the hyphæ have seized upon two cells (*a*, *a*) of *Cystococcus humicola*. B, more advanced stage; *sp*, *sp*, ascospores which have produced a web of hyphæ, enveloping the *Cystococcus* cells (*a*, *a*) in every direction. Magnified about 400. (After Bonnier.)

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 chlorophyll-bodies, 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. In many Lichens there are definite pores in the cortex, facilitating the gaseous interchange between the atmosphere and the gonidial layer. On the other hand, the rhizoids 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.

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 to the air 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.

The ascus-fruits of *Xanthoria parietina* are conspicuous to the naked eye as flat, shield-like discs on the upper surface of the thallus, generally of a rather deeper orange colour than the rest of the plant (see Fig. 98). 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. 98 and 101).

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;

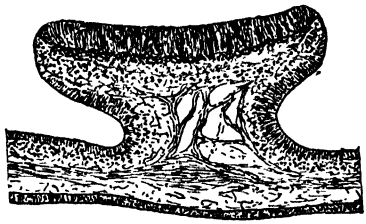


FIG. 101.—*Xanthoria parietina.* Vertical section through a young apothecium. Magnified 50. (O. V. Darbishire.)



FIG. 101*. — *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.)

each ascospore at maturity consists of two cells (Fig. 101*). The contents of the ascus are not, however, completely used up in the process of spore formation; a certain part remains over, lying between the spores; this unused substance becomes gelatinous, and in taking up water tends to swell, and so to burst the ascus. The dissemination of the spores, however, is not entirely due to the pressure from within the asci. The whole apothecium, including the paraphyses, endeavours to expand laterally when wetted, and this expansion is resisted by the rim of tissue at

the edge. Hence the asci are subjected to very considerable pressure, the result of which is that those which are ripe dehisce at the top, expelling all the eight spores with considerable force, so that they are shot up as much as a centimetre into the air. The asci open successively as they become mature, the dehiscence taking place whenever wet weather occurs.

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.

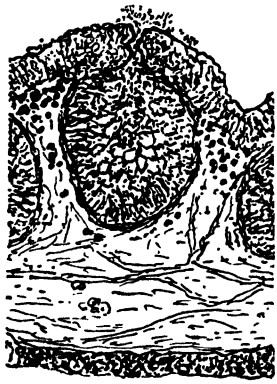


FIG. 102. — *Xanthoria parietina*. Vertical section through a spermogonium. Magnified 100. (O. V. Darbishire.)

There is another form of fructification consisting of small flask-shaped receptacles called *spermogonia* (Fig. 102), which, in our type and its near allies, are formed in groups on rounded prominences of the thallus. The opening at the top of the spermogonium is called the *ostiole*. The interior of the spermogonium is occupied by a net-work consisting of sterile and fertile cells. From the latter, excessively minute cells, the *spermatia*, are budded off (Fig. 103). Each spermatium contains one nucleus. The nature of these spermatia has been much disputed; there appears to be weighty evidence for regarding them, at least in certain cases, as the male cells of the Lichen.

In most species investigated the apothecium has been

found to arise from a special cellular filament, the *ascogonium*. Its lower end, which usually forms a coil, is embedded in the medullary tissue of the thallus, while the upper portion projects beyond the surface of the cortex, terminating in a long cell, the *trichogyne* (see Fig. 104). The trichogyne has a gelatinous cell-wall, to which numerous spermatia are found adhering. There is reason to believe that only those ascogonia, of which the trichogynes have been associated with spermatia, develop into ascus-fruits. The asci spring from cells of the coil, while the paraphyses arise lower down. It appears, then, that in these Lichens there may be a sexual process somewhat resembling that in the Rhodophyceæ and in certain Fungi. The details of fertilisation, however, still require to be worked out.

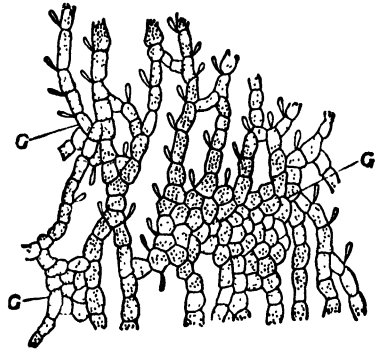


FIG. 103.—*Physcia pulverulenta*. Portion of the tissue inside a spermogonium, showing the groups of sterile cells (*G*), and the cells bearing spermatia. Highly magnified. (After Darbishire.)

In some cases, on the other hand, the spermatia have been observed to germinate, so their function as male cells seems not to be constant throughout the group. The illustrations (Fig. 103–104) are taken from a Lichen (*Physcia pulverulenta*), closely allied to our type. In certain free-living Discomycetous Fungi there is undoubtedly a process of fertilisation in the ascogonium.

The ascospores, as we have seen, reproduce only the fungal element of the Lichen; they must meet with algal cells in order to form a perfect Lichen-thallus.

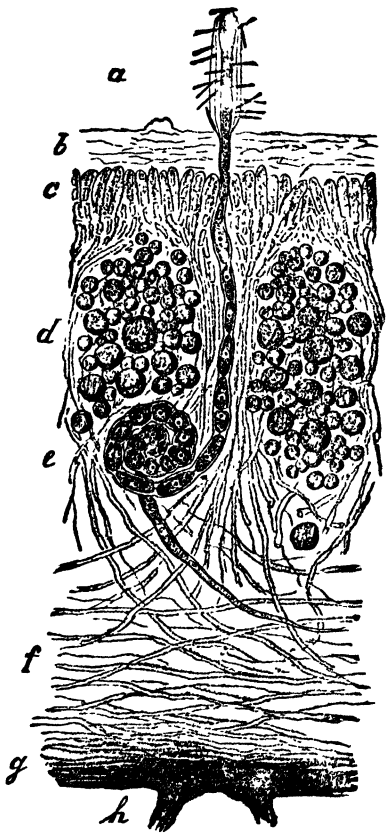


FIG. 104.—*Physcia pulverulenta*. Portion of a vertical section of the thallus, showing a complete ascogonium. *a*, projecting trichogyne, with swollen gelatinous cell-wall, in which numerous spermatia are caught; *e*, coiled part of the ascogonial filament; *b*, dead layers of upper cortex; *c*, living cortical hyphæ; *d*, groups of gonidia; *f*, medullary layer; *g*, lower cortex; *h*, rhizoids. Magnified about 1100. (After Darbishire.)

In many members of the group, however, though not in our type, there is a special provision for the reproduction of the compound organism as a whole. In these Lichens we find some of the apothecia replaced by patches of a powdery substance, each grain of the powder consisting of a few algal cells invested by fungal hyphæ. These little groups become isolated, and are dispersed by the wind or rain, or by the agency of insects. They are called *soredia*, and serve to reproduce simultaneously the algal and fungal constituents of the Lichen. In other Lichens similar bodies are formed on other parts of the thallus, sometimes in special organs.

Xanthoria then has served to illustrate, on the one hand, a highly

organised Ascomycete, with a complex fruit containing a large number of asci; while, on the other hand, it has made us acquainted with the remarkable phenomenon of *symbiosis*, or the associated life of two distinct organisms, each partner performing certain physiological functions to the benefit of the other. Of this widespread manner of life, the Lichens afford the most striking example among plants. Lichens live their lives as if they were single organisms, so perfectly are the two constituents of the thallus attuned to one another. Lichens, therefore, possess an individuality of their own. The association of Alga with Fungus enables both organisms to flourish in situations in which neither by itself could survive, and results in the formation of novel types of plant body not attained by Algæ or Fungi separately.

TYPE XXIII

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 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 light, 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 is mounted in water and examined under the microscope, it will be seen to consist of innumerable hyaline, spherical or oval cells, about 10–15 μ in diameter (Fig. 104*). In the centre of each cell is a large "vacuole," filled with sap, which is part of the nucleus. On the margin of the "vacuole" is a dense granule, the nucleolus, but this is only visible after staining. This is the modern view of the yeast nucleus, but there has been much dispute about its interpretation. 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.

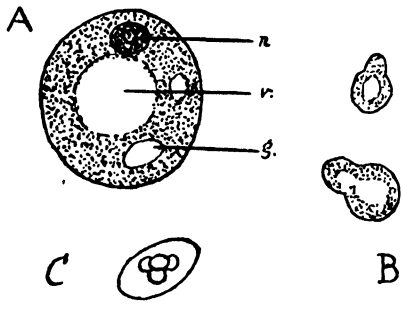


FIG. 104*. — *Saccharomyces*. A, cell; *n*, nucleolus; *v*, nuclear "vacuole"; *g*, glycogen. Magnified 3000. B, cells showing budding. C, cell with spores. B and C magnified 1000. (R. W. Marsh and W. J. Dowson.)

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. 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 con-

stituent 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.

In many yeasts "budding" is the only form of reproduction. In some, however, spores are formed under certain conditions, especially when the food in the surrounding medium is becoming exhausted, or when there is danger of desiccation. In the process of spore formation the protoplasm divides, usually into four portions, each of which becomes surrounded with a comparatively thick wall (Fig. 104*). When four spores are formed they are usually arranged tetrahedrally in the mother-cell. After a time the spores are liberated. By virtue of their thick walls the spores can remain alive under adverse conditions. On germination the spores bud and give rise to colonies of cells. It is in consequence of this method of spore formation that *Saccharomyces* and allied genera are included in the Ascomycetes, for the mother-cell, which gives rise to a definite and limited number of spores corresponds to an ascus. In some yeasts spore formation is preceded by a sexual fusion or conjugation of two ordinary cells. Subsequent to the union of the cells and the fusion of the two masses of protoplasm two spores are usually formed in each of the conjugating cells.

Like other Fungi, yeast cannot assimilate the carbon dioxide of the air. It can, however, utilise for food the carbon in comparatively simple organic substances, *e.g.* ammonium tartrate [$(NH_4)_2C_4H_4O_6$]. It also requires for its growth nitrogen (present in ammonium tartrate), sulphur, phosphorus, potassium, magnesium and calcium, as well as hydrogen and oxygen. A convenient nutritive solution for growing yeast consists

of potassium hydrogen phosphate [K_2HPO_4], magnesium sulphate [$MgSO_4$], calcium phosphate [$Ca_3(PO_4)_2$], and ammonium tartrate, dissolved in water. In this solution, yeast grows fairly well and gives rise to large numbers of new cells. If, however, glucose [$C_6H_{12}O_6$], a kind of sugar, is added to the nutritive medium, the yeast grows much faster and produces larger quantities of carbon dioxide than when grown in the simpler solution. In addition, a considerable quantity of alcohol [C_2H_5OH] will be found to accumulate in the medium as time goes on.

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 oxidation, alcohol being formed at the same time as follows :

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

As with normal respiration this process of decomposition of glucose without oxidation (known as *anærobic* respiration) results in the liberation of energy which is utilised for carrying out other vital activities. Even in the entire absence of oxygen, yeast can grow rapidly owing to its ability to 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 an enzyme, *zymase*, contained in its cells. By pounding up yeast cells the zymase can be extracted with difficulty from the protoplasm, and it will then decompose glucose precisely as the living yeast does. Zymase, like other enzymes, is a lifeless substance of very complex composition, which is formed by the protoplasm (see *Structural Botany*, Part I. Ch. I, III, k). 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 lævulose 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* (see Part I. Ch. III, II) 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. 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.

TYPE XXIV

PUCCINIA GRAMINIS

The group of Fungi (*Uredineæ* or Rust Fungi) represented by this type is a comparatively large one, but it shows a narrow range of diversity as compared with a great group like the Ascomycetes. The plants, however, are of much interest, for they afford one of the very best examples of typical parasitic Fungi, which have adapted themselves exclusively to life at the expense of other plants. Some of them, and especially that species which we have chosen as our type, are extremely injurious to important crops, and so possess a very considerable practical interest. The life-history of these parasites is singularly complicated, at least in some of their representatives.

Puccinia graminis is the cause of the Black or Stem Rust of Wheat and other cereals. Other species of *Puccinia* cause different rusts of cereals, some of which are much commoner in Britain than is *P. graminis*.

P. graminis occurs in summer on the leaves and stems of Wheat, Barley, Rye, and Oats, as well as on various wild grasses. In its early stage on these hosts the parasite is easily recognised, for it forms conspicuous rusty brown streaks between the veins of the leaf or along the surface of the stem, but it is usually much more abundant on the stems and leaf sheaths than on the laminæ. When the rust is mature, we see that these streaks are made up of a fine powder, bursting out through the epidermis of the host-plant, the powder consisting of the *conidia* or *uredospores* of the Fungus. Thus it is only the fructification of the parasite which is visible externally.

The vegetative part or mycelium is hidden in the tissues, and requires very careful microscopic examination for its detection. It does not spread throughout the whole plant, but is limited to isolated patches of the particular organs attacked. The mycelium consists of a dense web of excessively fine hyphæ, growing luxuriantly between the cells of the parts affected, and also sending out haustoria, which penetrate the cells themselves. The mycelium is multicellular, the transverse septa, however, only occurring at long intervals. The elongated form of the rust-streaks, which is most conspicuous on the stems, is due to the fact that the Fungus attacks the soft tissues, lying between the longitudinal bands of fibres, which accompany the vascular bundles.

The fructification characteristic of the rust-stage of the Fungus is produced in great quantities during the summer months. Preparatory to its formation, certain of the more superficial hyphæ pack themselves closely together, forming a dense layer just below the epidermis of the host plant. From this layer the conidia are formed. Each conidium is a single cell, borne at the end of a vertical unicellular stalk (see Fig. 105, E, *u*). They arise in great numbers close together, forming large groups or

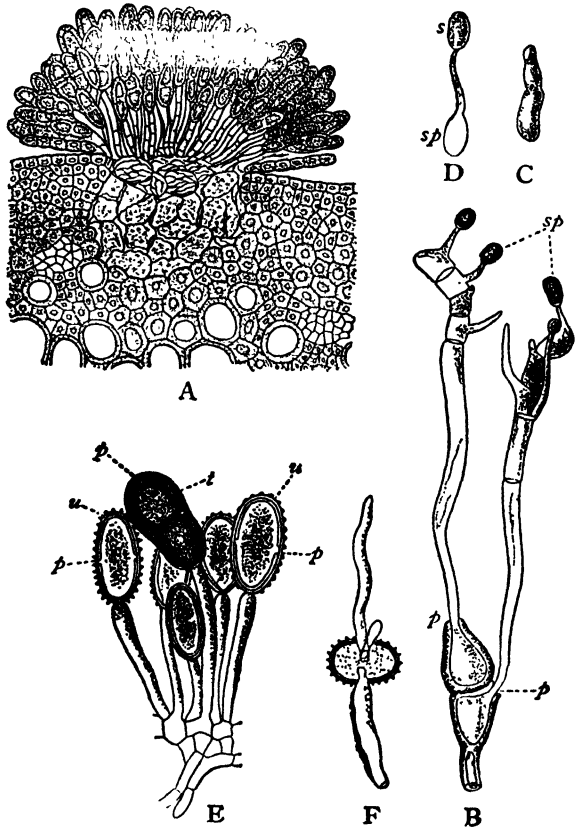


FIG. 105.—*Puccinia graminis*. A, section of the cortex of a wheat-stalk, showing a pustule of teleutospores, with the mycelium below. Magnified 150. B, teleutospore germinating; *p*, *p*, germ-pores; *sp*, sporidia borne on sterigmata arising from the promycelium. Magnified 230. C, sporidium germinating directly. D, sporidium (*sp*) germinating indirectly, forming a secondary sporidium (*s*). Magnified 370. E, part of a pustule, showing several uredospores (*u*) and a teleutospore (*t*); *p*, *p*, germ-pores. Magnified 300. F, uredospore germinating. Magnified 300. (After Von Tavel, Tulasne, and De Bary.)

pustules; in each pustule the development begins near the middle of the mass and spreads centrifugally. As the pustule develops, the epidermis lying above it is burst, and the ripening conidia are exposed to the air.

The single conidium, as it matures, acquires a rather thick cell-wall, consisting of two layers, the exospore and endospore, the outer of which is of a brownish colour and is covered with short spines, while the inner is colourless. There are usually four *germ-pores* or thin places in the cell-wall around the middle of the spore (see Fig. 105, E, *u*). In the cell-contents a quantity of oily, brownish-coloured pigment is present.

These conidia are called the *uredospores*, because they were formerly regarded as belonging to a distinct genus—*Uredo*—the species of which are now known to represent merely a particular form of fructification of the *Puccinia*. These uredospores become detached from their stalks, and are scattered by the wind and possibly also by the agency of insects. They are capable of immediate germination, and give rise to the same form of the Fungus as that which produced them, growing on the same kind of host plant, or at least on an allied species. The hyphæ grow out from the germinating spore through the germ-pores (see Fig. 105, F). If germination takes place upon a Wheat plant or other suitable host of the Grass family, the hyphæ grow along the surface of the epidermis until a stoma is reached, through which an entrance into the intercellular spaces of the host is effected. Thenceforth the hyphæ at once proceed to develop a new mycelium, from which new crops of uredospores arise. This form of fructification therefore serves for rapid propagation during the summer, though, as we shall see, it is not of necessity limited to that season.

Later in the summer another kind of spore, borne on

the same mycelium with the uredospores, begins to make its appearance. The external sign of the change of fructification is a change in the colour of the pustules, from reddish-brown to nearly black. This is due to the development of the *teleutospores*, which owe their name (meaning *final* spores) to the fact that they appear at the end of the season of growth. It is in consequence of the black streaks of teleutospores on the stems that *P. graminis* is often called " Black Rust."

It was to the teleutospore form of fructification that the name *Puccinia* was applied in the first instance, before the life-history was completely understood ; for this Fungus was originally put in three distinct genera, which are now known to represent stages in the development of one and the same plant. The teleutospore condition used to be known as the " *Mildew* " of wheat and other cereals. The teleutospores are produced in just the same way as the uredospores ; in fact both kinds of spore are often found in the same pustule (Fig. 105, E) during the intermediate period while the one fructification is being gradually replaced by the other. Later in the season we find pustules consisting of teleutospores only (Fig. 105, A).

The teleutospore is borne on a stalk like the uredospore, but is quite different from it in structure. The membrane is excessively thick, consisting of a stout outer coat of a dark-brown colour, and an inner colourless layer. The spore is made up of two cells, separated by a comparatively thin transverse septum. Within the cytoplasm of each young cell are two nuclei, which subsequently fuse into one, and there is also a vacuole containing oil. The surface of the cell-wall is smooth, unlike that of the uredospores. Each cell has a germpore, that is to say, a deep pit in its membrane ; in the upper cell this pit is situated at the apex, while in the lower it lies on one side, just below the septum (Fig.

105, B). These teleutospores represent the resting-stage of the Fungus, in which it passes through the winter.

This completes the history of the parasite, so far as its life on the Wheat or other gramineous [1] host is concerned. The damage which it does when it attacks the crop before the grain is set is very serious, though its immediate effect is only local. The chlorophyll of the part attacked is destroyed, and the tissues thus rendered useless for assimilation, while the cells affected ultimately become exhausted and die. Thus, if the seats of infection are numerous, the plant may gradually lose almost the whole of its effective assimilating tissue, and thus become starved and quite incapable of producing good grain. When the stems are severely affected the straw sometimes falls to the ground. Fortunately, early attack of cereals by *P. graminis* is now rare in Britain, but in N. America and certain other countries grave damage is caused by it in certain seasons.

The germination of the teleutospores in this species takes place in the following spring, and occurs while the teleutospores are still attached to the straw. Each cell sends out a hypha, which starts from the germ-pore, as shown in Fig. 105, B. These hyphæ do not develop into a normal mycelium, but are of limited growth, forming what is called a *pro-mycelium* (see Fig. 105, B) or *basidium*, which divides by transverse walls, cutting off a row of four cells from its terminal portion.[2] Each of these cells sends out a slender lateral outgrowth, which swells up at the end to form a small spore-like cell (Fig. 105, B). These cells are the *sporidia* or *basidiospores* ; the stalks on which they are borne are called the *sterigmata*. Hence we see that the teleutospore is incapable of directly repro-

[1] The family Gramineæ, or Grasses, includes all cereals.

[2] In water, however, the pro-mycelium may grow to a considerable length before producing sporidia.

ducing the typical form of the Fungus, for it only gives rise to a rudimentary mycelium, which proceeds at once to form yet another kind of spore. The sporidia become detached from their stalks, and are capable of direct germination ; but if they do not happen to be carried by the wind to their proper host plant, they form only a very short hypha, which at once gives rise to a secondary sporidium (Fig. 105, D), thereby gaining another chance of successful dissemination.

The sporidia, whether primary or secondary, are quite incapable of infecting any plant of the Grass Family. They are dependent upon a totally different kind of host, namely, the Barberry (*Berberis vulgaris*) or some of its allies. The sporidium, if it germinates on a young leaf of a Barberry bush, sends out a hypha which penetrates the cuticle instead of obtaining entry into the tissues by way of a stoma. In this respect the germinating sporidium differs from all the other forms of spore in this Fungus. When the mycelium is once started, it spreads in the tissues of the leaf, establishing haustoria in the cells, just as it did in the Wheat. The fructifications produced on the Barberry, however, are of a totally different kind from any of the forms already described.

During the late spring the Barberry may show signs of disease, consisting in the appearance of swollen discoloured patches on its leaves. When the disease has advanced further we find on the under-side of the leaf, seated upon the swollen place, clusters of exceedingly pretty little yellow cups containing spores (Fig. 106, A). This is the *Æcidium* form of the parasite, and, like the *Uredo* and *Puccinia*, was long described by botanists as belonging to a distinct genus.

When an *Æcidium*-fruit is to be produced, a group of hyphæ becomes densely felted together in an intercellular space of the leaf ; the inner hyphæ of the group

enlarge their cells, so as to give rise to a little nest of apparently parenchymatous tissue, surrounded by a

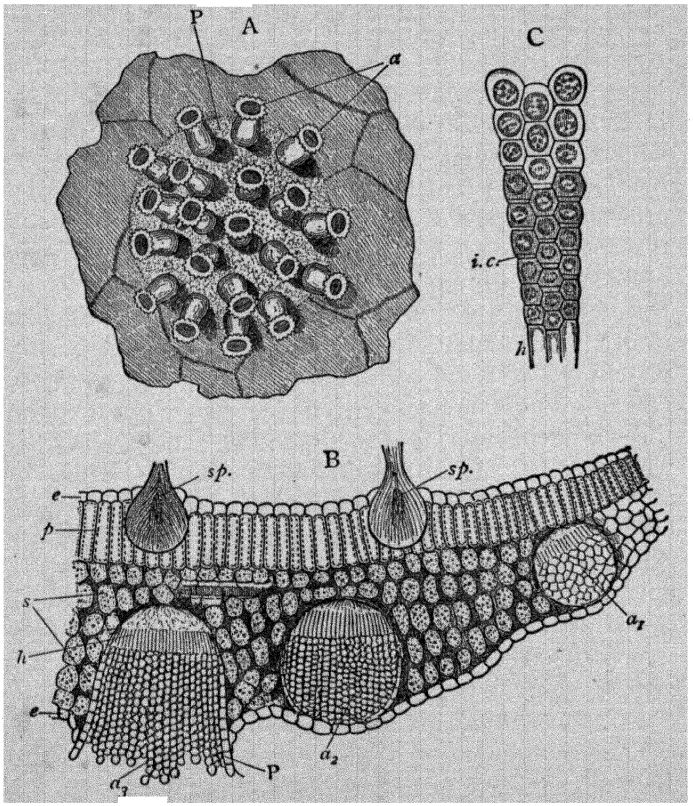


FIG. 106.—*Puccinia graminis*. A, part of the lower surface of a Barberry leaf; on the swollen part (P) is a cluster of *Æcidium*-cups (*a*). Magnified about 10. B, vertical section of the diseased part of the leaf; *e*, *e*, epidermis; *p*, palisade tissue; *s*, spongy tissue; *sp*, *sp*, spermogonia of the parasite; a_1, a_2, a_3, three stages in the development of the *Æcidium*-fruit; *P*, peridium; *h*, hymenium. Magnified 40. C, three chains of æcidiospores; *h*, hymenial cells; *i.c.* intercalary cells. Magnified about 200. (After Zopf and Kny.)

web of ordinary mycelium ; at the base of this mass a now of vertically elongated cells—the *hymenium* (Fig. 106, B, *h*)—is formed, and it is from these cells that the spores are formed. Each cell of the hymenium divides by transverse walls, and produces in basipetal order a long string of spores, separated from each other by intercalary sterile cells (Fig. 106, C). In this way the whole interior of the young *Æcidium* becomes filled up by numerous parallel chains of spores, which, as they grow, completely displace the cellular tissue by which the space was at first occupied. The wall or *peridium* of the cup is built up of vertical rows of sterile cells resembling the chains of spores, but connected together into a permanent tissue. This peridium at first completely encloses the fruit, but as the spores within increase in number, the enveloping layer is burst and thrown open, showing a toothed margin where its edges were torn apart (Fig. 106, B).

The æcidiospores, which are of a bright yellow colour, become separated by the breaking down of the sterile cells between them. The spores have a somewhat polygonal form, owing to mutual pressure while enclosed in the peridium, but they become approximately spherical on liberation. Their walls are thick, and each spore possesses a few germ-spores or pits, through which, on germinating, the hyphæ make their exit.

The æcidiospores germinate within a few hours of their discharge, if sufficient moisture be present. They do not, however, infect the host on which they were produced, but are only able to form a mycelium if conveyed by the wind or rain on to the leaves of some member of the Gramineæ, such as the Wheat or Rye. In this case a hypha is sent out through one or more of the germ-pores. The hypha receives the protoplasm from the spore and goes on growing, bending

first in one direction and then in another until its tip lights on a stoma. Then the hypha turns in through the pore of the stoma, and so makes its way into the intercellular spaces of the host, where it develops a mycelium from which uredospores are soon produced. Thus the cycle of the parasite's existence is completed.

There remains, however, yet another form of reproductive structure to be considered before we proceed to sum up the life-history. Accompanying the *Æcidium* on the Barberry, but usually on the upper surface of the leaf, are minute bodies called the *spermogonia*,[1] which are visible to the naked eye merely as little yellowish specks. They make their appearance before the cups on the opposite side of the leaf fully develop. Each of these spermogonia, when observed in a section vertical to the surface of the leaf (see Fig. 106, B, *sp*), is found to be a little flask-shaped body, consisting of a sheath of slender converging hyphæ, leaving a cavity in the middle. The spermogonium arises from the mycelium below the epidermis of the host, but ultimately breaks through it, so that the neck of the flask reaches the surface (Fig. 106, B). The hyphæ which project into the cavity form minute cells at their ends, a little row of such cells being formed on each filament. These minute cells—the *spermatia* [2]—are very much smaller than any other form of spore in the Uredineæ. They occur in enormous numbers, and sugary substances (" nectar "), secreted by the spermogonium, accompany their exudation through the opening (*ostiole*) at the top. Each spermatium contains a large nucleus and a little cytoplasm. Projecting beyond the ostiole are a few sterile *flexuous hyphæ*, which serve an important function (see later).

It used to be thought that the spermatia were functionless male cells, but it is now known that they play a very

[1] Sometimes called *pycnidia*. [2] Sometimes called *pycnospores*.

important part in the life-history of *P. graminis*. Like certain other Fungi (see p. 232) *P. graminis* is heterothallic, *i.e.* it exists in two sexual strains physiologically differentiated from each other. Unless these two strains are united by a kind of sexual process, æcidia and æcidiospores do not normally develop. Let us denote the two sexual strains of this Fungus as "A" and "B." It will be remembered that when the teleutospores germinate, each cell produces a pro-mycelium or basidium that forms four spores. Two of these spores belong to the sexual strain "A" and two to "B." Both "A" and "B" sporidia can infect Barberry leaves and give rise to mycelia and spermogonia. There will, however, be two kinds of sexually differentiated mycelia and spermogonia, "A" and "B" respectively, although they look alike. Unless the two kinds of mycelia become united, or unless "A" spermatia come into contact and fuse with hyphæ of the "B" type, or *vice versa*, thus leading to the formation of a mycelium having both "A" and "B" characters, æcidia do not fully develop. The ways in which an "A+B" mycelium becomes established are diverse. It has recently been shown that flies and other insects visit the spermogonia on the Barberry leaf to obtain the "nectar," in which there are large numbers of spermatia. In this way the "A" and "B" spermatia probably become intimately associated with *flexuous hyphæ* of opposite sex. Often, however, in nature the "A" and "B" types of mycelium develop in close proximity so that, *e.g.* "A" spermatia have abundant opportunity of coming into contact with "B" *flexuous hyphæ*. It may be that the nucleus of an "A" spermatium enters a cell of a "B" hypha, thus forming a cell with "A+B" nuclei. By nuclear division and migration other "A+B" cells may arise, and thus an "A+B" type of mycelium may become established.

As a consequence the æcidia develop and produce æcidiospores. The function of the spermatia is undoubtedly to give opportunity for the establishment of mycelia of the " A+B " type.

Before the discovery of the function of the spermatia it was known that the cells which give rise to the chains of æcidiospores were bi-nucleate and that each æcidiospore was also bi-nucleate. It is clear that one of each pair of nuclei is of the " A " type and the other of the " B " type. The " A " and " B " nuclei, however, do not fuse together at this stage. When the æcidiospores germinate the " A " and " B " nuclei divide simultaneously, and mycelia are formed consisting of bi-nucleate cells. The uredospores are also bi-nucleate, and so is each cell of a young teleutospore. The " A " and " B " nuclei, however, fuse together as the teleutospores mature. The " A " and " B " sexual characters again become separated from each other during the germination of the teleutospores. Thus processes of an undoubtedly sexual nature play an important part in the life-cycle of the Rust Fungi.

We are now acquainted with the full normal life-history of *Puccinia graminis*, which affords a typical instance of the phenomenon known as *heteræcism*, this term implying that the parasite at different stages of its career necessarily inhabits two distinct hosts. In this case we have seen that on the Wheat or other members of the Grass Family, two forms of spores—the uredospores and the teleutospores—are produced. The latter on germination give rise to sporidia which infect the other host, namely, the Barberry. It is only on the Barberry that the *Æcidium* fructification and the spermogonia are developed. The æcidiospores once more infect the Wheat or some allied plant, and the cycle is complete.

The fact that the Barberry has something to do with the appearance of Black Rust in Wheat was well known to

practical farmers, long before botanists found out the scientific explanation, or even allowed the truth of the observation. During the eighteenth century a vast amount of evidence was accumulated showing that Barberry bushes acted as centres of infection, from which rust spread over the cornfields. So strong was this conviction among agriculturists, that in the year 1760 a " Barberry Law " was enacted in the province of Massachusetts in North America, ordering the rigorous extirpation of Barberry bushes throughout the province. The preamble to the Act runs thus : " Whereas it has been found by experience that the Blasting of Wheat and other English Grain is often occasioned by Barberry Bushes, to the great loss and damage of the inhabitants of this province . . . " etc. The almost complete eradication of Barberry bushes from the vicinity of arable fields in Britain accounts for the comparative rarity of the Fungus nowadays. The true explanation " that the parasitic Fungus of the Barberry and that of Wheat are one and the same species," was first suggested by Sir Joseph Banks in 1805, and fully confirmed a few years later by the independent experiments of a Danish schoolmaster named Schoeler. Botanists, however, were still unwilling to accept the fact, because the *Puccinia* of the Wheat had quite different characters from the *Æcidium* of the Barberry. It was not till 1865 that the complete demonstration of all stages of the life-history of the parasite was accomplished by the German botanist De Bary. We now know of a great many other cases of heterœcism among allied Fungi.

We must not suppose, however, that the change of host is absolutely necessary for the perpetuation of a heterœcious parasite such as *Puccinia graminis*. In Australia, for example, Black Rust is prevalent on Wheat to a serious extent, though there are no Barberry bushes

nor any other plant on which the Æcidium form naturally develops. In such cases it is evident that the *Uredo* form must persist through the mild winter. Under such conditions, the teleutospores are useless, for their sporidia can only infect the other host, and not the Gramineæ.

There is another interesting feature about the parasitism of *Puccinia graminis*. Although this Fungus occurs on all the cereals, the uredospores taken from wheat cannot infect oats, or *vice versa*. It is evident therefore that *P. graminis* exists in several distinct *physiologic races* or *biologic forms*, physiologically, but not morphologically, distinguishable from one another. This kind of parasitism is known as *specialised parasitism* ; it is of common occurrence in many parasitic Fungi, especially in Powdery Mildews and Rusts.

Some other members of the *Uredineæ* have a very simple life-history compared with *Puccinia graminis*. In many of them all stages of the Fungus are passed through on the same host plant (*autœcism*), while in others certain of the stages are missing altogether.

TYPE XXV

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. 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 substratum 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. Such fusions have nothing to do with reproduction, and so far as we know serve no other purpose than to facilitate nutrition. Each cell of the mycelium contains numerous small nuclei in its cytoplasm.

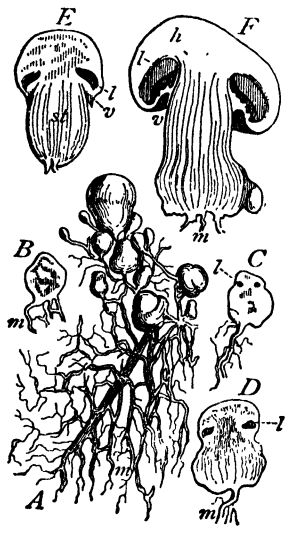


FIG. 107.—Development of a Mushroom. *A*, mycelium (*m*) giving rise to a number of young fructifications. *B*, very young mushroom in section; *m*, mycelium. *C*, slightly older; *l*, the gills just appearing. *D*, still older; *l*, gills; *m*, mycelium. *E*, older again; *l*, gills; *v*, velum; *st*, stipe. *F*, nearly ripe; *h*, pileus; other letters as before. Reduced. (After Sachs.)

The matured fructification consists, as everyone knows, of a thick stalk (the *stipe*) swollen at the base, supporting a hat-like expansion (the *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. 107, *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 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 halfway up, is a membranous ring or *annulus*, formed of the remains of the *velum*, which at an earlier stage covered in the lower surface of the pileus, as shown in Fig. 107, *E* and *F*.

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. 108). 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 lamella is called the *trama* (Fig. 108, *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 hyphæ which constitute the trama and sub-hymenial layer (Fig. 108). 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.

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 from two to four minute peg-like outgrowths (the *sterigmata*), each of which enlarges at the tip to form a *basidiospore* (see Fig. 108, *C*, *s*). The wild Mushroom has usually four spores on each basidium and the cultivated form two. The young spores are pink, but when ripe are purplish black; they contain oil, and have each two or four nuclei. These are derived from the basidium, which at an earlier stage possesses a single nucleus formed by the fusion of the two nuclei which it originally contained. The fused nucleus of the

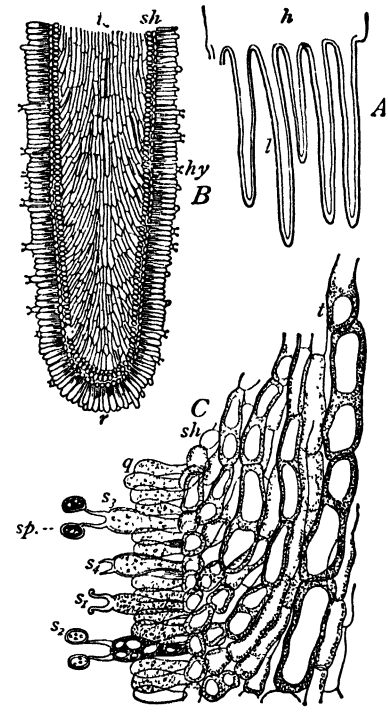


FIG. 108. — Gills of Mushroom. *A*, part of tangential section of pileus (*h*), showing gills (*l*). Slightly magnified. *B*, single gill in section; *t*, trama; *sh*, sub-hymenial layer; *hy*, hymenium; *r*, lower edge of gill. Magnified about 80. *C*, part of *B* enlarged; *t*, cells of trama; *sh*, sub-hymenial layer; *q*, paraphyses and very young basidia; s_1-s_4, stages in development of basidia; *sp*, basidiospores. Magnified 230. (After Sachs.)

basidium divides into four, and the daughter-nuclei pass into the basidiospores, one or two into each. They again divide, so that the mature spore has two or four nuclei. 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 just 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 the 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 the microscope.

This mode of fructification, consisting of basidia bearing spores on sterigmata, is universal throughout the great group to which *Psalliota* belongs, hence called the *Basidiomycetes*. The subdivision of this group, represented by *Psalliota*, is characterised by the hymenium being exposed to the air when ripe, and bears the name of the *Hymenomycetes*. The basidium, when it has once produced its two or four spores, is exhausted, and does nothing more ; but for a time new basidia may arise, growing up between the old ones.

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 time 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 basidial fructification is quite distinct from that of any other group of Fungi which we have described. There are, however, a number of doubtful forms among the lower Basidiomycetes which appear to connect that group with the Uredineæ, and the basidium of the Mushroom group is undoubtedly homologous with the promycelium produced from the teleutospores of the Uredineæ, the basidiospores corresponding to the sporidia. There are some Uredineæ, such as the *Puccinia* so common on hollyhocks (*P. Malvacearum*), in which the teleutospores germinate *in situ*, *i.e.* while still in the pustule and attached to the mycelium. In this case the resemblance of the pro-mycelium to the basidia of some of the simpler Basidiomycetes is very striking.

In Fig. 107 the development of the Mushroom-fruit is illustrated. The young Mushroom arises from a tangle of hyphæ borne on a strand of mycelium. The intertwined hyphæ group themselves into a tissue, thus forming a little oval tubercle. At first the Mushroom is all stalk; soon, however, the pileus begins to appear at the top. In the earlier stages there is no separation between pileus and stipe (Fig. 107, *B*, *C*). The gills are developed endogenously, while enclosed on all sides by continuous tissue (Fig. 107, *D*). Later on the pileus begins to spread out laterally (Fig. 107, *E*), but its under-side is still closed in. The tissue which connects

the edge of the pileus with the stalk, and thus encloses the gills from below, is called the *velum* or veil (Fig. 107, *F*). At last this becomes ruptured as the pileus expands, and its torn remains adhere to the stipe, forming the *ring*, which we mentioned in describing the ripe fructification.

Mushrooms develop normally in complete darkness, and in fact they are often cultivated in cellars and caves. The fruit bodies are sensitive to gravity, the stipe being negatively, and the gills positively, geotropic. These tropisms lead to the correct orientation of the fructifications for spore discharge. After being hurled from the sterigmata the spores fall downwards in the spaces between the gills and are then caught up by convection currents in the air and dispersed. If a ripe Mushroom be suspended in a dimly lighted room a faint cloud of spores can be seen arising from the lower part of the pileus. The occurrence of the hymenia on the under surface of the fruit body protects the basidia from rain and from excessive loss of water in dry weather, and the erection of the pileus above soil level facilitates the dispersal of the spores by air currents after discharge from the basidia. The fructification of the Mushroom is a most efficient mechanism for the formation and liberation of large numbers of spores.

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.

Although there are no true sexual organs in the Mushroom and its allies, the invariable fusion of nuclei in the young basidia is undoubtedly a kind of sexual process. Some Fungi closely related to the Mushroom are hetero-

thallic, the spores being of two sexual types, " A " and " B," as in the sporidia of *Puccinia graminis*. Unless a hypha from an " A " spore fuses with that from a " B " spore, thereby establishing an " A + B " type of mycelium, fertile fruit bodies are not formed. In such a heterothallic type one of the nuclei in the young basidium is of the " A," and the other of the " B," kind.

In the Mushroom no other form of spore than the basidiospores has so far been discovered. In some nearly allied Fungi, however, additional forms of spores, such as conidia, are produced on the mycelium.

We have now finished our series of types of Fungi. It has only been possible to consider a very few representatives, and many important groups have been left altogether untouched. We have gained, however, some slight idea of the great range of structure which the class presents, and in our later types we have seen how very far the higher Fungi have diverged from the simple forms with which we started our survey.

CHAPTER V

THE BACTERIA

THE Bacteria, which in these days are familiar, by name at any rate, to everyone, 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 both their carbon and nitrogen supplies usually from organic sources. They are, however, as we shall see, quite different from any known Fungi in structure and development, and constitute a wholly distinct class of organisms.

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. 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 has become in recent years of the greatest possible practical importance in relation both to medicine, as regards the parasitic 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.

TYPE XXVI

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 μ) in diameter and from $\frac{5}{1000}$ to $\frac{8}{1000}$ mm. (5–8 μ) 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) which are attached to the protoplasm and penetrate the wall (see Fig. 109, *a*, *d*).

Rod-shaped Bacteria, not forming spores, are usually referred to the genus *Bacterium*. Other Bacterial cells are spherical (*Micrococcus*), while some are comma-shaped (*Vibrio*) or are in the form of loose spirals (*Spirillum*). Some Bacteria form filaments which are spuriously branched (*e.g. Cladothrix*). Many Bacteria have no flagella and are non-motile.

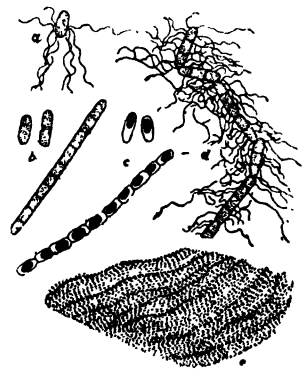


FIG. 109. — *Bacillus subtilis*. *a*, *d*, ciliated motile cell and filament; *b*, non-motile cells and filament; *e*, zooglœa, during spore-formation; *c*, cells and filament with endospores, from the zooglœa. *a-d*, × 1050. *e*, × 175. (After A. Fischer.)

The whole interior of the cell is occupied by protoplasm. Only in a few bacteria has the presence of a nucleus yet been determined.

For some time *B. subtilis* continues in the actively swarming condition, multiplying abundantly by the repeated transverse division of the cells. 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 iridiscent 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. 109). The spores in this species and in certain

other Bacteria, 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 comparatively thick and 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.

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. 109, *a*).

Fig. 110 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 (2·5 μ) 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. There is no kind of sexual reproduction in any of the Bacteria.

Bacillus subtilis, like most other living things, requires plenty of atmospheric oxygen in order to flourish. Some of the other Bacteria, however, have the remarkable peculiarity that they thrive best in the *absence* of free oxygen. This is the case, for example, with *Clostridium butyricum*, the organism to which the formation of butyric acid by the fermentation of sugar is due. In this case the oxygen necessary for respiration is not absorbed in the free state, but obtained from the breaking down of the organic substance in which the organism lives.

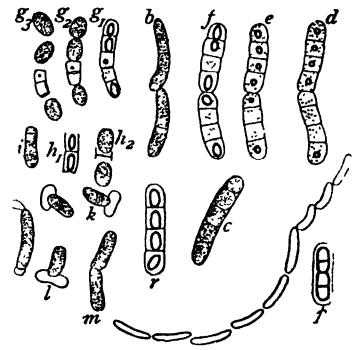


FIG. 110.—*Bacillus megatherium*. *a*, chain of vegetative rods, each consisting of two or more cells, but septa not shown. Magnified 250. *p*, four-celled rod, after treatment with alcoholic solution of iodine; *b*, vegetative rods; *c-f*, rods, showing the formation of endospores; *r*, four-celled 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.)

It may be mentioned here that numerous experiments have proved that bright light has a very unfavourable effect on Bacteria, completely stopping their growth and multiplication in many cases, and even, when intense enough, killing the cells outright. It is the rays towards the violet end of the spectrum and the ultra-violet rays which exercise the greatest retarding effect on the growth of these organisms. The action of light in checking the

increase of these agents of decomposition and disease is evidently a fact of great practical importance.

It was stated in Part I. (Ch. III. 1), that plants of the Pea and Bean kind, unlike ordinary green plants, are able, by the help of certain bacterial companions, to obtain their nitrogenous food from the free nitrogen of the atmosphere. The plants in question, including most if not all of our native Leguminosæ, invariably have swellings or tubercles on their roots. These tubercles are inhabited by a symbiotic bacterium, the entrance of which into the root is the cause of the first formation of the tubercle. It has been proved conclusively that it is only when this organism is present in the soil that the tubercles develop on the roots, and only when the tubercles are formed that free nitrogen can be assimilated. If the plants are grown in sterilised soil, *i.e.* soil which has been heated sufficiently to kill all living things contained in it, then no tubercles develop, and no nitrogen is absorbed from the air. When the tubercles are present, however, great quantities of nitrogen are assimilated, and the plant can thrive even if nitrogenous compounds be quite absent from the soil. A very important result of this fact is that leguminous crops actually enrich the soil in nitrogen. In Germany one sees whole fields of Yellow Lupine grown for no other purpose than to be ploughed in and so enrich the soil for other crops. In this country clover is often grown before wheat in the farm rotation of crops. The remains of the clover on being ploughed into the soil enrich it 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* or *Bacterium radicicola*. Moreover, the relation of this creature 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.

R. leguminosarum is only one of many kinds of Bacteria that play an essential part in the circulation of nitrogen in Nature. Certain Bacteria convert 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 processes of oxidation that lead to the formation of nitrites and nitrates. Still other soil Bacteria utilise atmospheric nitrogen in their own metabolism, and in this way " fix " it for the future benefit of the green plant. 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.

Before leaving the subject of Bacteria it may be mentioned that as a group they show an extraordinary range of different types of metabolism. It has already been implied that the nitrifying Bacteria obtain the whole of their food supplies from inorganic sources. In certain other Bacteria, carbon dioxide is decomposed under the influence of light, with the help of a purple pigment which seems to have similar properties to those of chlorophyll. In the curious group of the " sulphur bacteria " sulphuretted hydrogen is oxidised to sulphur and energy thereby gained, the sulphur being deposited as granules in the cell.

CHAPTER VI

THE MYXOMYCETES [1]

THE present type represents a group of organisms lying on the borderland of the animal and vegetable kingdoms. It may be doubted whether they have any right to a place in a book on Botany, but we give them the benefit of the doubt because of their great scientific interest; for in them we can study living protoplasm and its behaviour on a greater scale than in any other creatures. Myxomycetes, unlike Fungi and Bacteria, are of no practical importance, apart from a few which are parasitic on plants, *e.g. Plasmodiophora Brassicæ*, the cause of Finger and Toe or Club Root disease of turnips and cabbages. They are probably known to very few people except naturalists; yet they are common enough, easily visible to the naked eye, and in some conditions extremely conspicuous.

In the vegetative state a typical Myxomycete consists of a mass of naked protoplasm, sometimes several inches in extent, which creeps slowly about, on the surface of dead leaves or bark or wood. Such immense aggregations of living matter in so simple a form are quite unknown in any other group of organisms.

When reproduction is about to take place, the creature completely changes its character, gradually ceases to be active, and converts itself into a collection of fruits of rather complex structure, in which the microscopic spores are produced. The spores on germination give rise to

[1] Also called *Mycetozoa*.

swarm-cells, which unite together to build up the great protoplasmic body with which we started. Such are the rough outlines of a Myxomycete's career. We will now proceed to study a particular example more in detail.

TYPE XXVII

BADHAMIA UTRICULARIS

1. THE PLASMODIUM

This Myxomycete is common in some years, though rare in others; it occurs on the bark or wood of fallen trees, on old garden seats, and in fact in all places where timber is left exposed to damp and decay. In its ordinary state the organism forms irregular flat gelatinous masses of a deep chrome-yellow colour, spreading and creeping over the surface of the rotting wood, especially in damp weather. These creeping masses are called *plasmodia*. A small plasmodium is shown in Fig. 111. This specimen was only about half an inch across, but much greater dimensions are usually attained, the area covered by one plasmodium sometimes amounting to as much as six square inches. The plasmodium is not uniform in thickness throughout, but is traversed by thicker veins, which unite together to form a kind of network. The thinner protoplasmic layer between the veins is sometimes interrupted so as to leave some of the meshes empty. The whole plasmodium is a mass of living protoplasm which is in constant movement. The movement is of two kinds—(1) an advancing locomotion of the whole plasmodium, and (2) an internal circulation of the protoplasm, especially in the veins. The locomotion is a slow, creeping movement; the advancing edge of the mass (*a*, *a* in Fig. 111) is con-

stantly putting out feelers (*pseudopodia*, as they are called), which are sometimes withdrawn again, but more often maintain their position, and are increased by the flow of protoplasm from behind. The outer layer of the whole plasmodium is clear and transparent; the inner mass is very granular, and the granules are especially abundant in the veins. Many of the granules consist of lime (calcium carbonate), and it is around these lime-granules that the yellow colouring-matter is chiefly

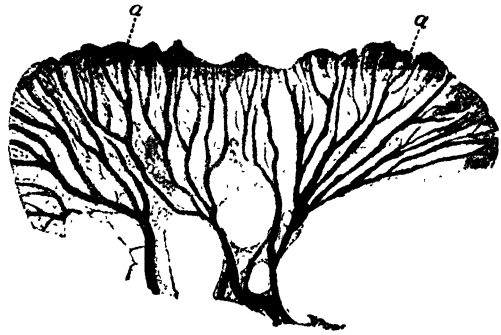


FIG. 111. — *Badhamia utricularis*; plasmodium, from a stained specimen, prepared by the late Mr. A. Lister, F.R.S. *a*, *a*, advancing margin. Magnified about 5. (R. S.)

deposited. The clear part of the protoplasm is colourless. When a pseudopodium is first extended it consists of the clear part (*hyaloplasm*) only; subsequently the inner granular substance flows into it and increases its mass.

The internal movement along the veins is extremely active, and can be followed with ease under the microscope by means of the granules which are swept along with the current. The flow is curiously rhythmical. In each vein the current sets steadily in one direction for from one and a half to two minutes, then it slackens

and stops altogether for an instant, only to recommence with equal energy in the opposite direction. This internal flow is closely related to the locomotion of the whole plasmodium, for it is found that the current lasts longest in that direction in which the plasmodium is advancing.

The movements do not go on at random, but take a definite direction in accordance with the needs of the organism. Thus an active plasmodium, if the wood be wetted on one side of it more than on the other, will move towards the damper side; if, however, the Myxomycete be about to form spores (for which moisture is not favourable) it will move the opposite way, in the dry direction. Generally speaking, a plasmodium will try to avoid intense light (which no doubt has a bad effect, as in the case of the Bacteria); for the purpose of spore-formation, however, it will leave any dark recess of the wood in which it may be hidden, and seek the light.

This particular Myxomycete, *Badhamia utricularis*, feeds on living Bacteria and Fungi, especially on members of the Hymenomycetes, which grow on decaying wood. If a piece of one of these Fungi be placed in its way, the advancing margin of the *Badhamia* at once begins to flow over it, and the whole plasmodium will turn aside in the direction of the prey. Individual hyphæ, or small pieces of the fungus, or even Bacteria living on the surface, become enclosed in vacuoles in the protoplasm of the *Badhamia* and digested, their useless remains being afterwards disgorged and left behind on the track. This way of feeding, by taking solid food into the body, and then digesting it, is characteristic of animals, and is not known among true plants. The Myxomycetes generally have this power, but in most cases they live on dead and decaying substances, such as fragments of

bark and wood, and to some extent their mode of nutrition may be saprophytic. As a reserve food material the plasmodium forms glycogen. Our type is exceptional in preying on living tissues. Its frequency in any particular season depends on the weather and the abundance of the Fungi which it grows on.

The plasmodium contains an immense number of nuclei, which are only absent from the clear external portion. The nuclei (see Fig. 112) have the same structure as those of higher organisms, possessing a nucleolus and a framework of delicate threads. They increase in number by division, as the plasmodium grows.

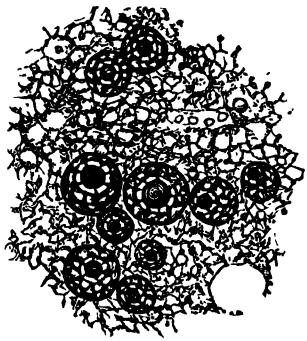


FIG. 112. — *Badhamia utricularis*; portion of plasmodium, showing a number of spherical nuclei, in each of which the fibrillar network and the nucleolus is seen. Magnified 1200. (From Lister's Monograph of the Mycetozoa.)

We see, then, that the plasmodium of a Myxomycete is a typical example of non-cellular structure, consisting of a perfectly continuous protoplasmic body of large size, containing vacuoles and numerous nuclei, but entirely destitute of any cell-wall.

Sometimes the plasmodium passes into a resting condition, a change which often, though not always, happens in consequence of drought. The movements cease, and the protoplasm becomes partitioned into a number of irregular *cysts* or cells, each containing about ten or twenty of the nuclei. The cysts are separated from each other by firm walls, which are hardened portions of the protoplasm. In this resting stage, which is known as the *sclerotium*, the plasmodium may remain alive for as long

as three years. The external appearance of the sclerotium of our type is that of a dry, horny, irregular mass, of a brick-red colour. When moistened, it revives, the walls of the cysts become absorbed, and the contents reunite and recommence the movements characteristic of active life.

2. The Sporangia and Spores

When a Myxomycete fructifies it completely changes its appearance. The whole of the active protoplasm is used up to form a sorus of sporangia in which the spores are contained. The sporangia are often brightly coloured; in *B. utricularis* they are ashy-grey. In Fig. 113 a cluster of sporangia (from an allied genus) is shown. The ripe sporangium is a rounded hollow case, borne on a stalk; it has a firm external wall, and its interior is traversed by a network of threads, among which lime is deposited (see Fig. 113, *b*). In the meshes of the network are contained the numerous spores.



FIG. 113.—*Leocarpus vernicosus*. *a*, group of sporangia on a fragment of dead leaf. Magnified 2½. *b*, portion of capillitium with spores. Magnified 120. (From Lister's Monograph of the Mycetozoa.)

When fructification is about to take place, the protoplasm accumulates at certain points, corresponding to the position of future sporangia. At each of these points the protoplasm heaps itself up to form a projecting mass; a portion of this hardens and becomes the stalk, while the living part continues to creep upwards, and constitutes the sporangium itself at the top. The outer layer of the terminal mass of protoplasm forms itself into the firm outer wall, while the interior part builds up a network of hollow branched

threads (the *capillitium*), which traverse the cavity in all directions (see Fig. 113, *b*). Between these threads masses of living protoplasm remain. After the wall and capillitium are completed, the formation of spores takes place. The protoplasm in the meshes breaks up into distinct masses, the nuclei of which all undergo division. It may be mentioned here that nuclear division, both in the sporangia and in the plasmodium as well, takes place in just the same complicated way as in the tissues of the higher animals and plants. Ultimately the whole of the living protoplasm in the sporangium further divides up into spherical spores, each of which includes a single nucleus.

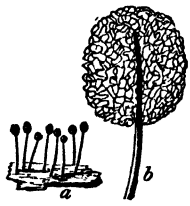


FIG. 114.—*Comatricha obtusata*. *a*, group of sporangia. Natural size. *b*, empty sporangium, showing capillitium. Magnified 16. (From Lister's Monograph of the Mycetozoa.)

The cell-wall of the spores, and also the substance of the sporangial wall and the capillitium, resemble the cuticularised membrane of vegetable cells. In a few cases cellulose has been found. It will be noticed that complicated as the structure of the sporangia is, there is no formation of distinct cells until the spores themselves are developed. In Fig. 114 the sporangium of another Myxomycete (*Comatricha obtusata*) is figured. Here the sporangial wall soon disappears, so that the whole capillitium in connection with the stalk becomes visible.

The sporangia of *Badhamia* open by the breaking down of the membrane, and the spores are exposed. They hang for a time on the threads of the capillitium, which acts as a supporting scaffolding, and are gradually scattered. The spores are brownish, spherical, and 9–12 μ in diameter. The spores can be kept dry for a

long time in a living condition, and germinate readily when wetted (see Fig. 115, from another Myxomycete). The membrane splits, and the whole contents become free. The protoplasmic body at first shows " amœboid " movements, changing its form by putting out and again withdrawing pseudopodia. After a few minutes a single flagellum is developed at one end, and now the pear-shaped swarm-spore is fully formed (Fig. 115, *d*). It contains one nucleus, placed near the thin end, and its cytoplasm is vacuolated; one of the vacuoles is contractile, expanding and contracting at regular intervals. The swarm-spore swims through the water with a dancing movement, or it creeps along the surface of any solid body like a snail.

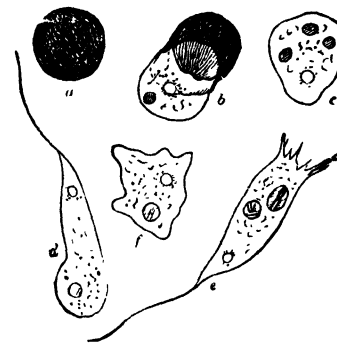


FIG. 115.—*Didymium difforme*. *a*, spore; *b*, swarm-cell escaping from the spore-membrane; *c*, newly-hatched swarm-cell, containing a nucleus and three vacuoles; *d*, flagellated swarm-cell; *e*, swarm-cell, with two vacuoles containing bacteria—another bacterium is just caught by the pseudopodia; *f*, amœboid swarm-cell. Magnified 720. (From Lister's Monograph of the Mycetozoa.)

These swarm-spores, like the plasmodia, can take in their food in the solid state, but they may also feed in a saprophytic manner. They catch minute objects in the water by means of pseudopodia put out at the broad posterior end. They are particularly fond of Bacteria, which are often caught in this way, the pseudopodia laying hold of the microbe, and in spite of its struggles dragging it in until it is enclosed in a vacuole of the cytoplasm, and ultimately digested (Fig. 115, *e*).

The swarm-spores multiply repeatedly by division

into two, the movement ceasing before the division takes place, and starting again when the daughter-cells are formed. The division of the nucleus precedes that of the cell. The swarm-spore may also become encysted, surrounding itself with a cell-wall, from which it afterwards escapes, resuming its active career. The encysted swarm-cells bear the name of *microcysts*.

From the swarm-spores the plasmodium is built up. Before this happens they withdraw their cilia, and henceforth confine themselves to creeping amœboid movements. When two creeping *myxamœbæ* (as they are called at this stage) meet, their protoplasm flows together into a single mass. According to recent observations on other Myxomycetes the nuclei of these *myxamœbæ* also fuse, so that the act of union appears to be a sexual conjugation. Then other swarm-spores, *microcysts* and *myxamœbæ* coalesce with the two cells that have fused sexually into one, and so the beginning of a new plasmodium is made (Fig. 116). The nuclei of the accessory swarm-spores, etc., are digested by the young plasmodium. The nuclei of the latter arise solely by division of the single nucleus formed by the sexual fusion of the first two *myxamœbæ* to coalesce. In some Myxomycetes sexual fusion occurs between motile swarm-spores instead of between *myxamœbæ*.

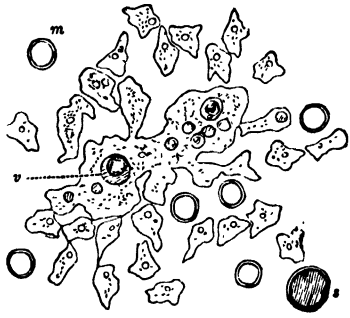


FIG. 116. — *Didymium difforme*; young plasmodium with attendant myxamœbæ. *m*, microcyst. One microcyst is being digested in a vacuole (*v*). *s*, empty spore-membrane. Magnified 470. (From Lister's Monograph of the Mycetozoa.)

Thus we see that a plasmodium is a compound struc-

ture, built up in the first instance by the union of a number of distinct protoplasmic bodies. As there is no fusion of nuclei in the later stages, only the first union can be regarded as sexual.

When a plasmodium has been started in this way it continues to grow, and the number of its nuclei increases by division to keep pace with its growth,—a fact which is now well ascertained.

Such are the outlines of the life-history of these extraordinary creatures, which in their whole structure and mode of development differ widely from any other organisms. We can study in them, better perhaps than in anything else, the behaviour of living protoplasm when untrammelled by the bonds of cellular structure. We see how closely movement and growth are connected; and when the period of fructification comes on, we can observe how the protoplasm by its active exertions literally builds up the new structure out of its own substance. It has been well said that in the plasmodium of a Myxomycete we have a type of the organisation of all plants, for we see in these organisms, freely exposed to view, the same movements and the same constructive activity of the living matter, on which the growth and development of the highest plants depend. In the latter, however, the living agent is concealed within the framework of the cells, and its successive changes of form are stereotyped by the rigidity of the structures which it has itself built up.

CHAPTER VII

THE FLAGELLATA

THE Flagellata are a large group of motile, unicellular organisms, some of which possess wholly animal characteristics, while others, like *Euglena viridis*, show a mixture of plant and animal characters. The Algæ may have evolved from pigmented forms like the Flagellata, and the Fungi from colourless members of this group or allied groups of the Protozoa. It is not possible to draw a hard-and-fast line between the Flagellata and certain unicellular Algæ (see p. 180).

TYPE XXVIII

EUGLENA VIRIDIS

Our type, *Euglena viridis*, is sometimes found in great abundance in shallow stagnant water, especially in water containing considerable quantities of nitrogenous substances, such as pools in farmyards and around manure heaps. In such situations *Euglena viridis* may be so plentiful as to colour the water a brilliant green.

Under the microscope the organism is seen to be actively motile, as in *Chlamydomonas*, but it may also exhibit a slow, crawling amœboid movement when not progressing rapidly. In the latter case *Euglena viridis* changes its shape gradually as it slowly moves. At one moment an individual may be pear-shaped or spindle-

shaped with a pointed posterior extremity, at another it may be nearly spherical. These changes of form are due to the fact that the organism is not bounded by a rigid cell-wall as in *Chlamydomonas*, and it is the absence of a cell-wall in the motile condition which is one of the most important differences between the Flagellata and the unicellular Algæ. The peripheral region of the protoplast of the motile *Euglena*, called the *periplast*, is somewhat more rigid than the interior and shows a faint spiral striation.

Euglena viridis moves rapidly through the water by means of a single protoplasmic thread, the cilium or flagellum (Fig. 117), which arises from the gullet and which by its own movements propels the organism onwards. The flagellum is about the same length as the cell. It is comparable with the cilia of *Chlamydomonas*, but is considerably coarser. The flagellum can generally be seen easily, although by running a little iodine solution under the coverslip it may be made clearer.

Within the cell is a bright green chloroplast of stellate form (Fig. 117), which enables the organism to carry out photosynthesis of the carbon dioxide dissolved in the water. The visible product of photosynthesis, however, is not starch, but an allied substance, paramylon, which does not stain blue with iodine. Grains of paramylon can be seen clustered round the "pyrenoid" in the central part of the chloroplast, and also in other parts of the cell. In a median position in the lower part of the cell is a relatively large nucleus containing a conspicuous nucleolus (Fig. 117). The nucleus is usually only visible after staining with iodine or other reagent. Towards the anterior part of the organism is a red eye-spot, which, as in *Chlamydomonas*, there are reasons for thinking renders the organism sensitive to varying light intensities. *Euglena* tends to move towards light of moderate in-

tensity. Also in the front of the organism and at one side is a large contractile vacuole, which is sometimes accompanied by subsidiary ones (Fig. 117). The contractile vacuole expands and contracts, and empties itself into the reservoir which connects with the exterior by a very narrow channel, the gullet.

Division takes place in *Euglena* after the organism has come to rest and has discarded its flagellum and surrounded itself with a somewhat gelatinous membrane. In this quiescent state the protoplast divides longitudinally into two and then into four portions, which soon become differentiated as complete individuals. These escape from the delicate membrane in an actively motile condition. At other times, especially when desiccation threatens, the individual comes to rest and surrounds itself with a thick membrane to form a *cyst* (Fig. 117). In the encysted condition the organism can withstand long periods of drought, and may be distributed by wind like particles of dust. In a favourable environment, *e.g.* an abundant supply of water, the protoplast within the cyst divides into two or four individuals which are liberated in an actively motile state when the wall of the cyst ruptures. There is no kind of sexual reproduction in *Euglena viridis*, and this is true of most of its nearest allies and of other Fagellata.

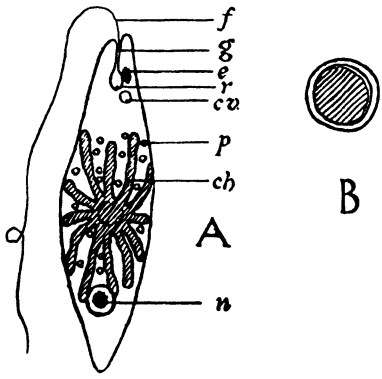


FIG. 117.—*Euglena viridis*. A, motile cell; *f*, flagellum; *g*, gullet; *e*, eye-spot; *r*, reservoir; *c.v.*, contractile vacuole; *p*, paramylon; *ch*, chloroplast; *n*, nucleus. B, cyst. Magnified 600. (R. W. Marsh, after Lemmermann.)

In so far as its mode of nutrition is that of an Alga, all the substances required for food being dissolved in the water, *Euglena viridis* is obviously plant-like, but in view of its power of movement, the absence of a cell-wall in the motile state, and of certain other structural features, it is also clearly a unicellular animal. Large numbers of the Flagellata possess a mixture of plant and animal characteristics, and this is probably an indication that both plants and animals have had a common origin in the very remote past.

If *Euglena viridis* is kept in water containing much organic food, its brilliant green colour tends to fade, and under such circumstances it feeds in a partly saprophytic manner. Other species of *Euglena* become entirely colourless and wholly saprophytic in their mode of nutrition if grown in darkness, in solutions of certain organic substances.

CHAPTER VIII

CONCLUSION

IT will be useful, at the conclusion of our series of types, to sum up very briefly what we have learnt from them, with reference especially to the relationships of the groups which they represent. Throughout the book we have followed on the whole a descending order, proceeding from the more complex to the more simple, though there have been many exceptions to this rule, because it is impossible to arrange any set of plants in a single linear series, whether according to increasing or decreasing complexity.

In the present summary we will follow the reverse order, starting where we left off, with the lowest forms, following up the various lines of affinity, and concluding with the highest plants, with which we began in Part I. This is the natural succession, and the attempt to follow it will at any rate teach us how complicated the relationships are, and how difficult it is to arrange naturally even a few types such as ours.

The two groups near the end of the series, with which we therefore begin our summary, have no clear and evident affinities with any of the rest. As regards the Myxomycetes, it is doubtful whether any such relationship exists at all. These organisms have attained a fairly high stage of development (so far at least as their fruits are concerned) on lines of their own; they have typical nuclei which appear to undergo a sexual fusion. They are best regarded as forming by them-

selves a short but distinct line of descent, which may have arisen very far back, among organisms not yet characterised as either animals or plants. In the swarming and plasmodial stages the Myxomycetes would most naturally be regarded as animals, especially when we consider their mode of feeding. In the formation of their fruits and spores, however, they rather suggest plants of the nature of Fungi, but probably this is only a case of parallel development, not indicating a real blood-relationship to any undoubted members of the Vegetable Kingdom.

The Bacteria are still more difficult to place, for though in some ways we know so much about them, we still do not know what they are. Possibly several heterogeneous groups are included among them. The more typical Bacteria, however (such as *Bacillus subtilis* and its allies), which are often characterised by the production of endospores, are very unlike any other plants, and might be placed in a neutral group lying at the base of both the animal and vegetable kingdoms. Bacteria, however, offer so few points for morphological comparison with other groups, that nothing definite can be said at present as to their relationships.

Nostoc, representing the Cyanophyceæ, is another extremely simple type, so far at least as our present knowledge enables us to judge. It is probable, however, that further research may show the cell-structure to be more like that of the higher plants than it appears at present. It is doubtful whether the Cyanophyceæ should be classed with the Algæ or not; some botanists group them with the Bacteria in a class by themselves—the Schizophyta. As already pointed out, however, this relationship seems remote, except perhaps in the case of certain filamentous Bacteria. Until the cell-structure of the Cyanophyceæ and Bacteria is better understood,

it may remain impossible to assign them to their true position. The absence of sexual reproduction and of ciliated swarm-cells tends to keep the Cyanophyceæ in an isolated position, though it now appears probable that they approach the Algæ in possessing bodies of the nature of incipient nuclei.

Leaving these dubious forms, we come to the Flagellata, a group of motile unicellular organisms, some of which are animals, while others are partly plant-like and partly animal-like. From the Flagellata both the Algæ and certain groups of the Protozoa may have evolved. *Euglena viridis* is an animal by virtue of its organisation, but a plant as regards its mode of nutrition.

Chlamydomonas is a remarkable unicellular Alga which betrays its relationship to simple animals of the group Flagellata by the fact that the cells display active movement throughout their ordinary vegetative life. In higher plants the power of locomotion becomes restricted to certain reproductive cells, and is ultimately lost altogether, its last appearance being in the spermatozoids of the Vascular Cryptogams and of such Gymnosperms as the Cycads. The sexual reproduction of *Chlamydomonas* ranges, in the different species, from isogamy, or the union of similar sexual cells, to heterogamy, in which the gametes are clearly differentiated.

From unicellular Green Algæ, or their ancestors among the flagellate Protozoa, quite a number of distinct lines of affinity branch out. In one direction we reach the Conjugatæ, some of which are themselves unicellular, while in others, such as *Spirogyra*, the cells are usually united in filaments. This group always remains at a low level anatomically, for no more complex thallus than a simple filament is ever produced. On the other hand, the histological structure shows a great advance, as indicated especially by the highly-differentiated chloro-

plasts, which not only assume strange and varied forms, but are much specialised internally, possessing protein bodies (pyrenoids) around which the formation of starch is partly localised. In many members of the group, namely among the Desmids, the external form of the individual cells is also very complex. The sexual process is well marked, but of the simplest kind, consisting in the union of the contents of similar vegetative cells, with, at most, only the slightest indication of any difference between the sexes. The Conjugatæ, so far as we know, do not lead on to any of the higher groups of plants.

In quite a different direction green unicellular organisms appear to have given rise to the remarkable group represented among our types by *Vaucheria*. Here the cell has become multinucleate, and grows out into a large and in some cases complex thallus, but without dividing, so that we find a highly organised plant with non-cellular structure. *Vaucheria* itself, though its thallus is simple compared with that of other Siphonales, has attained a very high level as regards reproduction, for its sexual organs are as sharply differentiated as in the higher multicellular plants.

Differences of sex appear quite independently in many diverse lines of affinity, among which that represented by *Vaucheria* is one of the most distinct.

Vaucheria is also of great interest because of its analogy with the lower Fungi. There can be no doubt of the close parallelism between such a Fungus as *Pythium* and such an Alga as *Vaucheria*. This parallelism, however, is no indication of affinity (see p. 223). Fungi and Algæ have probably been wholly distinct lines from a stage as simple as that of the unicellular Flagellata. Spermatozoids are not differentiated in *Pythium*, the male protoplasm being carried to the ovum by the fertilising tube. This condition has been compared to the

change from fertilisation by spermatozoids to fertilisation by a pollen-tube, in passing from Cryptogams to Phanerogams. In both cases the disappearance of motile male cells is correlated with the loss of aquatic environment.[1] The gradual extinction of zoospores among the allies of *Pythium* is due to similar causes, and has been fully traced above (p. 218).

The Zygomycetes, as represented by *Pilobolus*, are Fungi which are adapted to a terrestrial mode of life. Though they still show signs of analogy with non-cellular Algæ, there can here be no question of affinity.

When we come to the higher Fungi, beginning with such forms as *Sphærotheca*, we find it impossible, in the present state of our knowledge, to determine their relation to the lower forms. The ascus has been sometimes regarded as corresponding to the sporangium of the Zygomycetes; this, however, is probably untrue, for there is invariably a nuclear fusion in young asci and not in sporangia. In any case, the Ascomycetes have diverged very widely from the Phycomycete stock, as shown not only by their fructification but by their septate mycelium. This group reaches a very high development, the ascus-fruit having become a very complex structure in forms like *Xanthoria*. The Lichens, most of which are Ascomycetes, are the only Fungi which form a highly-organised aërial thallus. By their association with a green assimilating organism (the captive Alga) they have placed themselves on a level with the higher chlorophyll-containing plants.

Among the Ascomycetes the conidial form of fruit, though often important, is subordinate. In the remaining groups the conidia (the origin of which could already be traced in the Phycomycetes) and basidiospores have completely displaced the sporangia, and assume very

[1] See, however, p. 311.

various forms, constituting the great means of propagation. In the Uredineæ the æcidium is to be regarded as a sexually produced fruit, while the spermatia formed in the spermogonia play a very important part in the sexual process that leads to the development of æcidia. The uredospores, teleutospores, and sporidia, however, are all of an asexual nature.[1]

The Uredineæ are adapted to a strictly parasitic mode of life, and in habit differ greatly from other Basidiomycetes, especially if we consider a highly organised representative of the latter, such as the Mushroom. The fructifications of these highest of the Fungi are very complex, but the basidium itself appears to be comparable to a teleutospore germinating *in situ*, an homology which is strikingly confirmed by the occurrence of nuclear fusion, alike in the teleutospore and the basidium.

We see, then, that the Fungi form by themselves a highly-complex cycle of relationship, approaching the lower Algæ at one or two points, but otherwise distinct from the rest of the Vegetable Kingdom. Sexuality has proved to be far more general among this mass of saprophytic and parasitic organisms than was once supposed, though it often assumes a curiously reduced form comparable to the fusion of nuclei in apogamous Fern-prothalli.

We must now retrace our steps to the Algæ. The Red Seaweeds form a perfectly definite group by themselves, without clear connections either below or above. *Callithamnion* is a fair average type ; some forms are simpler, especially in the development of the fruit, but even the simplest of the undoubted Rhodophyceæ are highly

[1] It must be remembered, however, that the derivatives of the paired nuclei of the æcidiospores only fuse with one another in the young teleutospores (see p. 267).

organised plants, quite unlike any other group. Many are more complex than our type, but they are complex in their own peculiar way, and do not show any transition towards the higher groups of plants.

The sexual process in Rhodophyceæ is quite peculiar among Algæ, for no definite oöspore is ever formed as the result of fertilisation. The whole carpogonium when fertilised remains in complete continuity with the tissues of the thallus, and sends out branches, which ultimately produce numerous spores, usually after various subsidiary cell-fusions have taken place. This continuity of the spore-fruit with the thallus completely severs the Rhodophyceæ from the Bryophyta, with which there is otherwise a certain analogy, in so far as in both groups the result of fertilisation is a fruit. The Rhodophyceæ are also remarkable for the entire absence of motile ciliated cells, a point in which they differ from the great majority of the Algæ, though certain isolated groups, such as the Conjugatæ (which certainly have nothing to do with them), have the same peculiarity. The most striking result of recent work on the Rhodophyceæ has been to show that there is often a regular alternation between the sexual and asexual plants.[1]

The Phæophyceæ are also much isolated from other Algæ, but they have more in common with Chlorophyceæ than is the case with the Red Seaweeds. Ciliated cells are almost universal throughout the group, though in the highest Brown Algæ—the Fucales—they only appear as spermatozoids. Fertilisation usually, if not always, takes place *outside* the oögonium, a point in which these plants differ from the Green Algæ. The Fucales are on a much higher level than the rest of the group, but transitional forms are not altogether absent. On the whole, we may say that the Brown Algæ are a natural

[1] See also p. 208.

group, attaining very great complexity on their own lines, and not clearly related either to the lower or higher plants. In some of the Orders (*e.g.* the Laminariales and the Dictyotales) an alternation of sexual and asexual generations occurs.

We must now return to the Chlorophyceæ. We have in *Ulothrix* a form scarcely more complex than *Spirogyra*, but evidently on quite a different line of descent. Here the reproductive cells are all ciliated and active. It is between certain of these ciliated cells that sexual fusion occurs, and not between vegetative cells, as in *Spirogyra*. Evidently the origin of sexuality was quite distinct in these two groups. If we had been able to take a wider survey of the Vegetable Kingdom, we should have found evidence that this important step from asexual to sexual reproduction was made independently in many groups.

Ulothrix is also interesting from the great difference in subsequent development between the asexual and the sexual swarm-cells. The asexual zoospore merely reproduces the ordinary plant, whereas the zygospore gives rise to a dwarf individual quite distinct from the typical form. In fact we have here, coinciding with the first appearance of sexuality, some slight suggestion of regularly alternating generations. For this reason *Ulothrix* has been regarded as lying more or less in the direct line of descent of the archegoniate plants, in which regular alternation of generations is so striking a character. Of course this cannot be taken literally. No form now living can possibly be in the direct line of descent of any other form, any more than a man's cousin can be his ancestor! One cousin, it is true, may more than another inherit the characteristics of some remote ancestor, and this is all we mean in speaking of lines of descent with reference to recent plants. In the case of *Ulothrix*, however,

there is probably nothing more than a remote analogy with the course of development of Bryophyta. A better parallel is really found in the alternation of sexual and asexual individuals in some of the higher Algæ.

Œdogonium makes in some respects a great step in advance. Here the sexual cells are perfectly differentiated; instead of two similar fusing motile cells, we find a small moving spermatozoid and a large resting ovum. The casual difference in size sometimes observed in *Ulothrix* has here become fixed, and other differences are added. Evidently there is a more perfect adjustment of function here; for while both partners are still on equal terms as regards the union of their nuclei, it is the female cell alone which assumes the whole duty of accumulating food-supplies for the next generation. In order to do this most effectually, it remains at rest, in connection with the vegetative body of the plant. So far as the sexual division of labour is concerned, *Œdogonium* is almost as far advanced as any other plant.

The formation of dwarf male plants in some members of this group is without exact parallel in any other plants, and shows how far the specialisation of the sexes may go, even in simple organisms. This, however, is only a special case, for, as we have seen, there are some species of *Œdogonium* without dwarf males.

The division of the germinating oöspore into four swarm-spores is an interesting fact. These spores are just like the zoospores produced by the plant in its ordinary condition. The fact that they are always formed by the sexually produced resting-spore immediately on germination, indicates some approach to a regular alternation of sexual and asexual reproduction. In this respect, however, *Œdogonium* shows no advance on *Ulothrix*.

In another genus of green fresh-water Algæ, *Coleochæte*, the oöspore, while still enclosed in the oögonium,

divides up into a group of cells, in each of which a zoospore is formed. This process shows a remote analogy with the formation of the simplest forms of sporogonium in the Liverworts, among which there is a genus (*Riccia*) in which the fruit consists of nothing but a mass of spore mother-cells surrounded by an epidermis. There is, however, no trace of affinity between the Alga and the Hepatic, in which the simplicity of the fruit may be the result of reduction.

The sporophyte of the higher plants, whatever its origin may have been, is specially adapted to the formation of aërial, as distinguished from aquatic, spores. The spores of the Archegoniatæ, from the lowest Bryophyta upwards, differ from those of any of the Algæ in being almost always suited for dissemination by the air. The sporophyte which bears them is essentially the *aërial* generation, while the gametophyte is dependent on water for the act of fertilisation. The difference is very well shown in *Pellia*, where the sexual generation is a low-growing thallus, keeping close to the damp ground, or even living under water, while the sporophyte grows up high into the air, exposing its spores as freely as possible, so that they may be dispersed by the wind. The result in other cases is attained in a different way, but the general rule holds good, that the function of the sporophyte—the dissemination of spores—requires exposure to dry air, while the most important function of the gametophyte—the act of fertilisation—requires the presence of water.

It is improbable that the aërial, asexual spores of the Bryophyta are homologous with the aquatic, asexual spores of the Green Algæ ; a better comparison is with the *tetraspores* of the Rhodophyceæ and the Dictyotales among the Brown Seaweeds. The origin of the Archegoniatæ must have taken place in enormously remote geological ages,

when plants were first adapting themselves to terrestrial life, and we cannot be surprised that no transitional forms connecting them with the Algæ are known to us, unless it be among the remains of the older Devonian Flora. It is commonly assumed that the Bryophyta represent an earlier stage of evolution than the Pteridophyta, but palæontological evidence lends no support to this assumption.

So far as the vegetative structure of the thallus is concerned, *Pellia* is a very simple Liverwort; others are more complex, but in all alike the archegonium and antheridium are totally different from the sexual organs of any Thallophytes.

In the true Mosses both the sexual and asexual generations are more highly developed than in the Hepaticæ. Not only is the thallus replaced by a leafy stem (a change which is already accomplished in many Liverworts), but the anatomical structure is much more perfect, and a definite system of conducting tissue is differentiated. The sporophyte never develops into anything more than a "fruit," yet it is anatomically the more elaborate of the two generations, as shown not only by the arrangements for dispersing the spores, but also by the vegetative tissues of the sporogonium, which have some resemblance to those of vascular plants, especially in the possession of true stomata. The mosses are highly organised plants in their own way, but appear to have no direct affinity with superior groups.

If we found a wide gap to cross in passing from Algæ to Bryophyta, this is equally the case when we pass on to the Pteridophyta. The latter, as at present existing, form three quite distinct stocks—Horsetails, Ferns, and Club Mosses—but in none of the three is there the least evidence for any near relationship to the Bryophytes. The sexual generation presents little difficulty;

for instance, the thallus of a *Pellia* may well be compared with the prothallus of a Fern. It is the sporophyte which is so different in the two classes. Speaking broadly, the asexual generation in the Bryophyta is always a "fruit," while in Pteridophyta it is always a plant. Recently, however, among early Devonian fossils, organs with the structure of Bryophytic sporogonia have been found, borne on the stems of a simple form of Pteridophyte.

It is too soon to discuss the significance of these observations ; it may be that the further investigation of the oldest known land-plants will throw light on the origin of the two great divergent series of the Bryophyta and Pteridophyta. We have long had direct geological proof of the enormous antiquity of the Pteridophyta which appear to form the bulk even of the older Devonian Flora. At that period, however, some of them seem to have been of a relatively primitive nature, differing from any of the existing groups, and possibly combining their characters, while at the same time suggesting perhaps some lingering trace of old Algal affinities. The Devonian sporogonia, referred to above, are the first indications yet discovered of the high antiquity of a Bryophytic type of reproductive structure, though not of the Bryophyta themselves, as now understood.

The Pteridophyta are much more highly organised than any of the previous groups ; their advance is entirely confined to the asexual generation, for the gametophyte remains throughout at a very low level (below that of the simplest Bryophyta), and indeed degenerates as we reach the higher forms. No doubt the aquatic mode of fertilisation has kept back the gametophyte, which throughout the Pteridophyta is always a damp-loving organism, and never completely adapts itself to terrestrial life. The asexual plant, on the other hand, has attained

the greatest complexity, rivalling that of the Flowering Plants.

In all the three main groups both homosporous and heterosporus forms have occurred, though among the Horsetails heterospory is now extinct.

Most Ferns, like our type, are homosporous, though even here rudimentary purely male prothalli are not uncommon. Heterospory in plants of the Fern alliance is now limited to two small families. The origin of heterospory may be compared to the origin of sexual differentiation (see above, p. 306). Just as nutritive functions came to be assigned specially to the ovum, so here they are assigned specially to the female prothallus, which has to feed the embryo during its development. The male prothallus can safely be treated by the plant on strictly economical principles, for it has nothing more to do than to produce a few minute spermatozoids. We see this change beginning both among Ferns and Horsetails ; in the latter the smaller, less vigorous prothalli, are exclusively male. Then the difference extends further back. The insignificant male prothallus only needs a small spore to grow from, while the female must be fed well from the first, and so a large spore, full of reserve food, is set apart for its formation. On the other hand, it is an advantage to have plenty of males in order to ensure fertilisation. Thus we get a large number of microspores forming small male prothalli, and a small number of megaspores forming comparatively large female prothalli.

In *Selaginella* we have an extreme case of heterospory, with an enormous difference between microspores and megaspores. There is, however, another change going on concurrently with that just sketched. Both prothalli have become the mere bearers of sexual organs, and are losing the character of distinct organisms. Hence the

female prothallus, though so highly developed relatively to the male, is itself reduced, as compared with the prothallus of a homosporous Pteridophyte.

The homologies between *Selaginella* and a gymnospermous Flowering Plant, such as *Picea*, are quite clear, and have been fully demonstrated above (p. 31). It is certain, however, that there is no near affinity between *Selaginella* and the Gymnosperms, which, as palæontological evidence indicates, probably sprang from a stock quite unlike any existing Pteridophyte. In any case the homologies hold good, whatever the unknown heterosporous group or groups may have been from which the Gymnosperms sprang.

In the latter Class the female gametophyte has lost its independence altogether, and never leaves the megaspore, which itself remains shut up in the sporangium enclosed in an integument. Fertilisation leads to the formation of a seed—the characteristic structure of Flowering Plants, consisting of integument, sporangium, prothallus, and embryo, united to form one body, and fed entirely at the expense of the parent sporophyte.

Until the year 1896 there appeared to be a sharp distinction between Cryptogams and Phanerogams in the method of fertilisation, for active spermatozoids were supposed to be peculiar to the former, the generative cell in Phanerogams being carried passively to the ovum by the growth of the pollen-tube. The researches of the Japanese botanists Hirase and Ikeno, followed by those of Webber in America, first broke down this distinction, for they proved that in some Gymnosperms true motile spermatozoids are formed. The plants in which this important discovery was first made are the Maidenhair Tree (*Ginkgo biloba*), a tree of an ancient type, nearly related to the Coniferæ, and *Cycas revoluta* (see p. 34). In both these cases (to which others have

now been added) a pollen-tube is formed, which enters the nucellus, but does not reach the archegonia, and serves chiefly to anchor the pollen-grain in the right position. Two generative cells are formed in the usual way, but each of these gives rise to a large, spirally-coiled spermatozoid, with numerous cilia (see Figs. 118 and 119, which have been sketched from the original preparations, kindly sent by Prof. Ikeno and Dr. Hirase; Fig. 119*). The spermatozoids break out from the pollen-tube, and by their own active movements swim to the necks of the archegonia through a cavity, filled with fluid, which is formed in the upper part of the nucellus. These plants thus present a beautiful transition between the Cryptogamic and Phanerogamic methods of fertilisation. The male cells are conveyed for a short distance by the growth of the pollen-tube, but they have to com-

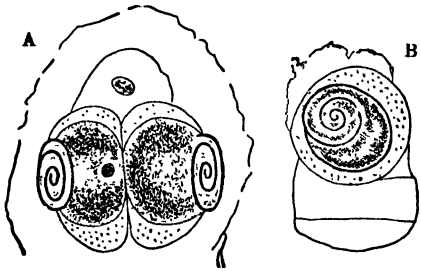


FIG. 118.—*Ginkgo biloba*. A, pair of generative cells in the pollen-tube. On the outer side of each cell a spiral coil is seen in connection with the nucleus. B, generative cell, showing the spiral spermatozoid in surface view. × 225. From a preparation by Dr. Hirase. (R. S.)

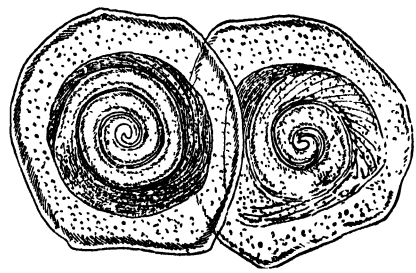


FIG. 119.—*Cycas revoluta*. Pair of generative cells from a pollen-tube, showing the spirally-coiled spermatozoids, surrounded by the cytoplasm of the cell. The fine striation overlying the spiral coil indicates the cilia. × 190. From a preparation by Prof. Ikeno. (R. S.)

plete the journey to the ovum by means of their own movements.

A condition still more cryptogamic has since been discovered by Caldwell in the Cuban Cycad *Microcycas calocoma*, in which each pollen-tube produces no less than eight pairs of generative cells, giving rise to sixteen spermatozoids. This multiplication of sperm-cells, probably unexampled among Seed-plants, is correlated with the immense number of archegonia (200 or more) produced in the embryo-sac of this strange plant.

These remarkable discoveries confirm, in the most striking way, the theoretical conclusions at which Hofmeister arrived in 1851.

From Gymnosperms to Angiosperms is another great step, and here the gulf has not yet been bridged. In Angiosperms the female prothallus has almost disappeared, and even the archegonia are no longer recognisable. The embryo-sac (the equivalent of the megaspore) proceeds, after only a few preliminary divisions, to the formation of the ovum, and the development of the endosperm is dependent upon fertilisation, — obviously an expedient arrangement, for it is not formed at all unless it is wanted. The processes in the pollen-grain are also simplified. The great characteristic of Angiosperms is the high development of the flower and fruit. Not only does the megaspore remain enclosed in the integumented sporangium or ovule, but the latter is itself enclosed in the ovary, so that fertilisation has to



FIG. 119*.—*Cycas revoluta*. Pollen-tube, branched above, and containing the two actively moving, ciliated spermatozoids. Magnified 44. (After Miyake.)

take place through the mediation of the stigma and style. The remarkable development of the floral leaves, characteristic of most Angiosperms, is connected with the occurrence of pollination by insects, for which so many Angiosperms are specially adapted.

At present we are not in a position to determine either the relation of Angiosperms to Gymnosperms, nor that of Monocotyledons to Dicotyledons. The latter classes are mainly distinguished by vegetative characters, the reproductive phenomena being the same in both. On both these questions, however, we may hope for further light, especially from palæontological research, for the first appearance of Angiosperms falls within a geological period from which abundant fossil remains have come down to us. Dr. Wieland's discovery that the Bennettitales, Mesozoic plants allied to Cycads, produced elaborate hermaphrodite "flowers" somewhat comparable to those of the Angiosperms, has already thrown some light on these questions.

This brief summary has had one main object,—to indicate the complicated and difficult nature of all questions as to the affinities of plants. Naturalists in these days are agreed that the different forms of plants and animals arose from one another by descent. If this be so, a natural classification of the Vegetable Kingdom would take the form of a genealogical tree, just like the pedigree of a family. The genealogical tree of plants must have been complex beyond all power of conception, with boughs, branches, and twigs of every degree starting from each other at every possible point,—some long and some short, a few reaching on to our own day, while the immense majority came to an end in the long-past geologic ages.

If we attempted to construct such a tree, say for our

twenty-eight types, almost every branch would be marked with a query. If the reader has gained some idea of the difficulty and complexity of the profoundly interesting problems which the comparative study of plants presents to us, the object of this concluding chapter will have been attained.

CHAPTER IX

APPENDIX

TYPE IV A

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 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. 120).

The stems bear crowded small green leaves of simple form, spirally arranged. The leaves are somewhat fleshy and terminate in a sharp point; they are attached to the stem by a rather broad base. The leaves, as in

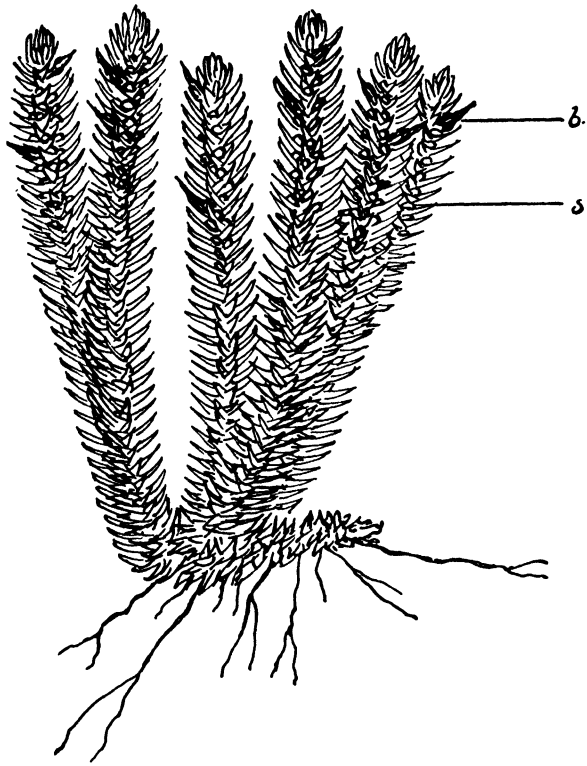


FIG. 120.—*Lycopodium Selago*; mature plant. *b*, bulbil; *s*, sporangium. (W. J. Dowson.)

all species of *Lycopodium*, have no ligule, and in this respect are unlike the leaves 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 : they are not always confined to the axils of the upper leaves, but may be present nearly down to soil level, or again they may occur in the upper and lower parts of the shoot with a sterile interval between. The reproductive part of the plant, therefore, is not differentiated into a cone as in *Selaginella Kraussiana*, where the sporophylls are distinct from the ordinary leaves.

In another British species, *L. clavatum*, popularly known as Stag's Horn Moss, which also occurs in mountainous districts, the habit of the plant is different. Here the branched stem creeps along the ground for a considerable distance, giving off roots at intervals. In *L. clavatum*, too, there are well-defined cylindrical cones which arise at the forked extremities of erect branches that are clearly differentiated from the trailing stems and have smaller widely-spaced leaves. The sporophylls are crowded and scale-like, and each bears a sporangium at its base.

To return to *L. Selago* : in the upper parts of the erect shoots a few of the leaves and their associated sporangia are commonly replaced by large green buds or *bulbils*, which later become detached. Each bulbil consists of a short stem and a few thick green leaves. The bulbils fall to the ground and may grow into new plants, thus serving as an accessory vegetative means of reproduction.

II. *INTERNAL CHARACTERS OF THE VEGETATIVE ORGANS*

a. The Stem

We will first describe the structure of the stem. If a transverse section of the stem, remote from a branch, is examined (see Fig. 121) it will be seen that there is a

single centrally disposed stele. If, however, the section is cut near a fork, two steles will be seen, one from each branch ; it is only at a lower level that the two steles coalesce into one. The stele consists of a more or less star-shaped mass of xylem with the phloëm between the " rays." In transverse section the xylem may appear to

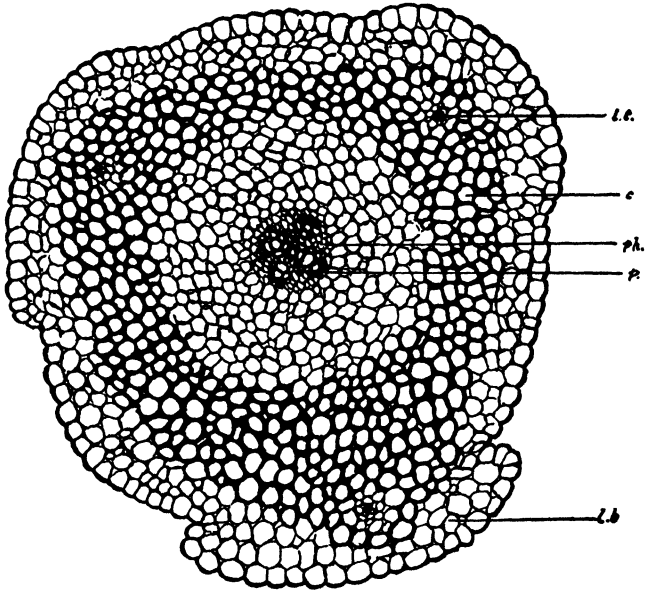


FIG. 121.—*L. Selago*; transverse section of stem. *c.*, middle cortex; *l.b.*, leaf base; *l.t.*, leaf-trace; *p.*, protoxylem; *ph.*, phloëm. Magnified about 70. (W. J. Dowson.)

be broken into separate groups, but these are found to connect together if traced longitudinally. The xylem consists wholly of tracheids, the smaller tracheids of the protoxylem occurring invariably at the fan-like extremities of the " rays." The xylem of the stem, therefore, differentiates centripetally as in *Selaginella*, and this is one of

the constant features of the anatomy of the *Lycopodiales*. In longitudinal section the protoxylem tracheids are seen to be spirally thickened, but the later formed tracheids (the metaxylem) are scalariformly pitted, as is usual in the Pteridophyta. A narrow zone of parenchyma occurs between the xylem and the phloëm, which latter consists of sieve-tubes. Bounding the xylem and phloëm is a parenchymatous sheath, outside which is an endodermis, usually ill-defined. In the cortex small leaf-traces can be seen (Fig. 121), which connect the vascular supply of the leaves with the stele of the stem. The outer cortical cells are thick-walled and serve to give rigidity to the stem. At the periphery of the stem leaf-bases are seen in transverse section. The outer walls of the epidermal cells are covered with a cuticle, an impervious layer which checks transpiration.

All growth of the shoot apex proceeds from a small group of *initial cells*, instead of from a single apical cell as in *Selaginella Kraussiana*. The stelar and cortical regions are differentiated quite near the apex. The leaves begin to develop from the surface layers just below the apical region.

b. The Leaves

As in *Selaginella*, the leaves of *L. Selago* are very simple in structure. Each leaf receives a single vascular bundle from the stem, which traverses it from end to end without branching. The bundle is embedded in the somewhat fleshy tissue of the leaf, so it is not visible to the naked eye as a midrib. The bundle consists of a few tracheids and sieve-tubes, only the former of which extend to the tip of the leaf. The stomata are scattered over the whole surface of the leaf. The epidermal cells, apart from the guard cells, are elongated and their outer walls have wavy outlines which fit into one another ; in section the outer

walls are seen to be strongly cuticularised. The mesophyll is undifferentiated; the cells, which are loosely arranged, contain numerous small chloroplasts. The walls of some of the mesophyll cells are rather thick and many of these cells are elongated in a direction parallel to the long axis of the leaf. In the middle of the leaf and towards its base there is often a considerable cavity between the upper and the lower parts of the mesophyll. The somewhat fleshy nature of the leaf and its well-marked cuticle are related to the exposed situation in which *L. Selago* lives.

c. The Root

The roots arise endogenously from the prostrate portion of the stem. They are very slender and branch dichotomously at intervals. Growth in length proceeds from a small group of meristematic cells at the apex, which is covered by a delicate root cap.

Each root is traversed by a single stele of simple structure. In transverse section the xylem usually appears to be in the form of a crescent, with the protoxylem at the two extremities. The phloëm with parenchyma occupies the bay between the horns of the crescent. Surrounding the xylem and phloëm is a band of parenchyma, but the endodermis is ill-defined. A broad zone in the outer cortex consists of thick-walled cells which serve to give rigidity to the slender root. The outermost cells are thin-walled and many of them grow out into root-hairs.

In *L. Selago* roots may also arise endogenously in the tissues of the erect stem, but such roots rarely emerge; they grow vertically downwards in the cortex for some distance and then usually cease to develop further. These roots are sometimes seen in transverse sections of the erect stem.

III. *REPRODUCTION AND LIFE-HISTORY*

a. The Sporangia and Spores

The sporangium begins to develop as a slight swelling on the upper surface of the base of the sporophyll, but owing to subsequent growth it often appears to arise in the axil (see Fig. 122). The very young sporangium consists of a single row of archesporial cells, surrounded by a layer of cells destined to form the sporangial wall.

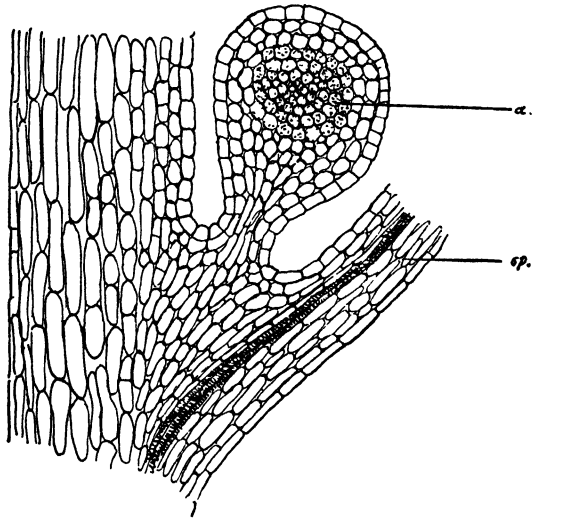


FIG. 122.—*L. Selago.* Longitudinal section through a young sporangium. *a*, archesporium; *sp*, sporophyll. Magnified about 70. (W. J. Dowson.)

Divisions proceed so that at a later stage a considerable number of archesporial cells are enveloped by the sporangial wall which is three cells thick except towards the base where a short multicellular stalk is differentiated. The innermost layer of the sporangial wall is the tapetum, which later undergoes disorganisation. After repeated

divisions the archesporial cells become separated from one another as spore mother-cells, and the cell-walls of the outer sporangial layer become thicker. Each spore mother-cell then divides twice in rapid succession, producing a tetrad of spores. The walls of the spores become thickened and ornamented on the surface. Owing to the breaking down of the walls of the mother-cells the spores come to lie freely in the sporangial cavity. At maturity the sporangium is kidney-shaped. The cells of the wall lose water in dry weather, and eventually the sporangium dehisces by a vertical slit, thus liberating the spores.

Throughout the genus *Lycopodium* the spores are all of one kind, a condition known as *homospory* in contrast to the *heterospory* of *Selaginella*. In this respect *Lycopodium* is similar to most of the Ferns and the Horsetails.

b. The Prothallus and Sexual Organs

The spores alight on the soil and are often washed down below the surface by rain, where they germinate to produce the *prothallus* or sexual generation (gametophyte). Not much is known about the early stages in the development of the prothallus, as young prothalli are difficult to find in nature and it is even more difficult, if not impossible, to cultivate them from spores artificially. The prothallus of *Lycopodium* long escaped discovery because it is generally subterranean, but we now have a fairly complete knowledge of the prothallus of the commonest species. In *L. Selago* the young prothallus develops underground from the spore as a colourless mass of cells shaped like a minute inverted cone. Some of the superficial cells grow out into slender rhizoids, and we now know that unless some of these rhizoids become infected at an early stage by a particular fungus from the soil the young prothallus ceases to grow and quickly perishes. After successful invasion of the rhizoids, the fungus

invades a broad band of cells in the lower part of the prothallus (see Fig. 123), but it never penetrates the upper region where the meristematic tissue is situated. The fungus undoubtedly absorbs food materials (including

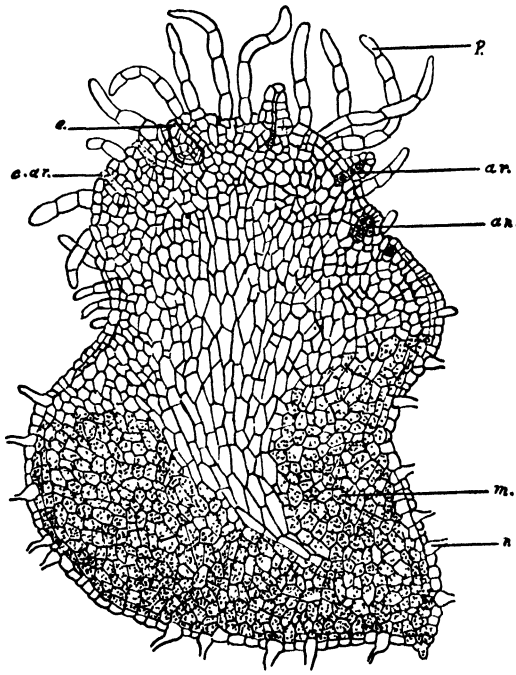


FIG. 123.—*L. Selago.* Median longitudinal section of prothallus. *an*, antheridium; *ar*, archegonium; *c. ar*, collapsed archegonium; *e*, very young embryo; *p*, paraphysis; *m*, tissue containing fungus; *r*, rhizoid. Magnified about 35. (W. J. Dowson, after Bruchmann.)

organic carbon compounds) from the soil, which are of benefit to the young prothallus. Furthermore, in the layer of infected cells bordering on the upper, fungus-free region, the hyphæ of the fungus and their contents

are digested by the host protoplasm, thus providing further food for the prothallus. This strange intimate association of a fungus with a subterranean organ of a higher plant is called a *Mycorrhiza* (literally, *fungus-root*). Without it the subterranean Lycopod prothalli could never develop to the stage of producing sexual organs, for being devoid of chlorophyll their tissues cannot assimilate carbon from the air. In passing, it may be mentioned that mycorrhizal associations between the roots of forest trees and certain fungi are quite common, especially where the soil contains much humus, although in such trees photosynthesis proceeds normally. The prothallus continues to grow by the active division of the cells at the top, and starch grains are found in quantity in the cells between the meristematic zone and the fungus-invaded zone below. The prothallus of *L. Selago*, which when young is in the form of an inverted cone, becomes roughly cylindrical as it approaches maturity, when it is about 2 mm. across. At other times, especially if the young prothallus is somewhat deeply situated in the soil, it assumes a slender cylindrical form and may reach a length of about 5 mm. There is, in fact, considerable diversity of shape in these subterranean prothalli. Furthermore, in *L. Selago* the upper part of the prothallus occasionally reaches the surface of the soil, when by marginal growth small lobes are formed which become green owing to the development of chlorophyll. In certain tropical and sub-tropical species of *Lycopodium* the upper part of the prothallus is invariably green. In another British species, *L. clavatum*, the prothallus is wholly subterranean and devoid of chlorophyll.

In the simplest form of the adult prothallus of *L. Selago* which we have described, antheridia and archegonia are formed on the upper surface, as indicated in Fig. 123. Near the sexual organs superficial cells of the prothallus

grow out into short septate filaments, the *paraphyses*, between which water is retained by capillarity, thus enabling the spermatozoids to move. The antheridia are spherical and slightly sunken in the tissues ; the wall, one cell thick, encloses a number of spermatozoid mother-cells, each of which forms a single spermatozoid (see Fig. 123). At maturity, the wall breaks down and the spermatozoids are liberated into the soil water. The spermatozoids are biciliate and very similar to those of *Selaginella*. The archegonia are produced on the same prothallus, in close proximity to the antheridia. They are similar to the archegonia of *Selaginella*, but the necks are somewhat longer (see Fig. 123). The venter of the archegonium containing the ovum is surmounted by a neck of about six tiers of cells in the middle of which is a number of canal-cells arranged in a single row from the top of the neck to the ovum. When ripe, the canal-cells break down and the neck cells at the top separate somewhat, leaving an open channel down to the ovum. The spermatozoids are probably attracted to the archegonia by some secretion, as in Mosses and Ferns. In the process of fertilisation a spermatozoid passes down the channel in the neck and fuses with the ovum. As can be readily understood, there is some hazard about the spermatozoids reaching the archegonia through the soil water, and fertilisation may not be achieved until the prothallus is several years old.

The fertilised ovum surrounds itself with a wall and then divides into two cells, the upper one of which (*i.e.* the one towards the neck of the archegonium) becomes the *suspensor*, which, however, is less well developed than in *Selaginella*. The lower of the first two cells then divides transversely and longitudinally to produce a small mass of tissue, the embryo proper, from which the foot (which absorbs food material from the prothallus), the stem and

the first root (which arises exogenously) soon become differentiated. The stem grows upwards and produces the first green leaf which is sometimes called the *cotyledon.* The portion of the stem between its attachment to the prothallus and the cotyledon may be called the *hypocotyl,* the length of which depends on the depth to which the prothallus is buried in the soil, as the cotyledon does not develop fully until the surface is reached. As the stem grows above the soil other leaves are formed in rapid succession and new roots arise endogenously from the inner cortex. The young sporophyte is now launched on an independent existence. It is characteristic of Lycopod prothalli to die once a new sporophyte has been successfully established.

c. Life-History and Comparison with Selaginella

The life-history of *Lycopodium Selago* is thus completed in two sharply contrasted stages. The erect green plant as seen in its natural habitat is the sporophyte which produces spores in sporangia. A spore on germinating forms the somewhat fleshy, usually subterranean, prothallus or gametophyte on which both kinds of sexual organs, the antheridia and archegonia, are borne. The fertilised ovum develops into a new sporophyte. Thus there is a regular alternation of generations in the life-cycle. The only complication is that bulbils serve to reproduce the sporophyte indefinitely without interruption by the gametophyte generation.

We will now briefly compare *Lycopodium* with *Selaginella.* The leaves of the former are devoid of a ligule, but in the latter they possess one. *Lycopodium* is homosporous but *Selaginella* is heterosporous. The gametophyte of *Lycopodium* bears both antheridia and archegonia, whereas there are two kinds of gametophytes in *Selaginella,* the male gametophyte being exceedingly

reduced. The prothallus of *Lycopodium* is more massive than the female gametophyte of *Selaginella* and in many species is a subterranean structure, devoid of chlorophyll, which is nourished by association with a fungus. On the other hand, there are close relationships between the two genera : the vascular organisation of their sporophytes is similar, their leaves are invariably small, the mode of development of their sporangia is practically identical, and in both the spermatozoids are bi-ciliate. For these reasons the two genera are placed together in the *Lycopodiales*.

GLOSSARY

ÆCIDIOSPORES.—The spores produced in chains in the cluster-cups (Æcidia) of Rust Fungi.

AMPHITHECIUM.—The outer layer of the young capsule in Bryophytes.

ANALOGOUS.—Corresponding in function.

ANDROSPORE.—The small zoospore producing a dwarf male in some Œdogoniaceæ.

ANNULUS.—1. The rows of cells, which causes a Fern sporangium to open.

2. The ring of abortive leaves at the base of an *Equisetum* cone.

3. The ring of cells in a Moss capsule, which splits when the lid comes off.

4. The ring underneath the pileus of a mushroom.

ANTHERIDIUM.—The organ in which the male cells are produced in Flowerless Plants.

APICAL CELL.—The large cell at the growing point, by the divisions of which, in many Flowerless Plants, all the new tissues and organs are ultimately produced.

APOGAMY.—The production of a sporophyte from a gametophyte without the intervention of the sexual organs.

APOPHYSIS.—The basal, sterile portion of a Moss capsule.

APOSPORY.—The production of a gametophyte from a sporophyte without the intervention of the spores.

APOTHECIUM.—The open, disc-shaped fruit of some Lichens and Ascomycetes.

ARCHEGONIUM.—The organ in which the female cell is produced in Gymnosperms, Pteridophyta, and Bryophytes.

ARCHESPORIUM.—The cell or cells from which the spores are ultimately produced in a sporangium or sporogonium.

ASCOGONIUM.—The female organ of Ascomycetes, which gives rise to the ascus or ascogenous hyphæ.

ASCOSPORES.—Spores produced in an ascus.

ASCUS.—The characteristic reproductive cell of the Ascomycetes, producing a definite number of spores, usually 4 or 8, in its anterior.

AUXILIARY CELLS.—The cells which fuse with the fertilised carpogonium or outgrowths therefrom in certain Red Algæ.

BASIDIOSPORES.—Spores produced on a basidium.

BASIDIUM.—The cell which gives rise externally to certain spores in the Basidiomycetes.

BIOLOGIC FORM.—A physiological variety of a species of parasitic fungus confined to a particular host or hosts.

BIPINNATE.—When the leaflets of a pinnate leaf are themselves pinnate.

CALYPTRA.—The envelope enclosing the young capsule in Bryophytes.

CAPILLITIUM.—A web of threads investing the spores : *e.g.* in the sporangium of a Myxomycete.

CAPSULE.—The spore-case in Bryophytes.

CARINAL.—Opposite a rib of the stem.

CARPOGONIUM.—The cell from which the fruit originates in Red Algæ.

CARPOSPORES.—The sexually produced spores of Red Algæ.

CHLAMYDOSPORE.—A thick-walled spore in Fungi usually formed in a hypha.

CHROMATIN.—The essential nuclear substance, which stains readily with dyes.

CILIA.—Protoplasmic threads, by means of which spermatozoids and other motile cells move.

CIRCINATE.—Coiled like a crozier or a snail.

COLUMELLA.—The central, sterile part of a Moss capsule and of the sporangium of certain Fungi.

COMMENSALISM.—The association of two different organisms for mutual benefit, as the Alga and Fungus in a Lichen.

CONCEPTACLE.—The cavity containing the sexual organs in Fucales.

CONIDIA.—Propagative cells of Fungi, asexually and externally produced.

CONIDIOPHORE.—The organ which bears the conidia.

CONJUGATION.—The union of two similar sexual cells.

CYST.—A thick-walled resting cell, *e.g.* the compartments of the resting plasmodium in Myxomycetes.

CYSTOCARP.—The sexually produced fruit of Red Algæ.

DICHOTOMY.—The equal division of the growing point to form two equivalent branches.

DICTOSTELE.—A stele in the form of a complicated network.

ELATERS.—1. The arm-like appendages attached to the spore in *Equisetum*.

2. The spirally thickened cells in the capsule of Liverworts, helping to disperse the spores.

ENDOSPORE.—A spore formed inside a cell in some Bacteria.

ENDOTHECIUM.—The inner layer of the young capsule in Bryophytes.

EPIBASAL.—Forming the upper part of the embryo.

EPIPHYTE.—A plant which grows on another plant without obtaining food material from it.

EPITHECIUM.—The layer formed by the tips of the paraphyses above the asci in the fructification of a Lichen.

FERMENTATION.—The production of gases, especially CO_2, by certain micro-organisms under anærobic conditions.

FLAGELLA.—See CILIA.

FLEXUOUS HYPHA.—A hypha projecting from the spermogonium of a Rust Fungus which serves as a receptive organ for spermatia of opposite sex.

FOOT.—The part of the embryo which absorbs food from the prothallus in Pteridophyta.

GAMETE.—A sexual cell.

GAMETOPHYTE.—The sexual generation.

GEMMÆ.—Cells or buds serving to propagate the plant.

GLYCOGEN.—A substance related to starch found in Fungi, etc.

GONIDIA.—The algal cells of Lichens.

HAUSTORIUM.—The sucker of a parasite, absorbing food from the host plant.

HERMAPHRODITE.—Containing both sexes, in the same flower or the same conceptacle.

HETEROCYSTS.—Large, thick-walled cells occurring in *Nostoc* and its allies.

HETERŒCIOUS.—Infecting different host plants, at different stages of its life-history (used of parasitic Fungi).

HETEROGAMY.—The sexual fusion of unlike gametes (♂ and ♀).

HETEROSPOROUS.—Producing two kinds of spores: microspores (male) and megaspores (female).

HETEROTHALLISM.—The occurrence of physiologically, but not morphologically, distinct sexual forms in certain Fungi.

HOMOLOGOUS.—Corresponding in origin.

HOMOSPOROUS.—Producing one kind of spore only, as Ferns and Horsetails.

HORMOGONIA.—Actively creeping filaments, in *Nostoc* and its allies.

HYALOPLASM.—Clear protoplasm, free from granules, as in a pseudopodium of a Myxomycete.

HYMENIUM.—The layer of cells producing the spores in certain Fungi.

HYPHÆ.—The filaments of which Fungi are composed.

HYPOBASAL.—Forming the lower part of the embryo.

HYPOTHECIUM.—The part of the fructification of a Lichen below the hymenium.

INDUSIUM.—A membranous envelope enclosing a group of sporangia, or sometimes a single sporangium, in Ferns.

INTERCALARY.—Lying between apex and base, used of growing points which are not terminal.

INVOLUCRE.—An envelope enclosing the reproductive organs ; as the pocket round the archegonia in *Pellia*.

ISOGAMY.—The sexual fusion of similar gametes.

LAMELLÆ.—The " gills " of a Mushroom or Toadstool, which bear the spores.

LIGULE.—A membranous scale borne on the upper side of the leaf-base in *Selaginella*, *Isoëtes*, and their fossil allies.

MALIC ACID.—$C_4H_6O_5$: occurs in apples and most fruits.

MEGASPORANGIUM.—A spore-sac containing one or more megaspores.

MEGASPORE.—The large spore, which produces the female prothallus in heterosporous Pteridophyta.

METAXYLEM.—The part of the primary xylem differentiated after the protoxylem.

MICROCYST.—A swarm-spore, which has enclosed itself in a cell-wall, in Myxomycetes.

MICROSPORANGIUM.—A spore-sac containing microspores.

MICROSPORE.—A small spore, producing a male prothallus.

MICROZOOSPORES.—The minute swarm-cells of certain Green Algæ.

MONOSTELIC.—Containing a single vascular cylinder.

MYCELIUM.—The vegetative part of a Fungus, as Mushroom spawn.

MYCORRHIZA.—The intimate association of a fungus with the subterranean organs of a higher plant.

MYXAMŒBÆ.—The creeping swarm-spores of Myxomycetes.

OCTANTS.—The eight cells into which the fertilised ovum divides in some Petridophyta.

OÖGAMY.—The sexual fusion of a stationary female gamete with a male gamete.

OÖGONIUM.—The cell which contains the ovum or ova in many Algæ and Fungi.

OÖSPORE.—The fertilised ovum.

OPERCULUM.—The lid of a Moss capsule.

OVUM.—The female cell which, when fertilised, gives rise to the new generation.

PALEÆ.—Chaffy scales, as those of Ferns.

PARAMYLON.—A substance related to starch found in certain Flagellata.

PARAPHYSES.—Sterile hairs accompanying reproductive organs.

PARASITE.—A plant which grows on another plant and feeds on it.

PELTATE.—Shield-shaped.

PERIDIUM.—The wall of the fruit in certain Fungi, as in the Æcidium of the Rusts.

PERIPLASM.—The outer part of the protoplasm in an antheridium or oögonium, when not used in the formation of the sexual cells.

PERISTOME.—The ring of teeth round the mouth of a Moss capsule.

PERITHECIUM.—The envelope enclosing the ascus or asci in some Fungi, as in *Sphærotheca*.

PHYSIOLOGIC RACE.—See BIOLOGIC FORM.

PILEUS.—The upper, expanded part of the fruit in a Mushroom or Toadstool.

PINNATE.—Compound, with the leaflets arranged along each side of a common midrib.

PLANOGAMETE.—An actively moving sexual cell.

PLASMODIUM.—A naked protoplasmic body, containing many nuclei and capable of creeping movements.

PROCARP.—The female reproductive branch in Red Algæ, before fertilisation.

PROTHALLUS.—The sexual generation in Vascular Cryptogams, and, in a modified form, in Flowering Plants.

PROTONEMA.—The filamentous growth developed from the spore (or other cells) of a Moss, and giving rise to the leafy plants.

PROTOSTELE.—A simple stele consisting of a solid mass of xylem surrounded by phloëm.

PSEUDOPODIA.—The protrusions of living protoplasm put out, *e.g.*, by the moving plasmodium of Myxomycetes.

PUSTULE.—Dense aggregations of the spores of Fungi on the host.

PYCNIDIUM.—A flask-shaped fructification in certain Fungi which forms conidia (pycnospores).

PYRENOID.—A protein body, round which starch is formed, in the chloroplasts of many Algæ.

RAMENTA.—The chaffy scales or hairs of Ferns.

RECEPTACLE.—The end of a branch, on which the reproductive organs are borne.

RHIZOID.—A filamentous organ, discharging the function of a root, in the prothallus of Pteridophytes and in Bryophytes and Thallophytes.

RHIZOME.—An underground or prostrate stem, from which roots and herbaceous stems arise.

RHIZOPHORE.—A leafless branch, bearing the roots, as in *Selaginella*.

SAPROPHYTE.—A plant which lives on dead organic matter.

SCALARIFORM.—Like a ladder, as the pitted walls of the tracheids in Ferns.

SCLERENCHYMA.—Thick-walled, fibrous tissue, serving as a mechanical support.

SCLEROTIUM.—The thick-walled, resting condition of the plasmodium in Myxomycetes and the compact mycelium of certain Fungi.

SETA.—The stalk of the sporogonium in Liverworts and Mosses.

SOREDIA.—Detached groups of associated algal cells and fungal hyphæ, serving for the propagation of Lichens.

SORUS.—A group of sporangia.

SPECIALISED PARASITISM.—The occurrence of distinct physiological forms of a parasitic Fungus on particular hosts.

SPERMATIUM.—A male cell, which has no power of active movement, in some Algæ and Fungi.

SPERMATOZOID.—A male cell, which has the power of active movement by means of cilia.

SPERMOGONIUM.—The organ in which spermatia are produced in some Fungi.

SPORANGIOLE.—A small sporangium, containing one or a few spores, in Zygomycetes.

SPORANGIOPHORE.—An organ, in some Vascular Cryptogams, specially adapted for bearing sporangia ; also used in Fungi.

SPORANGIUM.—A sac or case in which spores are produced.

SPORE.—The asexual reproductive body in Cryptogams, usually consisting of a single cell.

SPORIDIUM.—A small spore, formed on the promycelium of Rust Fungi.

SPOROGONIUM.—The upper part of the asexual generation, in Liverworts and Mosses.

SPOROPHYLL.—A leaf, bearing sporangia.

SPOROPHYTE.—The asexual generation.

STELE.—A vascular cylinder, consisting of xylem and phloëm, usually associated with other cellular tissue.

STERIGMA.—The little stalk on which a basidiospore or sporidium is borne.

STIPE.—The stem or stalk of a Mushroom or Toadstool.

SUSPENSOR.—1. A filament of cells, forming a temporary organ of attachment for the embryo : as in *Selaginella* and most Flowering Plants. 2. The hypha which bears a sexual cell in Zygomycetes.

SYMBIOSIS.—The association of two organisms living together for mutual benefit, as the Fungus and Alga in a Lichen.

TAPETUM.—The layer of cells immediately surrounding the spore-producing tissue (archesporium).

TELEUTOSPORE.—The spore of Rust Fungi which produces the promycelium on germination.

TETRASPORANGIUM.—The cell which divides up to form the tetraspores.

TETRASPORES.—The asexual spores, usually produced in fours, in Red Seaweeds.

THALLUS.—The vegetative body of the plant, when not differentiated into stem and leaf.

THECA.—The capsule of a Liverwort or a Moss.

TRABECULÆ.—Cell filaments connecting the stele with the cortex, as in *Selaginella*.

TRAMA.—The tissue underneath the hymenium in the higher Fungi.

TRICHOGYNE.—The hair-like organ which receives the male cells in Red Algæ.

TROPISM.—The bending movement of a plant organ in response to an external stimulus.

TUBER.—A short and thick underground branch, serving for propagation.

UREDOSPORE.—The unicellular summer spore of the Rust Fungi.

VALLECULAR.—Opposite a furrow of the stem.

VELUM.—The membrane which covers the gills in a young Mushroom or allied Fungus.

VENTER.—The lower part of an archegonium, containing the ovum.

WHORL.—A ring of leaves or other organs all inserted at the same level on the stem.

ZOOGLŒA.—The gelatinous colony formed by certain Bacteria in the resting condition.

ZOOSPORE.—An actively moving ciliated spore in Algæ and Fungi.

ZYGOSPORE.—The product of the conjugation of two similar sexual cells.

ZYGOTE.—The product of two gametes, whether similar or dissimilar.

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