LECTURES

ON THE

EVOLUTION OF PLANTS

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BY

DOUGLAS HOUGHTON CAMPBELL, Ph.D.

PROFESSOR OF BOTANY
IN THE LELAND STANFORD JUNIOR UNIVERSITY

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PREFACE

In the present volume I have endeavored to present in as untechnical a manner as seemed feasible the more striking facts bearing upon the evolution of plant forms. While there are numerous excellent text-books in which most of the statements here given are clearly presented, there is none, at least in English, so far as I am aware, where a connected account of the development of the plant kingdom from an evolutionary standpoint has been attempted. Of course every modern system of classification is based upon the assumption of a genetic connection between the different groups, and must take into account the origin of plant forms; but these phylogenetic problems are necessarily subordinated in the general text-books. Moreover, these text-books are, for the most part, avowedly prepared for the use of botanical students alone.

It seemed to the writer that an accurate, if somewhat general, and not strictly technical, statement of our present knowledge concerning the data from which the genealogical history of the vegetable kingdom may be traced, might be of interest not only to such botanists as have not concerned themselves specially with this phase of the science, but also to zoölogists, and those general readers who are interested in biological problems.

The substance of the following chapters was presented in the form of a course of lectures at Stanford University during the past year. These lectures have been carefully revised, and a number of drawings prepared, which it is hoped will be helpful in elucidating the text.

Very little originality can be claimed for the matter presented, beyond its arrangement. The writer has availed himself freely of the materials accumulated through the labors of botanists during the past fifty years, which have made possible such a general presentation of the subject as has been here attempted. It was intended, at first, to prepare a bibliography of the more important works bearing on the subject; but it was soon evident that the magnitude of a bibliography, which would be in any way complete, rendered this impracticable.

Most of the drawings have been made by the author from nature. Where these have been borrowed, due acknowledgment has been made.

Special thanks are due my colleague, Dr. G. J. Peirce, for most valuable assistance in the reading of the proofs.

<div style="text-align: right">DOUGLAS HOUGHTON CAMPBELL.</div>

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EVOLUTION OF PLANTS

CHAPTER I

INTRODUCTION

With the acceptance of the theory of evolution, the question of the origin and affinities of the manifold forms of life making up the organic world becomes of absorbing interest to the biologist, and the hope of solving some of these problems has been the great incentive to much of the most brilliant work, both of zoölogists and botanists, during the latter half of the nineteenth century.

When we survey the vast assemblage of living organisms, the thought of arranging these in orderly sequence seems hopeless; and indeed when we take into account how many forms must have disappeared and left no trace behind, it must be admitted that the task is one whose completion, if ever reached, must lie in the distant future. Nevertheless the data are slowly but surely accumulating through the efforts of biologists whose patient researches are constantly adding to our knowledge, both by the discovery of new forms and by a more thorough examination of those already known. The constant improvement in the technical appliances for research, such as the microscope and

microtome, improved methods of staining, etc., as well
as the extension of explorations to the remoter parts of
the world, have all contributed to these advances in
knowledge, and have been fruitful sources for new
materials.   The brilliant results already attained make
it reasonable to hope that others of equal importance
are yet to follow.

Very much remains to be done, and any conclusions
based upon the data now at hand must be subject to
change as new facts are brought forward ; nevertheless
enough is at present known to warrant an attempt, at
least, at an arrangement of the larger groups of plants,
showing their mutual affinities.   Some of these groups,
however, like the Diatoms, stand very much by them-
selves, and it must be admitted that their relationships
with other plants are extremely problematical.

In spite of the almost infinite diversity of structure
shown by plants and animals, it is found that only a
very small number of the seventy or more chemical
elements known at present, enter into their composition.
Carbon, oxygen, hydrogen, nitrogen, and probably sul-
phur are always present, and usually at least, potassium,
phosphorus, calcium, magnesium, and iron.   In addition
to these are a number of elements usually present, but
apparently not essential for the manifestation of life.
These elements are combined into extraordinarily com-
plex substances whose exact analysis often baffles the
chemist, owing to their excessive instability.   Inasmuch
as none of the elements found in living matter are
peculiar to it, but are also found in the so-called " in-
organic " substances, and since all living bodies are
directly or indirectly dependent upon the latter for

their growth, it is at once evident that any attempt to make a hard and fast line separating organic and inorganic substances must necessarily prove futile.

There are, however, certain properties peculiar to living organisms which may be said definitely to characterize them, *i.e.* the power of spontaneous movement, nutrition, and reproduction. All of these functions are associated directly with that remarkable substance protoplasm, most happily designated by Huxley the physical basis of life. So far as ordinary chemical and physical tests go, the protoplasm of all living organisms is much alike; of course this does not imply that protoplasm is a definite chemical compound such as starch or sugar; it is rather to be considered as a mixture of excessively complex and unstable substances, more or less similar in the elements of which they are made up.

The constituents of this protoplasm are evidently very unstable, as every manifestation of life in the living protoplasm is necessarily bound up with chemical changes in its substance. Where the protoplasm is present in sufficient quantity to be handled in mass, as in those curious organisms, the Slime-moulds, by-products are usually present which interfere with an accurate analysis.

The simplest forms of life, like the Bacteria, often show little structure beyond a mass of apparently homogeneous protoplasm surrounded by a delicate membrane, but it is exceedingly doubtful whether this extreme simplicity is more than apparent, owing to the excessively minute size of these organisms. The presence of a nucleus, or at any rate nuclear substance in bacteria, is by no means improbable. Among ani-

mals the so-called " Monera," which were formerly
supposed to be composed of structureless protoplasm,
are now known to possess a nucleus, so that we cannot
assert positively that any known forms consist of un-
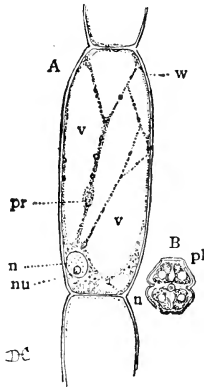differentiated protoplasm as was once supposed to be
the case. As a rule the
protoplasm is segregated in
masses of definite form, usu-
ally furnished with a more
or less evident envelope and
provided with a special
structure, the nucleus.
These nucleated masses of
protoplasm are generally
called cells, although the
name is occasionally re-
served for such as are pro-
vided with a single nucleus
and a definite membrane,
each nucleus with its ac-
companying protoplasm be-
ing designated an "energid."
We shall, however, for con-
venience' sake use the term
cell in its ordinarily accepted
sense.

Fig. 1. — A, a cell from a hair at the
base of the stamen of a spider-
wort (Tradescantia), showing
the parts of a typical plant cell;
w, the cell-wall; *pr*, the proto-
plasm in which is imbedded the
nucleus, *n*, with the nucleolus,
nu; *v*, vacuoles, spaces filled
with watery cell-sap. B, a Des-
mid (Cosmarium), a plant con-
sisting of a single cell; *pl*, one
of the chloroplastids; *n*, the
nucleus.

In all but the lowest forms of life the cells always show
at least two parts, the cell-plasm or cytoplasm, and the
nucleus. The latter is usually of definite form, globular
or lenticular (Fig. 1, A, *n*), and bounded by a definite
membrane, which, however, is apparently not chemically
different from the cytoplasm in which it is imbedded.

The nucleus shows a complicated structure, being composed of a very much twisted filament, more or less fused together at certain points, of a substance (linin) which does not readily take up the ordinary stains used in histological studies. In this linin-thread are numerous granules of a peculiar substance, chromatin, characterized by its avidity for various nuclear stains. A colorless fluid, or semi-fluid substance fills the space of the nuclear cavity not occupied by the linin-thread. There are in most cases one or more nucleoli present, globular bodies which gen-

FIG. 2. — An Amœba — a unicellular organism consisting of a nucleated mass of protoplasm without a cell-wall. *n*, nucleus; *v*, one of the contractile vacuoles.

erally stain strongly, but whose nature is still somewhat doubtful. Of the various constituents of the nucleus, the chromatin is probably the most important, and it is likely that in this substance are contained the elements which determine the peculiar properties of the cell, and in the reproductive cells transmit hereditary characters. The nucleus is an essential part of the cell, and is always formed by division of a preëxisting nucleus. There is no evidence that it can ever arise *de novo*.

Nuclear division is of two kinds, direct and indirect. By the first method a nucleus simply becomes constricted and forms two similar nuclei, or the part separated may be smaller than the main part of the nucleus. This form of division is confined to the lower types of plants, or it may occur secondarily in old cells of some

of the higher forms, such as the long cells in the stems
of a good many flowering plants.

Much more commonly the division of the nucleus is
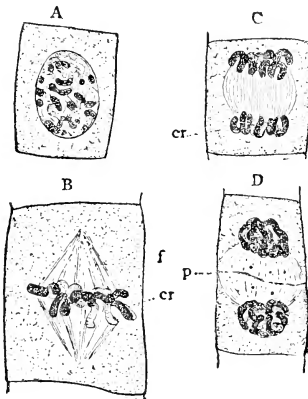preceded by a number of complicated changes, result-
ing in the breaking
up of the linin-thread
into separate pieces
or segments (chro-
mosomes) and a fur-
ther splitting of these
segments into halves.
Two groups of
segments are thus
formed, which sep-
arate and rearrange
themselves to form
the daughter-nuclei.
This indirect division
(Mitosis, Karyokine-
sis) is the only form
found in the actively
dividing cells of the
higher plants.

Fig. 3. — Four cells from the growing tip of
the root of an onion, showing different
stages in the division of the cell-nucleus.
In B the nuclear membrane has disap-
peared and the nuclear segments or chro-
mosomes (cr) are arranged in a plate at
the equator of the nuclear spindle, which
is composed of the "spindle-fibres," f.
In C the two groups of chromosomes
have moved to the poles of the nuclear
spindle. In D the young division-wall,
p, has been formed.

Besides the nucleus
there are found in
most plant cells certain bodies known as "plastids."
(Fig. 1, B, pl.) These are similar to the cytoplasm in
composition, and are very important in the nutrition of
the cell. Among them are the green corpuscles —
"chloroplastids" or chromatophores — in which are
contained the green pigment, chlorophyll, which plays
so important a rôle in the green plants. The red and

yellow corpuscles found in many flowers and fruits also belong in this category.

Associated with the nucleus in most animal cells, and sometimes found in those of plants, are certain small bodies, the centrospheres, each enclosing a minute corpuscle, the centrosome. These are usually considered to be of great importance, especially in the process of nuclear division, but their absence from many plant cells would indicate that their importance has been over-rated.

In the young plant cell the cytoplasm nearly or quite fills the cell, but as the latter enlarges there is an accumulation of fluid in the cell, and this occupies the greater part of its bulk. This watery cell-sap is contained in cavities (vacuoles) which it has been claimed are integral parts of the cell, and multiply by division; but this view is by no means universally admitted.

New cells may arise in several ways. The commonest is by fission, or division into two parts, usually equal. This division is preceded by division of the nucleus, after which a cell-wall is formed dividing the cavity of the cell. (Fig. 3, D.) Less commonly there is a repeated division of the nucleus, followed by a simultaneous division of the protoplasm into as many parts as there are nuclei. This "internal division" is most common in the formation of spores and other reproductive cells.

The study of the cell, and especially the changes in the dividing nucleus, have been the subjects of some of the most important researches of recent years, and have developed a distinct department of biology, cytology, with results of far-reaching importance. Nevertheless,

we are still far from understanding the ultimate struct-
ure of the cell, although many ingenious hypotheses
have been formed to explain the structure of the proto-
plasm.

We have seen that cells multiply by division.   In
the lowest organisms the cells thus produced usually
separate at once, resulting in the formation of two or
more individuals exactly like the parent.   In case this
division is repeated at short intervals, as happens, for
example, in the Bacteria and many infusorians, the
result is the production of an enormous number of in-
dividuals in a surprisingly short time.   In all but the
lower forms of life the cells do not usually separate
after division, the result being a multicellular organism.
The cell-aggregates, of which these higher plants and
animals are composed, are known as tissues, and these
may be combined to form special organs.   The cells of
growing parts of the higher plants resemble the simple
unicellular forms in structure, but as they grow older
they may become extremely modified to fit them for
special functions.

If we examine one of the lower vegetable forms, such
as a desmid (Fig. 1, B), we find that the single cell of
which the plant is composed is at once vegetative and
reproductive.   Such a green cell is capable of perform-
ing all the life-functions.   It can absorb water con-
taining certain food elements in solution, including the
oxygen necessary for respiration, and, by virtue of the
chromatophore containing chlorophyll, is able in the pres-
ence of light to decompose carbon dioxide and water,
and from the oxygen, hydrogen, and carbon so separated,
to manufacture the primitive carbo-hydrates necessary

for the growth of the cell. The power to manufacture these carbon compounds is, so far as is positively known, confined to cells which contain chlorophyll. Finally, by division the cell gives rise to two new ones, which become at once independent individuals, each containing a nucleus and chromatophores like the parent cell. This brief cycle, feeding, growth, and division, constitutes the whole life-history of many of these lowly organisms.

As we compare these simple plants with the more perfect higher forms, we find a more and more marked specialization of parts fitting them for special functions. Thus there is very early shown a modification of certain cells for purely reproductive purposes. These cells are evidently descendants of vegetative ones, and in their earliest phases of development are often indistinguishable from the latter ; finally, however, they become extremely modified, and can serve for reproduction only. In extreme cases this results in the formation of sexual cells, when two sorts of cells, male and female, are produced, each of which is incapable of developing further except as the result of a union of the two.

An analogous differentiation of the vegetative parts of the plant is seen as we pass from the lower to the higher forms. While in the unicellular plant the same cell serves to perform all of the functions, in the higher plants special organs are developed for special purposes. This, of course, reaches its maximum in the seed-bearing plants, or " flowering plants," as they are more commonly known. Here not only is the plant body multicellular, but the cells show great variety of form

and structure, and constitute tissues of different kinds
which are in turn aggregated to form special organs.
Thus a special subterranean root system is present, and
the green assimilative tissue is mainly confined to the
leaves, which are preëminently organs for carbon assimi-
lation.   The extreme of specialization is reached in the
flowers of these plants, which are beyond doubt the
most complicated structures which occur in the plant
kingdom.

Between the extremes found in the unicellular plants
at the bottom of the series, and the complicated seed
plants at the top, are numberless gradations of structure
which throw much light upon how these advances in
structure have been brought about.   A similar progress
from the simple to the complex is, of course, evident in
the evolution of the animal kingdom ; but the animal
type reaches a far greater degree of complexity and
specialization than is ever found even in the highest
plants, which differ much less from the lower ones than
is the case among animals.

At the bottom of the scale the two kingdoms con-
verge.   There are many forms to be met with whose
position is more or less doubtful, and in some cases it
is practically impossible to determine to which great
division they belong.   We can only say that we have
to do with organisms which are not yet sufficiently
differentiated to determine whether the animal or
vegetable characters predominate.   It is the study of
these primitive organisms, and the realization of the
close similarity in the structure and functions of the
animal and plant cell, which emphasize the intimate
connection between the two kingdoms, and the impos-

sibility of making any absolute separation between them.

A popular misconception of the province of biology assigns to it only a study of animal functions ; but the scientific biologist recognizes the fundamental likeness in the structure and functions of plants and animals, and realizes that any complete survey of the science must take equal cognizance of both.

For practical purposes, inasmuch as all but the lowest forms of life are readily to be assigned to one kingdom or the other, it is desirable to retain the old divisions of zoölogy and botany ; but this does not imply any absolute differences between the two great divisions of living things. The popular belief that plants and animals differ essentially in their life-processes is erroneous. Plants feed, breathe, and reproduce, exactly as do animals. It is true that the green cells of plants are able to absorb carbon dioxide from the atmosphere, and to utilize it in the manufacture of carbon compounds, a power, which, so far as we know, is lacking in animals. This assimilation — or as it has been better termed " photo-synthesis " — is not to be confounded with respiration, which takes place in all plants precisely as in animals, but, being less energetic, is masked by the evolution of an excess of oxygen in those green cells which are exposed to sunlight. This photo-synthesis, and the character of the cell-wall, which in young plant cells is always composed of the carbo-hydrate cellulose, are the most marked characteristics of ordinary plants ; but as cellulose occurs in some animals, i.e. certain Tunicates, and very many plants like the Fungi, and many parasites and sapro-

phytes among the higher plants, such as the common dodder and Indian pipe, are quite destitute of chlorophyll, and hence incapable of carbon assimilation, it is clear that neither of these criteria can be used as absolutely decisive. Nevertheless, the power of carbon assimilation, with the accompanying presence of chlorophyll, and the cellulose cell-membrane, are characters constant in all typical plants.

As already indicated, it is near the bottom of the two great series of organisms that they approach, and as these ascending lines of development are traced they diverge widely, the peculiar animal and plant characters becoming more and more pronounced as we ascend. That special department of biology, known as Taxonomy or Classification, is the attempt to group all these divergent forms of life so as to indicate their relationships.

So long as plants were considered as so many isolated objects without any genetic connection, the earlier systematists, especially Linné, sought simply for some obvious external characters which would serve for identification, without any thought as to any real relationship. Later botanists, although they did not assume any genetic relationship, nevertheless in the so-called natural system, did make an attempt to arrange them in a sequence which seemed to imply some such connection, and, in many instances, really succeeded, although, through the selection, in many instances, of characters of secondary importance, many mistakes were made.

An ideal system of classification of plants would show the genealogy of the whole vegetable kingdom

in all its numberless ramifications. Such a complete classification can never be hoped for, inasmuch as the plants which now exist are in many cases but scattered remnants of groups once much more numerous than at present, which have left no recognizable fossil traces. Some forms are so much isolated, and have so little in common with other groups, that at present any attempt to give them their proper place in the system is little better than pure guesswork.

It is thus clear that at present the question is very far from settled; indeed, hardly more than a beginning has been made in the establishment of a system which can be said to represent real genetic relationships. Our present knowledge of the vast majority, even of many of the commoner plants, is extremely imperfect, being confined often to purely superficial characters. It is necessary to investigate thoroughly the structure and development of a great many forms before the data can be had for constructing a classification which we can hope will be permanent, and a beginning only of this vast work has yet been made. In addition to the careful structural study of the existing plants, a thorough examination of the fossil species is necessary, involving even more arduous labor than does the investigation of living forms. Palæo-botany has already yielded results of the greatest importance, and it is but reasonable to hope that further investigations will add much to the materials already accumulated. These researches must, however, consist of something more than mere collecting and naming of dubious fragments. What is imperative is a more complete knowledge of the remains already discovered, rather than the

accumulation of doubtful and imperfectly studied forms.

While it is true that the great majority of the fossil remains of plants are too imperfect to make possible a satisfactory study of their finer structure, it happens occasionally that the tissues are preserved with extraordinary completeness, so that a microscopic study of the cellular structure is possible, and in this way much light has been thrown upon the real nature of many fossil plants. A few types, like the Diatoms, have silicified cell-walls which have remained unaffected by the changes to which they have been subjected, and have sometimes been preserved in immense quantities, and so perfectly that even the species can be determined without difficulty. Other forms, with calcified cell-membranes, like the Coralline algæ and Characeæ, have also been preserved very perfectly. In the vascular plants the preservation of the cell-structure is usually due to the infiltration of silicious matter after the death of the plant. These silicified tissues, such as the familiar fossil woods, often show the cell-structure with marvellous clearness, but unfortunately the more perishable tissues are very seldom preserved in this way, and these are usually of especial importance in classification. Thus the flowers of the seed plants, and the spore-bearing parts of the lower ones, are seldom preserved in a recognizable state, and this makes a careful study of such few forms as have survived, doubly important, as these are the surest means of deciding the relationships of these fossil plants to each other and to their living descendants. At best, the geological record is extremely fragmentary, and we

must therefore look to other sources of information in our quest for the ancestors of the present flora of the earth.

Much can be learned as to the relationships of plants from a study of their external structure, and the classification, especially of the higher plants, is based largely upon purely external characters. While such characters are usually reliable when dealing with nearly related forms, they are likely to be misleading when we try to trace out the affinities of plants whose kinship is not so obvious. Here it is important to take into account, for comparison, the more obscure points of structure, — for it not infrequently happens that resemblances may thus be traced which are not evident at first sight. Thus, in comparing the Mosses and Ferns, it is the minute reproductive organs and embryos which show the unmistakable relationship of these plants, while their more conspicuous external structures are very different.

There is little question that, as in the study of animal forms, it is the careful investigation of the life-history of the plant which affords the surest clue to its affinities with other forms. The generally accepted view that in animals the developing germ repeats in a general way the evolution of the race, is also applicable, in some degree at least, to plants, and by far the most important discoveries, with reference to the origin of plant forms, have been due to studies of this nature. Very often the early stages of the embryo and reproductive organs in different plants reveal resemblances, while the adult stages may have, apparently, very little in common. These embryonic phases are less affected

by external influences, and as they represent presumably primitive conditions, the importance of a study of these early stages of the plant's existence is evident.

When we consider the manifold sources of error, it is not to be wondered at that botanists have not yet been able to establish a perfect system of classification, and that it must be a long time before anything approaching this can be hoped for.

The plant kingdom is usually divided into a number of primary divisions, "branches," or "sub-kingdoms," as to whose limits there is not complete accord among botanists. Excluding a number of groups of doubtful affinity, sometimes put together under the name Protophyta, botanists usually recognize the following sub-kingdoms: 1. Algæ (green plants below the Mosses); 2. Fungi (a group parallel with the Algæ, but destitute of chlorophyll); 3. Archegoniatæ (Mosses and Ferns); 4. Spermatophyta (seed-plants— the "flowering plants" of the older botanists). Of these divisions, the Fungi and Algæ are often united into a single great division, Thallophyta, and the Archegoniatæ divided into two sub-kingdoms, Mosses (Bryophyta) and Ferns (Pteridophyta); but the arrangement here given seems to the writer more in accordance with what we know of the relationships of the different members of these groups.

CHAPTER II

THE CONDITIONS OF PLANT LIFE

No matter how simple or how complicated they may be, all plants agree in their essential life-processes, and certain conditions are necessary for these. All feed, grow, and reproduce, and all exhibit to a greater or less degree the power of movement, although this is, as a rule, much less evident than in animals. For the manifestation of the various functions, certain external conditions are essential. Thus a certain amount of moisture is necessary in order that they may grow, and of course the requisite food elements must be supplied. In green plants, where alone, as we have seen, the assimilation of carbon dioxide goes on, this is dependent upon the presence of light, and there are certain limits of temperature also which regulate the activity of the plant. The amount of moisture, heat, and light necessary may vary greatly, however, in different plants. Many water plants, especially algæ, often flourish in water whose temperature is very near the freezing point, and some of them may be actually frozen into the solid ice without injury; but these same plants are quickly killed if they are placed, even for a short time, in warm water. In strong contrast to these are certain low plants, e.g. species of Oscillaria and various bacteria, which thrive in hot springs im-

pregnated with sulphur and other mineral substances usually inimical to plant life.

When in a dormant condition, the protoplasm is able to resist much greater extremes both of heat and cold than is possible while it is in an active state. Thus seeds, spores, and the twigs of woody plants can endure without injury a degree of cold which would at once kill the protoplasm were the cells in a growing condition. On the other hand, the same dormant parts, especially spores of various kinds, can endure a comparatively high temperature without injury, this being especially marked in the case of the spores of certain bacteria, which can endure exposure for several hours to a temperature above the boiling point of water without being killed.

The amount of moisture necessary for plant growth also varies extremely. Water plants are quickly killed by exposure to air of ordinary dryness, while many desert plants, such as cacti, may remain uprooted and exposed to the hot sun for weeks without being killed. These desert plants are provided with very perfect means of resisting loss of water, both by a great reduction of the evaporating surface through the partial or complete suppression of leaves, and also by the development of a thick, and almost impervious covering to the exposed surfaces.

In all green plants the arrangement of the chlorophyllous tissue is always regulated by the amount of light. If this is weak, the green cells are spread out so as to expose a large area to its action ; but if the light is too intense the area is reduced, and the cells are screened by the development of more or less opaque

tissue above them.   Plants growing in deep shade have usually larger and more delicate leaves than those fully exposed to the sun.

The principal sources of plant food are carbon dioxide and oxygen, obtained from the atmosphere, and water with various inorganic substances in solution, usually absorbed by the higher plants from the earth.   When the plant is completely submerged, as are many algae, and a considerable number of flowering plants also, the food substances dissolved in the water may be taken in at almost any point.   Except in a few doubtful cases among the lowest plants, all food taken in must be in a gaseous or fluid form.

Where the plant is unicellular, of course this single green cell must perform all the nutritive functions, and is at the same time reproductive.   Such a simple plant consists of a single globular or oval cell surrounded by a membrane of cellulose, within which is the nucleated protoplasmic mass with one or more chromatophores or chloroplasts.   Such a cell can absorb water with various food substances, including free oxygen and carbon dioxide in solution.   The chromatophores, in some way not clearly understood, decompose the carbon dioxide and water, and of the elements carbon, hydrogen, and oxygen, manufacture the carbo-hydrates upon which the protoplasm is dependent for its growth. The first product of this process which can be recognized, is usually starch, which appears in the form of granules within the chloroplasts shortly after they are exposed to the action of light, which, as we have seen, is a necessary condition for photo-synthesis.

As a result of the assimilation of the food absorbed,

the cell increases in bulk, and sooner or later divides
to form new ones which become at once new individuals,
so that the single cell exhibits all the characteristics of
a typical plant; *i.e.* it feeds, grows, and reproduces
itself, and all these functions are performed by one
and the same cell. Such a unicellular plant cannot
properly be considered as strictly undifferentiated,
since the permanent constituents of the cell, *e.g.*
nucleus and chromatophore, must be regarded as defi-
nite organs.

As we pass from the unicellular plants to the simpler
multicellular forms (see Fig. 9, F) we find the first
indications of a specialization of certain cells. Thus the
basal cell has very little chlorophyll, but is modified
into a root-like organ for the attachment of the plant,
while the other cells with their numerous chloroplasts
are alone concerned with the nutrition of the plant.
Very much more complicated are many of the large
sea-weeds, some of which, like the great kelps (see
Fig. 17), reach an enormous size. In these plants
there are various sorts of cells aggregated into definite
organs. The chloroplasts are mainly confined to the
outer part of the plant, where they may be fully exposed
to the light, while the inner tissue has little or no
chlorophyll, and the cells are modified for conducting
purposes. In the most highly organized of these marine
algæ, like the gulf-weed (Fig. 18), a further advance
is seen in the formation of flattened leaves to which
the chlorophyll-bearing cells are mainly restricted.
Indeed these highly specialized sea-weeds bear a most
remarkable superficial resemblance to the flowering
plants in the development of a definite branching axis

bearing leaves. This is one of many instances where in response to similar needs there has been a parallel development in groups which genetically are widely separated.

It is, of course, among the Spermatophytes (seed-bearing or flowering plants) that the highest degree of specialization, both of the plant body and tissues, is reached. The plant usually shows a definite main axis or stem, to which are attached a variety of appendicular organs — leaves, roots, and branches. The tissues of which these various organs are composed show much variation in the cells of which they are made up. The green tissue is mainly restricted to the leaves, where it is so placed as to be most favorably situated with reference to the light. As a rule the outer or epidermal cells are not provided with chloroplasts, but serve as a protection for the delicate green cells lying below them, and in case the plant is exposed to great heat or dryness, the epidermal cells become much thickened and almost impervious to water, so that the loss of water from the green cells is effectively checked. Familiar examples of this kind are seen in the leaves of the laurel, oleander, and many other evergreens. As it is necessary, however, for the green cells to have communication with the atmosphere in order to obtain the necessary carbon dioxide and oxygen, this is provided for by the development of the stomata or breathing pores always found upon the leaves, and these communicate with the numerous air-spaces between the green cells which are thus brought directly into contact with the atmospheric gases.

Within the green cells the decomposition of the car-

bon dioxide and water is accomplished, and from their elements are manufactured the organic carbon compounds. When these green cells are exposed to the light, starch can soon be detected in them, but it disappears if the plant is placed for a short time in darkness.

The presence of other pigments, such as the red and yellow ones in the marine algæ, and also the similar ones often found in young leaves, doubtless advantageously modify the light which passes through them before reaching the chlorophyll.

Movement is not generally associated with one's idea of a plant, but it is a property which all plants possess to some degree, and is usually associated with the sensitiveness of living protoplasm within the cells. In every living cell the protoplasm shows more or less marked movements which may not be at once perceptible, but sometimes are very active indeed. These movements are very familiar to botanists in the cells of many water plants, *e.g.* the eel-grass (Vallisneria) and stone-wort (Chara), and are also very active in the cells forming the hairs upon the surface of many land plants. This is especially true of the hairs upon various parts of many flowers.

Spontaneous movements of the plant as a whole are confined to a comparatively small number of low aquatic forms (see Fig. 6). Here the plant moves by means of vibratile protoplasmic threads or cilia, which propel it through the water, precisely as many of the lower animals move. The extraordinary resemblance between these low ciliated plants and the lower animals is one of the strongest evidences of the relationship

which exists between the lowest members of the two great organic kingdoms. This power of free locomotion is also found in some of the reproductive cells of most plants except the highest ones, and even in a few of the seed plants these have recently been discovered, the male reproductive cells having the form of ciliated spermatozoids which are actively motile. This power of spontaneous locomotion is finally lost, and in nearly all the seed plants is completely absent, although even here the plant exhibits more or less marked movements of various kinds. Some of these movements are apparently spontaneous, such as the revolution of the apex of the growing stem and root, and of tendrils, but others are influenced directly by external agencies, light, moisture, contact, and gravity. The spontaneous movements of the growing apex of many plants is called nutation, and is apparently quite independent of external agencies. The effect of light in plants is well known. The response of actively growing plants to this stimulus is often very rapid, although the exact mechanism of these movements is not entirely clear. Occasionally plants are negatively heliotropic, *i.e.* they grow away from the light, as is seen in the common ivy. Light is, in most cases, necessary for the formation of chlorophyll, as well as for the performance of photosynthesis in those cells which contain the chlorophyll.

Doubtless the cause of the movements of plants is largely due to the direct effect of light upon the sensitive protoplasm of the cells of the motile parts. This is indicated by the activity of naked swarmspores and plasmodia (masses of naked protoplasm found in certain low organisms, such as the Slime-

moulds, Fig. 4), when exposed to light, the green swarm-spores of algæ almost always being very quickly attracted to the light.

Geotropism, or the movements induced by gravity, are either negative or positive. In the higher plants, the aerial parts, especially the stems, are usually negatively geotropic, *i.e.* grow upward, the roots positively geotropic.

The marked movements of the sensitive plant (Mimosa), as well as the similar movements especially of the floral parts of many plants, and the so-called "sleep movements" of such leaves as the locust, clover, and many others, are connected with changes in the turgor of the cells of special parts of the motile organs. These movements are undoubtedly, like the movements due to simple heliotropism, intimately associated with the sensitiveness of the protoplasm, and are induced by a variety of stimuli, such as shocks, light, and electricity.

The absence of locomotion in the higher plants is in large measure due to the investment of the cells with a firm membrane, and it is only when the protoplasm escapes from the cell, as in the case of swarm-spores and spermatozoids, that the primitive power of locomotion is regained, and recalls the possession of this animal character by the ancestors of all the higher plants.

It is a popular fallacy that plants and animals supplement each other in their method of respiration. It is not necessary to remind the botanist that this mistake is based upon a confusion of terms. During the process of carbon assimilation in the green cells, there is a large amount of free oxygen liberated — much in excess of

the amount used by the cells in respiration ; hence when exposed to light the cells give off an excess of free oxygen which escapes into the surrounding atmosphere. So soon, however, as the light ceases to act, it is found that these cells, like the colorless ones, consume free oxygen, and the oxidation in the protoplasm is accompanied by an evolution of heat, precisely as in animals, although, as a rule, it is less energetic. Occasionally this evolution of heat is quite perceptible and can be easily measured. A thermometer thrust into a mass of germinating seeds, or into the spathe of one of the larger Aroids like the common "calla-lily," will show a rise of several degrees, this evolution of heat in the latter case being most energetic while the pollen is being shed.

The gradual evolution of the reproductive parts of plants is very instructive, especially when we consider the fact that it closely parallels the development of these parts in animals, this being especially true of the sexual reproductive elements.

In the lowest forms of life, both plant and animal, the entire unicellular organism is at once vegetative and reproductive. In these forms, after the cell has attained its maximum size, it divides directly into two or more parts, each of which becomes at once an individual. The power of forming new individuals non-sexually persists in many multicellular animals, and in most plants. In animals the power of producing new individuals by budding or fission is found in a considerable number of the lower groups of Metazoa, such as the Corals, Sea-anemones, etc., and the renewal of lost parts may take place even in Vertebrates, *e.g.*

in lizards the renewal of the tail, but, owing to the
great complexity of the higher animals, they are unable,
except in rare instances, to produce new individuals
except from eggs. With plants the case is different,
and even among the highest ones some forms of non-
sexual multiplication by budding is almost universal.
This is no doubt largely due to the much lower degree
of specialization in the tissues of even the highest plants.

The first evidence of sex is manifest very early among
both animals and plants. Sexual reproduction consists
essentially in the formation of a germ by the union of
two cells which fuse completely into one. In many
unicellular plants, such as the desmids (Fig. 1, B) and
lower green monads (Fig. 6, F), there is no apparent
difference between the sexual and non-sexual cells, but
two individuals fuse into one, or at least the protoplasm
and nuclei of the two cells fuse, the resulting cell then,
as a rule, secreting a new wall about itself, and either
forming a new plant at once, or by division giving rise
to two or more new plants. In these lowest forms the
two uniting cells are entirely similar, and we cannot
speak of male and female cells.

The first indication of the separation of the sexes is
seen in the formation of sexual cells or gametes, of un-
equal size (Fig. 6, F). These cells are usually motile,
being provided with cilia, and resemble exactly the non-
sexual swarm-spores, except that they are incapable of
germinating unless two of them unite to form the
"zygote," or germ of the new plant. The larger of
the gametes is the female, the smaller the male cell. It
is interesting to note that in some of the lowest forms
where gametes occur, these may under certain condi-

tions germinate without fusion, showing that they may properly be considered simply as modifications of cells once purely non-sexual in character.

As the sexual cells become more differentiated, the difference in size becomes very marked, the female cell being many times larger than the male (Fig. 6, D, E). The former also shows a tendency to become passive before fertilization, even in such forms as still retain the primitive ciliated condition, and finally all power of motion is lost, and usually the female cell, or egg, is retained within the cell where it is formed, and is there fertilized by the small, active male cell or spermatozoid.

As the plant body becomes multicellular, the reproductive function, except in the lowest types, becomes restricted to special cells which differ in appearance and size from the vegetative cells. This is accompanied by the more perfect differentiation of the sexual cells, resulting as already stated in the formation of a large, passive female cell or egg, and a small, actively motile male cell or spermatozoid. In extreme cases, such as the ferns and mosses, the spermatozoid is mainly reduced to the nuclear substance of the mother-cell, a small portion only, including the locomotive organs (cilia), being composed of the cytoplasm or cell-plasm.

It is an interesting fact that a very similar evolution of the sexual cells has taken place in the animal kingdom, and has also developed independently in several widely separated groups of plants. Thus we have still existing, every phase of development of these sexual cells in the Brown Algæ, the Volvocaceæ, the Siphoneæ, and Confervaceæ, and less perfectly in several other groups.

While in the lower groups the sexual cells are borne in cells differing but little from the vegetative ones, the higher algæ, mosses, and ferns have them contained in multicellular structures of very characteristic form which may properly be considered as true sexual organs.

A marked degeneration of the sexual cells is observed in many fungi where, when present at all, they are usually reduced in structure and sometimes apparently functionless, while in very many of them no traces of sexual organs have as yet been discovered.

Among the flowering plants there are produced special accessory structures connected with reproduction but not to be considered strictly themselves as reproductive. The various parts of the flower are of this nature, the true reproductive organs being special minute structures within the pollen-grain and ovule. The development of brightly colored and sweet-scented flowers is doubtless connected with the fertilization of the germ-cells within the ovule, and the same is true of the various mechanical devices for insuring pollination through insect agency. The correlation of structures in flowers and insects is often extraordinary, and is sometimes so great that a single species of flower and insect are absolutely dependent on each other for their existence. We shall, however, consider this question more at length in a later chapter.

A high degree of specialization is also seen in the subsidiary reproductive parts of plants other than the seed plants, although less marked than in those. Thus in the mosses and ferns there are very perfect mechanical devices for distributing the ripe spores. The

mechanism of these devices is usually dependent upon moisture. Of these may be cited the ring of thickened cells which surrounds the spore-case in most ferns, and the strongly hygroscopic elaters of most liverworts, and the curious structures forming the "peristome" about the opening of the spore-bearing capsule of the common mosses.

The fruits and seeds of the flowering plants offer numberless examples of specialized structures, evidently adaptations to special environment. In the lower members of the group, such as the pond-weeds and similar simple aquatic types, the fruits are very simple and the seeds are set free through its decay, falling to the bottom of the water, where they remain until conditions are suitable for germination. A similar condition of things prevails among a good many land plants, *e.g.* some of the grasses, but in very many of the higher types special contrivances have been evolved by means of which the distribution of the seeds is facilitated. The violent opening of many seed vessels; the wings and floats developed by many seeds and fruits; the hooks, prickles, etc., found in many fruits and seeds, by means of which they adhere to animals, and are thus transported, are a few of these many devices, and the presence of edible parts in fruits and seeds is largely to be placed in the same category.

Summary

All plants agree in requiring for their existence certain food substances which must be absorbed in the form of solutions or gases. Of these food substances

the carbon is directly available only for those plants which possess chlorophyll; and where the plant is destitute of this, as in most saprophytes and parasites, it must obtain its carbon from organic compounds. All plants breathe by taking in free oxygen and giving off carbon dioxide.

Water is essential for the manifestation of life, but the amount varies greatly in different plants as does the temperature at which they will grow.

Light is necessary to all green plants, and to most others as well, but among these, the optimum illumination is extremely variable.

We see, in passing from the simple unicellular plants, where all the functions are performed by a single cell, how there is a gradual division of labor, first in a separation of the vegetative and reproductive cells, and later a further specialization of both vegetative and reproductive functions, which reaches its highest expression in the seed plants where there are special complicated organs — leaves — for carbon assimilation, an extensive system of roots for attachment and absorption of food from the soil, extremely modified tissues for conduction, storing of food, and other functions; and finally extraordinarily varied structures — the flowers — connected with the reproduction of the plant and the distribution of seeds.

The power of independent locomotion is confined to a small number of the lower plants, or to certain reproductive cells of higher ones; but all plants exhibit more or less marked movements which may be spontaneous, or influenced by various external agencies, such as light and gravity.

CHAPTER III

THE SIMPLEST FORMS OF LIFE

THE simplest conceivable living being is a mass of undifferentiated protoplasm, and it was claimed by Haeckel and others that such simple forms of life do actually exist. Haeckel described under the name Monera a considerable number of organisms to which he attributed this simple structure; but the great improvements made of late years in microscopic technique have shown that these are really much less simple than was supposed. A nucleus can in most cases be demonstrated, as well as other evidences of differentiation.

There are, however, a good many organisms of such simple structure that we cannot positively assert that they belong to either the animal or vegetable kingdoms. There are in particular two groups of these indifferent organisms, those included by Haeckel in his Monera, such as Vampyrella and Protomyxa, and those curious organisms the "Slime-moulds," — Myxomycetes or Mycetozoa. These two groups, which are generally considered respectively as the lowest of the animal and plant series, have a good many characters in common. They are all, in their vegetative condition, naked masses of soft, slimy protoplasm — "plasmodia,"—which show

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active movements and other evidences of life (Fig. 4, A). The Monera are aquatic, often parasitic, organisms and their life-history is a simple one.   After the plasmodium has reached its maximum size it contracts and develops a firm covering and the contents of this cyst divide into a great many parts, each of which is provided with a nucleus. These minute nucleated masses escape in the form of actively swimming bodies which may form a new plasmodium by simple growth; but sometimes, by the fusion of a great number of the separate spores, as in Protomyxa, a large plasmodium may be formed at once.
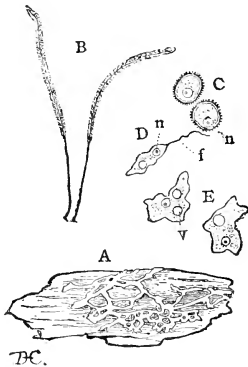
Fig. 4 (Mycetozoa). — A, a Slime-mould growing upon a bit of rotten wood ; B, two of the fruiting structures (sporangia) of another form (Stemonitis) ; C, two ripe spores of Trichia ; D, the active motile protoplasmic mass which escapes from the spore when it germinates ; *f*, the flagellum or motile organ ; *n*, the nucleus ; E, two amœboid later stages which have lost the flagellum and later unite with others to form the larger "plasmodium," shown in A. *v*, the contractile vacuole.

In the Mycetozoa, or Slime-moulds, which are often regarded as plants, the life-cycle is somewhat more complicated, due to the fact, perhaps, that they are terrestrial in their habits.   The active condition in these is also that of a plasmodium, these naked masses of white or yellow slimy matter often reaching a large size.   The commonest of these is one found growing upon old tan-bark where the light-yellow soft mass may often be met with in damp, cloudy weather, the plasmodium shunning too strong lights

and needing moisture for its growth. If threatened
with drying up it may contract and secrete a protec-
tive covering about itself.

The reproduction is purely non-sexual, and consists
in the breaking up of the protoplasm into a great many
parts, as in the Monera; but in the slime-moulds the
cells thus formed secrete a definite protective covering
or cell-wall, and closely resemble the spores or repro-
ductive cells of the Fungi, with which these organisms
are often classed; but the general opinion at present
is that they are forms allied to the Monera, which have
not yet become sufficiently differentiated to show defi-
nite animal or plant characters.

The most specialized forms among the slime-moulds,
like the ones figured (Fig. 4), show a curious resem-
blance to true plants in their reproductive parts,
although these resemblances are purely superficial.
Thus they form spore-cases or " sporangia " of definite
and characteristic shapes (B), within which the proto-
plasm divides into a great many nucleated fragments,
as in the Monera; but here, as we have seen, each por-
tion secretes a definite cell-membrane and forms a
spore, much like an ordinary plant-cell (Fig. 4, C),
and capable of being dried up without losing its vital-
ity. With these spores are found in the higher forms
curious thread-like structures of various kinds.

The spores, on being placed in water, soon burst open
and set free the contained protoplasm, which assumes
the form of a free-swimming, naked cell or swarm-
spore, like that of the Monera, and resembling closely
certain low animal forms, the flagellate infusorians
(Fig. 4, D). In this condition the slime-mould con-

D

tinues for a longer or shorter time, and may multiply
by fission and thus produce a large number of indi-
viduals which finally lose the single cilium or flagellum,
and creep about like amœbæ (E). Finally, as in the
higher Monera, these individuals fuse into a single large
mass or plasmodium.

A study of these two groups, Monera and Myceto-
zoa, illustrates in a very instructive way how a consid-
erable degree of differentiation is possible within the
limits of a group whose structure is of the simplest
character. The two classes are probably offshoots of
a common stock very near the bottom of the scale of
living organisms. It is not likely that either class has
much in common with the higher plants or animals,
but the constant occurrence in both of flagellate swarm-
spores indicates that the latter may, perhaps, represent
the simplest expression of living things known to us,
and that from some such forms have sprung not only
the Monera and Mycetozoa, but also the higher animals
and plants.

SCHIZOPHYTA (*Fission Plants*)

Under this name are now united a large number of
plants of very simple organization, of which the most
familiar are the Bacteria. Owing to the extreme
minuteness of many of them, it is not possible to deter-
mine positively how far their apparently excessive
simplicity is real. With better methods of fixing and
staining, and improved microscopic lenses, the bacteria
are revealing structures which formerly escaped detec-
tion, and it is reasonable to suppose that there is still
much to be learned as to their minute structure.

Most bacteria appear, under the microscope, as extremely small, often apparently homogeneous bodies of various shapes — round, oblong, rod-shaped, etc. (Fig. 5). They frequently exhibit active movements which are due to the presence of excessively fine cilia. They multiply with extraordinary rapidity
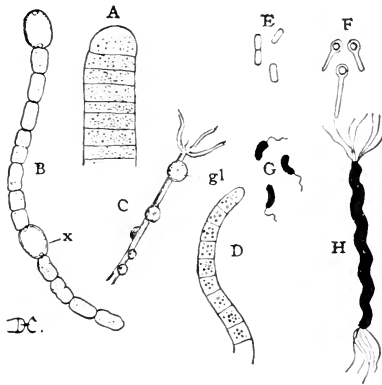
FIG. 5 (Schizophyta). — A, the tip of a filament of Oscillaria, one of the Fission Algæ (Schizophyceæ). The cell is filled with granular protoplasm, but no definite nucleus or plastids can be made out. B, part of a filament of Anabæna, a fission alga, showing two sorts of cells; *x*, one of the "heterocysts" which separate the filament into segments; C, a water-plant with colonies of a fission alga (Gloeotrichia), *gl*, growing upon it; D, Beggiatoa, a form without chlorophyll, allied to Oscillaria; E–H, different forms of Bacteria (Schizomycetes); E, typhus germ (*Bacillus typhi*); F, Tetanus bacillus (*B. tetani*), showing spore formation; G, cholera bacillus (*Microspira comma*); H, *spirillum rubrum*; G and H are stained to show the cilia. (Figs. D–H after Migula.)

by transverse fission, but may also produce internally special resting-cells, or spores (F). These latter are thick walled, and often capable of enduring an astonishing degree of heat without injury. Organic decomposition is mainly due to the activity of bacteria, and it is unnecessary to dwell upon the various forms

of disease germs, nearly all of which are bacteria.   The great importance of these minute organisms in the economy of nature is at once evident when we reflect that, without their assistance, the decomposition of dead organic matter would practically cease, and it would remain inert and useless as food for the higher plants. The presence of bacteria in the soil is of the greatest importance, as it is through their agency that the nitrogen compounds are put in such form that they can be absorbed by the roots of the higher plants.

While the position of the bacteria is unquestionably very low in the scale, their relation to the higher plants is somewhat problematical.   The presence of cilia has suggested a possible connection with the flagellate infusorians.   Related to them is a peculiar group of simple, green plants known variously as "Cyanophyceæ" — Blue-green Algæ — or " Schizophyceæ " — Fission Algæ.   Like the bacteria they multiply ordinarily by simple, transverse fission, but may also produce resting-spores.   Being provided with chlorophyll, however, they are to some extent independent, but they often occur in such positions as to indicate a partial dependence on other plants for food.   Some occur regularly within the bodies of higher plants, and are probably parasitic to a limited extent.   More commonly they live free upon damp earth, or in stagnant water (Fig. 4, A, B, C).

Like the bacteria, the cell-structure is very simple, and it is doubtful whether a perfectly organized nucleus is ever present, although a central structure of doubtful nature has been considered by some botanists to be a genuine nucleus.   They resemble the bacteria, also, in

being exceedingly resistant to extremes of heat and cold that would be fatal to most plants of higher organization. They often occur in thermal springs which are impregnated with various substances usually inimical to plant life. The name Cyanophyceæ has been given to this class, because in addition to the chlorophyll they usually possess a blue pigment (phyco-cyanin) which is readily soluble in water.

The similarity in the structure and reproduction of the Cyanophyceæ and Bacteria have led botanists to unite them into a common group, the Schizophyta, based upon the prevailing method of reproduction by simple, transverse fission. Whether this group is directly related to any other group of plants is questionable; but there is good reason to suppose that they represent an extremely primitive type of vegetation, and it has even been suggested that similar organisms were probably among the first to make their appearance upon the earth before the conditions were fit for higher forms of plant life.

It seems probable that the earliest forms of life could manufacture carbon-bearing compounds without possessing chlorophyll, and that the restriction of this power to green cells is a secondary condition.[1]

While both the Slime-moulds and Schizophytes show but doubtful affinity with the higher plants, there is a third group of low organisms, sometimes united with these two under the name of Protophytes, which are of especial interest in connection with the evolution of

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[1] Certain bacteria, although destitute of chlorophyll, are independent of organic food. Such forms, however, possess a red or purple pigment, which serves as a substitute for chlorophyll.

the higher plants. These are known as the Volvoca-ceæ, or Volvocineæ, and have been claimed by zoölo-gists as animals, although there seems no question of their close relationship with the lower green plants. It is true that they are actively motile, and show other animal properties, but they usually possess a cellulose membrane, and the characteristic green chromatophore of the typical plant cell, and inasmuch as they are con-nected with unmistakable plants by a complete series of intermediate forms, there seems to be no valid reason for not considering them as low plants. It is interesting to note, however, that the lower mem-bers of the series of Volvocineæ are very much like the animal flagellate infusorians and also the swarm-spores of the slime-moulds, from which they differ mainly in the presence of a green chromatophore. The frequent recurrence of this free-swimming, flagellate type among both the lower animals and plants suggests some similar forms as the ancestral type for both of the great series of organic beings, which here converge.

The simplest of the Volvocineæ are round or oval cells, which in their ordinary condition are actively motile, swimming by means of two delicate cilia. In the younger stages these cells are quite destitute of a membrane, but older cells usually have a distinct cellu-lose wall, with openings through which the two cilia protrude. The structure (Fig. 6, B) is that typical of the lower green plants. The green chromatophore (chloroplast) has the form of a cup and fits into the lower part of the oval cell-cavity. Within the hollow of the chromatophore is included a mass of protoplasm in which is imbedded the nucleus. The forward end

of the cell is occupied by colorless protoplasm, and near the outside is a bright red pigment-mass — the "eye-spot" (*e*), near which can generally be detected one or two pulsating or contractile vacuoles, such as frequently occur in the lower unicellular animals and in the slime-moulds. .

If these free-swimming green cells are placed in a glass vessel full of water, and placed where they are more strongly illuminated from one side, as for example in a window, it will be found that very soon they collect on the lighted side, and, if they are present in large numbers, may be seen to form a green line close to the side where the light is strongest. There is reason to suppose that the red eye-spot is in some way connected with this sensitiveness to light, as it is nearly always present in those motile green cells which show sensitiveness to light, and is
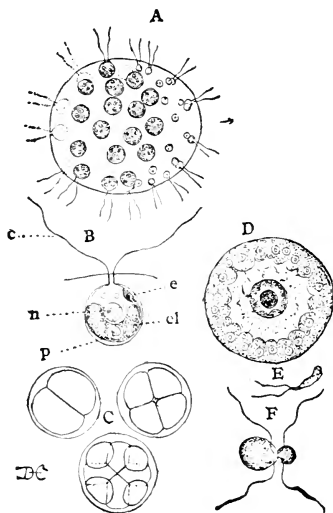
FIG. 6 (Volvoceæ). — **A**, a plant of *Pleodorina Californica*, showing the ciliated cells of which it is composed; the arrow shows the direction in which it moves; **B**, one of the smaller cells, much enlarged, showing the two long cilia, *c*, the eye-spot, *e*, the nucleus, *n*, the pyrenoid, *p*, imbedded in the cup-shaped chloroplast, *cl*; **C**, three stages in the division of one of the large cells; **D**, the egg; **E**, spermatozoid of Volvox; **F**, two gametes of Pandorina fusing together to form the zygote, or resting-spore. (Figs. B, C, after Shaw; D, E, after Overton; F after Pringsheim.)

always at the end which is directed toward the light when they are in motion. Moreover, in the multicellular forms (Fig. 6, A) it is those cells which are in the forward part of the colony which have the eye-spot best developed.

The multiplication of the lower Volvocineæ, *i.e.* the unicellular forms, is accomplished by an internal division of the cell-contents after the withdrawal of the cilia and the development of a firm cell-membrane. This division is accompanied by a preliminary division of the nucleus and chromatophore, but the eye-spot and contractile vacuoles are probably formed anew in the daughter-cells. The latter escape from the mother-cell and, developing cilia, become at once complete individuals.

In the higher members of the group, like Pleodorina (Fig. 6, A), the plant is multicellular, and the new individual arises by the repeated fission of the mother-cell, but the resulting cells remain connected, and form a multicellular complex of definite form, each cell of which has the structure of the simpler unicellular forms. In some of these multicellular genera the cells are all alike, and are at the same time vegetative and reproductive, any cell having the power of dividing repeatedly and thus giving rise to a new plant. In the most specialized forms in the group, such as Pleodorina, each individual has cells of two kinds, small, purely vegetative ones and large, reproductive ones. In the genus Volvox only a small number of cells have the power of dividing, and these have completely lost the cilia and eye-spot. Even in the largest specimens, where the vegetative cells number several thousand,

there are not more than a dozen of these large gonidia or reproductive cells.

Within the group of the Volvocineæ there is very perfectly exhibited the evolution of the sexual cells. The lowest members of the series show no marked differences between vegetative and reproductive cells, and the latter are much the same whether they are sexual or non-sexual. Thus, in the genus Pandorina (Fig. 6, F), the sexual cells are hardly distinguishable from the vegetative ones, or those which give rise to a new individual by simple fission; but these sexual cells separate, and, escaping from the colony, swim about as unicellular individuals for a short time. Two of these free-swimming cells then come together and fuse into a single one which becomes later a resting-spore, which in time will give rise to new individuals. This fusion of two similar cells is the simplest type of sexual reproduction.

In the higher Volvocineæ, there is a gradual differentiation of the reproductive cells, at first indicated by a slight difference in the size of the male and female cells, which are much alike; but in the genus Volvox, which is the highest of the series, the male cell is very small and ciliated, and is now called a spermatozoid (E), while the female cell is very much larger and quite destitute of motion. This large, non-motile cell is called the egg, or germ-cell (D).

If we compare the different members of this order we find them forming a continuous series in which differentiation has proceeded in two directions, while all, nevertheless, retain the primitive power of active locomotion. While the lower members of the series are

strictly unicellular, the higher ones are multicellular, this being most marked in the genus Volvox, where there are several thousand cells in each individual, all connected by protoplasmic threads. We have seen, too, that, in the simpler types, all the cells are alike, and there is no clear distinction between vegetative and reproductive cells, nor between sexual and non-sexual ones, while in the higher ones special cells are set apart for reproductive purposes, and sexuality is well marked. It must be remembered, however, that the evolution of the plant body in such specialized Volvocineæ, as Volvox, is in a direction away from that which leads up to the more typical plants, and there is no evidence that this peculiar line of development has ever advanced beyond such forms as Volvox, which seems to represent the highest expression of this type of structure. We must regard the whole series of the Volvocineæ as an offshoot of the main line of development of plants. The simplest of the group, such as Chlamydomonas, are closely related to the lowest of the typical green plants, the so-called Protococcaceæ, and may be considered to represent a primitive stock which has given rise to two branches, one, the Volvocineæ, culminating in Volvox, the other, the Protococcaceæ, which leads directly to the higher green plants.

THE PROTOCOCCACEÆ

The Protococcaceæ, employing this term in its widest sense, form a rather poorly defined group of unicellular plants, some of which are of doubtful autonomy, since many supposed members of this group have been shown

to be merely stages in the development of higher algæ, which, nevertheless, may grow independently for a long time, giving rise to many generations of unicellular individuals before the definitive form is reached. Many of the Protococcaceæ, however, such as the curious water-net (Hydrodictyon) (Fig. 7, B, C), are unquestionably distinct.

The lowest members of the group, like Pleurococcus (Fig. 7, A), recall in structure very strongly the resting-stages of many Volvocineæ, and it is interesting to note that in most of the Protococcaceæ the reproductive cells are actively motile, and closely resemble the active cells of the Volvocineæ. These reproductive cells are generally
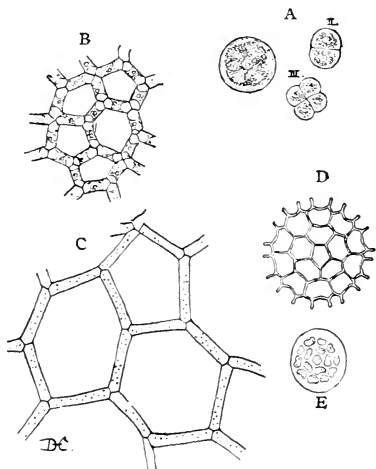
FIG. 7 (Protococcaceæ). — A, Pleurococcus, one of the unicellular Protococcaceæ; I., a full-grown individual; II., III., division stages; B, part of a very young water-net (Hydrodictyon), formed of coherent unicellular individuals, each with a single nucleus and chloroplast; C, part of a much older net, less highly magnified; each cell has many nuclei, and the chloroplast has broken up into many parts; D, E, Pediastrum; D, a full-grown colony; E, young colony, the individual cells still separate, but the whole enclosed in the membrane derived from the wall of the mother-cell.

formed by internal divisions of the protoplasm of the mother-cell, from which they escape in the form of biciliate naked cells almost identical with the Volvox cell. These motile cells soon come to rest, become invested with a cell-wall,

and soon assume all the characters of the parent-cell.

In the more specialized forms, like the water-net (Fig. 7, B, C), which may be said to bear somewhat the same relation to the lower forms that Volvox does to the lower Volvocineæ, the young individuals become united into a colony of definite form. The zoöspores, or ciliated, reproductive cells, remain within the mother-cell, where they grow together into a small net which is set free by the gradual dissolution of the wall of the mother-cell. The sexual cells, however, are ejected from the mother-cell, and unite two and two into spores which, in time, after several intermediate stages, give rise to several new nets. In nearly all these forms, both non-sexual and sexual cells show a reversion to the primitive biciliate cell, resembling closely in its structure the individual cells of the lower Volvocineæ from which these forms have presumably originated, but having only a very limited period of independent, active existence.

Within the Protococcaceæ we find considerably less specialization than exists among the Volvocineæ. Thus none of them can be properly considered as truly multicellular, for such forms as the water-net and its allies are really colonies of originally unicellular units, and all the individuals of the colony are alike. So, too, sexual cells, when they exist at all, are of the simplest type, with no difference between the male and female cells or gametes, which closely resemble the non-sexual zoöspores.

As the lower Protococcaceæ are very intimately connected with the series of green algæ which are the un-

doubted progenitors of the higher plants, their evident relationship with the Volvocineæ points to the latter as the starting point for the whole series of green plants above the Schizophyceæ.

Summary

We have seen that at the bottom of the two great series of organisms — plants and animals — there is an assemblage of extremely simple forms, many of which have not reached a stage of differentiation where it is possible to say that they are either plant or animal. Of these the Slime-moulds and Monera represent two evidently related branches of a common stock, which is perhaps, on the whole, more animal than vegetable in its nature. The slime-moulds, however, owing to their aerial habits have developed fructifications which superficially closely resemble the sporangia of many higher plants, and the spores are also plant-like in character. These spores on germinating give rise to uniciliate, monad-like zoöspores, which closely resemble the lower flagellate infusorians and suggest a relationship with them. The relationship of the slime-moulds to the other plants must be considered extremely doubtful.

The second group of low plants, the Schizophytes, while certainly to be considered as plants, are nevertheless very widely separated from any forms above them, and their connection with these higher plants must also be considered as, at least, uncertain. Whether the forms with chlorophyll among the Schizophytes are to be considered as the primitive types from which the bacteria or those forms without chlorophyll have been

secondarily derived, cannot be settled, but it is extremely likely that the whole group is a very ancient one and adapted to conditions quite unsuited to ordinary types of vegetation. The presence of cilia in many of the bacteria suggests possible affinity with the primitive motile forms from which the higher plants have originated.

Finally we have to consider the third group of these low plants, the Volvocineæ, which, while showing marked similarity to the lower animals in the actively motile vegetative cells, still in the possession of a cellulose membrane and definite green chromatophore, as well as in their nutrition and reproduction, are typical plants. Within this group there is considerable differentiation of the plant body and the reproductive cells, but it is among the lowest members of the group that we are to look for the point of contact with the higher plants as well as possibly with the lower animals.

By the loss of active motion we may assume that forms like the lower Protococcaceæ arose, the firm cellulose investment of the cell, found in most plants, precluding the active movements typical of the lower animals and of the Volvocineæ. This stationary green cell, with its definite cell-membrane, may be properly considered as the starting-point for the series of Green Algæ, or Chlorophyceæ, which in their turn are the progenitors of the much more perfect green land plants.

The two series, the Volvocineæ and Protococcaceæ, may be looked upon as offshoots of a common ancestral type, probably resembling the existing unicellular Volvocineæ. In one direction development has proceeded without loss of motion in the cells, re-

sulting in the higher types of Volvocineæ, like Volvox; in the other, by the loss of motility, there have first arisen non-motile unicellular plants like Pleurococcus, from which later have been developed the multicellular green algæ.

CHAPTER IV

ALGÆ

ABOVE the Schizophytes and Mycetozoa is a large assemblage of plants, sometimes all united under the name of Thallophyta, but probably better divided into two divisions of equal value, to which the rank of sub-kingdom may with propriety be applied. The primary division is based upon the presence or absence of chlorophyll, and although a few of them which have no chlorophyll are structurally similar to certain green forms, and possibly to be considered as derived from them, most of the forms without chlorophyll differ profoundly in their structure from all green plants, and may properly be relegated to a sub-kingdom of their own. To the forms which possess chlorophyll, the name of Algæ has been given, while those where chlorophyll is absent are known as Fungi. The two low groups of green plants, — the Protococcaceæ and Volvocineæ, — which were considered in the last chapter, are usually included with the Algæ, and very properly so, as they doubtless represent the lowest members of the sub-kingdom.

The Algæ are readily divisible into three main divisions or classes, which are easily distinguished by their color. All of them possess chlorophyll, but in two of the classes there are other pigments present, giving

them respectively a more or less pronounced red or brown color. On this basis of color, the three classes are denominated the Green Algæ (Chlorophyceæ), Brown Algæ (Phæophyceæ), and Red Algæ (Rhodophyceæ). While, at first sight, it would seem that such a classification is an artificial one, it is found, on more careful study, that these color differences are associated with constant and characteristic differences of structure, which really make the division a very natural one. Of these three classes, the two latter are mainly marine, and the peculiarities and color and structure are, with little question, largely the result of their peculiar environment.

The Green Algæ (*Chlorophyceæ*)

The Green Algæ are for the most part fresh-water plants, and although most of them are more complicated in structure than the very simple Protococcaceæ and Volvocineæ, still as a whole the members of the class are of simple structure, and, so far as the vegetative parts are concerned, much inferior to their larger red and brown relatives. In spite of the low organization of the green algæ, it is among these, rather than among the more complicated and larger marine red or brown ones, that we must look for the ancestors of the lowest green land plants, — the Mosses, — as there is strong evidence that these originated from aquatic plants allied to certain existing green algæ.

In spite of their simplicity, the latter show a considerable degree of variation among themselves, both as to their vegetative and reproductive parts, and upon

E

these differences there are based several well-defined
orders.

Attention has already been called to the probable
origin of the higher green algæ from the Volvocineæ,
and we have seen how, by the loss of free locomotion,
the latter gave rise to the simpler Protococcaceæ, which,
however, give an indication of their origin from motile
ancestors by the frequent reversion to the primitive
free-swimming condition in their reproductive cells.

Tracing up the line of ascent in the green algæ a
step further, there is found a group of forms which
consist of rows of perfectly uniform cells, all alike and
individually closely resembling in structure the unicel-
lular Protococceæ. Sometimes, among the simpler
forms of filamentous algæ, it is not uncommon to have
the filaments break up into separate cells, giving rise
to colonies of unicellular individuals which are not to
be distinguished from true Protococcaceæ. It is easy
to see how the latter, by the repeated division of a cell
in a single plant, without separation of the daughter-
cells, could give rise to a simple cell-row or filament
such as really makes up the plant body in many Chloro-
phyceæ. Indeed, if we follow the life-history of some
of these, we find that its individual development fol-
lows very closely what we may suppose has been the
history of the whole group. Thus the non-sexual re-
productive cells are very commonly free-swimming cells
(zoöspores), which show exactly the structure of the
lower Volvocineæ (Fig. 8, C). Such zoöspores are
often biciliate, possess a single chromatophore, eye-
spot, and contractile vacuoles, and are very sensitive
to light, collecting quickly on the lighted side of the

vessel in which they are placed.   After a short period
of active movement, they settle down, become invested
with a cell-membrane, and enter what may be called
the Protococcus stage, in which they sometimes remain
for a long time, giving rise to large colonies of unicellu-
lar plants by repeated fission and separation of the cells.
Indeed these unicellular stages of many algæ have been
given special names, under the mistaken impression that
they were really autonomous forms instead of simply
transitory stages in the development of a filamentous
alga.   Usually, however, the zoöspore, after coming
to rest, elongates, and, by the formation of a transverse
wall, becomes two-celled, and, by further elongation
and repeated cross-divisions, assumes the filamentous
form of the adult plant.   (Fig. 9, D, E, F.)

THE CONFERVACEÆ

The order which seems to be most directly connected
with the Protococcaceæ is that known as the Confer-
vaceæ, especially important in a study of the evolution
of plants, as it probably represents, more nearly than any
other existing group, the direct ancestral forms of the
higher plants.

The lowest members of the order are simple un-
branched filaments, composed of perfectly similar cells
(Fig. 8, A).   Somewhat higher in point of develop-
ment are a number of common forms, *e.g.* Chætophora,
Cladophora (Fig. 8, B), which are branched, while many
of these, as well as such of the unbranched forms as
are attached, often show a modification of the basal cell
into a root-like organ.   Where this is the case of course

the filament shows a distinction between base and apex. The most specialized forms, *e.g.* Coleochæte (Fig. 10), have the form of a flattened disk, and recall somewhat the structure found in the simplest mosses.
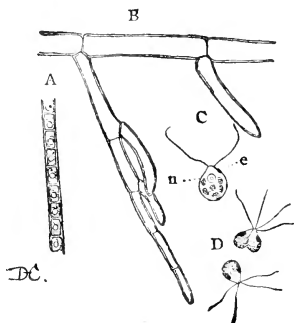
Fig. 8 (Confervaceæ).— A, a filament of Microspora, composed of entirely uniform cells; B, part of a plant of Cladophora, showing the branching habit; C, a zoöspore of Cladophora, showing the two cilia, the eye-spot, *e*, and the nucleus, *n*: D, gametes, or sexual cells, of Ulothrix, showing the process of conjugation. (Fig. D, after Dodel.)

Within the Confervaceæ there is found a similar advance in the reproductive parts to that described in the Volvocineæ. Some of the lowest forms have as yet shown only non-sexual reproductive cells, but it is not improbable that sexuality will be shown for all of them. In these forms where only non-sexual zoöspores have been observed, they may be either uniciliate or biciliate. These zoöspores may arise singly, by the escape of the whole of the contents of a cell as a single zoöspore; or there may be a division of the cell-contents into two or more parts which then escape. When the zoöspores are large (Fig. 9, D), they sometimes have more than two cilia, but otherwise resemble closely the typical Volvox cell.

The simplest type of sexual reproduction among the Confervaceæ consists in the formation of cells (gametes), which differ from the zoöspores only in being, as a rule, smaller, but with no distinction of sex. These gametes

are always biciliate, and are set free in the water where they unite in pairs to form a single cell (zygote) with four cilia (Fig. 8, D), which either at once grows into a new plant, or first passes into a resting stage (spore), which then gives rise to new individuals by first forming one or more zoöspores.

In the higher members of the order, the so-called oögamous forms, there is a sharp separation of the sexual cells, the female cell becoming here a large passive cell, the egg-cell, usually borne in a specially modified and enlarged cell called the oögonium (Fig. 9, *og*). In the form figured, the egg closely resembles in its formation and structure the large zoöspores, with which it agrees except in the absence of cilia,
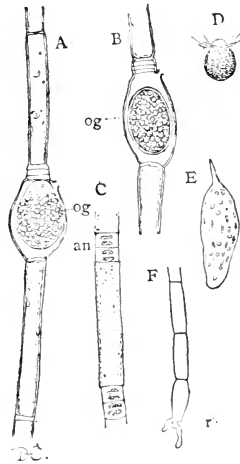
FIG. 9. (Confervaceæ). — A, B, portions of two female plants of Œdogonium : *og*, the oögonium : in A, the egg-cell has not yet been fertilized, in B, the fertilized egg has become transformed into a thick-walled resting-spore ; the spermatozoid enters through the pore at the top ; C, part of a male plant of the same species, showing the antheridium, *an* : D, a zoöspore or motile non-sexual reproductive cell ; E, one-celled plant derived from a zoöspore ; F, the lower part of an older plant showing the root-like outgrowths (*r*) of the basal cell.

and there is no question that here also the gametes are modifications of originally non-sexual zoöspores. The male gametes (spermatozoids) in these oögamous Confervaceæ are also borne in special cells (antheridia) (Fig.

9, C, *an*), and closely resemble the zoöspores except in size, and the partial or complete loss of chlorophyll. The spermatozoid has a large nucleus with relatively little cytoplasm, as the nucleus is probably of the most importance in the act of fecundation.

At maturity the oögonium opens and permits the entrance of the motile spermatozoid, which at once penetrates into the egg-cell where its nucleus fuses with that of the egg, thus fertilizing it. As the result of fertilization the egg becomes invested with a heavy cell-wall and forms a resting-spore which remains dormant for a long period, and is capable of resisting, unharmed, freezing and drying up.

FIG. 10.— A, a plant of *Coleochæte scutata*, one of the highest of the Confervaceæ; B, fragment of another species, *C. pulvinata*, with an oögonium, *og*; C, the germinating spore seen in section, showing its division into a nearly globular cell-mass; each cell later gives rise to a single biciliate zoöspore. (Figs. B and C after Oltmanns.)

In the highest type of all, represented by the peculiar genus Coleochæte (Fig. 10), the oögonium, with the contained oöspore, becomes, after fertilization, invested with a protective covering formed by the growth of adjacent cells, so that the influence of the act of fertilization extends beyond the egg-cell. Coleochæte, as we shall see

later, shows certain interesting analogies with the lower
mosses, and is on the whole, the type of the green algæ
which most nearly approaches them.   When the oöspore
germinates, instead of forming a plant like the original at
once, or having its contents divided into zoöspores which
then germinate, there is first developed a cellular body
(Fig. 10, C), which may be considered as a small plant
of very limited growth, differing from the normally de-
veloped sexual individuals.   From each cell of this small
plant is produced a single biciliate zoöspore, which then
develops into a normal individual.   This formation
from the resting-spore of an individual entirely devoted
to the formation of non-sexual spores, from which the
sexual plants are finally developed, is very much like
what occurs in the life-history of the mosses which
probably arose from the Algæ by a further development
of this alternation of sexual and non-sexual plants.
Where there is a marked difference in structure between
these phases, such as we find in the mosses and ferns,
the terms gametophyte and sporophyte have been ap-
plied respectively to the sexual and non-sexual phases.
The first indication of this differentiation is seen in such
forms as Œdogonium (Fig. 9), where the resting-spore
on germination does not at once produce a filament like
the parent plant, but first divides into four zoöspores
which, on escaping, give rise to as many new individuals.

While the Confervaceæ probably form the direct
line of ascent from the Volvocineæ to the mosses, there
are several other orders of green algæ which, starting
from about the same point, show specialization in various
directions.   Two of these, the Siphoneæ and Conjugatæ
are obviously related to the other green forms, but a

third order, the Characeæ, is made up of very peculiar
plants of doubtful affinities.

THE SIPHONEÆ

This order contains a good many types differing a
good deal among themselves and showing in some cases
a high degree of special-
ization. They differ
from the other green
forms in the almost
complete absence of
division walls within
the plant body, although
they can hardly with
propriety be considered
as strictly unicellular
since the protoplasm
contains a large number
of nuclei. The plant
may be a simple tubular
filament, or it may be extensively branched and form a
body of considerable size showing a remarkable degree
of external differentiation, actually mimicking the struct-
ure of the higher plants in the development of stem,
leaf, and root (Fig. 11); but even in such cases the
hollow cavity of the thallus is undivided by partition
walls. The wall is lined with a protoplasmic layer in
which are imbedded the numerous nuclei and chloro-
plasts. The division of the nuclei, of course, is not
accompanied, as in most cells, by the formation of a
division wall.

FIG. 11.—Part of a plant of *Caulerpa
plumaris*, one of the Siphoneæ, show-
ing external differentiation into stem,
root, and leaf in a non-cellular plant;
x, the growing point; *r*, rootlets.

The exact affinities of many of the Siphoneæ are still obscure, and it is by no means impossible that the group has had a multiple origin, *i.e.* all the members of the order may not neces-sarily be genetically related, but there may have been a develop-ment of this peculiar type from several an-cestral forms. While the lowest of the or-der show much in common with the Protococcaceæ, and may, perhaps, have arisen from them, others like the com-mon genus Vaucheria (Fig. 12) are struct-urally more like some of the Confer-vaceæ. There are a number of genera among the latter where the elongated cells are multinucle-ate and there is a partial suppression of the division walls,

Fig. 12.—*Vaucheria sessilis*, one of the fresh-water Siphoneæ; A, plant with unopened antheridium, *an*, and oögo-nium, *og*; B, an older plant with the antheridium empty, and the oögonium containing the resting-spore, *sp*; C, the end of a filament with a zoösporangium; D, zoöspore showing the pairs of cilia corresponding to the individual nuclei in its outer part; E, a germinating zoöspore.

nuclear division and cell division being quite independ-ent of each other. By the complete suppression of the division walls in forms like these, it is conceivable that

a thallus of the type found in Vaucheria may have arisen.

The largest members of the order, which reaches its highest development in the tropical seas, generally have the large thallus made up of closely interwoven, much-branched filaments, which, however, seldom show any divisions except those by which the reproductive organs are cut off. In regard to the latter, these large marine Siphoneæ are less highly developed than some of the otherwise much simpler fresh-water genera.

Within the series we find much the same progression in the development of the reproductive parts that has been described in the Volvocineæ and Confervaceæ. Most of them show both non-sexual and sexual reproduction, the latter being of a low type in the greater number of them, with little or no difference between the male and female cells. The genus Vaucheria, however (Fig. 12), shows perfectly differentiated sexual cells, the larger passive egg-cell being retained within the oögonium, where it is fertilized by the minute biciliate spermatozoids.

The Siphoneæ exhibit great variety also in the non-sexual reproduction. Most of them produce zoöspores, which are usually provided with two cilia, but, in the case of Vaucheria, are apparently multiciliate, owing to the fact that the individual biciliate zoöspores are discharged in a mass and never separate. Besides the zoöspores, there are various forms of non-motile spores, and the plants often increase in number by the separation of a portion of the thallus. Indeed in Caulerpa (Fig. 11) this is the only known method of reproduction.

THE CONJUGATÆ

The members of the second subsidiary order of the green algæ, the Conjugatæ, are mostly fresh-water plants, having very marked characteristics, and distin-
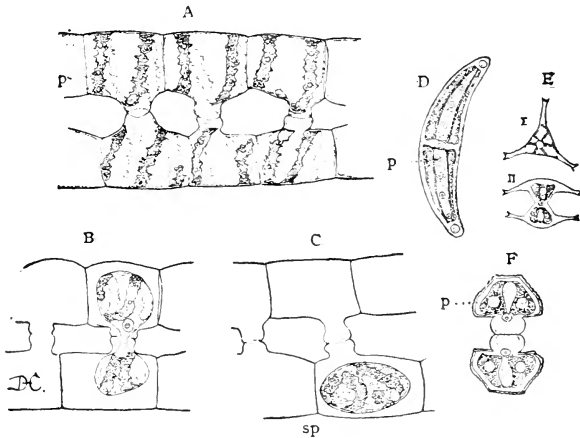
FIG. 13 (Conjugatæ).—A, two filaments of Spirogyra showing the beginning of conjugation; each cell contains a single large spiral chloroplast with the pyrenoids, *p*; B and C, later stages of conjugation; in C the contents of one of the conjugating cells has passed completely over into the other, the united protoplasmic masses forming the resting-spore, *sp*; D, Closterium, one of the Desmids or unicellular Conjugatæ; *p*, a pyrenoid; E, two views of another Desmid, Staurastrum; the shaded portion represents the chloroplast; F, a Desmid, Cosmarium, in process of cell-division.

guished from most of the other algæ by the complete absence of ciliated cells. The most familiar members of the group are the "pond-scums," which occur in large, frothy masses, floating in quiet water. The lowest of the order are the Desmids, perhaps the most beautiful of all unicellular plants (Fig. 13).

The lowest of the desmids are simple oval cells, with

a single chromatophore, and the cell may be compared
structurally to that of the Protococcaceæ or Volvocineæ,
and it is probably from these that the lower Conjugatæ
have arisen. Reproduction takes place in the lower des-
mids either by the division of the cells (Fig. 13, F), or
by the fusion of two of them into a single cell, or spore,
which subsequently by internal division gives rise to
several new individuals very much like the production
of zoöspores within the resting-spores of many Pro-
tococcaceæ and Confervaceæ.

From these simple unicellular types, it is easy to trace
the development of the series in one direction, by
specialization of the individual cells, to the higher
desmids; in the other, by cohesion of the cells, to the
filamentous pond-scums. The latter, probably, do not
all form one group, but have originated from several
types of unicellular ancestors, as there are several genera
of unicellular desmids, which, in the form of their pe-
culiar chloroplasts, closely resemble the different genera
of the pond-scums. Thus Mesotænium closely resembles
the individual cell of the filamentous Mesocarpus, and
Spirotænia bears the same resemblance to Spirogyra.

The chloroplasts of the Conjugatæ are always large
and usually have the form of a flattened band or plate
in which are imbedded one or more roundish bodies,
pyrenoids, such as are common in the chloroplasts of
most other green algæ (see Fig. 13).

The absence of motile reproductive cells necessitates
a special contrivance for fertilization. Except in a few
of the lowest forms where the unicellular individuals
fuse together completely, union of the sexual cells is
accomplished by the formation of protuberances, grow-

ing out from them, which unite to form a tube connecting the cells (Fig. 13, A, B, C). Sometimes the protoplasm of one of the cells passes over into the other one and fuses with its protoplasm; or the protoplasm may leave both cells and unite in the middle of the connecting tube. In either case the result of the fusion is the formation of a thick-walled resting-spore (zygospore). This process of conjugation is characteristic of the whole order, and, except in the very lowest forms, consists in a fusion of the cell-contents only, the wall of the resting-spore being an entirely new one.

The Characeæ

Probably no group of green plants is more puzzling to the systematist than the Characeæ, or stone-worts, as they are sometimes called, on account of the heavy coating of calcium carbonate frequently deposited in their outer cell-walls, which renders the plant rigid and brittle. These curious aquatics are all closely related among themselves, but show no very obvious affinity with any other group of algæ, and at present all attempts to connect them with the other algæ are little better than mere conjecture.

All the Characeæ are characterized by the regular division of the axis into nodes and internodes which bear a definite relation to the first divisions in the large apical cell which terminates each growing shoot. The plants are remarkable for the great size of the internodal cells, which often reach a length of several centimetres with a diameter of a millimetre. The protoplasm of these long cells shows a very active rotation within

the cell, and the cells have long been favorite subjects
for demonstrating this phenomenon. The original
nucleus of these elongated cells becomes early divided
into many, but these secondary nuclei are not formed
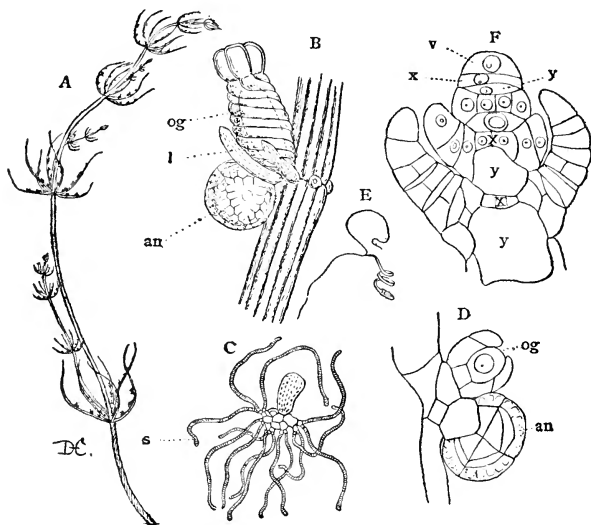
FIG. 14. — A, a plant of Chara, one of the Characeæ, showing the division
of the stem into nodes and internodes, and the method of branching;
B, part of a leaf with an antheridium *an*, and oögonium, *og*; *l*, leaflets
at the node of the leaf; C, a group of filaments from the interior
of the antheridium; each cell of the long filament contains a biciliate
spermatozoid; D, a section through the node of a young leaf showing
the young antheridium, *an*, below the oögonium, *og*; E, a single
spermatozoid; F, a longitudinal section of the stem-apex, showing the
apical cell, *v*, from the division of which all the parts of the plant
arise; *x*, the nodes, *y*, the internodes.

by the ordinary nuclear division, or karyokinesis, but
result from a direct constriction, or fragmentation of
the primary nucleus, a phenomenon which has also
been met with in the elongated cells of the stems of
some flowering plants.

No special non-sexual reproductive organs occur in these plants, beyond the separation of small fragments, usually nodes, which may, under proper conditions, develop into new individuals.

The sexual organs, antheridia and oögonia, are extremely complicated, especially the former, and differ very much from those of all other algæ. They show certain analogies with the reproductive organs of some of the lower mosses, this being especially the case with regard to the spermatozoids, which are strikingly similar to those of some mosses. A single large spore results from the fertilization of the egg-cell, which is surrounded by a protective covering formed by a series of cells about it.

The spore on germination produces a simple conferva-like filament, or "protonema," upon which the fully developed plant arises as a lateral branch. As this is somewhat like the formation of the leafy stems in the common mosses, it has been suggested that there may be some genetic connection between the latter and the Characeæ; but this is highly improbable in view of the great differences in the structure of the plants of the two groups, although the analogies in the structure of the reproductive organs may indicate a remote relationship between them.

THE BROWN AND RED ALGÆ

While the green algæ are for the most part inhabitants of fresh water, the two other great groups of Algæ are mostly found only in the sea, where they constitute the most conspicuous features of the marine flora. Both classes include plants of much greater size and complexity than any green algæ, some of the great

kelps being plants of gigantic size. Both groups differ
in many respects from the green algæ, and it is an open
question whether they have been derived from the latter,
or whether they are to be traced back to unicellular
ancestors, in which their peculiar pigments were already
developed. These red and brown pigments are doubt-
less associated with the process of photo-synthesis, and
are probably the results of the peculiar environment of
these sea-weeds.

THE BROWN ALGÆ (*Phæophyceæ*)

Before examining the more highly organized plants
to which the term Phæophyceæ is usually applied, it
may be well to consider a number of simple forms pos-
sibly allied to them, and, although minute in size, of
great importance in the economy of nature. Some of
these are inhabitants of fresh water, but the greater
number are free-swimming or pelagic organisms occur-
ring in the open ocean, and forming an important con-
stituent of the so-called "plankton" or floating life of
the ocean.

The simplest of these (Fig. 15, A, B) are very minute
ciliated organisms recalling the green, fresh-water Vol-
vocineæ, and possibly related to them. Like these they
show evident resemblances to the flagellate infusorians,
from which they differ mainly in the presence of chromat-
ophores, and the absence of an opening by which solid
food can be ingested. These plants have chromato-
phores which contain a pigment much like that of the true
Phæophyceæ, and possibly may bear the same relation to
this class that the Volvocineæ do to the green algæ.

A second group of unicellular plants, resembling the Phæophyceæ in color, but otherwise more like some of the green algæ, are the Diatoms (Fig. 15, C,D), a group including many thousand species, which often occur in enormous masses. Although these are unicellular, they are often united into colonies of definite form, but more commonly are free. The chromatophores are usually two in number and flattened in shape, but may be numerous and of the round or oval form commonly found in the higher Phæophyceæ. As in the latter there is present a

Fig. 15. — A, B, Peridineæ; C, D, Diatomaceæ. A, *Hemidinium nasutum* (after Stein); B, *Peridinium divergens* (after Schütt); C, *Pinnularia viridis*; I, from above, II, from the side, showing the overlapping valves of which the shell is composed; D, Navicula sp. ? showing the two chromatophores, *cl*.

brown pigment (diatomin) which quite conceals the chlorophyll. A further peculiarity of these plants is the presence of a silicious shell, composed of two valves, one fitting into the other (Fig. 15, C., II). This glassy case is often sculptured in a most beautiful manner, and the fine markings are favorite tests for microscopic lenses. The diatoms often exhibit creeping movements, but are never ciliated. The multiplication of the diatoms is either by fission, or by the formation of so-called "auxospores," which may be formed either sexually or asexually.

While diatoms are common in fresh water, it is in

the ocean that they are of most importance. Here, especially in the colder parts of the sea, they form the greater part of the floating vegetation, and sometimes occur in such enormous masses as to discolor the water over wide areas. It is these masses of floating unicellular plants which are the primary source of food for all the hosts of animal life in the ocean, and it is to these minute organisms that the manufacture of organic substances is due, and they serve as food for innumerable smaller animals, and sometimes larger ones as well, which, in their turn, are devoured by higher forms.

In the warmer waters, the diatoms are largely replaced by the other unicellular plants already referred to, as well as others whose affinities are still obscure. As the larger sea-weeds, with few exceptions, are attached, they are of necessity confined to a narrow zone of shallow water skirting the shore, and in spite of their large size, are of slight importance as compared with the hosts of minute pelagic plants.

The silicious shells of diatoms are almost indestructible, and have been preserved in a fossil condition so that even the species are readily determined. These deposits are often of great thickness, showing that, formerly, as at present, these plants occurred in immense numbers. However, geologically speaking, the group is not an extremely old one, but appears somewhat suddenly in the later secondary, and early tertiary rocks.

THE PHÆOPHYCEÆ

The true Phæophyceæ are almost exclusively marine and form a clearly defined class with no certain affinity

with the other Algæ. They include by far the largest
of the sea-weeds, and are familiar objects of the sea-
shore. With the exception of
a few forms like the gulf-weed
(Sargassum), which seems to be
really a floating plant, they are
usually firmly attached to rocks
and other objects by means of
highly developed root-like or-
gans or holdfasts. They may
grow where they are completely
submerged, but many of them
occur between tide-marks so
that they are partially or com-
pletely exposed at low tide. A
common feature of many of
them is the development of
floats, or air-bladders by which
the plant is buoyed up and
brought near the surface and
thus exposed to the light.

FIG. 16. — *Ectocarpus granu-
losus*, one of the simpler
Brown Algæ or Phæophyceæ:
A, part of a plant showing
the sporangia, *sp*; B, a uni-
locular sporangium, *sp*, more
highly magnified; C, young;
D, older plurilocular spo-
rangium; *cl*, the irregular
chromatophores; E, a single
gamete of *E. Siliculosus*,
showing the lateral position
of the cilia. (Fig. E after
Berthold.)

Within this class there is
great range of structure as well
as size. The simplest forms are
delicate, branching filaments
much like many Confervaceæ,
except for their brown color.
Others are gigantic plants reaching a length of a hun-
dred metres or more, rivalling the largest of terrestrial
plants. As might be expected, these giant kelps show
a considerable degree of specialization in their tissues,
but there is to be found almost every intermediate con-

dition between these and the simplest types, like Ecto-
carpus (Fig. 16). Among the most characteristic of
these larger forms
may be mentioned the
great bladder-kelps of
the Pacific (Macro-
cystis, Nereocystis)
(Fig. 17), and the
smaller Laminarias of
the Atlantic. Many
of the larger kelps
grow where they are
exposed to the full
force of the heavy
surf, and this ac-
counts for the tough,
leathery consistency
of many of them, and
the powerful hold-
fasts or roots.
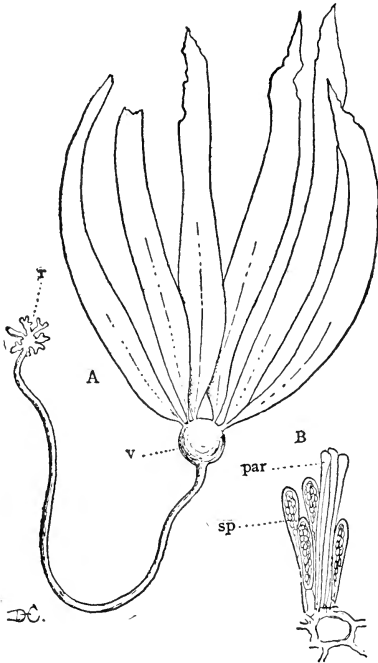
FIG. 17. — A young plant of *Nereocystis
Lutkeana*, one of the large kelps,
much reduced, showing the holdfast,
r, and the float, *v*, with the large
leaves at its summit; the fully grown
plant may reach a length of a hun-
dred feet or more; B, the simple uni-
locular sporangia, *sp*, and sterile
hairs, or paraphyses, *par*, much mag-
nified.

An examination of
the whole class shows
that within it there
has been much such
an evolution of the
reproductive cells as
we have seen in sev-
eral groups of the
green algæ; but this
is by no means paral-
leled by the vegetative parts, as the largest, and, so far as
the plant-body is concerned, the most specialized forms,

including all the giant kelps, show only the simplest possible form of reproduction, *i.e.* purely non-sexual zoöspores. Many of these larger kelps show an external differentiation which simulates closely the parts of the higher terrestrial plants. A definite axis, with lateral leaf-like outgrowths, has its base modified into a mass of firm root-like organs, forming a most efficient holdfast or anchor, which, in some of the largest kelps, when torn away may carry with it a mass of rocks and shells weighing several hundred pounds.

FIG. 18 (Fucaceæ).—A, a fragment of the common gulf-weed, Sargassum, showing the definite stem and leaves, and the berry-like floats, *v*; B, the egg of the common rock-weed (*Fucus vesiculosus*), being fertilized by the minute biciliate spermatozoids; C, a single spermatozoid more highly magnified.

The leaves of the large kelps are often several metres in length, and although structurally they differ widely from those of the higher plants, yet functionally they must be considered as equivalent to these. It is in these organs that the greater part of the chlorophyll-bearing cells are situated. The peculiar floats or air-bladders found in these plants are formed by the accumulation of gases within certain parts of the plant, resulting in a distention of the thallus at these points, but the details of their development cannot be given here.

While some of the forms, including the larger kelps, appear to possess only non-sexual zoöspores, others, like

the rock-weeds (Fucus) (Fig. 18, B), and the gulf-weed (Sargassum) (Fig. 18, A), have clearly marked, sexual cells, large, non-motile eggs, and small, ciliated spermatozoids, closely resembling the biciliate zoöspores of the kelps.

The lowest forms where sexual cells occur, *i.e.* Ectocarpus, have similar motile gametes, while in others, like Cutleria, there is a marked difference in size, although both gametes are motile.   The most highly specialized forms, *i.e.* Fucus and Sargassum, produce large non-motile eggs and minute spermatozoids, both of which are discharged into the water when the egg is fertilized, in a manner which recalls that of many low animals, such as the starfish or sea-urchin.

THE RED ALGÆ (*Rhodophyceæ*)

Among the most beautiful of all plants are the Red Algæ or Rhodophyceæ, whose brilliant colors and graceful forms are familiar to the most superficial student of the marine flora.   They differ in structure so much from the other Algæ, that they are sometimes considered to form a group entirely apart from these.   However, the lower members of the class show sufficient resemblance to the green algæ to make it seem likely that there is a relationship between the two classes, although it is probably a remote one.

While not so strictly marine as the typical Phæophyceæ, still the great majority of the Rhodophyceæ occur only in salt water.   The few members of the class which grow in fresh or brackish water are insignificant in size and dull in color, and belong to the lower orders of the class.

A remarkable characteristic of the class is the absence of the motile reproductive cells so common in the brown and green algæ. In the lowest members of the class, the Bangiaceæ, the reproductive cells are said to show a slight amœboid movement, but in all the others even such movement is quite wanting. Another peculiarity is the very evident protoplasmic connections between the cells of the thallus, these being constantly present in all but the lowest types. These connections have the form of extremely delicate filaments joining the protoplasmic bodies of adjacent cells (Fig. 19, A).

They all possess in addition to the chlorophyll an additional pigment, which, in most forms, is a more or less pronounced red. This pigment (phycoerythrin) is least developed in the fresh-water species, which show a more or less decided green tinge, olive or blackish rather than red. Many of the salt-water species, however, show a brilliant rose-red or purple color, to which they owe much of their beauty. This red pigment is soluble in fresh water and when it is extracted from the plants the chlorophyll-green becomes visible. The phycoerythrin seems to be related in its nature to chlorophyll, and probably is associated with it in the process of photo-synthesis.

The red algæ are small plants compared to the gigantic kelps, but are as a rule larger than the green algæ. Some are exceedingly delicate, consisting of simple or branching filaments much like some of the Confervaceæ. Others are composed of single plates of cells, which form an excessively delicate, filmy thallus. Some, however, like the common Irish moss (Chondrus), and other species which grow where they are exposed

to the action of the waves, are comparatively large, and
tough and leathery in consistence like the kelps, which
they also resemble in the general arrangement of the
cells in the thallus.   One peculiar family, the so-called
Coralline algæ, are characterized by the deposition of
large amounts of carbonate of lime, which makes them
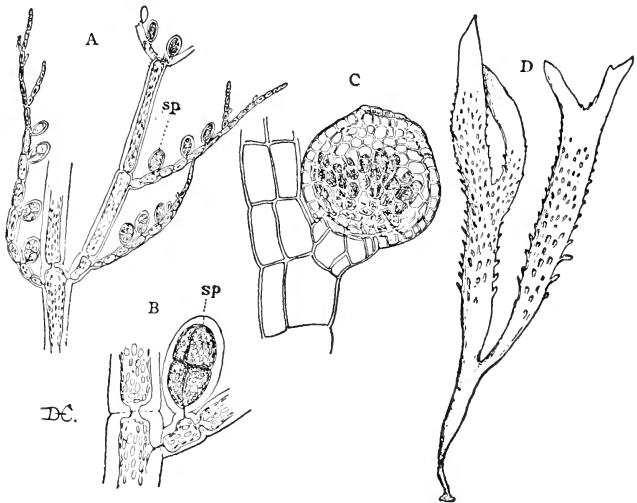
Fig. 19 (Red Algæ). — A, *Callithamnion floccosum*, a simple red sea-weed,
    showing the protoplasmic connections between the cells, and the non-
    sexual reproductive bodies, tetraspores, *sp*; B, a single tetraspo-
    rangium with the four contained spores; C, the spore-fruit, or cystocarp
    of a somewhat more complicated form, Polysiphonia; D, one of the
    larger red sea-weeds, *Gigartina spinosa*, reduced about one-half.

resemble corals in form, and in their stony hardness.
Some of these often grow associated with true corals,
and play an important part in the building up of coral
reefs.   Like the true corals, these corallines have been
preserved very perfectly in a fossil condition, and they
appear to be quite ancient forms.

As a rule, the fresh-water Rhodophyceæ are simpler in structure than their marine relatives, and probably represent a more primitive type of structure from which the others have been derived. It is not impossible that these simple fresh-water forms may also be intermediate between the green algæ and the higher Rhodophyceæ. It must be admitted, however, that, with the exception of the Bangiaceæ, a group whose affinity with the true Rhodophyceæ has been questioned, all the fresh-water forms, although simpler in structure, are typical Rhodophyceæ, so far as the reproductive parts are concerned.

The motile zoöspores of the brown and green algæ are replaced in most Rhodophyceæ by the so-called tetraspores, formed four together in a common mother-cell, much as zoöspores are formed. These escape from the mother-cell and form new plants at once (Fig. 19, A, B).

The sexual reproduction shows certain peculiarities which are not found elsewhere in the vegetable kingdom, although there are certain analogies in the fertilization of some fungi. The antheridium (Fig. 20, C) is made up of a great number of small cells which arise, as short branches, very much crowded together. The contents of the terminal cells escape in the form of a naked, but non-motile cell, or spermatium, which differs in structure from the spermatozoids of other algæ, mainly in the absence of cilia. So far as is known, the conveyance of the sperm-cell to the female reproductive organ, or procarp, is dependent upon the movements of the water.

The female reproductive organ of the Rhodophyceæ

the procarp, or carpogonium is, in the lowest forms (Fig. 20, A), a single cell much like the oögonium of the green algæ, but there is no contraction of the egg-cell

preliminary to fertilization. There is a more or less evident prolongation, known as the trichogyne (t), developed from the carpogonium, and the motionless spermatium, on coming in contact with this, fuses with it and the walls of both cells are dissolved at the point of contact, and the contents of the male cell pass into the trichogyne and effect fertilization. It is probable that in most cases there is a fusion of the nuclei of the spermatium and carpogonium, but it has been claimed that sometimes this does

FIG. 20. — Fructification of the Red Algæ; A, procarp, or female organ of one of the simpler Rhodophyceæ, Batrachospermum; t, the trichogyne; c, the carpogonial cell; B, the same after fertilization; an, the spermatium united with the trichogyne; sp, spores budding out from the carpogonial cell; C, the antheridium of Polysiphonia; D, the multicellular procarp of Spermothamnium; t, the trichogyne; E, diagram of the procarp in the higher Rhodophyceæ; t, the trichogyne; x, the auxiliary cell which is secondarily fertilized and produces the spores. (Figs. A, B after Davis; E, after Phillips.)

not occur, the fusion of the protoplasm being sufficient to insure fertilization. The result of fertilization is not a resting-spore as in the green algæ, but the carpogonial cell sends out a large number of short branches

whose end-cells are the "carpospores" (Fig. 20 B, sp);
the whole mass of spores budded off from the fertilized
carpogonial cell forms the "sporocarp" or "spore-fruit."

In the higher Rhodophyceæ, however, the cell which
bears the trichogyne does not itself produce the spores,
but there are certain accessory cells (Fig. 20 E, x) which
are impregnated, secondarily, by outgrowths from the
carpogonial cell, known as "oöblastema filaments." A
direct protoplasmic connection is thus established be-
tween the carpogonial cell and these auxiliary cells,
whereupon the latter begin to bud freely and produce the
spores much as these are formed from the carpogonial
cell in the lower forms. In certain types the auxiliary
cells are numerous and widely separated from the car-
pogonial cell. In such cases several very long oöblastema
filaments grow out from the latter after fertilization, and
these apply themselves to the auxiliary cell, which
thereupon produces a group of spores in the usual
way. In extreme cases a single oöblastema filament
may be sufficient for impregnating more than one aux-
iliary cell.

From some recent investigations it appears that some-
times parthenogenesis may occur, *i.e.* the procarp may
give rise to spores without fertilization. How exten-
sive this phenomenon is, must be determined by future
investigations; but the rarity of antheridia in some
species, and the absence of spontaneous movement in
the spermatia make it not unlikely that parthenogene-
sis is not so rare a phenomenon as has usually been
supposed. Among the green algæ parthenogenesis is
known to occur in *Chara crinita.*

Summary

The green algæ are probably the most primitive of the three classes of Algæ, and may have given rise to the other two, although an independent origin of the red and brown forms from unicellular ancestors is not impossible, and in the case of the Phæophyceæ is quite probable, as certain unicellular forms, the Peridineæ and Dinoflagellata show a close resemblance to the zoöspores of the higher brown algæ, and may represent their ancestral forms.

Among the green algæ the simpler Volvocineæ probably represent the most primitive forms from which the others have sprung. These actively motile plants also show possible affinities with such low animals as the flagellate Infusoria.

With this free-swimming cell as the starting-point, specialization has apparently proceeded in several directions. First of all, within the group of the Volvocineæ themselves there has been specialization in two ways, first, the production of a multicellular plant body; second, a high degree of differentiation of the reproductive parts which reaches its most complete expression in the genus Volvox. The series of forms leading up to the latter is very complete, every grade of development being represented by existing genera.

The second line of development is illustrated by the Protococcaceæ. By the loss of motility in the vegetative cells, and the formation of a continuous cellulose membrane, these have lost their power of locomotion. Within this series are also found multicellular plants,

but these are more properly aggregates or colonies of unicellular units than individual plants. The reproductive cells of the Protococcaceæ are always very primitive in character, and usually are motile, much like their unicellular volvocineous ancestors. The third line of development, represented by the Confervaceæ, may be assumed to have arisen from the lower Volvocineæ through the simpler Protococcaceæ, with which they agree closely in their development. The origin of the typically multicellular Confervaceæ from the unicellular Protococcaceæ has been brought about by the cohesion of the cells after fission is complete. By repeated divisions in a single plane the simpler filament of the lower Confervaceæ may thus be assumed to have arisen.

The differentiation of the plant body first resulted in the establishment of a basal and apical region in the unbranched filament, and, later, there arose branched forms or a flat thallus. The development of the reproductive parts parallels very closely that of the Volvocineæ, but the sexual cells in the higher types are borne in special organs, antheridia and oögonia.

The genus Coleochæte is the most specialized member of the order, and in the formation of a rudimentary spore-fruit (sporophyte) suggests a possible relationship with the lowest mosses.

The three orders—Volvocineæ, Protococcaceæ, and Confervaceæ — form, then, a continuous series leading up to the higher plants, while the other algæ are to be considered as offshoots of the main stock. Of these, the Siphoneæ have, perhaps, had a multiple origin, the simplest one being related to the lowest Volvocineæ or

Protococcaceæ, while others may have sprung from forms allied to the Confervaceæ.

The second subsidiary order of green algæ, the Conjugatæ, originated probably from unicellular forms near the bottom of the scale, and have retained a very primitive type of structure, as regards both the vegetative and reproductive parts.

In the Characeæ we encounter a very circumscribed and specialized group of plants of doubtful affinities, showing no certain relationships with any other groups of algæ, and possibly best removed from the Algæ altogether and made the type of a special sub-kingdom.

Among the brown algæ specialization has been largely in the direction of great increase in size, accompanied by a considerable degree of differentiation, both of external organs and of the tissues. The evolution of the reproductive cells has not, in all cases, followed the development of the plant body, and the larger forms, especially the giant kelps, are in this respect exceedingly primitive, producing non-sexual reproductive cells only. Within the class, however, there is a development of the sexual cells comparable to that in the principal groups of the Chlorophyceæ, but even in the highest types both egg-cells and spermatozoids are discharged into the water like the zoöspores of the lower forms.

The red algæ show a marked divergence from the Chlorophyceæ, not only in their color, but especially in the complete absence of motile cells. In most of them the spores are not formed directly from the fertilized carpogonial cell, but from certain auxiliary cells which are fertilized secondarily. This is rendered possible by the establishment of direct protoplasmic connections be-

tween the cells. Parthenogenesis is probably a not infrequent phenomenon, and marks the extreme point of divergence from the typical green algæ.

Both Phæophyceæ and Rhodophyceæ reach a far higher degree of specialization of the plant body than is ever met with among the Chlorophyceæ, but there is no evidence that either group has given rise to any higher types of plant structure than exist at present within the classes themselves, the most specialized of the existing forms representing probably the highest expression of these peculiar structural types.

The assumed relationships of the main group of Algæ may be illustrated by the following diagram : —
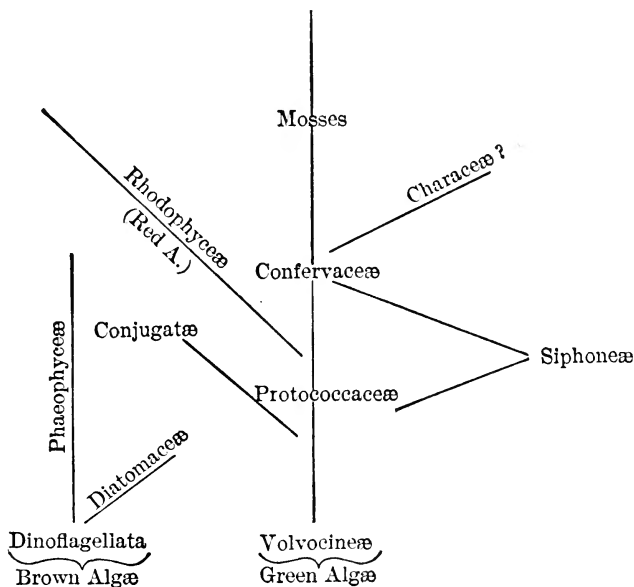
CHAPTER V

THE FUNGI

ALL of the plants considered hitherto, except the bacteria, have been characterized by the presence of chlorophyll and the accompanying power of assimilating carbon dioxide as food. While the latter property may be said to be characteristic of all typical plants, it must be remembered that there are very many plants, especially among the Thallophytes, where this power is wanting, and which are quite destitute of any trace of chlorophyll. It is usually supposed, although this is not universally admitted, that these plants are the descendants of green ancestors, and have lost their chlorophyll through the adoption of parasitic or saprophytic habits, *i.e.* feeding upon living or dead organic bodies from which they derive the carbon compounds necessary for their growth. All of these chlorophylless plants below the mosses are known as Fungi, and constitute a sub-kingdom which may be considered to have been developed parallel with the Algæ, or possibly may have been derived from them. The Fungi are very numerous, far exceeding the Algæ in number of species. Most of them are probably plants of comparatively modern origin, as very many of them are dependent as parasites upon various flowering plants, often being confined to a single species as host,[1] and presumably have

[1] Host — the animal or plant upon which a parasite lives.

acquired their specific peculiarities from this association.

The structure of these parasites and saprophytes has become so profoundly altered in consequence of their peculiar mode of life that it is exceedingly difficult to decide as to their relationship with the green plants. Naturally all trace of carbon-assimilating organs has disappeared, and the cell-structure differs much from that of the Algæ except in a small number of forms. The reproductive parts, too, as a rule are very different from those of the Algæ, and it is difficult to see any structural affinity between the majority of the Fungi and any green plants.

There are, however, a number of fungi which show unmistakable resemblances to certain algæ, and it is probable that these are really related to the latter. From this resemblance to algæ they are commonly known as the Phycomycetes, or "Alga-fungi," and are opposed to the "Mycomycetes," or True Fungi, the latter showing no certain affinity with the Algæ, although it is not impossible that they may be connected with them through the Phycomycetes. It must be said, however, that the whole question of the origin and affinities of the higher fungi is very far from being satisfactorily settled.

THE PHYCOMYCETES

This class embraces a considerable number of fungi, some of which show unmistakable resemblances to certain algæ, while the relationships of others to any green forms are by no means certain. Of the former class may be cited the water-moulds (Saprolegniaceæ) and

G

the fungi known as white-rusts and mildews. Of the latter the potato-fungus, Phytophthora infestans, the cause of the destructive "potato-rot," is one of the most familiar.

The water-moulds (Saprolegniaceæ), (Fig. 21, A, D) are aquatic fungi, either saprophytes on the dead bodies
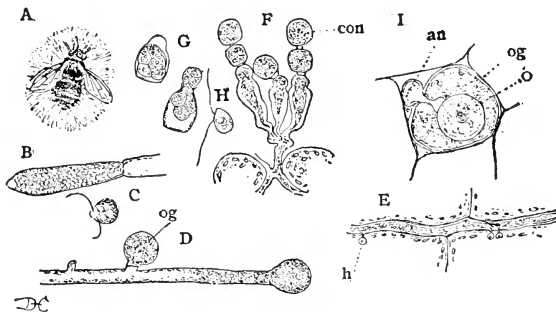
FIG. 21 (Phycomycetes).—A, a dead fly covered with a growth of water-mould (Saprolegnia) ; B, a sporangium of Saprolegnia about to open ; C, a single zoöspore ; D, part of a plant of Saprolegnia with two young oögonia, *og*; E, a filament of white-rust (*Cystopus candidus*) within the tissues of the host-plant, showing the suckers or haustoria (*h*) by which it absorbs its food from the cells of the host ; F, conidia, or non-sexual spores of Cystopus being cut off from the ends of the filaments ; G, two germinating conidia ; H, a free zoöspore which has escaped from the conidium ; I, the oögonium, *og*, with the egg, *o*, in process of fertilization by the tube sent into the oögonium from the antheridium, *an*.

of insects and crustaceans, or in a few cases, like *Saprolegnia ferax*, which is a very destructive enemy of young fish, they are true parasites. The latter species often causes great damage to young fish in hatcheries.

These water-moulds, and their immediate allies, closely resemble in general structure such siphoneous algæ as Vaucheria, being, like the latter, made up of branching filaments which show no division walls, but the proto-plasm lining the wall of the tubular filament having

numerous nuclei. In the common water-moulds the reproductive cells are also similar to those of the Siphoneæ. There are sporangia (Fig. 21, B) formed by the cutting off of the end of a filament, and the protoplasm of this sporangium then divides into a large number of biciliate zoöspores (C), which, on escaping, germinate promptly and form new plants.

The sexual organs of the water-moulds also recall those of Vaucheria, but the oögonium usually contains more than a single egg-cell, and fertilization is not effected by motile spermatozoids, but directly by a tube which is sent out from the antheridium and penetrates the wall of the oögonium. Through this tube the contents of the antheridium is transferred to the egg-cell, where by a fusion of the nuclei of the two cells, fertilization is effected. The fertilized egg thereupon secretes a thick wall and becomes transformed into a spore, as in the green algæ.

In some species of Saprolegnia the spores develop without fecundation, antheridia being entirely absent. There are some interesting intermediate conditions where the antheridium is present, but is entirely functionless. This degeneration of the reproductive organs is probably correlated with the parasitic or saprophytic habits of the plants, and is a phenomenon of frequent occurrence among the higher fungi, as we shall see, where the great majority show no trace of any sexual reproduction.

Still more like the algæ are the species of the rare genus Monoblepharis, where fertilization is effected by ciliated spermatozoids. Another remarkable genus, Myrioblepharis, recently discovered by the American

botanist Thaxter, has large multiciliate zoöspores much like those of Vaucheria.

Besides these aquatic alga-like fungi there are other Phycomycetes which are not aquatic. These may be either parasites upon the tissues of living plants, or they may be saprophytes either upon animal or vegetable substances. Of the first a good example is the so-called "white-rust" (*Cystopus candidus*) which infests the common shepherd's purse, Capsella, as well as other cruciferous plants. The masses of spores form conspicuous chalky-white blisters upon the stem, leaves, and flowers of the host, and the growth of the fungus also causes great enlargement and distortion of the parts attacked. The structure of the fungus is much like that of the related water-moulds, and it betrays its aquatic ancestry by the formation of ciliated zoöspores much like those of the water-moulds (Fig. 21, H). These zoöspores are formed when the spores germinate.

The fungus lives within the body of the host plant, occupying the intercellular spaces and sending into the cells of the host little suckers (Fig. 21, E, *h*) by means of which it feeds. Non-sexual spores are formed in rows cut off from the free ends of branches, just below the epidermis of the host. The epidermis is pushed out by the growth of these chains of spores, forming the blisters already referred to, and finally is ruptured and the spores then are shaken off as a fine white powder. Under proper conditions of temperature and moisture, the contents of these spores divide into a number of parts which escape as biciliate zoöspores. This ordinarily takes place when the leaves are wet with rain or heavy dew. Oögonia and antheridia are formed in

large numbers as the fungus grows older, but these are borne upon branches situated deep down within the host. Fertilization is effected by the formation of a fertilizing tube as in the water-moulds (Fig. 21, I). After the ripe oöspore is set free by the decay of the tissues of the host, it germinates by forming zoöspores, much as do the non-sexual spores.

There are now known a number of algæ which are more or less parasitic, and which in their manner of life suggest these parasitic Phycomycetes which may very well have originated from similar algæ. Such a parasitic alga is Phyllosiphon, which is a genuine parasite within the tissues of the leaves of a species of Arisarum, where it causes considerable damage. This plant is a most interesting example of an alga on the way to become a fungus. It still possesses some chlorophyll, but that it is a true parasite is at once shown by the injury which it inflicts upon the host. A probably analogous case among the flowering plants which possess chlorophyll is seen in such semi-parasites as the mistletoe and Gerardia.

Of the Phycomycetes which show less evident relationship to the algæ, the most familiar are the black-moulds. In these the structure of the plant is much like those already described, i.e. a branching, but undivided, tubular thallus. The reproductive parts are, however, quite different, none of the reproductive cells ever showing motion. The sexual cells, or gametes, are usually alike, and fertilization is effected by the fusion of two similar cells (Fig. 22, D), somewhat as in some of the desmids and pond-scums among the algæ. It has been suggested that possibly the black-moulds

(Mucorini) may have originated from algæ like the Conjugatæ, just as the water-moulds are supposed to

have originated from green forms resembling Vaucheria; but the structure of the thallus and the non-sexual spores of the black-moulds are so very different from those of the Conjugatæ that it seems much more likely that the similarity in the sexual cells is purely accidental.
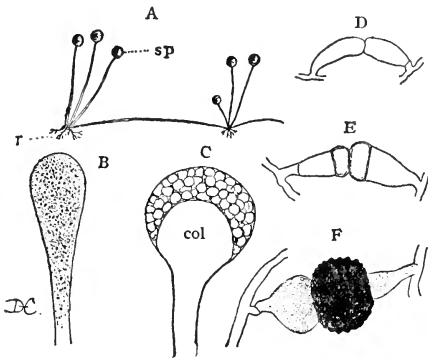
FIG. 22 (Phycomycetes).— A, a plant of a common black-mould (*Mucor stolonifer*), with groups of stalked sporangia, *sp*, arising from the creeping filament; *r*, rhizoids, or rootlets; B, young; C, mature sporangium seen in optical section, showing the columella, *col.*; D–F, successive stages in the development of the sexual spore or zygospore.

At any rate these fungi and their near relatives the insect-fungi (Entomophthoraceæ) must be regarded as much further removed from the algæ than the water-moulds and white-rusts with their ciliated zoöspores, and distinct oögonia and antheridia.

THE MYCOMYCETES

Most of the Fungi differ in structure so widely from the green plants that it is difficult to find any points of resemblance. These typical Fungi or Mycomycetes differ in nearly all respects from other plants, both in their structure and their methods of reproduction.

Some of them, it is true, show some resemblance to certain of the Phycomycetes, and may possibly have been derived from them; but most of the group are so different that any attempt to determine their origin is little more than pure conjecture.

These higher fungi are for the most part made up of filaments (hyphæ) which are divided by transverse walls formed in regular succession from the end of the filament, *i.e.* the hyphæ show a definite apical growth. The body of the fungus (mycelium) may be an indefinite tangled mass of hyphæ, or the plant, at least the spore-bearing portion, may have a definite form and firm texture owing to the compact interweaving, and often actual cohesion, of the hyphæ into a firm tissue, such as is encountered in the spore-fruits of the large fleshy fungi, like the mushrooms, puff-balls, etc. Occasionally, as in the large shelf-shaped fungi (Polyporus) and many of the so-called "black fungi," the walls of the hyphæ become hard and woody in texture.

The Mycomycetes may be either parasites or saprophytes, and occur under a very great variety of conditions. Owing to the complete absence of sexual reproduction in many of them, as well as the development of several very different types of spores, even in the same species, much confusion has arisen in the attempts to classify them, as not infrequently the same plant has received several different names based upon different stages of growth. This remarkable polymorphism has been the cause of endless mistakes in nomenclature, and at present the classification of the whole group is in a chaotic condition.

The question of sexuality in the higher fungi has

been the subject of much controversy, some investigators going so far as to deny that it exists in any members of the group. Recent investigations, however, have proved conclusively that in some of the simpler forms, at least, not only are there genuine sexual organs present, but the actual fertilization has been demonstrated beyond any question. In these forms, of course, a direct comparison can be made of the reproductive organs and the structures arising as the result of fertilization; but where sexuality has been completely lost, which appears to be the case in most of the larger forms, it is often impossible to determine positively which form of spores represents properly the product of fertilization in those forms where fertilization occurs. Especially is this the case where several sorts of spores are developed in the same plant.

Where parasitism occurs in the Mycomycetes, it often attains a degree of specialization unparalleled elsewhere in the vegetable kingdom, and recalls the behavior of certain animal parasites. This peculiarity consists in the passing from one host to another, one form of spores being produced upon one host, another upon the other. One of the first cases of this "heterœcism" to be studied was that of one of the fungi which cause the rust of wheat. It was observed that the presence of barberry bushes in the vicinity of wheat fields was accompanied by an unusual amount of rust upon the growing grain. It was finally discovered that the fungus, which in the spring formed what were popularly called "cluster-cups" upon the barberry leaves, was really only one stage of the same fungus which later, passing from the barberry to the wheat, caused the latter to rust, and

that in order for the plant to complete its life-cycle, it was necessary that it should grow in turn upon both hosts.

In the eastern United States there is another very conspicuous case of this heterœcism in the fungus causing the enlargements on the twigs of the red cedar known as "cedar-apples" (Fig. 23, A). These morbid growths are due to the attacks of a fungus (Gymnosporangium) related to the wheat-rust, and in the spring the large orange-colored masses of spores are exceedingly conspicuous, especially after a rain, when the gelatinous mass in which they are enveloped swells up. The spores in these masses (B, C) give rise on germination to secondary spores which germinate at once in case they fall upon

FIG. 23 (Æcidiomycetes). — A, a branch of red cedar attacked by a parasitic fungus (Gymnosporangium), forming the excrescence known as a "cedar-apple"; sp, masses of spores growing out from the surface of the cedar-apple; B, two spores of Gymnosporangium, one of which is beginning to germinate; pr, the young promycelium; C, a germinating spore which has given rise to a promycelium from each cell; the secondary spores, x, produced upon the promycelium do not germinate upon the cedar, but produce upon the hawthorn the so-called "æcidia," or cluster-cups; D, a leaf of cockspur thorn, with two groups of cluster-cups, ae; E, section through an æcidium of another rust (Uromyces caladii).

the young leaves of the wild crab-apple or hawthorn, but will not grow upon the cedar. The fungus pro-

duced from these spores upon the thorn (D) is abso-
lutely different in appearance from that upon the cedar,
the spores being very much smaller and produced in
chains within curious cup-shaped receptacles, much like
the barberry cluster-cups. These spores on being car-
ried back to the cedar produce upon it the form which
gives rise to the cedar-apples. This change of host in
these parasites is exactly paralleled by the life-history
of such animal parasites as Trichina and the tapeworms,
which also require more than one host for their com-
plete development.

The more familiar of the larger fungi, such as toad-
stools and puff-balls, are for the most part saprophytes,
the vegetative portion, or mycelium, being buried in
the substratum consisting of vegetable mould or earth
rich in organic matter, where it feeds and grows, and
finally sends up the spore-bearing fruit (spore-fruit,
sporophore), which is the familiar toadstool or puff-ball,
ordinarily supposed to be the whole plant.

The Mycomycetes (apart from the lichens) may be
arranged in three orders, which, however, show but
little in common. These are the Sac-fungi (Ascomyce-
tes); the Mushrooms and their allies (Basidiomycetes);
and Rusts (Æcidiomycetes).

THE ASCOMYCETES

The distinguishing mark of this order is the produc-
tion of spores in sac-shaped cells or asci, whence the
name. In the lowest of the series, such as the fungus
which causes the distortion of peach leaves known as
"curl," the spore-sacs are formed without any definite

arrangement; but in all the higher ones they are borne in definite spore-fruits of characteristic form. This spore-fruit is undoubtedly, in many instances, the result of fertilization, being produced by the formation of a peculiar cell, the archicarp, which corresponds to the oögonium of the Phycomycetes. This is usually fertilized by direct contact with the antheridium, and from it, more or less directly, are produced the spore-sacs or asci.

A good example of these simpler Ascomycetes is offered by the mildews which infest many plants, e.g. Sphærotheca, the common rose mildew. These are true parasites, but grow entirely upon the surface of the host, into whose epidermal cells are sent suckers by means of which the parasite obtains nutriment from the host. The mycelium of the fungus sends up vertical branches from which are successively cut off oval cells — spores or "conidia," — which germinate promptly and through whose means the fungus may spread rapidly.
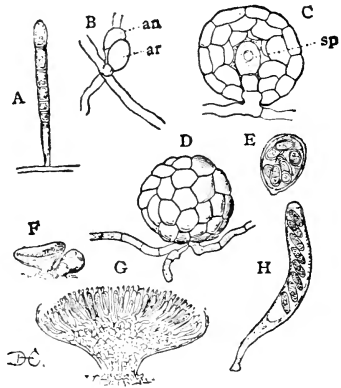
Fig. 24 (Ascomycetes). — A, a chain of conidia or non-sexual spores of a mildew (Sphærotheca), one of the simpler sac-fungi, or Ascomycetes, growing upon the leaves of the dandelion ; B, the sexual reproductive organs, archicarp, ar, and antheridium, an ; as the result of the fusion of these there is formed the spore-fruit, C, containing the single spore-sac, or ascus, sp, which is derived directly from the fertilizer archicarp ; D, the ripe spore-fruit seen from without ; E, a single spore-sac containing eight spores ; F, a cup-fungus (Ascobolus) ; G, section of the spore-fruit of Ascobolus showing the numerous spore-sacs, which are also derived from a fertilized archicarp ; H, a single ascus of Ascobolus.

The spore-fruit in these mildews is very simple, and in most cases is preceded by the formation of an archicarp and antheridium (Fig. 24, B), both of which are simple cells cut off from special branches. These organs unite, and the contents, including the nuclei, fuse, and thus a true fertilization is effected, much as in the white rust described under the Phycomycetes. In the simplest of the mildews the fertilized archicarp divides into a few cells, one of which grows directly into an oval sac in which, after a preliminary division of the nucleus into eight, there is formed about each of these nuclei an aggregation of protoplasm which becomes surrounded by a cell-wall and forms a spore. There are still simpler Ascomycetes where the fertilized archicarp becomes at once transformed into the ascus. From the filaments close to the archicarp there grow out a number of short branches which form a compact covering about the asci, the whole structure forming the " perithecium " or spore-fruit of the mildew. In many of the mildews the cells forming the wall of the perithecium develop hair-like appendages of curious and characteristic shapes, which constitute one of the best means of distinguishing the different genera and species.

Closely related to the mildews is the common blue-mould, Penicillium, and the herbarium-mould, Eurotium. These are saprophytes, and the spores are borne on branching conidiophores instead of in simple chains.

The spore-fruit of some of the larger Ascomycetes is very conspicuous, and in the case of the pretty cup-fungi of various vivid colors, scarlet, orange, yellow, etc. These large spore-fruits are usually the product of a number of archicarps, *i.e.* they are compound in nature,

but in many cases they seem to arise in a purely vegetative way without any formation of sexual organs.

Many of the Ascomycetes show remarkable polymorphism, this being especially marked in the "Black-fungi" or Pyrenomycetes, of which the ergot of the rye and the "black knot" of cherries and plums are examples. In these there are, in addition to the ascospores, several different forms of conidia cut off from the tips of the hyphæ.

THE BASIDIOMYCETES

The Basidiomycetes include most of the more familiar large fungi, known popularly as mushrooms, toadstools, puff-balls, etc. These fungi have no very evident affinity with the sac-fungi, and as yet none of them have shown any traces of sexual reproduction. The great majority are saprophytes, the mycelium or vegetative filaments ramifying extensively through the substratum, which usually is earth rich in decaying vegetation, rotten wood, or similar dead organic matter. From this mycelium the spore-fruit arises, apparently in all cases as a purely vegetative growth. Most Basidiomycetes produce but one kind of spores, borne upon club-shaped cells known as basidia (Fig. 25, E), and it is still an open question whether the spore-fruit in these can properly be compared to that of the Ascomycetes.

The basidia are swollen, club-shaped cells, borne at the end of hyphæ, and from each basidium grow out several, usually two or four, little protuberances, each of which produces a single spore at the tip. These basidia are usually formed upon special parts of the

spore-fruit, which may have a definite character, as in the mushroom, where the "gills" (Fig. 25, A, *g*) are of this nature. The spores on germination form a new mycelium, which in time produces spore-fruits.
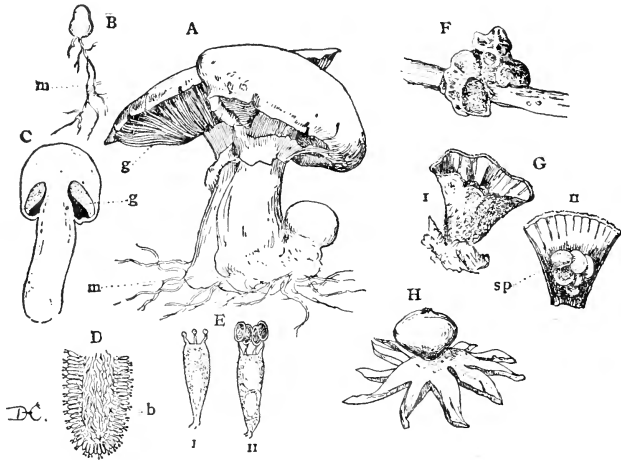
FIG. 25 (Basidiomycetes). — A, a cluster of spore-fruits of the common mushroom, arising non-sexually from the mycelium, *m*, which is buried in the ground; B, a very young mushroom; C, a section of an older one showing the gills, *g*, upon which the spores are borne; D, diagram showing a section of a gill with the spore-bearing "basidia," *b*, covering its surface; E, I, young, II, mature basidium of a toadstool (Coprinus), showing the spores borne at the summit; F, spore-fruit of Tremella, one of the lower Basidiomycetes; the spores cover the whole surface of the irregular spore-fruit; G, a bird's-nest fungus (Cyathus): the spores are borne inside the "sporangia," *sp*, within the cup; H, earth-star (Geaster), one of the Gasteromycetes allied to the puff-balls. (Figs. A, B, after Warming; C, after Atkinson.)

The lowest of the Basidiomycetes show analogies with the rusts (Æcidiomycetes), and do not have the basidia restricted to any definite part of the spore-fruit, but they may be produced all over it, as in the soft gelatinous Tremella (Fig. 25, F), whose convoluted soft yellow or orange masses are not uncommon on

rotten twigs or stumps. In all of the higher ones, however, the "hymenium" or spore-bearing areas are restricted to definite portions of the spore-fruit.

In the highest group of all, represented by the puff-balls (Lycoperdon) and their allies, the spores are borne within the spore-fruit, and are only exposed when they are perfectly ripe.

THE ÆCIDIOMYCETES

Under the name of Æcidiomycetes are included the parasitic fungi, known popularly as "rusts" and "smuts," which are among the most destructive of plant parasites. The various forms of wheat-rust, and the corn-smut, are familiar examples of this class. Both of these orders show certain analogies with the lower Basidiomycetes, and are possibly related to them. As in the latter, no trace of sexual organs has yet been discovered. Unlike the Basidiomycetes they often show a remarkable tendency to polymorphism, which reaches its most marked development in the rusts, where, as we have seen, in the wheat-rust and cedar-rust, it is complicated by the habit of heterœcism, or the passing from one host to another in the course of development. Owing to the absence of sexual organs, the same difficulty is experienced here as in the Basidiomycetes, of deciding which form corresponds to the spore-fruit in the Ascomycetes when this is developed as the result of fertilization.

While some of the rusts resemble the lower Basidiomycetes, the smuts show certain analogies with the Phycomycetes, but it is doubtful if the latter resem-

blances indicate any real relationship, and it is quite as likely that they are signs of degeneration, the most marked resemblance being the absence of division walls in the hyphæ. On the whole, the smuts seem to be really much more nearly related to the rusts.

We have finally to consider, among the Fungi, the peculiar organisms, the yeast-plants, which are the principal agents in alcoholic fermentation. They are unicellular forms, the individual cells being oval in shape and multiplying rapidly by the peculiar mode of cell-division known as budding. They may also, under special conditions, develop a number of spores by internal division. The structure of the cells is extremely simple, and the presence of a definite nucleus is still open to question.

The relation of the yeast-fungi to the other members of the group is still a matter of controversy. Some authorities consider them to be very low organisms, having some affinity with the bacteria; others, on the strength of their forming spores internally, somewhat like the Ascomycetes, regard them as the lowest members of this group; still others have thought that they represent a permanent conidial stage of forms related to the smuts, as in the latter the spores under certain conditions may bud much as do the yeast-cells: that is, the yeast-cells are supposed to be spores arrested in their development so that they never form filaments or hyphæ. Which of these hypotheses is the correct one, must at present be left unanswered.

THE LICHENS

In connection with the true Fungi there must be considered the Lichens. While there is no doubt that these are sufficiently distinct to form a separate class, nevertheless their obvious relationship to other fungi, mostly Ascomycetes, forbids the establishment of a subkingdom coördinate with Algæ and Fungi.

These curious organisms exhibit a remarkable type of parasitism, or perhaps better, symbiosis, where two plants, an alga and a fungus, are so intimately associated as practically to form a single plant. An examination of the thallus of a lichen shows it to be made up of densely woven and more or less coherent hyphæ, among which are found numerous green cells. The latter are usually aggregated near the outside of the thallus, and a careful examination shows them to be certain low algæ, which can be readily identified as species often growing quite apart from the lichen. If these algæ are isolated, and given proper conditions for growth, they flourish perfectly, showing that they are not, in any true sense of the word, really dependent upon the lichen for their existence. While in some respects the hyphæ of most lichens differ somewhat from those of other fungi, still the general structure is very similar, and the fructification corresponds exactly with that of typical fungi, especially the Ascomycetes, to which most lichens are undoubtedly related. A few, however, are Basidiomycetes.

It was supposed by the earlier students of the lichens that the green cells were direct outgrowths of the colorless hyphæ, but the more careful investigations of later

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years have proved conclusively that the lichen thallus is a compound organism, consisting usually of an ascomycetous fungus parasitic upon an alga. While the alga probably derives some benefit from this association with the fungus, and by the shelter afforded by the fungus can probably grow where otherwise it could not, still the advantage is much more on the side of the fungus, which without the alga is incapable of growth and soon perishes. Through this peculiar form of parasitism the fungi have become decidedly altered, so that they differ very considerably from any other Ascomycetes; but the algæ are identical, even to the species, with forms which live quite free from the lichen. The germinating spores of a lichen produce a mass of colorless filaments, like those of other fungi, and if these come in contact with the proper algal form, they will attach themselves, and in time the fully developed lichen thallus is produced. If, however, no algal cells are within reach, the mycelium soon dies unless supplied artificially with carbonaceous food.

The lichens, no doubt, represent a very specialized group of plants, but they cannot properly be separated from the Fungi, as they are so obviously related to them, and it is the fungus element of the lichen which is the predominant one. Moreover, not all the lichens are related among themselves, as it is perfectly evident that this peculiar form of parasitism has arisen quite independently in different groups of the Ascomycetes, as well as in the Basidiomycetes. The algal elements found in lichens belong also to a number of widely separated groups, e.g. Protococcaceæ, Cyanophyceæ, Confervaceæ.

Summary

The Fungi as a whole must be considered as having but slight affinities with the green plants. While the Phycomycetes or Alga-fungi show undoubted resemblances to certain green algæ, especially the Siphoneæ, even here there are marked differences, although not so great but that a possible derivation of the former from green ancestors is conceivable. The Phycomycetes are not, however, to be considered as a homogeneous class, but rather as an assemblage of chlorophylless plants derived independently from diverse green ancestors, in much the same way that various colorless parasites and saprophytes among the flowering plants have arisen independently.

While the question of the origin of the Phycomycetes is fairly clear, this is by no means the case with the much more numerous and varied Mycomycetes, or true Fungi. It is true that there are certain points of similarity between the lower Ascomycetes and the Phycomycetes, and the smuts also recall in some respects the latter; but it is by no means universally admitted that such a connection does really exist, and the origin of the Mycomycetes must for the present be considered as at least doubtful.[1]

Moreover, the interrelationships of the Mycomycetes are very obscure. The complete lack of sexuality in so many of them makes a determination of the homologies in their structure exceedingly difficult; and as

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[1] One very peculiar family of Ascomycetes, the Laboulbeniaceæ, which are parasites in insects, show many analogies with the red algæ, and may possibly have been derived from them.

the groups now exist, the three classes, Ascomycetes, Æcidiomycetes, and Basidiomycetes, have very little in common, although it is probable that the two latter have had a common origin.

The Lichens must be supposed to have had a multiple origin, like the Phycomycetes. The majority have been derived from different groups of ascomycetous fungi, but some of them are allied to the Basidiomycetes.

We may then consider the Fungi as an aberrant group of plants, probably — but not certainly — derived from originally green ancestors, but which have diverged so widely from the parent stock that they have lost nearly all of their original characteristics.

CHAPTER VI

MOSSES AND LIVERWORTS (*BRYOPHYTA*)

The Fungi form, as we have seen, an aberrant assemblage of plants, probably derived from green ancestors, but not giving rise to any higher forms. In seeking for the point of connection between the higher green plants and the Thallophytes, we must look then to the Algæ, and the forms among these which show the most evident relationship with the lower terrestrial green plants are the Green Algæ, or Chlorophyceæ.

While the Algæ are practically all aquatics, the plants we are now to consider are for the most part terrestrial. The lowest of these are the Bryophytes or Mosses, using this term in its broadest sense. These are readily divisible into two classes, the Liverworts, or Hepaticæ, and the true Mosses, Musci. Of these the former show the most evident resemblances to the Algæ, and will be considered first.

These plants are usually moisture-loving forms, a few being actually aquatic, but many of them are so constituted that they may be completely dried up without injury, quickly reviving when supplied with moisture.

The lowest liverworts (Fig. 27, A, C) are little flat green plants of very simple structure, and may be readily compared to some of the green algæ, such as Coleochæte. However, when the reproductive parts

are examined, it is seen that even the lowest mosses
are far more complicated than any of these algæ.

The zoöspores, or motile non-sexual reproductive cells
of the algæ, are wanting completely in the mosses, but
among the lowest liverworts there have been discovered
certain cells which perhaps represent them.   In these
forms the contents of an ordinary thallus cell are
ejected in the form of a unicellular or two-celled body
very much like the zoöspores of many algæ, but desti-
tute of cilia.   The method of development of these
bodies suggests that in them we have the last trace of
zoöspore formation, the absence of cilia being corre-
lated with the terrestrial habit of the liverworts.   Spe-
cial non-sexual reproductive bodies (buds or gemmæ)
of an entirely different kind are not uncommon in
many of the higher forms, both among the Hepaticæ
and the true mosses.

The lower Hepaticæ are of especial importance in a
study of the origin of the higher plants, as there is good
reason to believe that they represent the most primitive
of existing chlorophyll-bearing terrestrial plants, and
probably have given rise to all the higher types of
vegetation.

The liverworts, in common with the other mosses and
the ferns, have the egg-cell borne in a peculiar organ, of
very uniform structure in all of them, known as the
archegonium (Fig. 26, A, B) ; and on account of this
uniformity of structure, mosses and ferns together are
often united into one great division, the Archegoniatæ.
The archegonium usually has the form of a long-
necked flask in whose enlarged base, or venter, is found
the egg-cell.   The nearest approach to this structure

among the algæ is found in the stoneworts (Characeæ), but the differences in the vegetative parts between these and the Hepaticæ are too great to admit of the idea of any but the remotest relationship existing between the two, and at present it must be admitted that the gulf between Algæ and Archegoniates is a very deep one.

FIG. 26. — A, longitudinal section of the archegonium of a liverwort (Targionia), showing the central row of cells; B, a similar section of the ripe archegonium of Riccia: the cells of the axial row are disorganized and the egg, o, lies free in the enlarged venter of the archegonium; C, longitudinal section of the antheridium of Riccia, showing the mass of sperm-cells surrounded by a single layer of peripheral cells; D, a free spermatozoid of *Fimbriaria Californica*.

The antheridium is not so different from that of some algæ, but is much more complicated than in any but the Characeæ. In the Archegoniates it has the form of a capsule (Fig. 26, C), which in the lower forms is usually stalked. The central part is divided into many small cells, in each of which is developed a spermatozoid. The latter is very much like those of most algæ, and like them is provided with cilia (Fig. 26, D).

Throughout the whole group of the Archegoniates water is necessary for the opening of both archegonium and antheridium, the water swelling up the mucilaginous cell-walls of the interior of the organs, thus forcing them open. The liberated spermatozoids then swim to the open archegonium, which in the mean time has dis-

charged the disintegrated cells of the canal traversing the neck, and thus cleared the passage to the egg-cell within the venter. The spermatozoids enter the open archegonium and make their way to the central cell, where one of them penetrates the egg-cell, thus effecting its fertilization.

The necessity of water for the effecting of fertilization is significant, as it would seem to be a reversion to the aquatic condition of the algal ancestors of the Archegoniates.

ALTERNATION OF GENERATIONS

The alternation of sexual and non-sexual individuals is met with in many algæ, but there is usually little difference in the structure of the two, aside from the reproductive organs. Thus in Œdogonium, or Vaucheria, there is no apparent difference between the plants which produce zoöspores and those which bear the sexual cells; and sometimes, at least, the formation of one sort of reproductive cells or the other is entirely a question of nutrition.

In the higher Chlorophyceæ, and this is suggested in Œdogonium, it will be remembered that the spore produced as the result of fertilization does not at once grow into a plant like the parent, but there is first a division of its contents into four zoöspores which give rise to as many new individuals. In Coleochæte (see Fig. 10), the genus which on the whole approaches most nearly to the lower Archegoniatæ, the germinating resting-spore produces a multicellular body, from each of whose cells a zoöspore is produced which then develops into the new plant.

In the Archegoniates the structure arising from the fertilized egg is much more complicated than in any of the algæ. Here, also, the egg after fertilization secretes a cell-wall about itself, but instead of remaining at rest for a long time, growth begins almost at once. The plant thus formed is entirely different from the one which produces the sexual organs, and the reproductive cells to which it gives rise differ entirely from those of the sexual plant. These cells are purely non-sexual in character and capable of germinating at once. They are spores which differ from the corresponding ones of the green algæ in being destitute of cilia and provided with a very firm membrane which enables them to resist extremes of temperature and dryness.

The spores in all the Archegoniates are formed in groups of four from the division of a common mother-cell. The tissue from which the sporogenous cells arise is termed the "archesporium." These spores on germination give rise, not to another spore-bearing plant, but to the sexual one. This alternation of sexual and non-sexual individuals is a constant characteristic of the Archegoniates, and the two phases are known respectively as the gametophyte (sexual) and sporophyte (non-sexual), — convenient terms which will be adopted in the future discussion of the group.

Among the lower Archegoniates, as in the algæ, it is the gametophyte which is predominant and the sporophyte is small and inconspicuous, looking like a mere appendage of the gametophyte; but as we ascend, we shall see how the gametophyte becomes more and more subordinated to the sporophyte, which finally becomes an independent long-lived plant, while the gametophyte

simply lives long enough to produce the sexual organs and to nourish the embryo-sporophyte until it becomes self-supporting.

THE LIVERWORTS (*Hepaticæ*)

Like the Confervaceæ among the green algæ, the Liverworts seem to represent a low generalized assemblage of plants showing affinities with several other groups, and, indeed, they probably represent the ancestral forms from which have arisen all the higher plants. While the lower Hepaticæ are but little more complicated than some of the Confervaceæ, others show a considerable degree of differentiation of the gametophyte. The latter, in the simplest cases (Fig. 27, A, C), is a small flat body or thallus composed of almost uniform green cells, the whole fastened to the ground by numerous delicate hairs or rhizoids.
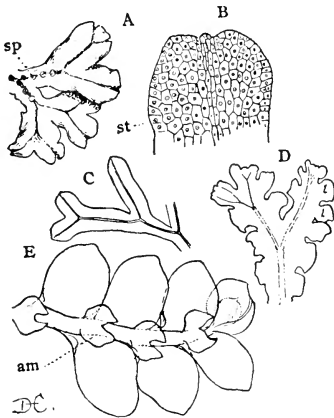
FIG. 27 (Hepaticæ). — A, B, C, thallose liverworts; A, Riccia, *sp*, the very small sporophyte; B, Conocephalus, *st*, stomata; C, Metzgeria; D, Blasia, a liverwort which shows the first formation of leaf-like organs, *l*; E, Lejeunia, a foliose liverwort with definite stem and three rows of leaves, large dorsal ones, and small ventral ones, *am*.

This thallus grows by the divisions of a definite apical cell, which differs in different genera, or even in different species of the same genus.

Starting from this simple type, the development of the gametophyte has proceeded in several directions, two of which are specially noteworthy. In the first place, while the gametophyte has retained its primitive thallose form, there has been a very considerable amount of differentiation in the tissues, which are divided into a dorsal region, mainly occupied by an elaborate system of assimilating tissues, and a ventral mass of colorless cells. The assimilative apparatus in the most highly specialized forms consists of a series of large chambers into which the chlorophyll-bearing cells project, which communicate with the outside atmosphere by means of curious pores which may be compared functionally at least with the stomata of the higher plants (Fig. 27, B). The rhizoids are also peculiarly modified, and scales are developed from the ventral surface of the thallus. In the higher members of this group (Marchantiaceæ), the sexual organs are borne upon modified branches, and in some cases peculiar non-sexual reproductive bodies, gemmæ, are produced in special receptacles.

The second type of differentiation is shown by the foliose or leafy Hepaticæ, the "scale-mosses." These comprise much the greater part of the existing liverworts, and are distinguished from the lower forms by having a distinct axis with definite leaves or assimilative organs (Fig. 27, E). Both stem and leaves are of the simplest possible structure, all the cells being alike, and the leaves are composed of but a single layer of cells, but these simple leaves form very efficient assimilating organs. The scale-mosses are much the commonest of liverworts, and their adaptation to various

conditions, as well as their abundance and variety, indicate a more modern type than the thallose forms with which they are connected by various intermediate conditions (Fig. 27, D).

Some of the foliose Hepaticæ, especially certain tropical types, show extremely curious modifications of the leaves to form reservoirs of moisture or even traps for small Crustacea, recalling those found in some flowering plants, such as the bladder-weed (Utricularia).

The range of structure in the sporophyte of the Hepaticæ is great, and a study of the different types is most instructive in showing the growing importance of the sporophyte in passing from the lower forms to those which approximate the structure of the higher plants.

The simplest sporophyte is met with in the genus Riccia (Fig. 27, A, Fig. 28, B), which comprises a number of small thallose liverworts, where there is no trace of any differentiation of the gametophyte into stem and leaves; but the thallus is not so primitive as in certain other forms which have a more highly developed sporophyte. The sexual organs are borne upon the dorsal surface of the gametophyte, but not arranged in any definite order. They have the typical structure found in other Hepaticæ. The archegonium (Fig. 26, B) contains the egg in the enlarged ventral portion, and when the plants are covered with water, it opens and allows the spermatozoids, which have at the same time been liberated from the ripe antheridium, to swim into it. The spermatozoid penetrates the egg-cell, which thereupon is stimulated into active growth, and develops into the sporophyte, or sporogonium, as it is commonly termed in the mosses. The development of

the sporophyte in Riccia is very simple, recalling that of Coleochæte (Fig. 10, C) among the algæ, and there is no difficulty in understanding how a sporophyte of the type of that in Riccia may have originated from that of Coleochæte.
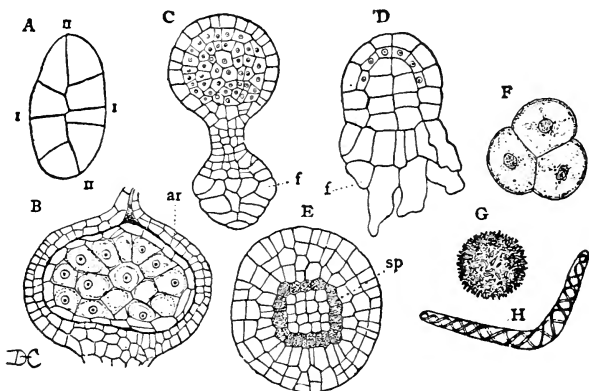
FIG. 28 (Development of the sporophyte in Hepaticæ). — A, young embryo-sporophyte of Targionia ; I, II, the first division walls in the fertilized egg ; B, longitudinal section of the young sporophyte of Riccia, included within the archegonium, *ar* ; all of the cells, except a single peripheral layer, produce spores ; C, longitudinal section of the young sporophyte of Sphærocarpus ; only the upper part produces spores, the lower half forming an organ of absorption, the foot, *f* ; D, a similar section of the embryo of Anthoceros ; the nucleated cells represent the archesporium or sporogenous tissue ; E, cross-section of an older sporophyte of Anthoceros, showing the small amount of sporogenous tissue, *sp* ; F, section through a spore-tetrad of *Fossombronia longiseta* ; only three of the four spores show ; G, a ripe spore of the same species ; H, an elater.

The first result of fertilization is the formation of a cellulose membrane about the egg, which thus is transformed into a spore directly comparable to the resting-spore of such an alga as Œdogonium. Here, however, instead of remaining at rest for a long period, it germinates at once. It first divides by a transverse wall

into equal parts, and this is followed by two other walls at right angles to the first, and the globular "embryo," as it is now called, is composed of eight nearly equal cells. Soon there are formed a series of walls by which a single layer of peripheral cells is separated from the central mass of tissue (Fig. 28, B), and the cells of the latter, after several preliminary divisions, separate, and each one divides into four equal parts or spores. This division is preceded by a double division of the cell-nucleus, and it is not until the four nuclei are complete that the division-walls arise between them, by which the sporogenous cell is divided into the four tetrahedral spores. These are at first thin walled (F), but later develop a thick membrane (G), and the spore as it ripens becomes filled with oil and other nutritive substances. The mature sporophyte in Riccia is simply a globular capsule, completely filled with a mass of thick-walled spores. No assimilative tissue is developed by the sporophyte, and it is entirely dependent for its subsistence upon the gametophyte. The venter of the archegonium continues to grow with the enclosed sporophyte, and forms a protective covering about it, much as do the enveloping cells in Coleochæte, although in the latter the protective cells are entirely undeveloped before fertilization.

The mass of spores remains enclosed within the archegonium-venter ("calyptra") until they are liberated by its decay, as the older parts of the thallus die. After a period of rest, these spores germinate if they are supplied with the proper conditions of light, heat, and moisture. The spores give rise, not to a sporophyte, but to a gametophyte, and it is interesting to

note that in its earlier stages it is much simpler than the mature gametophyte, but closely resembles the fully developed thallus of certain Hepaticæ whose sporophyte is much more highly developed than that of Riccia.

In all the other liverworts the sporophyte shows a certain amount of vegetative tissue, only a portion being devoted to the formation of spores. The first step in this separation of sporogenous and sterile tissue is the division of the fertilized egg into two cells by a transverse wall, the upper part developing into the spore-bearing portion or "capsule," the lower giving rise to an organ of absorption, the "foot" (Fig. 28, C, f), and usually an intermediate region, which forms a stalk or pedicel which elongates at maturity, and causes the sporophyte to rupture the archegonium-venter, and thus facilitates the scattering of the spores. In most of the Hepaticæ the vegetative tissue develops but little chlorophyll, and the growth of the sporophyte is mainly at the expense of the gametophyte, from which, by means of the foot, it absorbs nourishment very much as a parasitic fungus does from its host. In all of the Hepaticæ, except Riccia and one or two closely related genera, only a part of the sporogenous tissue or archesporium produces perfect spores. The others either remain undeveloped and serve to nourish the growing spores produced from the other cells, or more commonly they remain undivided and form peculiar cells known as "elaters." These elongate and develop upon the inner face of the cell-wall thickened spiral bands which, when fully developed, are strongly hygroscopic, and by their movements, induced by changes in moisture after the

capsule is ripe, help to distribute the spores (Fig. 28, H).

In contrast to the simple sporophyte of the lower liverworts, there is found in one group a sporophyte which reaches a high degree of complexity, and becomes almost independent of the gametophyte. This reaches its highest expression in the genus Anthoceros (Fig. 28, D, Fig. 31, C). Here the gametophyte is very primitive and consists of a simple thallus composed of almost perfectly uniform cells, and without any differentiation into stem and leaves. Indeed, it represents almost the lowest type of the gametophyte among the Hepaticæ. A suggestion of an origin of this type of thallus from the Algæ is seen in the single chloroplast in each cell, much like that in Coleochæte. The sexual organs of Anthoceros, while on the whole like those of the other liverworts, are peculiar in being sunk in the thallus, and recall, in this respect, those of the more primitive ferns.

It is the sporophyte, however, which is of the greatest interest. This reaches a relatively large size (Fig. 31, C, *sp*) and shows a considerable degree of independent growth. Between the large foot and the upper portion is a zone of growing tissue, which enables the sporophyte to grow in length as long as the gametophyte remains active, and from this growing zone new tissue is constantly added to the base of the sporophyte. The latter has its outer parts developed into a perfect assimilating tissue with several layers of spongy green tissue whose air-spaces communicate with the outside atmosphere by means of stomata or pores in the epidermis, precisely like those found upon the leaves of the higher plants.

The spores arise from a single subepidermal layer
of cells (Fig. 28, D), which later becomes deeper
seated through the further division of the superficial
cells (E). Within the sporogenous layer, or arche-
sporium, is a central cylinder of sterile cells forming
the "columella," which both in origin and position
seems to represent the axial vascular bundle or strand
of conducting cells found in the young sporophyte of
the ferns, and it is not impossible that it may also serve
as a conducting tissue, thus representing a primitive
vascular bundle physiologically as well as structurally.
Owing to the absence of a root connecting the sporo-
phyte with the earth, it remains dependent upon the
gametophyte for its supply of water and also for cer-
tain food elements, and if the gametophyte perishes, the
sporophyte necessarily soon dies as the supply of water
is cut off. Otherwise, owing to the perfect assimilative
system, it is quite independent, and if a root were pres-
ent would be entirely so.

THE TRUE MOSSES (*Musci*)

The second class of the Bryophytes, while greatly
outnumbering the liverworts, shows very much less
range of structure and is evidently a much more spe-
cialized group. These "True Mosses," with few ex-
ceptions, show an almost stereotyped plan of structure,
the differences between them being mostly of minor
importance. There are a few, however, notably the
peat-mosses (Sphagnaceæ), which show affinities with
the liverworts, especially with Anthoceros.

The gametophyte of the Musci usually exhibits two

phases, the protonema and gametophore. The spore on germination produces a filamentous, or occasionally flat, alga-like growth, the protonema (Fig. 29, A, B, C, *pr*), and upon this arise special buds or branches which grow into leafy stems, the gametophores (Fig. 29, A, B, C, *k*), which bear the sexual organs. The leaves of the gametophoric branches are commonly arranged spirally, and the branches seldom are flattened as in the foliose Hepaticæ. While there are certain superficial resemblances between the leafy stems of the mosses and foliose liverworts, there are differences which make it extremely improbable that the former have been derived from the latter. The two forms are rather to be considered as parallel developments. In the Musci the structure of both leaves and stem is as a rule much more complex than in the Hepaticæ, and there is usually present a central strand of conducting tissue, quite wanting in both stem and leaf in the latter group.

FIG. 29 (Musci or True Mosses). — A, the liverwort-like protonema of a peat-moss (Sphagnum) with the leafy shoot, *k*, budding out from it; B, the filamentous protonema, *pr*, of a common moss (Funaria), with a very young leafy bud, *k*; C, an older stage of the same moss; D, the full-grown leafy gametophore, *g*, with the sporophyte, *sp*, still connected with it; *ar*, the remains of the archegonium carried up by the growth of the sporophyte.

The mosses which approach most nearly to the Hepaticæ are undoubtedly the species of Sphagnum, the common peat-mosses. In these the protonema arising from the germinating spore is a flat thallus, very much like a simple liverwort in appearance (Fig. 29, A). From the margin of this, secondary protonemal branches arise which are filamentous and closely resembling those of the higher Musci.

If, as seems probable, the Musci have arisen from the Hepaticæ, Sphagnum probably represents an intermediate form, and the flat, liverwort-like protonema must be considered to be more primitive than the filamentous type which has been derived secondarily from it. The suppression of the flat thalloid stage is probably correlated with the development of the leafy gametophoric branches, which become more and more important.

The sporophyte in Sphagnum is, in its early stages, remarkably like that of Anthoceros, especially in the origin of the archesporium. Like Anthoceros the sporophyte possesses a well-developed assimilative system of green tissue with numerous stomata, which are not always, however, functional.

The gametophyte of Sphagnum, in spite of its large size, shows a simpler structure than that of the typical mosses, the central strand of tissue being absent from the stem, and the leaves being destitute of a midrib. There are a few forms intermediate, to some extent, between Sphagnum and the typical mosses ; but a very large majority of the Musci belong to a single order, the Bryineæ. While these show great diversity in their habits, their essential structure is remarkably uniform.

They occur in almost all situations except in salt water and actual deserts, some being submersed aquatics, others growing upon the ground, or upon rocks and trees, and indeed in any situation where they can occasionally obtain moisture. Many of them may be completely dried up for an indefinite period without losing their vitality.

In the growth of the stem and leaves, as well as in the structure of the reproductive organs, the gametophyte is very uniform. Both leaves and stem show a definite apical growth, and the leaves are, with few exceptions, arranged spirally about the stem. The sexual organs are in the main like those of the Hepaticæ, but show a definite apical growth in both archegonium and antheridium.

The sporophyte is highly specialized and shows a certain degree of independence in the development of a well-marked assimilative system of tissues, as in Anthoceros and Sphagnum. It differs in its growth from that of the liverworts in the presence of a definite single apical cell, to whose regular divisions the early growth of the embryo is due. Later this apical growth is replaced by a basal growth much as in Anthoceros.

The young sporophyte is a cylindrical body which later develops an enlarged upper portion, the capsule or theca, borne upon a long stalk, or seta (Fig. 29, D, *sp*). The latter is usually traversed by a strand of conducting tissue, possibly homologous with the columella in the sporophyte of Anthoceros, or the vascular bundles in the young fern-sporophyte.

The assimilative tissue in the sporophyte of the higher Musci is very perfect. The basal part of the capsule

(Fig. 30, A, *a*) is composed mainly of a spongy green tissue which is also present in the upper part of the capsule, surrounding the large air-spaces between the sporogenous tissue and the outer part of the capsule. This green tissue recalls the "mesophyll" or spongy green tissue in the leaves of the higher plants, and like the mesophyll communicates with the outside atmosphere by stomata. In a few cases, this basal part of the capsule (apophysis) is a very much enlarged special organ, comparable physiologically, although hardly structurally, with the leaves of higher plants.
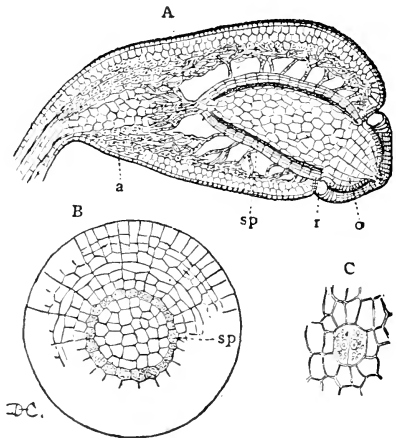
Fig. 30 (Musci). — A, a longitudinal section through the upper part of the sporophyte of Funaria; *a*, the apophysis or enlarged basal part of the capsule, containing chlorophyll and with stomata in the epidermis; *sp*, the sporogenous tissue; *o*, the operculum, or lid, which finally falls away and allows the escape of the spores; *r*, the ring of cells where the lid *o* separates from the urn, or theca; B, cross-section of a young capsule, showing the position of the sporogenous cells; C, a young stoma or breathing pore from the base of the capsule. The structure of the stoma is like that found upon the leaves of the higher plants.

The formation of spores is restricted to a very small part of the sporophyte, the sporogenous tissue comprising but a single layer of cells forming a cylinder in the middle region of the capsule, and surrounding the central columella (B, *sp*). The upper part of the capsule usually

becomes detached as a little lid (operculum), and the detachment of this is aided by the formation of an elaborate system of tooth-like structures (peristome) about the mouth of the capsule. These teeth are extremely hygroscopic, and by their movements they not only help to throw off the operculum, but also to empty the capsule and disperse the spores, which, when ripe, lie loosely in the capsule, owing to the drying up and withering of the delicate interior tissues.

SUMMARY

While there is little question that the Bryophytes have arisen from forms similar to certain green algæ, it must be admitted that so far as existing forms are concerned the relationship is at best a remote one. It is true a direct comparison can be made between the sporophyte in Coleochæte, for example, and that of Riccia, and the change from the motile zoöspores of the one to the spores of the other can be explained by the abandonment of the aquatic habit by the Bryophytes. The gametophyte, itself, offers no serious difficulties, retaining in Anthoceros, for instance, apparently the single chloroplast in each cell found in so many algæ, e.g. Coleochæte, and the structure of the thallus is hardly more complex than in these; but when an attempt is made to compare the sexual reproductive organs it must be admitted, especially as regards the archegonium, that the difference between the two groups is a very great one. The nearest approach in this respect is found in the Characeæ, which otherwise differ profoundly from the Mosses, and so far as our

knowledge goes at present, the gulf between Algæ and Archegoniates is a deep one.

The dependence of all Archegoniates upon water for fertilization, and especially the presence of ciliated spermatozoids, are strong arguments for the derivation of the group from aquatic ancestors, but at present this is about all that can positively be asserted.

Among the Archegoniates themselves, the relationships are much more obvious. Undoubtedly the lowest forms are the Hepaticæ, shown both by comparison with the algæ and with the other Archegoniates, and probably these are to be considered as the primitive forms from which the others have sprung.

Among the Hepaticæ, the lower Jungermanniaceæ, such as Metzgeria (Fig. 27, C), seem, on the whole, to be the simplest, although the sporophyte even in the lowest ones is more perfect than in Riccia, which has the lowest type of sporophyte found among the Archegoniates. Assuming that the lower thallose Jungermanniaceæ are the most primitive of Hepatics, we have seen that, from this type, several others have been developed. In one line (Marchantiaceæ) differentiation has resulted in the specialization of tissues, the plant retaining its primitive thallose form (Fig. 27, A, B). In the leafy liverworts, the tissues have remained very simple and the differentiation has been purely external, resulting in a definite axis or stem bearing three rows of leaves (Fig. 27, D, E). A third line of development has given rise to the complex leafy gametophyte of the true mosses.

In the simpler Hepaticæ the sporophyte is small and exclusively devoted to spore-production, *e.g.* Riccia.

In the higher types it becomes more and more independent through the development of green assimilative tissues. This reaches its highest expression in Anthoceros and the Musci.

The latter group is probably the most modern and specialized one. This is indicated both by the greater number of species and their wider distribution, as well as by a much more stereotyped structure. These have probably arisen from liverworts resembling Anthoceros, and it is not likely that they have given rise to any higher forms, but represent the end of their own special line of development.

In the evolution of the sporophyte there has been little external differentiation, the most highly specialized forms being found in the Musci, where the sporophyte shows a foot seta and capsule; but there are no leaves or other appendicular organs, although the peculiar apophysis found in a few mosses perhaps approaches this condition.

In Anthoceros, although the external differentiation is very slight, there is one respect in which it stands alone, *i.e.* the unlimited growth of the sporophyte. This, in connection with the highly developed assimilative tissue, makes the sporophyte of this plant the nearest approach to the entirely independent sporophyte of the ferns. Were the foot of the sporophyte in Anthoceros prolonged into a root penetrating the earth, it would become quite independent of the gametophyte, and were a special assimilate organ or leaf developed, a condition directly comparable to the sporophyte of the lower Pteridophytes or ferns would result. It is prob-

able that the origin of the latter is to be looked for among Hepaticæ, which like Anthoceros had a very simple gametophyte, and a large, nearly self-supporting sporophyte with a relatively small amount of sporogenous tissue.

CHAPTER VII

THE FERNS (*PTERIDOPHYTA*)

THE Pteridophytes or Ferns, using the latter term in its widest sense, include those plants sometimes known as the Vascular Cryptogams, which while evidently related to the mosses differ from them in the very much more highly developed sporophyte, which here becomes an independent plant. Indeed, it is the sporophyte or non-sexual generation of the ferns which is the plant as it is ordinarily understood, the gametophyte being usually small and inconspicuous and of short duration.

It will be remembered that in considering the Bryophytes great differences were noted in the relative development of gametophyte and sporophyte; that while in Riccia, for example, the sporophyte is nothing more than a capsule filled with spores, in Anthoceros the spore-formation is subordinated to a considerable extent, and there is developed a well-marked assimilative issue, consisting of green cells with large intercellular spaces, and stomata communicating with the outside as in the vascular plants. Moreover, this sporophyte is not limited in its growth, but continues to elongate as long as the gametophyte remains alive. Owing to the absence of a root, however, the sporophyte still remains dependent upon the gametophyte for water, and to some extent for food also; but the well-developed

green tissue enables it to utilize the carbon dioxide of the atmosphere.

It is not a long step from such a sporophyte as that of Anthoceros to that of the lower Pteridophytes. In the latter, owing to the early development of a root in the sporophyte, the latter soon becomes quite independent of the gametophyte, which is generally short lived, although occasionally it reaches a considerable size and may live for several years, especially where the sporophyte fails to develop (Fig. 31, A).

The sporophyte in even the lowest Pteridophytes exhibits a complexity far exceeding that of the highest moss. This is especially

FIG. 31.—A, gametophyte of a fern (Marattia), showing a forking of the growing point, and the development of secondary buds, k ; B, gametophyte of the same fern, with the young sporophyte, sp, attached : C, a liverwort, Anthoceros, with several sporophytes, sp, attached to the gametophyte, g. The sporophyte is capable of long-continued growth, but does not develop a root, and hence never becomes entirely independent.

the case in regard to the external differentiation. While in all Bryophytes there is very little development of special external members in the sporophyte, in ferns there are very early developed several characteristic external organs, viz., stem, leaf, and root. The foot, or absorbent organ of the embryo, is much like the corresponding organ in the moss-embryo.

Corresponding to this development of external mem-

bers, the tissues of the sporophyte show a much greater
degree of complexity than is found in any of the plants
below the ferns.   This is especially seen in the develop-
ment of the so-called " vascular bundles," which are met
with for the first time in their fully developed con-
dition in the sporophyte of the ferns.   These tissues
are, however, hinted at in the sporophytes of some of
the mosses.   Thus the central strand of tissue in the
seta of the moss-sporogonium, and the columella in
Anthoceros, both in origin and appearance, suggest the
young vascular bundles in the organs of the young
fern-embryo, and may probably be fairly considered
as the homologues of these.

It is in the ferns, however, that we first encounter
the peculiar tracheary tissue characteristic of the woody
portions of the bundles in the vascular plants.   This
tracheary tissue is made up of empty cells with woody
walls, and is a very important element in the conduc-
tion of water in the vascular plants.   These empty cells
are known as tracheids, but occasionally in the ferns
there are encountered true vessels, or rows of tracheids
whose partition walls have been absorbed.   In the ordi-
nary ferns the woody tissue or " xylem " is surrounded
by a mass of " phloëm " or " bast," containing as its
most characteristic element the sieve-tubes, similar in
appearance to the tracheary tissue of the xylem, but
without lignified walls and containing living proto-
plasm.   The vascular bundles form a complicated system
of strands in the stem of the sporophyte, and with these
are connected the bundles traversing the roots and
leaves.

A well-marked epidermal tissue is always present,

especially well developed upon the leaves, where it is furnished with stomata communicating with the green tissue of the leaf, and also is often provided with hairs and scales of characteristic form. The remaining tissue, usually known as the "ground-tissue," shows a much greater diversity of structure than is met with in any of the lower plants, and closely approaches in this respect the higher flowering plants.

While in the mosses the existence of the sporophyte usually ends with the dispersal of the spores, in the ferns spore-formation is subordinated to the vegetative existence of the sporophyte. The spores themselves, instead of arising from a large, continuous archesporium, are here restricted to certain definite structures of the sporophyte called sporangia (Figs. 34, 35). A faint indication of this segregation of the sporogenous tissue is seen in the Anthocerotaceæ, among the liverworts, where there is an imperfect separation of small sporogenous areas by means of sterile tissue between them.

In the ferns, as a rule, the development of spores usually takes place only after the sporophyte has reached an advanced stage of development, and this is often not accomplished for many years in some of the large ferns, although in a few cases the sporophyte lives but a single season.

A study of the development of an individual case illustrates very clearly the homologies which exist between ferns and the lower mosses. It is well known to botanists that the germinating fern-spore does not at once produce the leafy sporophyte, but there is first formed a much simpler plant, the gametophyte (Fig. 32). On first germinating, the unicellular spore usually pro-

duces a slender filament or cell-row, much like the sim-
pler green algæ. This condition soon gives place to a
delicate flat thallus, closely resembling some of the
simpler liver-
worts. At this
stage growth is
effected by a
single apical cell
(Fig. 32, B, x)
precisely as in
such simple liv-
erworts as An-
eura. The degree
of development
of this thalloid
g a m e t o p h y t e
varies much in
different ferns,
but it may reach
a length of sev-
eral centimetres,
branching ex-
tensively, and
living for sev-
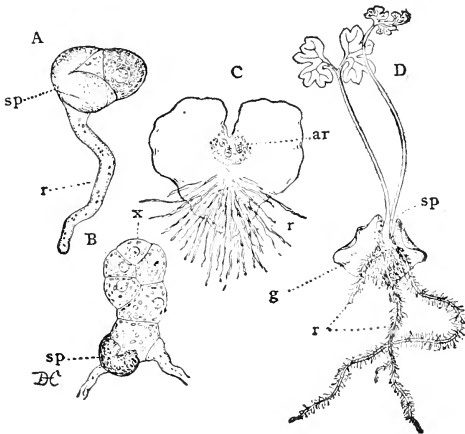
FIG. 32. — A, the germinating spore of the ostrich
fern (*Onoclea struthiopteris*), showing the rup-
tured spore-coat, *sp*, and the first rhizoid, *r*; B,
a somewhat older plant (gametophyte) with a
single apical cell, *x*; C, female gametophyte
seen from below, showing the archegonia, *ar*;
D, young sporophyte, *sp*, still attached to the
gametophyte, *g*; the sporophyte has developed
leaves and roots, *r*, so that it is quite inde-
pendent of the gametophyte.

eral years, especially when the archegonia remain unfer-
tilized (Fig. 31, A). The largest of these "prothallia"
occur in certain tropical ferns, especially species of
filmy-ferns (Hymenophyllaceæ) and Vittaria. In the
latter genus they sometimes have numerous branches,
radiating from a common centre and forming circular
disks ten centimetres or more in diameter, and closely
resemble a large liverwort. These large gametophytes

are usually sterile, and seem to be the result of excessive vegetative activity. They not infrequently multiply by means of special buds, or gemmæ, by which the number of the gametophytes may be rapidly increased exactly as in the liverworts.

In some species of Trichomanes (Fig. 35, E), a genus of the filmy-ferns, the gametophyte may have the form of an extensively branched filament, closely resembling an alga; and it has been suggested that this may be the primitive type of the gametophyte. However, as many closely allied species produce the usual flat thallus, and all of the forms, when exposed to excessive moisture, show a tendency to assume a filamentous stage, it is quite as likely that this is an adaptation to a moist environment, rather than being the primary condition.

Another group of ferns, the so-called Eusporangiatæ, which includes the adder-tongue (Ophioglossum) (Fig. 34, A) and its allies, as well as certain interesting tropical forms, the Marattiaceæ (Figs. 31, 34), show a long-lived gametophyte of a somewhat different type. In all of these, so far as they are known, the gametophyte is massive and quite different from the thin, delicate thallus of the filmy-ferns and Vittaria, but like these the gametophyte may live for a long time, often for several years, and not infrequently remains alive long after the young sporophyte is quite independent. The gametophyte in the Marattiaceæ, especially (Fig. 32, A, B), is extraordinarily like a simple thallose liverwort, both as regards the thallus itself and the sexual organs developed upon it. In the adder-tongues the gametophyte, so far as at present known, is subterranean and quite destitute of chlorophyll; but whether this is originally

the case remains to be seen, as the earliest stages are
very imperfectly known.

The Horse-tails (Equisetineæ) (Fig. 36) and the
Club-mosses (Lycopodineæ) (Figs. 37, 38), while differ-
ing in some minor details, agree closely in the main with
the eusporangiate ferns in the characters of the gameto-
phyte.

Upon this thalloid gametophyte are borne the repro-
ductive organs, antheridia and archegonia, structurally
very much like those of the Bryophytes, especially the
liverworts, which with little question are the nearest
relatives of Pteridophytes among the lower plants. The
resemblances are especially marked in the Anthocero-
taceæ, which are also the nearest approach to the ferns
in the structure of the sporophyte.

Within the antheridium are produced motile sperma-
tozoids, which, in the true ferns, have many cilia (Fig.
33, C) instead of the two possessed by the moss-sperma-
tozoid, and these require the presence of water in order
that they may reach the egg-cell in the open arche-
gonium ; and water is also necessary, as in the Bryo-
phytes, for the opening of the ripe reproductive organs.

We have already indicated in a preceding chapter
that the motile spermatozoids of the algæ are to be con-
sidered as modifications of originally non-sexual zoö-
spores, which in turn are a reversion to the originally
free-swimming ancestral type from which all the green
plants originated. The recurrence of these ciliated re-
productive cells in the Pteridophytes is a strong argu-
ment in favor of considering these plants as being also
derived from originally aquatic ancestors. Fertilization
is effected in these as in the mosses, and the gameto-

phyte may be described as amphibious, inasmuch as it must become aquatic, so to speak, in order that fertilization may be effected.

The spermatozoid, attracted by the substance ejected from the open archegonium, swims to it and makes its way through the canal in the neck to the central cavity, where it quickly penetrates the egg-cell and slowly fuses with its nucleus, after undergoing a series of changes. As a result of fertilization the egg begins to grow, having in the mean time secreted a wall about itself, and thus forms what may be called a spore,

FIG. 33. — A, the open archegonium of the ostrich-fern, showing the egg-cell, *o*, within the venter; B, the antheridium of the same species; C, a free spermatozoid, showing the numerous cilia; D, the fertilized archegonium containing the young embryo sporophyte; E, the archegonium of a liverwort, Riccia, with the young sporophyte, showing the close resemblance between the ferns and mosses in regard to the young sporophyte; F, longitudinal section of an older embryo of the ostrich fern, showing the division into stem, *st*; leaf, L; root, R; and foot, F.

comparable to the resting-spore of such green algæ as Œdogonium, or to the fertilized egg-cell in the moss archegonium. Like the latter it germinates at once instead of passing through a long dormant period, as in most green algæ.

The early divisions in the young embryo, developed

K

from the egg, agree exactly with those in the liverwort-embryo, and the great similarity in the structure of the young sporophyte in Bryophytes and Pteridophytes (Fig. 33, D, E) is one of the strongest evidences of the intimate relationship of the two great divisions of the Archegoniatæ. The young embryo consists at first of four nearly equal cells, arranged like the quadrants of a sphere, and in the lower ferns the young sporophyte retains this globular or oval form for a considerable time, and closely resembles the corresponding stages in certain low liverworts, *e.g.* Riccia. In the common ferns, however, there very early appears a marked deviation from the type found in the mosses. This is the indication of external members, absent in the embryo of the latter. Usually each of the four original quadrants of the young embryo becomes the starting-point for a special organ, and soon these are evident as the rudiments of the primary leaf or cotyledon, the stem or axis of the young sporophyte, the primary root, and the foot (Fig. 33, F). Each of these organs in the more specialized ferns shows a definite apical cell, and this apical growth in each of the members soon causes the young sporophyte to assume the character of an independent plant, the young fern, in short. The root elongates rapidly and soon fastens the young sporophyte to the earth, and as soon as the primary leaf is expanded, the little fern is quite independent of the gametophyte with which it is still connected by means of the foot, through which it is nourished until its own primary members are fully developed (Fig. 32, D).

In the more generalized and lower ferns, the sporophyte retains much longer its undifferentiated character,

and is dependent upon the gametophyte for a long period — indeed in some of these the gametophyte remains alive for months, or even years, after the sporophyte has become quite capable of self-support.

It is the development in the sporophyte of these external members — stem, leaf, and root — which at once distinguishes the fern from the moss, and it is the presence of these which enables the sporophyte to become independent of the gametophyte, which soon perishes. It must be remembered, however, that the young sporophyte in the ferns is also dependent for a longer or shorter period upon the gametophyte, just as is the case permanently in the mosses, and the cases known among the former, where the existence of the gametophyte does not necessarily end when the sporophyte has become independent, recalls at once the normal condition of things among the Bryophytes.

Of the original quadrants into which the fern-embryo divides, one, as we have seen, becomes the apex of the future stem, and this cell may retain its identity, persisting as the apical cell of the axis of the plant. Thus in the gigantic tree-ferns, the single initial cell at the apex of the stem is the direct descendant of one of the four primary cells into which the embryo was first divided. The growth of all of the other original members of the embryo is limited, the cotyledon and primary root very soon dying and giving place to others.

The size which the sporophyte finally reaches varies extremely. Thus in some of the tiny filmy-ferns (Fig. 35, C) the delicate stem is hardly thicker than a hair, and the fully developed leaves less than a centimetre in length; on the other hand, some of the giant tree-

ferns may have an erect stem ten or fifteen metres in
height, with leaves five or six metres long. These gi-
gantic sporophytes offer a strong contrast to the insig-
nificant sporophyte of the mosses, and corresponding to
this is the late appearance of the sporogenous tissue,
which may not be formed until after many years. This
extreme subordination of the sporogenous tissue is a
wide departure from the condition existing in such low
liverworts as Riccia, where practically the whole sporo-
phyte is composed of sporogenous cells.

In all of the Pteridophytes the sporogenous tissue is
restricted to certain definite areas, these being confined
to more or less distinct organs, sporangia. The latter
are possibly foreshadowed by the imperfect segregation
of the sporogenous tissue in the Anthocerotaceæ, the
highest of the liverworts. Among the ferns, the forms
which approach nearest the condition existing in the
Anthocerotaceæ are the species of Ophioglossum or
adder-tongues, where the limits of the sporangia are
scarcely indicated at all upon the surface (Fig. 34,
A, B, C). In these ferns the sporogenous tissue occurs
in masses of considerable size, but is not clearly sepa-
rated from the surrounding tissue. The archesporial
cells are separated from the epidermis of the leaf
(sporophyll) by several layers of cells, and the spores
finally escape through a cleft which opens at the sur-
face of the sporophyll. The archesporium is at first
of sub-epidermal origin, as in Anthoceros, the latter
being in this particular more like the ferns than like
the typical mosses, where the sporogenous cells are
originally derived from the central part of the sporo-
phyte. Even in Anthoceros, however, the separate

groups of sporogenous cells are much less definite than in Ophioglossum, and do not have a separate opening for each; still it is quite conceivable that the simple

sporangia of Ophioglossum may have originated from structures not unlike the groups of sporogenous cells found in the Anthocerotaceæ.

In the ferns, as in the mosses, each sporogenous cell gives rise to four spores, which develop in an absolutely similar way, and offer another striking proof of the close relationships of the two groups.

If we admit that Ophioglossum shows the most primitive type of sporangium among the ferns, we may say that passing from this type to that found in the most specialized ferns, the so-called "Leptosporangiatæ," we

Fig. 34 (Eusporangiate Ferns). — A, sporophyte of an adder-tongue fern (*Ophioglossum vulgatum*); *sp*, the sporangial spike; B, longitudinal section of the sporangial spike of another species (*O. pendulum*), showing the cavities containing the spores; C, cross-section of the sporangial spike of *O. pendulum*; D, separate sporangia of Botrychium; E, leaflet of Marattia, showing the synangia, or coherent sporangia; F, a single synangium cut to show the separate sporangial cavities; G, Angiopteris, one of the Marattiaceæ with nearly separate sporangia, *sp*.

encounter an almost perfect series of intermediate forms leading up to the exceedingly specialized sporangium of the latter, and this series may be assumed to represent the evolution of the sporangium of the leptosporangiate ferns from the simpler type found in

Ophioglossum.   This specialization consists in a more
definite limitation of the sporangium, and the restric-
tion of the primary sporogenous tissue or archesporium
to a single cell (Fig. 35, E, F).   The genus Botry-
chium, which is obviously related to Ophioglossum,
has, within its limits, species which illustrate the
change from a large indefinite sessile sporangium much
like that of Ophioglossum, *e.g. B. simplex*, to the
much smaller obviously stalked sporangium found in
such large species as *B. Virginianum* (Fig. 34, D).
This evolution of the sporangium is accompanied by a
growing complexity in the divisions of the leaf, as well
as correlated modifications of the tissues of the sporo-
phyte, which approximate the structures of the typical
Leptosporangiatæ.   Another group of ferns, intermedi-
ate in some respects between the lower (Eusporangiatæ)
and the leptosporangiate ferns, are the Osmundaceæ,
including the royal fern *Osmunda regalis*, and in east-
ern America the common cinnamon-fern, *O. cinna-
momea*.   In these the sporangia and the tissues,
especially the vascular bundles, show undoubted re-
semblances to the Eusporangiatæ, although, on the
whole, they are nearer the leptosporangiate type.

In the latter the sporangia can be traced back to a
single epidermal cell, the early divisions of which are
extremely regular, and result in the formation of a
single central archesporial cell surrounded by a single
layer of outer cells.   The so-called "tapetal cells"
(Fig. 35, F, *t*) are cut off from the archesporium, but
are later broken down, so that at maturity the wall of
the sporangium consists of a single layer of cells.   A
constant character of these ferns is the formation of

the "annulus," a row of cells with thickened walls whose contraction plays an important part in the opening of the ripe sporangium and the discharge of the spores (Fig. 35, G, H, *r*).

On comparing the Eusporangiatæ and Leptosporangiatæ, one is at once struck by the great disparity in the numbers of the two groups. Probably all living species of Eusporangiatæ, including the peculiar genus Isoëtes, whose position here is by no means certain, scarcely exceed one hundred, while the Leptosporangiates, the typical ferns, number probably at least 3500 to 4000 species. In

Fig. 35 (Leptosporangiate Ferns).— A, leaflet of a shield-fern (Aspidium), showing the sori, or sporangial groups, *s*; B, a single sorus covered with the kidney-shaped indusium, *in*; C, a filmy-fern (Trichomanes) with the sorus surrounded by a trumpet-shaped indusium; D, longitudinal section of the sorus, showing the sporangia borne upon the elongated columella; E, F, young sporangia of *Polypodium falcatum* seen in section; the sporogenous cell is shaded; *t, t*, the tapetal cells which later are broken down; G, a ripe sporangium of the same species showing the ring or annulus, *r*, and the stomium, *st*, where the opening occurs; H, sporangium of a climbing fern (Lygodium) with terminal annulus, *r*.

spite of this extraordinary difference in numbers of species, the former group shows much greater range of structure, so much so that it is necessary to make two and perhaps three orders to include them, and the relationships of these are very doubtful. The Lepto-

sporangiates, in spite of their numbers, might all be included in a single order, Filices, were it not for a small number of the heterosporous forms, *i.e.*, those having two kinds of spores, which are, however, evidently related to the Filices. A study of the different orders of the Eusporangiatæ indicates that we have to do with remnants of once much larger groups, of which most of the members have become extinct. The much greater homogeneity of the Leptosporangiatæ, as well as their numbers, indicate on the other hand a specialized and presumably more modern type of vegetation, and this is borne out by a study of their distribution.

None of the Eusporangiatæ ever occur in any great numbers together, although some of them are cosmopolitan. One order, the Marattiaceæ, are strictly tropical plants, and usually occur as isolated individuals or in small groups. Among the Leptosporangiates, on the other hand, the plants are often gregarious, and form conspicuous features of the vegetation. The common brake, *Pteris aquilina*, and in the tropics, species of Gleichenia, form tangled thickets and cover extensive tracts almost to the exclusion of other vegetation. If we analyze the fern-flora of those tropical regions where ferns form an important feature of the vegetation, the disproportion in numbers between the eusporangiate and leptosporangiate species is even greater than in temperate regions. Thus in Jamaica, which is exceptionally rich in ferns, out of about five hundred species described from the island, less than a dozen are eusporangiate, and of these none are common enough to make any impression upon the general character of the vegetation, although an occasional gigantic Marattia

attracts the attention of the botanist. The Leptosporangiates, on the other hand, occur everywhere in the most astonishing profusion and variety, often constituting the most conspicuous feature of the flora of certain districts, especially in the higher mountains.

The conclusion is irresistible that in the Leptosporangiatæ we have to do with a comparatively modern type of plants, eminently adapted to existing conditions and competing successfully with the highly specialized flowering plants. The small number, both of species and individuals, among the Eusporangiates points to the opposite condition in their case. They show every evidence of plants that are being worsted in the struggle for existence by their more specialized competitors.

A study of the anatomy of the sporophyte as well as the gametophyte confirms this view. We find that the gametophyte in the Eusporangiates approaches that of the liverworts much more closely both in its structure and long duration, and the reproductive organs are much more like the liverwort type than are those of the leptosporangiate ferns. The embryo also remains much longer connected with the gametophyte, and the differentiation of its members does not take place until a later period. Finally, the sporophyte has simpler tissues, and the sporangium is of a less specialized type, approximating the conditions found in the highest liverworts. In short, the theory of the Eusporangiatæ being primitive and presumably an older type than the Leptosporangiatæ is borne out by every detail of their structure.

That the Leptosporangiates have been derived from the Eusporangiates is indicated by the number of

transitional forms, like Osmunda, which connect perfectly the two groups. We should naturally expect that the most specialized forms, *i.e.* those which have diverged most widely from the primitive stock, would be the prevailing forms at the present time, and such really is the case. The Polypodiaceæ, which include all the commoner ferns and are with little question the most specialized of the ferns, far outnumber all the other families combined, and are preëminently the modern type.

It is interesting to note that the conclusions reached by a study of comparative morphology are confirmed by the geological record. The oldest ferns known are beyond question Eusporangiates, all of the ferns found in the Carboniferous and pre-Carboniferous rocks probably being of this character, while undoubted Leptosporangiates first appear in the Mesozoic formations, from which time they appear to have increased in number and variety, gradually replacing the eusporangiate ferns of the earlier formations. There is no evidence that the Leptosporangiates have ever been any more abundant than at the present time, and they are probably to be considered as a distinctly modern type.

CHAPTER VIII

PTERIDOPHYTA — *Concluded*

BESIDE the true ferns there are two other classes of existing Pteridophytes, — the Equisetineæ (horsetails, scouring-rushes) and the Lycopodineæ or club-mosses.

The former, while showing certain points of resemblance to the ferns, still differ so widely from them that they are properly included in a separate class. All the known living forms belong to a single genus, Equisetum, which comprises about twenty-five species, mostly belonging to the northern hemisphere, and especially well represented in the United States. The peculiar sporophyte (Fig. 36, A), with its jointed, grooved stems, and sporiferous cones, is familiar to every botanist.

The gametophyte is less generally known and shows many points of resemblance to that of the ferns, especially the Eusporangiatæ. The green spores germinate promptly if sown as soon as they ripen, but soon lose their power of germination. After about a month the male gametophyte is mature, the female plant requiring a somewhat longer time. In its earlier stages the gametophyte is much like that of the common ferns, but is more irregular in shape, developing more or less definite lobes, which are especially conspicuous in the female plant. The growth of the latter is a good deal like that of the gametophyte of Marattia or Osmunda,

except for the conspicuous lobes referred to above.
The reproductive organs are very much like those of
the eusporangiate ferns, and the spermatozoids, which
are large and multiciliate, closely resemble those of
Osmunda.
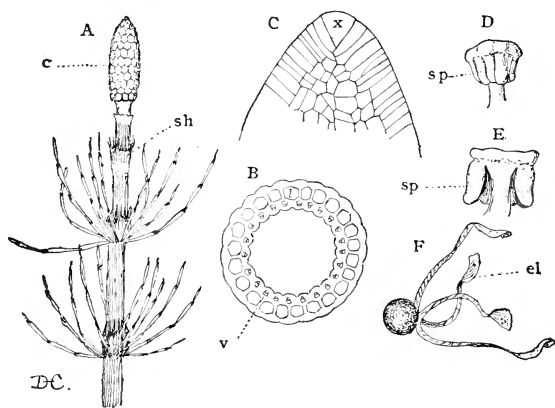
FIG. 36 (Equisetineæ). — A. upper part of a sporiferous shoot of a horse-
tail (*Equisetum pratense*), showing the division into nodes and inter-
nodes, the rudimentary sheath-leaves, *sh*, and the strobilus or cone of
sporophylls, *c*; B, a cross-section of an internode of *E. maximum*,
showing the arrangement of the vascular bundles, *v*, and the air-spaces,
or lacunæ, *l*; C, longitudinal section of the apex of a young shoot of *E.
maximum*, showing the single large apical cell, *x*; D, a single sporophyll
of the same species with the sac-shaped sporangia, *sp*; E, median sec-
tion of the sporophyll; F, a ripe spore, with the elaters, *el*.

The sporophyte, however, shows many points of dif-
ference which are early manifest.   Thus, in the embryo,
it is the stem-quadrant which grows most actively,
while the development of the leaves is subordinated to
it, as it is throughout the life of the sporophyte.   In-
stead of the short stem and large leaves of the ferns,
the stem in Equisetum is very much elongated, while the
leaves are reduced to the toothed sheaths which sur-

round the nodes or joints of the stem. These reduced leaves are practically useless as assimilative organs, and their office is assumed by the internodes of the stem and branches, where the green tissue is largely developed, and connected with the outside by numerous stomata in the epidermis. The leaves serve as protective organs only, forming a thick covering over the apex of the young shoot, and also covering the buds from which spring the lateral branches.

In studying the development of the tissues of the sporophyte, one is struck by the almost mathematical regularity in the divisions of the cells at the stem-apex, as well as in the roots. The shoot in all species terminates in a single apical cell (Fig. 36, C), having the form of an inverted three-sided pyramid from whose lateral faces segments are cut off in regular succession, and the tissues of the mature stem bear a definite relation to the early divisions in these segments. A similar regularity exists in the early divisions of the cells at the apex of the root. The stem is traversed by a regular system of lacunæ, or air-passages (Fig. 36, B, *l*), and the vascular bundles are arranged in a circle, recalling the arrangement in the stem of the typical Dicotyledons. In the arrangement of the woody tissue and bast, they recall the flowering plants rather than the ferns, although among the latter the Ophioglossaceæ show a somewhat similar type of vascular bundle, — the "collateral" form, — and also other structural resemblances.

The sporangia of Equisetum occur upon peculiar umbrella-shaped sporophylls which are arranged in whorls about the apex of certain shoots, and crowded together so

as to form a cone or strobilus. In their development, the sporangia are much like those of the eusporangiate ferns, but in their method of opening they are more like the sporangia (anthers) of the flowering plants. The early stages in the development of the spores follow the regular type found in all Archegoniates, but the ripe spore is very peculiar, being provided with curious appendages (elaters), formed by a splitting of the outer membrane (Fig. 36, F).

The existing species of Equisetum differ a good deal in size, varying from small forms not more than ten to twenty centimetres in height, to the giant of the genus, *E. giganteum* of tropical America, which may reach a height of ten metres, with a stem diameter of two or three centimetres. In spite of these differences in size they all agree closely in the structure of the sporophyte.

While all the living members of the class can be placed in a single genus, it is different with the numerous fossil forms which are known. Especially during the Carboniferous epoch was there a rich development of this peculiar group of plants, which formed a conspicuous feature in the vegetation, where they were represented by numerous genera and species. The modern genus Equisetum probably extends back to the coal-measures, where it was associated with numerous extinct types which reached a far greater size and complexity. The largest of the fossil Equisetineæ were the species of Calamites, which attained tree-like dimensions and whose remains show evidences of a secondary thickening of the vascular bundles of the stem, like that in the trunks of existing trees. It is interesting that a trace of this

peculiarity has been recently detected in one of the living species of Equisetum.

Associated with some of the fossil forms there are found cones, which evidently belong with them, and resemble those of the existing Equisetum. In a few instances they have been preserved so perfectly that the inner structure can be accurately made out, and it is evident that the tissues and sporangia of these plants closely resembled those of Equisetum, although most of them exhibit a degree of specialization not found in any of their living relatives. The Equisetineæ rapidly diminish in importance in the later geological epochs, until, as we have seen, but a single genus has survived to the present time, and this is one of the less specialized types.

Fig. 37 (Lycopodineæ). — **A**, part of a plant of a club-moss (*Lycopodium clava-tum*) with two sporangial spikes, *sp*: **B**, a sporophyll from the spike of *L. den-droideum*, bearing a single large sporangium. *sp*: **C**, cross-section of the stem; *vb*, the central vascular cylinder.

LYCOPODINEÆ

The third class of Pteridophytes, the Club-mosses, is intermediate in point of numbers between the two already considered. There are three well-marked orders, of which the first, Lycopodiaceæ, includes the common club-mosses belonging to the genus Lycopodium. The second order, Selaginel-

laceæ, or smaller club-mosses, is closely related to the Lycopodiaceæ, and includes a single genus Selaginella, with several hundred species, mostly tropical (these are common in greenhouses, where they are usually mis-named "Lycopodium"). The third order, Psilotaceæ, includes two peculiar tropical genera, Psilotum and Tmesipteris, evidently closely related genera, but doubt-fully associated with the other Lycopods, and possibly more nearly allied to certain extinct Pteridophytes.

The gametophyte is at present known only in Lyco-podium and Selaginella, and until its character in the other genera is known, it will be impossible to assign them their proper place in the system. In Lycopodium the gametophyte varies greatly in different species, in some being a green lobed thallus somewhat like the gametophyte in Equisetum, while in others it is desti-tute of chlorophyll, at least in its older stages, and is apparently truly saprophytic in its habits. The earliest stages of these colorless gametophytes are not known, and it is possible that they may at first possess chloro-phyll. The sexual organs are much like those of Equi-setum and the eusporangiate ferns, but the spermatozoids have only two cilia, as in the Bryophytes.

The embryo in the club-mosses differs from that of the other Pteridophytes in being derived from one only of the two cells resulting from the first transverse division of the egg-cell. The other cell forms a structure known as the suspensor (Fig. 38, G, *sus*), which is much like the similar organ found in the embryo of most flowering plants. The embryo in Lycopodium remains for a long time dependent upon the gametophyte, and may develop several leaves before the first root is formed.

In Selaginella (Fig. 38), while the embryo closely resembles that of Lycopodium, the gametophyte is very different. The sporophyte produces two sorts of spores, large and small. The former, the macrospores, produce a rudimentary gametophyte, which bears only archegonia (Fig. 38, E). The gametophyte projects from the spore but little, and until its later stages is contained entirely within the macrospore. In germination there are first
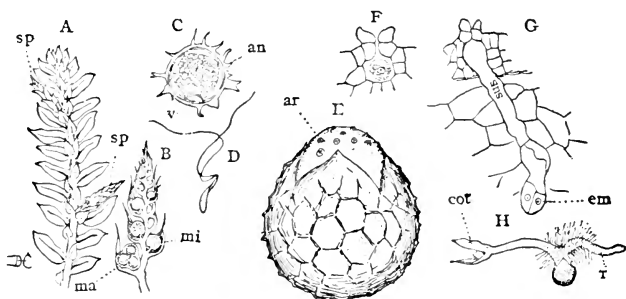
FIG. 38 (Lycopodineæ). — A, a branch of one of the smaller club-mosses (Selaginella) with two sporangial spikes, *sp*; B, longitudinal section of spike showing a single macrosporangium, *ma*, and several microsporangia, *mi*; C, germinated microspore containing the rudimentary male gametophyte; *v*, the single vegetative cell; *an*, the antheridium; D, a spermatozoid (after Belajeff); E, germinating macrospore with the female gametophyte protruding; *ar*, archegonia; F, a single archegonium; G, a young embryo, *em*, attached to the suspensor, *sus*, whose base remains within the archegonium; H, young sporophyte, still attached to the gametophyte within the macrospore; *cot*, cotyledons; *r*, root.

produced within the spore numerous free nuclei, between which, later, cell-walls arise, forming a continuous tissue much as in the "embryo-sac" of the flowering plants. The formation of the gametophyte begins in Selaginella before the spores are set free from the sporangium. The small spores or microspores produce an even more rudimentary gametophyte (C), which is

reduced to a single vegetative cell, and a single anthe-
ridium in which are developed biciliate spermatozoids
like those of Lycopodium (D).

In both Lycopodium and Selaginella, the stem of the
sporophyte is long and extensively branched, while the
leaves are small and moss-like. The tissues, especially
the vascular bundles, are not unlike those of the ferns.
Sometimes the stem and root grow from a single apical
cell, sometimes a group of initial cells is present, but
even when there is a single apical cell, it never shows the
almost mathematical regularity in its divisions found in
the leptosporangiate ferns or in Equisetum.

The sporangia in both Lycopodium and Selaginella
are borne singly, either upon the inner face of the
leaves, or upon the axis just above a leaf. They are
kidney-shaped capsules, which open by a longitudinal
cleft (Fig. 37, B). The sporophylls are usually
crowded together into a cone or strobilus, somewhat
as in Equisetum. In Lycopodium all the sporangia are
alike, but in Selaginella the oldest one (or ones), at the
base of the cone, matures but four spores (macrospores),
which are very much larger than the numerous micro-
spores produced in the upper sporangia (Fig. 38, B).
The development of the two kinds of spores is the same
up to the point where each mother-cell divides into the
four spores. In the microsporangia all the spores de-
velop, but in the macrosporangium only one tetrad comes
to maturity, the others serving simply as food for the
developing macrospores. These begin to germinate
within the sporangium, and besides using up the other
spore-tetrads as food, are nourished from the sporophyte
through the cells of the sporangium-wall, which re-

main alive and active up to the time the spores are ripe.

A third genus, Phylloglossum, allied to Lycopodium, includes a single species from Australia, and is apparently a very primitive type, as it resembles closely the embryonic condition of some species of Lycopodium. Unfortunately, all attempts to germinate the spores have failed, and the gametophyte is entirely unknown.

The order Psilotaceæ, which is commonly associated with the club-mosses, includes two tropical genera, Psilotum and Tmesipteris. They are usually epiphytes, *i.e.* grow upon the trunks and branches of trees, and Tmesipteris shows some evidences of being partially parasitic. The sporangia are large and all alike, but as yet nothing is known of the nature of the gametophyte produced from them, so that it is impossible to compare it with that of the other Pteridophytes, and at present the systematic position of these curious plants must be regarded as doubtful.

Like the Equisetineæ, the club-mosses were once much more abundant than at present, and many of them far exceeded in size and complexity any of the existing species. Members of this class probably existed as far back as the upper Devonian, and in the Carboniferous rocks they form one of the most conspicuous features of the fossil flora. The most striking forms are the species of Sigillaria and Lepidodendron, which reached tree-like dimensions and showed a secondary thickening of the stems like that of the living coniferous trees. Many of these fossil Lycopods are preserved in an extraordinarily perfect manner, so that the histological details are perfectly recognizable and can readily

be compared with those of existing species. Occasionally even the spore-bearing parts have been well preserved, and it is evident that Lepidodendron and its allies were structurally much like the living genera Lycopodium and Selaginella. Especially does Lepidodendron resemble the latter in the character of the spores, which are of two kinds, macrospores and microspores. The genus Lycopodium seems to be very old, fossils apparently very close to the living species occurring in the older rocks. These simpler forms have held their own in the struggle for existence, while the more highly specialized ones seem to have been crowded out by the still more specialized seed plants, some of which may be their direct descendants.

HETEROSPORY

In all of the principal groups of Pteridophytes, in passing from the simpler to the more specialized forms, a striking phenomenon manifests itself, *i.e.* "heterospory," or the development of two sorts of spores, producing respectively male and female gametophytes. In the lower members of each series, the "homosporous" forms, the spores are all alike, and on germination produce a thallus of considerable size showing more or less resemblance to that of the lower liverworts, and in extreme cases living for several years. Upon this thallus the reproductive organs are borne, antheridia and archegonia usually growing upon the same plant, but sometimes upon separate ones. Where the gametophyte is unisexual, as in Equisetum and some ferns, the male plants are smaller, in extreme cases being

reduced to a few vegetative cells and a single antheridium. In all of these homosporous types, however, there is nothing in the appearance of the spore to indicate whether the resulting gametophyte is to be male or female, and indeed this is sometimes, to a certain extent at least, a matter of nutrition.

In each of the principal groups of Pteridophytes, however, we find at least one genus which develops two very distinct forms of spores, *i.e.* is heterosporous. In all but the Equisetineæ there are existing examples of heterosporous genera, but in the latter class the single living genus is homosporous, although some of its fossil relatives are known to have been heterosporous.

Among the eusporangiate ferns it is an open question whether there are any undoubted cases of heterospory, although it is probable that the peculiar genus Isoëtes (Fig. 39, A), where heterospory is very pronounced, is related, although remotely, to the homosporous Eusporangiatæ. It certainly seems to be nearer to the ferns than to the club-mosses with which it is usually associated.

In Isoëtes the sporangia (Fig. 39, B), which are very large, and borne singly at the bases of the closely crowded rush-like leaves, are alike in structure and external form, but there is an enormous difference in the size of the macrospores and microspores. The male plant produced from the microspore (Fig. 39, C) is exceedingly rudimentary, consisting of a single minute vegetative cell and an antheridium which produces but four spermatozoids, and is the most reduced known among the Pteridophytes, and approximates nearest the condition found in the flowering plants. The macrospore is very large and

filled with accumulated food substances which serve to supply the developing female gametophyte with food, as the latter does not contain chlorophyll. The gametophyte, as in Selaginella, is almost entirely included within the large macrospore, and the formation of the
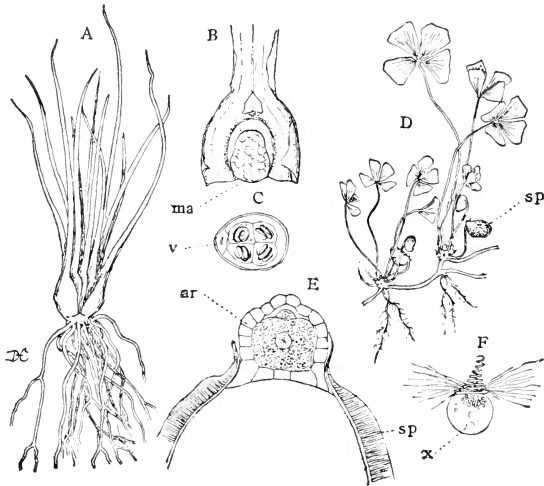
Fig. 39 (Heterosporous Ferns). — A, sporophyte of *Isoëtes echinospora;* B, a single leaf showing the enlarged base bearing a single macrosporangium, *ma*; the microsporangia are much the same; C, a germinated microspore with the contained gametophyte reduced to a single vegetative cell, *v*, and an antheridium with four coiled spermatozoids; D, *Marsilia vestita,* a heterosporous form allied to the leptosporangiate ferns; *sp*, the "sporocarp" or modified leaf-segment within which are borne the sporangia; E, section of the upper part of the macrospore and female gametophyte, here reduced to a single archegonium, *ar*; the body of the macrospore, *sp.* remains undivided; F, spermatozoid of Marsilia; *x*, the remains of the central part of the sperm-cell.

cells is preceded by a repeated division of the nuclei as in the formation of the gametophyte or "endosperm" of the flowering plants. Germination, however, does not begin until the spores have been set free. The arche-

gonia in Isoëtes are very much like those of the eusporangiate ferns, and the spermatozoids are multiciliate like those of the typical ferns, and it is largely for these reasons that the writer is inclined to consider Isoëtes as related to the ferns rather than to the club-mosses.

Among the Leptosporangiatæ heterospory has developed quite independently in at least two places. The two families, Marsiliaceæ and Salviniaceæ, usually associated under the name of Hydropterides or water-ferns, are obviously not closely related, and they show evidence of having been derived independently from two widely separated families of homosporous ferns. The Salviniaceæ show certain resemblances to the filmy ferns, while the Marsiliaceæ are more like the Polypodiaceæ. Both families agree in having the macrospores reduced to a single one in each macrosporangium, through the abortion not only of the other spore-tetrads, but also of the three sister-spores of the macrospore. The latter becomes very large, and its outer membranes much modified (Fig. 39, E).

In the Salviniaceæ, especially Salvinia, the female gametophyte is much larger than in the Marsiliaceæ, or indeed than in any other heterosporous Pteridophyte. It has abundant chlorophyll and does not differ very essentially from the green gametophyte of the homosporous ferns. The male plant, too, is less reduced than in other heterosporous forms. In the Marsiliaceæ, the female gametophyte is reduced to little more than a single archegonium (Fig. 39, E), and the male plant to a single antheridium with one or two rudimentary vegetative cells.

In the genus Marsilia the development by the gameto-

phyte is exceedingly rapid, in marked contrast to the long-lived gametophyte of the homosporous ferns. The ungerminated dried spores of *Marsilia vestita* (Fig. 39, D), for example, a common species of the western United States, on being placed in water will complete their whole development within less than twenty-four hours, the sexual organs being matured and fertilization effected within that time.

In the Equisetineæ, heterospory, as already noted, is known only in a few fossil forms, and in these there is much less difference in the size of the two sorts of spores than is the case in the heterosporous ferns.

The club-mosses, as we have seen, show very marked heterospory in the genus Selaginella, which includes the majority of the existing species, mostly tropical in their distribution. In Selaginella, as in Isoëtes, the formation of the female gametophyte is preceded by a repeated division of the nucleus of the macrospores, and closely resembles the endosperm formation of the flowering plants. The male gametophyte is reduced to a single vegetative cell as in Isoëtes, but the number of sperm-cells is much greater, and the spermatozoids are biciliate as in Lycopodium or the mosses, and not multiciliate like those of the other Pteridophytes.

In Selaginella the germination of the spores begins while they are still included in the sporangium, whose wall-cells remain active, the inner layer of cells acting as nourishing cells for the developing spores with the contained gametophyte. The latter derives its sustenance, not from reserve matter within the spore, but directly from the sporophyte. In this respect Selaginella approaches the condition found in the flowering plants, where the

macrospore remains permanently within the sporangium.

SUMMARY

In reviewing the Pteridophytes or Ferns, we have seen that the three existing classes are sharply separated from each other by the characters of the sporophyte. In the ferns proper the leaves are greatly developed, while the stem is often short and inconspicuous. In the other two classes, the horsetails and club-mosses, it is the stem which is especially developed, while the leaves are small and sometimes quite functionless as organs of assimilation, as seen in Psilotum or Equisetum.

In the lower or homosporous members of all the series, the gametophyte is comparatively long-lived, and there is a good deal of similarity of structure in all of them, especially in regard to the sexual organs. Both the gametophyte itself and the sexual organs show marked resemblances to certain liverworts, especially the Anthocerotaceæ. These are so great as to warrant the assumption of an origin of the Pteridophytes from liverwort-like ancestors which must have resembled in many respects the Anthocerotaceæ.

The resemblances between ferns and Equisetum in the structure of the reproductive organs, and especially the spermatozoids, are very marked, and suggest a possible common, but very remote, origin for the two. The small biciliate spermatozoids of the Lycopods, on the other hand, seem to indicate a more direct origin of these from forms like existing liverworts; but as yet no Bryophytes are known which possess the large

multiciliate spermatozoids of the ferns. There is no very satisfactory evidence of the origin of any of the existing classes from either of the others, although there are certain characters which the lower members of all the series have in common.   It is probable that all have originated from either the same or closely related ancestral forms, but the three classes as they now exist may be considered as coördinate.

The geological evidence shows conclusively that the club-mosses and horsetails are to be considered as remnants of groups once much more important than at present, which probably reached their maximum development during the Carboniferous era.

With the ferns the matter seems different. Of the two main divisions, the Eusporangiatæ, *i.e.* the Marattiaceæ and Ophioglossaceæ, show strong evidence of being primitive forms. This is indicated not only by the large long-lived gametophyte and the form of the reproductive organs, but also by the simplicity of the tissues of the sporophyte, especially the undifferentiated sporangia, which show an approach to the condition found in certain liverworts. The evidence of comparative anatomy is confirmed by the geological record, which shows conclusively that the oldest fossil ferns were undoubtedly of the eusporangiate type. The Marattiaceæ, especially, were very much better represented than at present.

From the primitive eusporangiate stock, which, as might naturally be expected, shows certain affinities with the lower members of the Lycopodineæ and Equisetineæ, the more specialized and modern Leptosporangiatæ have arisen, and at present they form the prevail-

ing type of Pteridophytes, which has largely crowded out the more primitive Eusporangiates. Certain genera, like Osmunda, are probably intermediate in character between the two. The Leptosporangiatæ have diverged further and further away from the parent stock, reaching their highest expression in the heterosporous forms like Marsilia and Salvinia. It is doubtful whether the latter have given rise to any higher types.

It is possible that another important group of plants, the Angiosperms or highest of the flowering plants, has arisen from the Eusporangiatæ. There are numerous striking resemblances in the structures of the two groups, and it is possible that the peculiar genus Isoëtes may represent a transitional condition. The relation of the latter to the ferns is by no means admitted by all botanists, but on the whole it seems to be more nearly related to these than to the Lycopods. If this is true, it is not impossible that from some similar forms the lower Monocotyledons have arisen.

Another group of flowering plants, admittedly the lowest of all, shows almost certain affinity with the eusporangiate ferns. These are the Cycads, whose recently discovered spermatozoids break down the last barrier between ferns and flowering plants.

The Equisetineæ, so far as we can judge, never developed beyond the large heterosporous forms found fossil, but the Lycopods, through forms like Selaginella, and much larger but similar fossil types like Lepidodendron, may perhaps have been the ancestors of a part at least of the Gymnosperms, or lowest group of seed-bearing plants. The similarity of the tissues of the sporophyte, and especially the remarkable resemblances in the gam-

etophyte and embryo of Selaginella and the Conifers, are very noticeable, and in connection with Conifer-like Lepidodendrons and other arborescent ancient types, suggest a direct origin for the Conifers from such ancestral forms.

We see, then, that, starting from a common form, or at least from similar ancestral forms, probably allied to existing liverworts, the three existing classes of Pterido-phytes have developed along parallel lines. In all cases there has been a reduction of the gametophyte among the higher members of each series, with a corresponding perfecting of the sporophyte. This has resulted finally in heterospory, which in at least two cases — *i.e.* eu-sporangiate ferns and Lycopods — has resulted in the production of seed-bearing plants. In the one case the result was the Angiosperms and perhaps the Cycads; in the other the Conifers. From the Eusporangiatæ were also developed, as a second branch, the modern group of leptosporangiate ferns.

The accompanying diagram will show the relations of these groups.
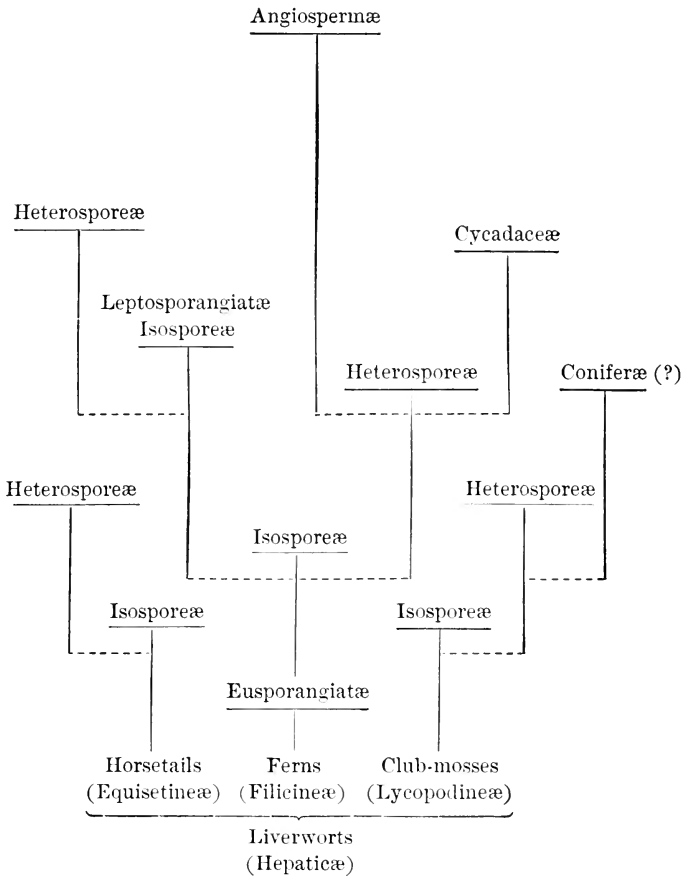
Diagram to illustrate the relationships between the three existing classes of Pteridophytes and the Spermatophytes.

CHAPTER IX

SEED PLANTS (SPERMATOPHYTA) (*GYMNOSPERMÆ*)

ONE of the most notable peculiarities of the higher Pteridophytes is the extreme reduction of the gametophyte and the corresponding specialization of the sporophyte. This culminates in the various heterosporous types, where the gametophyte may lack all power of independent growth and serve merely to develop the reproductive organs and nourish the embryo-sporophyte until it is self-supporting. In Selaginella the gametophyte is partially developed within the spores while they are still included within the sporangium, and is nourished directly from the sporophyte through the sporangium wall, which serves thus not only to protect the spores, but also to nourish them during the early stages of germination. Finally, however, the spores are discharged from the sporangium, and the gametophyte completes its development away from the sporophyte.

In the highest of all plants, the seed-bearing, or, as they are commonly called, the "flowering plants," heterospory is carried one step further, and the macrospore remains permanently within the sporangium. Not only is the germination of the spore completed within the sporangium, but the fertilization of the archegonium is effected and the development of the embryo-sporophyte

is begun. The microspores, however, although the germination begins within the sporangium, are finally discharged and complete their development outside the sporangium, precisely as in the Pteridophytes.

The Spermatophytes do not differ in any essential structural points from the Pteridophytes. Like them they produce sporangia, usually upon special leaves (sporophylls), which are here known as carpels and stamens. Upon the former are borne macrosporangia (ovules), upon the latter the microsporangia (pollen-sacs). These sporangia agree closely in their structure and development with those of the higher Pteridophytes. In the microsporangium the development of the spores (pollen) corresponds in the minutest particulars with that of the microspores of the heterosporous Pterido-phytes, but in the macrosporangium, especially in the higher Spermatophytes, the Angiosperms, there is not always the division of the spore mother-cell into four daughter-spores. The macrospore in these forms is usu-ally known as the "embryo-sac."

The development of the female gametophyte within the embryo-sac, especially in the lower types (Gym-nosperms), agrees very closely with that in Selaginella and Isoëtes. After the germination is complete and the embryo has developed from the fertilized egg-cell of the archegonium, the wall of the macrosporangium hardens and forms a firm protective covering for the enclosed embryo, which generally is imbedded in the tissue of the gametophyte. The latter becomes filled with food-substances, such as oil, starch, and nitrogenous compounds, for the future growth of the embryo. The sporangium now falls away from the sporophyte, and is

known as a seed. This peculiar modification of the macrosporangium to form a seed is the real distinguishing characteristic of the Spermatophytes.

The microspores or pollen-spores of the seed plants differ very little from those of the ferns either in form or development, and indeed are strictly homologous with the spores of all Archegoniates, where, as we have seen, the spores invariably arise from the division of the sporogenous cell into four equal parts.

Owing to the position of the archegonium within the macrosporangium, the method of fertilization is different from that in the Pteridophytes, where the free gameto-phytes are directly exposed to the action of water, and motile spermatozoids are produced in the antheridium. The pollen-spore of the Spermatophytes on germination produces a long tubular filament within which is contained the very rudimentary antheridium with usually two sperm-cells. In its growth the pollen-tube grows down through the tissues above the apex of the female gametophyte, and finally reaches the archegonium, where it discharges the sperm-cells, one of which fuses with the egg-cell, thus effecting fecundation. Until very recently it was supposed that the absence of motile spermatozoids formed an absolute distinction between Pteridophytes and Spermatophytes, but the discovery of large fern-like spermatozoids in certain Cycads, as well as in the curious genus Gingko, has broken down the last barrier between the two groups.

The "flower" in most Spermatophytes is a collection of sporophylls, or spore-bearing leaves, the carpels, bearing macrosporangia (ovules), and the stamens, bearing the microsporangia (pollen-sacs). These sporophylls

may be compared directly with those of the **Pterido-phytes**, which are sometimes grouped in a spike or strobilus, as is seen in the horsetails and club-mosses, and this strobilus is structurally much like the flower of some of the lower Spermatophytes, especially the Coniferæ.

In the Cycads, which are the lowest known Spermatophytes, the foliar nature of the sporophylls is very obvious (Fig. 40, A), but in the higher forms this is not usually so evident, especially as regards the carpels. In addition to the sporophylls, most of the higher Spermatophytes have accessory floral leaves, sepals and petals, which, however, are by no means necessarily present.

The seed-bearing plants are commonly divided into two great divisions, Gymnosperms and Angiosperms. The former, which include the Cycads, the Conifers, and a third less familiar order, the Gnetaceæ, or "joint-firs," are characterized by having the macrosporangium borne upon an open carpellary leaf; hence the name, Gymnospermæ, or naked-seeded plants. In the Angiosperms, the second group, the carpel (or carpels) forms a closed cavity, the ovary, in which the ovules, and later the seeds, are completely enclosed. It is this last group which comprises the vast majority of the flowering plants.

M

The Gymnospermæ

In the Gymnosperms the flowers are of the simplest character, consisting entirely of sporophylls of one kind. Macrospores and microspores are always borne in different flowers and very often upon different plants.

The Cycads (*Cycadaceæ*)

Without question the lowest types of seed-bearing plants known are the Cycadaceæ, a group of palm-like plants of which the best known is the so-called "sago-palm" of the greenhouses, *Cycas revoluta*. About seventy-five living species of Cycads are known, widely distributed through the warmer regions of both the Old and the New worlds. Most of them are strictly tropical, but one species, *Zamia integrifolia*, is found as far north as Florida, and *Cycas revoluta* probably extends beyond the northern tropic in Japan. They recall in many ways certain ferns, and a careful examination of the tissues of the sporophyte shows that these resemblances are more than superficial. The tissues of the fern-like leaves resemble those of the lower ferns, and the leaves when young are coiled up much as in the ordinary ferns (Fig. 40, F). The plant, however, may develop a primary tap-root like that of the Conifers or Dicotyledons, and there is a more or less marked secondary thickening of the vascular bundles of the stem, which, however, also occurs in a few ferns.

In Cycas the macrosporangia are borne upon leaves which differ but slightly from the ordinary ones (Fig. 40, A). The sporangia are very large, sometimes being

of the size of a large plum. The very large macrospore (Fig. 40, B, *ma*) has a definite thick membrane like that of the ferns, but is retained permanently within the sporangium. So far as it is known, the development of the
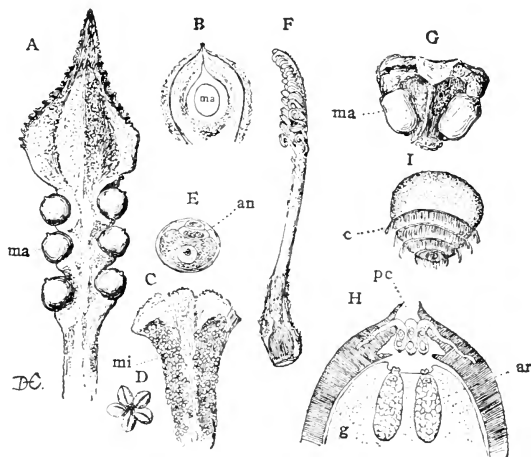
Fig. 40 (Cycadaceæ). — A, a sporophyll of *Cycas circinalis*, with six ovules (macrosporangia), *ma*; B, longitudinal section of a young ovule of *C. revoluta*, showing the single large macrospore, *ma*; C, a sporophyll from the male cone of *C. revoluta*, showing the lower surface covered with groups or sori of microsporangia, *mi*; D, a single sorus of five microsporangia; E, a microspore (pollen-spore), showing the rudimentary antheridium, *an*; the larger antheridial cell later gives rise to two large spermatozoids; F, a young leaf of *C. revoluta*, showing the fern-like coiling of the divisions; G, a scale from the female cone of *Zamia integrifolia*, with two ovules, *ma*; H, section through the ovule at the time of fertilization; *pc*, the pollen-chamber with three germinating pollen-spores; *g*, the vegetative tissue of the female gametophyte contained within the macrospore; *ar*, two archegonia; I, a spermatozoid of Zamia, showing the numerous cilia, *c*. (Figs. H, I, after Webber.)

gametophyte is much like that of Isoëtes or Selaginella, but the details are still somewhat imperfectly known. The gametophyte, if fertilization is not effected, may grow out beyond the spore and develop chlorophyll,

and thus is capable of a certain degree of independent existence, a condition not known in any other Spermatophytes. The several archegonia produced upon the gametophyte do not differ in any essential particular from those of the true Archegoniates.

The microsporangia occur in great numbers upon the backs of sporophylls which are arranged spirally about a thick axis and form a cone or strobilus. The microsporangia are very much like those of the ferns, and are usually grouped in clusters or sori (Fig. 40, C, D). The microspore on germinating produces a rudimentary plant with a simple antheridium containing two sperm-cells. From these are produced the spermatozoids, much like those of the ferns, but, especially in Zamia, enormously larger than any other known spermatozoids. These are formed shortly before fertilization takes place.

The pollen falls upon the top of the ovule (macrosporangium), where there is an opening in the integument with which it is surrounded, and this opening at the time of pollination is filled with a fluid which on evaporating deposits the pollen-spores upon the top of the sporangium itself, where they germinate by sending out the pollen-tube, which forces its way through the upper part of the ovule to a cavity just above the archegonium (Fig. 40, H). Simultaneously with the ripening of the latter, the two spermatozoids within the pollen-tube are discharged into the cavity, which is filled with a watery fluid derived from the distended pollen-tubes, and in this they swim to the archegonium by means of the numerous cilia with which they are furnished. Fertilization is thus effected precisely as in the Arche-

goniatæ, and the egg thereupon begins to grow and develops into the embryo-sporophyte, while the surrounding cells of the gametophyte become filled with food-materials and are known as the "endosperm." The wall of the sporangium now hardens, while the outer tissues of the integument become pulpy, so that the ripened seed looks very much like the fleshy fruit of a plum or cherry.

That the Cycads represent a very ancient type is shown by their fossil remains, which indicate that during the Mesozoic age they were among the most abundant plants. They occurred in great numbers, and comprised many more genera and species, as well as individuals, than at present. The first evidences of the existence of Cycads occur in the Carboniferous rocks, but in small numbers; but in the Mesozoic rocks, as already stated,
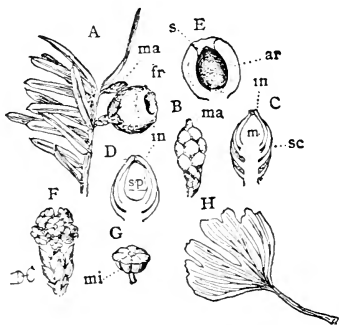
FIG. 41 (Coniferæ). — A, a branch of a female plant of the common yew (Taxus), one of the simplest Conifers; *ma*, young female flower; *fr*, ripe fruit; B, a single female flower, consisting of an ovule, or macrosporangium, *ma*, surrounded by a number of scale-leaves; C, a section of the flower, showing the terminal sporangium (ovule), *m*, surrounded by the integument, *in*, and the scales, *sc*; D, section of an older ovule, showing the large macrospore ("embryo-sac"), *sp*; E, the ripe fruit, with one side of the cup-shaped aril, *ar*, cut away to show the seed, *s*; the seed is the matured ovule, the aril a special structure which grows up about the seed; F, a male flower of Taxus, showing the umbrella-shaped sporophylls, each bearing several microsporangia upon the lower surface; G, a single sporophyll; *mi*, the sporangia; H, a leaf of Gingko, showing the fern-like form and venation. (Figs. F, G, after Eichler.)

they occur in great numbers. The oldest forms closely resembled the existing genus Cycas, which has persisted while many of the more specialized types have become quite extinct.

Perhaps allied to the Cycads, and like them also a very old type, is the curious genus Gingko (Fig. 41, H), represented at present by a single species no longer known in a wild state, but much planted about temples in China and Japan, where gigantic trees, hundreds of years old, are standing. From the fern-like venation of the leaves, the tree is sometimes called the maiden-hair tree, and this peculiarity of the leaves probably indicates a real affinity with the ferns. Many fossil species, much like the existing one, are known, the oldest ones from the Permian rocks, and therefore somewhat more recent than the oldest Cycads.

Gingko is usually referred to the Coniferæ, but the development of the gametophyte, especially the production of multiciliate spermatozoids like those of Cycas, as well as the fern-like character of the leaves, suggest that its affinities are rather with the Cycads than with the Conifers.

THE CONIFERÆ

Although the Cycads and Coniferæ are usually associated in a common group, Gymnospermæ, it is at least doubtful in view of the recent discoveries in regard to the former, as well as because of other differences in structure, whether these two orders are really related to each other.

The Coniferæ are the familiar "evergreen" trees of

our northern forests, and while a much more ancient type than the Angiosperms, they are still a predominant type of vegetation in many regions, where the forests are often composed almost exclusively of these trees. In contrast to the Cycads, which rarely attain tree-like proportions, and whose leaves are large and fern-like, the Conifers usually become trees, often of gigantic size, and in most of them the leaves are small and needle-shaped. In the relation of stem and leaves the Conifers recall the club-mosses, while the Cycads are very much like the ferns, and it is not impossible that this may indicate an entirely independent origin for the two groups from Lycopods and ferns respectively. The recurrence of fossil forms of an intermediate character supports such a hypothesis.

The sporophyte in the Conifers, as already stated, is always large, usually becoming arborescent, and sometimes a hundred metres and more in height. These giant trees reach their greatest development on the western slopes of the mountains of Pacific North America, where a number of species attain a height of one hundred metres, or it is claimed one hundred and fifty metres, with trunks from five to six metres in diameter; or, in the case of the great Californian Sequoias, ten metres or even more. The extraordinary height of coniferous trees, which almost always exceeds that of their deciduous companions, is due to the persistence of the original apical bud, which, unless injured by accident, remains active, so that a definite central axis is formed which may grow in length for hundreds of years. The regular whorls of branches formed at the base of each year's growth in many spe-

cies gives them the strikingly symmetrical conical form
so characteristic of most of the group.

The leaves of the Conifers are usually slender
"needles," or are small and scale-like, as in the cypress
and arbor-vitæ. Usually they remain attached to the
stem for several years, but in a few cases, like the larch
and bald cypress, they are shed annually. Like the
Cycads, the Conifers generally have a main tap-root,
which, like the stem, shows a continuous secondary
growth in thickness. This in the stem results in the
formation of the well-known annual growth-rings. This
secondary growth is much like that found in the stems
of normal Dicotyledons, and on the strength of this the
older botanists united these with the Gymnosperms
under the name "Exogens"; but the great differences
in the structure of the flower, and especially in the
gametophyte, forbid the idea of such a union, and
botanists are now agreed that no near relationship exists
between the two.

The flowers of the Coniferæ are very simple in struct-
ure. In the lowest types, like the yew (Taxus) (Fig.
41, A–G), the macrosporangium is borne directly at the
end of a shoot, and is in fact its transformed apex. It
becomes invested with an integument like that found
in Cycas, and is protected while young by several over-
lapping scale-leaves. Within is produced a group of
sporogenous cells, from one of which is developed the
single macrospore which gives rise to a gametophyte
of considerable size with several archegonia. The
microsporangia are formed, several together, upon um-
brella-shaped leaves, which are arranged in a cone which
suggests that of Equisetum (F, G). The germinating

microspore produces a rudimentary antheridium with two sperm-cells, much as in Cycas, but so far as known at present, the formation of spermatozoids is completely suppressed. It would not be surprising, however, if some trace of such structures should be discovered. The germination of the pollen-spore when it falls upon the ovule is like that of Cycas, but the pollen-tube penetrates through the neck of the archegonium, and the sperm-nucleus is discharged directly into the egg.

In the higher Conifers, such as the pines and firs, the macrosporangia are developed upon special sporophylls (carpels) which not infrequently are borne in the axils of sterile bracts. The sporophylls are arranged spirally about the axis of a shoot, forming the familiar "cones" of these trees. As in the yew, the single macrospore which is finally formed in the sporangium produces the large female gametophyte, much like that of Selaginella. The archegonia are several in number, with very large egg-cells, but the neck parts relatively small, as they are in all Gymnosperms. The sporangium is invested with a single integument as in the other forms described.

The microsporangia are also borne upon special sporophylls, and are usually arranged in a cone like those bearing the ovules. These microsporangia or pollen-sacs correspond in every detail of their development with those of the Pteridophytes. The ripe pollen-spores in the pines (Fig. 42, E) and firs are provided with wing-like outgrowths of the outer membrane, which form very efficient sails by which they are more easily scattered by the wind. As the pollen must depend upon the wind for its distribution, the number of

pollen-spores produced is enormously in excess of the
macrospores. Indeed, so abundant is the pollen, that
the ground in the neighborhood of the trees is some-
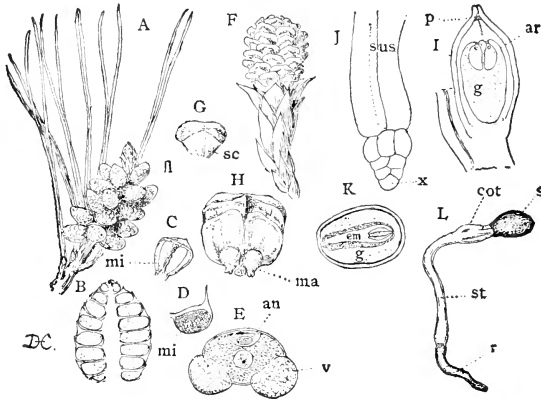
Fig. 42 (Coniferæ). — A, branch of a pine (*Pinus contorta*) with male
flowers, *fl*; B, longitudinal section of a single flower, showing the
arrangement of the sporophylls; C, a single sporophyll, showing the
two microsporangia, *mi*, upon its lower surface; D, a section through
the microsporangium; E, a single microspore, showing the antheridium,
an, and the vesicular outgrowths of the wall, *v*, which serve as sails;
F, a female flower of the same pine; G, a single sporophyll from the
female flower, showing the small scale, *sc*, by which it is subtended; H,
a sporophyll from an older cone, showing two macrosporangia (ovules),
ma, upon its inner face; I, longitudinal section of an ovule (macro-
sporangium); the large macrospore contains the gametophyte, *g*,
bearing several archegonia, *ar*; *p*, a pollen-spore sending down the tube
by which the archegonia are fertilized; J, a young embryo; *sus*, sus-
pensor; *x*, apical cell; K, section of a ripe seed, containing the embryo,
em, imbedded in the prothallial tissue, *g*; L, young sporophyte, show-
ing the cotyledons, *cot*; stem, *st*; root, *r*; *s*, the empty seed-coat.

times covered with a layer of the sulphur-colored
powder.

The germination of the pollen-spores and the fertili-
zation of the archegonium are effected as in Taxus. As
in that genus, no trace of motile spermatozoids has yet

been found in the higher Coniferæ, and it is not likely that in these spermatozoids exist.

The development of the embryo in the Conifers shows a good deal of difference in different genera. Sometimes but a single embryo arises from each egg-cell, as in most other plants; but sometimes, for instance in the common pines and firs, each egg gives rise to a group of (usually four) embryos, and the ripe seed may contain more than one young sporophyte. Generally, however, one of the growing embryos crowds out the others, and only this one matures. As in Selaginella and the lower Gymnosperms, a long suspensor (Fig. 42, J, *sus*) is formed from the upper part of the egg, while the lower portion only gives rise to the embryo itself. By the rapid lengthening of the suspensor the growing embryo is pushed down into the tissue of the gametophyte, whose cells become gradually filled with nutrient substances upon which the developing embryo feeds. These are not all consumed, however, but a considerable part persists in the ripe seed as the "endosperm," in which the young sporophyte is imbedded, and upon which it draws for nourishment in the early stages of the germination of the seed. The young sporophyte within the ripe seed already has all its primary organs developed. The stem is prolonged downward into the primary root, which is directed toward the opening in the integument (micropyle), while the upper end of the embryo terminates in the conical stem-apex about which is arranged a circle of primary leaves, or cotyledons, ranging in number from two to half a dozen or more.

The ripe seed has a hard, usually dark-colored coat, effectually protecting the delicate inner tissues; some·

times attached to it are membranaceous wings to facilitate its distribution by the wind.

Before the seed germinates, the enclosed sporophyte absorbs water rapidly, and the dormant protoplasm of its cells resumes its activity. The little plant increases quickly in size, growing at the expense of the food stored in the surrounding endosperm. The root elongates, and pushes out through the micropyle, turns downward, and buries itself in the earth, and thus fastens the young sporophyte into the ground. In the meantime the cotyledons have enlarged and turned green, and finally pull themselves out of the seed, whose empty shell is thrown aside. The young sporophyte is now quite independent, and in course of time assumes its perfect form.

The stem of the seedling sporophyte contains a circle of separate vascular bundles, not unlike those in the stems of some Pteridophytes, but there is soon developed in each bundle a zone of growing tissue, finally connected with that of the other bundles by means of a similar zone developed in the tissue lying between the separate bundles. This zone of growing tissue, or "cambium," characterizes the older stems of all Conifers, and to its continued activity is due the annual growth-rings found in these trees. A similar secondary growth in thickness is known to have taken place in the stems of the fossil Lepidodendrons, which it has been suggested may have been the progenitors of the modern Coniferæ.

Unless injured, the original stem-apex of the embryo persists in the older sporophyte, and to this is due, as we have said, the extraordinary height which some of the Conifers attain.

The Gnetaceæ

The last order of the Gymnosperms, the Gnetaceæ, are forms familiar only to the botanist, the only examples occurring in the United States being a few species of Ephedra in the deserts of the Southwest. The other two genera are strictly tropical. It is a question how closely the three genera are related, as they differ very much from one another, as well as from the other Gymnosperms. Some of them show certain analogies with the Dicotyledons, and they are sometimes regarded as forms connecting the Gymnosperms with the latter. Their development is not known with sufficient completeness, however, to make this at all certain, and the few fossil remains attributed to this order are much too imperfect to throw much light upon their geological history.

Fossil Conifers

Most of the living genera of Conifers are also found fossil, and some of them which are now restricted to a very limited area were evidently much more widespread in earlier geological times. None of the living genera can be traced with certainty further back than the earlier Mesozoic rocks, although a number of fossils from the coal measures have been doubtfully assigned to existing genera. In the later Mesozoic and early Tertiary rocks, however, there are abundant evidences of the existence of many living genera, or, in a few instances, even species. A notable case is that of the genus Taxodium, with two existing species in the southeastern United States and Mexico. Of these, the common bald cypress of the

Gulf States is represented in Tertiary deposits by an apparently identical species, which at that time had a wide range over nearly the whole northern hemisphere. The genus Sequoia is another striking example of the survival, in a limited range, of a once widely distributed type. At present the two species, *S. sempervirens,* the coast redwood of California, and *S. gigantea*, the giant tree of the Sierra Nevada, are all that remain of a genus once represented by numerous widely distributed species.

Besides the genera still existing there are a number known only as fossils, some of which extend back to the Carboniferous. The exact relation of these extinct forms to the existing Coniferæ is somewhat doubtful.

The Cordaiteæ

Probably allied to the Conifers is a peculiar group of fossils, the Cordaiteæ. These first appear in very old formations, some writers claiming that they are found in the Silurian rocks. The occurrence of seed-bearing plants in such ancient formations is, to say the least, unexpected. They are most abundant in the coal measures and disappear soon after. The flowers have been preserved in some instances in an astonishingly perfect condition, even the pollen-spores with an enclosed structure supposed to be the gametophyte being recognizable. The latter is much more highly developed than in any living seed plants, and this shows the primitive nature of these plants. In regard to the structure of the flowers, they show certain resemblances to both

Cycads and Conifers, but on the whole they are probably nearer the latter.

Summary

Compared with the Angiosperms, the Gymnosperms are an ancient primitive group of plants showing very evident resemblances to the Pteridophytes, from which they have doubtless originated. It is not likely that the existing Gymnosperms constitute a homogeneous class, but it is more probable that they are remnants of at least three lines of development. Of these the Cycads show evident relationships to the ferns, this being evinced by the character of the leaf and flowers, and still more by the form of the spermatozoids. The geological record shows that the Cycads were once a much more important group than at present. Perhaps related to these is the genus Gingko, also a very old type, with but a single living representative.

The Conifers are a more recent type than the Cycads, but still are older than the Angiosperms. In the general habit of the sporophyte, especially the sporophylls, they suggest a direct connection with the Lycopods, and this is borne out by a study of the gametophyte, which closely resembles that of Selaginella. The presence in the Carboniferous rocks of gigantic Lycopods now extinct, suggests these as possible ancestors for the existing Conifers.

There is very little in common between the third order, the Gnetaceæ, and the other Gymnosperms, and it is questionable whether the theory that the Gnetaceæ

are forms intermediate between the other Gymnosperms and the Angiosperms will prove to be correct. It seems quite as likely that the latter have originated independently directly from the Pteridophytes, or possibly from low forms allied to the Cycads.

CHAPTER X

THE second great division of the seed-bearing plants, the Angiosperms, is preëminently the prevailing modern plant type. These are the plants ordinarily thought of as "flowering plants." They are at once distinguished from the Gymnosperms by the development of a closed ovary formed from the carpel, or by the union of two or more carpels. Within this closed cavity are borne the ovules or macrosporangia, which are usually, but not always, outgrowths of the carpellary leaves. Sometimes the apex of the floral axis or shoot is transformed directly into the ovule.

The flowers of the Angiosperms exhibit extraordinary variety, and contrast strongly with the very uniform character of the flowers of most Gymnosperms. In the simplest types (Fig. 43) the flowers of the Angiosperms are nearly as simple as the simplest Gymnosperms, but as a rule they are far more complex. This arises primarily from a multiplication of the sporophylls, but is further complicated by the development of accessory leaves, sepals and petals, never found in the Gymnosperms.

In most Angiosperms both sorts of sporophylls are usually associated in the same flower; *i.e.* the flower contains both carpels and stamens, which are sur-

rounded by the floral envelopes, corolla and calyx, made up respectively of the petals and sepals. The base of the carpel forms the ovary, while above it is prolonged into the style tipped by the stigma, or portion upon which the pollen falls (Fig. 44, A).

In the number of parts in the flower, as well as in their arrangement and form, the Angiosperms show almost infinite variety. The petals are very frequently brightly colored, and this, together with many modifications in the other structures, is intimately associated with pollination through insect aid, which has undoubtedly played an important part in the evolution of the floral structures of the Angiosperms.

The gametophyte in the Angiosperms is so much reduced and so inconspicuous that it is usually quite ignored in the ordinary study of these plants; but it must be borne in mind that the gametophyte is always present, although in a very reduced form. As in the Gymnosperms, the ovule corresponds to the macrosporangium of the heterosporous Pteridophytes, and within it is formed the single macro-

FIG. 43. — Flowers of a pondweed (Naias); the male flower, A, and the female, B, are much alike. Each consists of a single sporangium invested with an integument, *in*, the whole enclosed in a tubular leaf with spiny processes at the summit. This sheath-like leaf is usually considered in the female flower to be a carpel. Fig. C shows a section through the base of the female flower, with the enclosed macrosporangium, or ovule, *ma*, and two integuments, *in*, and the contained embryo-sac, or macrospore, *sp*.

spore or embryo-sac (Fig. 44, A, *ma*, B), which in its origin corresponds closely to that in the Gymnosperms and in such Pteridophytes as Isoëtes. As in the Gymnosperms, the macrospore remains permanently within the ovule. The gametophyte is usually extremely reduced, showing in the typical forms a very constant structure.

The single nucleus of the macrospore divides, and one of the two resulting nuclei moves to each end of the spore-cavity or embryo-sac. Here each nucleus divides twice, so that there result four nuclei at each end of the sac. Three of them remain at the ends,

FIG. 44.—A, diagram showing the arrangement of parts in a typical angiospermous flower; *ca*, the calyx made up of individual leaves, sepals; *co*, the corolla, composed of petals; *an*, the androecium, composed of the stamens; *gy*, the gynoecium, made up of the carpels (here but a single carpel). The upper part, anther, *an*, of each stamen has usually four microsporangia, or pollen-sacs; the macrosporangia, or ovules, are contained in the ovary, formed by the base of the carpel, or united carpels; *p*, a pollen-spore germinating upon the stigma, and sending its tube, *pt*, down through the central part of the gynoecium or pistil; B, diagram showing the structures within the embryo-sac at the time of fertilization. The three cells at the upper end form the "egg-apparatus," consisting of the two synergids, *sy*, and the egg-cell, *o*. At the lower end are the three "antipodal-cells," *ant*, and in the centre are the two "polar nuclei," *pn*, which afterward unite into a single one, the "endosperm-nucleus"; C, young pollen-spore of Naias, showing the antheridial cell, *x*; D, a germinating pollen-spore of the sweet-pea: *pt*, pollen-tube; *x*, sperm-nucleus.

while the fourth one from each end moves toward the centre of the embryo-sac where these two "polar nuclei"

(Fig. 44, B, *pn*) coalesce. About the three nuclei at
the upper or micropylar end of the embryo-sac there is
formed an aggregation of protoplasm resulting in three
naked cells, which constitute the so-called "egg-appa-
ratus." The three nuclei at the other end become also
surrounded by protoplasm, which usually is bounded
by a definite cell-wall. These three cells are called the
antipodal cells (Fig. 44, B, *ant*).

In some of the simpler Monocotyledons, *e.g.* the
grasses, the number of antipodal cells is more numer-
ous, and a few cases are known where there seems to
be a multiplication of the other cells within the embryo-
sac; but these are not yet sufficiently understood to
throw much light upon the homologies existing between
the female gametophyte of the Angiosperms and that
of the Gymnosperms and heterosporous Pteridophytes.
Whether the egg-apparatus is to be considered as a
single archegonium, or whether each of its cells is to
be so regarded, cannot be positively decided at present.
The other cells, *i.e.* the antipodals and the endosperm
cells formed later, represent probably the vegetative
part of the gametophyte.

The microsporangia are much less modified, and the
development of the microspores (pollen) corresponds
exactly with that of the Gymnosperms and the Arche-
goniates from the mosses up, even to the final division
of the mother-cell into four spores. The ripe pollen-
spore shows exactly the same structure as the spores
of the Archegoniates. On germination two cells are
formed, a large vegetative one and a small antheridial
cell (Fig. 44, C). The former, when the spore falls
upon the pistil, develops into the pollen-tube, and the

antheridial cell passes into it. Either before this happens, or later, the antheridial cell divides into two sperm-cells, but no motile spermatozoids are formed.

The upper part of the pistil, the stigma, is usually provided with papillæ which hold the pollen, and the surface is often adhesive owing to a peculiar secretion which at the same time probably serves to induce the germination of the pollen. In some cases there is an open tube through the pistil, through which the pollen-tubes grow, but more commonly the central part of the style is occupied by a peculiar conducting tissue serving to nourish the growing pollen-tube, which grows through it much as a fungus hypha grows through the tissues of its host. On reaching the ovary, the pollen-tube grows along the placenta or tissues from which the ovules spring, until finally it reaches the micropyle, or opening of the ovule, which it then enters, and penetrates through the overlying tissues of the apex, to the egg-apparatus. The expulsion of the generative cell is effected much as in the Conifers, and one of the sperm-nuclei makes its way into the egg-cell, the lowest of the three cells of the egg-apparatus (Fig. 44, B, *o*), the two others, the synergidæ (*sy*), probably assisting in the transference of the male nucleus from the pollen-tube to the egg.

The effect of pollination is usually marked by a rapid growth of the ovary, as well as the development of the ovules into seeds. The development of the latter is quite similar to that in the Gymnosperms, but the further changes in the carpels, to form the "fruit," is peculiar to Angiosperms. We cannot here go into details as to the great variety shown in the fruits of

Angiosperms, but shall refer to this later.   The effect
of fertilization may extend beyond the fruit itself and
involve the calyx, as in the apple or pear, or even the
summit of the floral axis, as in the strawberry or fig.

The embryo-sporophyte in different Angiosperms
shows a very different degree of development at the
time the seed ripens.   Sometimes, especially in para-
sitic plants, it consists merely of a small mass of cells
without any external differentiation.   On the other
hand, as in the pea family, it finally occupies the whole
cavity of the seed, and all the parts, stem, root, and
cotyledons, and the terminal bud, are perfectly formed.

The remarkable complexity shown by the fully devel-
oped sporophyte of the Angiosperms offers a marked
contrast to the extremely reduced gametophyte, and it
is in this group that the development of the sporophyte
reaches its most complete expression.   From minute
undifferentiated aquatics like the little duckweed
(Lemna) (Fig. 45, D), every grade of development is
encountered, up to trees rivalling the giants among the
Conifers in point of size, and far surpassing them in the
perfection of their parts, especially the flowers.

In marked contrast to the Gymnosperms, which are
restricted in their range, some forms of Angiosperms oc-
cur under all conditions.   Some are aquatics, even grow-
ing in the ocean, while others are inhabitants of almost
absolute deserts.   Some are stately trees, while others
are minute, almost microscopic, herbs living but a few
weeks.   Especially in the tropics, where the struggle
for existence is keen, do we find Angiosperms taking
advantage of every opportunity offered, — some lift
themselves by tendrils or by twining their stems about

other plants, until they reach the light, while myriads of parasites and air-plants cover the trunks and branches of the trees, all striving to hold their own in the fierce competition. The variety shown in the flowers and fruits of these plants, as well as in the leaves and stems, is almost infinite, and in these respects the Angiosperms stand far above all other plants. In spite of this extraordinary variety, the essential structure of the flowers and seeds of the Angiosperms is remarkably uniform, and with little question they constitute a perfectly homogeneous class.

The Angiosperms fall naturally into two subclasses, — Monocotyledons and Dicotyledons. These show many points of similarity in their structure, but the differences are sufficient to make somewhat doubtful the exact relationship of the two.

The Monocotyledons

The Monocotyledons are usually simpler than the Dicotyledons, both as regards their tissues and their flowers, although among them are certain groups, like the orchids, which are among the most specialized of all Angiosperms. As a rule they have narrow leaves with unbranched veins, and the vascular bundles never exhibit secondary thickening. The roots therefore never become very thick, and a tap-root is never developed. While it is true that the parts of the flower are usually arranged in whorls of three, there are so many exceptions to the rule that it cannot be used as a satisfactory diagnostic character of the group as a whole.

The embryo of the Monocotyledons is characterized

by the presence of a single primary leaf, or cotyledon, which usually arises from the apex of the embryo, the stem-apex of the young sporophyte in most cases being formed laterally (Fig. 45, G). Of the Pteridophytes, Isoëtes shows the nearest approach to the conditions found in typical Monocotyledons. There is much uncertainty at present as to which of the Monocotyledons are to be considered as the most primitive, and their relation to the other Spermatophytes is also a question about which there is much disagreement. These points can be settled only after much more is known than at present about the development of the flower and embryo in the simpler types of the group. The principal disputed point at present is whether the forms with the simplest flowers are really the most primitive, or whether this simplicity is a reduction from a more specialized type.

The Monocotyledons which possess the simplest flowers are aquatics, the simplest of all being probably the genus Naias (Fig. 43). In this genus, which is composed of completely submerged aquatics, the flowers are reduced to a single carpel or stamen, the latter usually showing but a single pollen-sac or sporangium, produced directly from the transformed apex of a shoot; the ovule originates in precisely the same way. Both kinds of sporangia are remarkably alike in their early stages, and the origin of the sporogenous tissue is the same in both, and suggests that of many Pteridophytes. Whether or not this simple structure of the flower in Naias is the result of reduction from a more specialized type, it is certainly more like the sporangia of the Pteridophytes than is that of any other Angiosperm. A similar type of flower, but somewhat more

complicated, is found in a number of aquatic forms allied to Naias, and also occurs in some of the terrestrial types among the aroids. In the latter (Fig. 45, A–C), while the individual flowers are often of the simplest
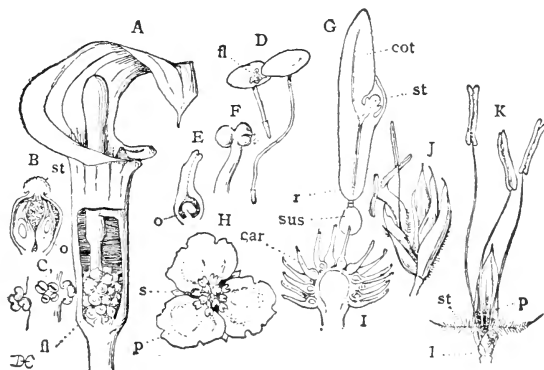
FIG. 45 (Lower Monocotyledons). — A, female inflorescence of the Indian turnip (Arisæma), the enveloping bract cut away at the base to show the inconspicuous flowers, *fl*; B, a single flower cut longitudinally to show the ovules, *o*: *st*, the papillate stigma; C, a group of male flowers, each consisting of four stamens; D, two plants of duckweed (Lemna), a minute floating aroid: *fl*, the inflorescence consisting of two male and one female flower; E, the female flower cut longitudinally; F, the male flower, consisting of a single stamen; G, longitudinal section of the embryo of Naias, showing the characters of the typical monocotyledonous embryo; the cotyledon is terminal, and the stem-apex, *st*, of lateral origin; *r*, the root; *sus*, suspensor; H, male flower of arrow-head (Sagittaria), consisting of a group of stamens surrounded by three white petals, *p*, and three sepals, *s*; I, section through the head of separate carpels, *car*, from the female flower; J, inflorescence (spikelet) of a grass (Dactylis): the lowest flower has the three stamens, and the two feathery stigmas protruding; K, a separate flower of Dactylis, consisting of a single carpel and three stamens in the axil of the bract, *p*; at the base of the carpel are the two small bracts (lodicules), *l*.

description, they are usually aggregated to form a compact, elongated inflorescence, the spadix, which may reach a large size and be very conspicuous, especially when, as often happens, it is surrounded by a showy bract, as in the common "calla lily" or some species of

Anthurium. This bright-colored "spathe" serves here the purpose of the showy corolla of the higher forms.

Somewhat higher in the scale are found plants whose flowers are made up of numerous but separate sporophylls. These may have carpels and stamens together in the same flower, or they may be separated, as in the common arrow-head (Sagittaria), (Fig. 45, H, J). In these there are also found the accessory leaves, sepals (s) and petals (p), the latter often large and showy. These forms show certain analogies, both in the structure of the flowers and the tissues, with some of the lower Dicotyledons, especially the buttercup family (Ranunculaceæ), and it has been suggested that the latter may have been derived from Monocotyledons of this type.

Of the simplest of the Monocotyledons, the Naiadaceæ, or pond-weeds, have been referred to. Other groups which are considered to be very primitive are the Cat-tail rushes (Typhaceæ), the Bur-reeds (Sparganiaceæ), the Screw-pines (Pandanaceæ), as well as several other less-known groups.

The Aroids (Araceæ), of which the common calla lily is perhaps the best-known representative, show many evidences of being a primitive group, especially in the simplicity of the flowers, although there is considerable variety among them in this respect. They are for the most part tropical, although a few genera, Arum, Arisæma, Symplocarpus, and others, are inhabitants of the temperate regions. Some of the tropical aroids are plants of considerable size, the largest being climbers, whose long stems may reach to the top of lofty trees. These climbing aroids are among the most striking of

tropical growths, especially in the American tropics, where some species of Philodendron and Monstera are among the most conspicuous plants met with. The smallest and simplest of the family are the duckweeds (Lemna), minute floating plants, the smallest of all flowering plants (Fig. 45, D). These are usually considered to be degenerate relations of the more specialized aroids. Some of the latter possess true compound leaves, which are almost unknown elsewhere among the Monocotyledons, and in this respect they resemble the ferns and many Dicotyledons.

Probably remotely connected with the aroids are the Palms, a large order mainly restricted to the tropics, and one of the most striking types of the vegetable kingdom. A few genera, like the palmettoes of the Gulf States and the fan-palms of southern California, extend beyond the tropics, but it is in the hot, moist regions of the tropics that they reach their most perfect development. Most of the palms, as is well known, are unbranched trees, with a crown of gigantic leaves, either pinnate or fan-shaped. The apparently compound leaves of palms are caused by the tearing into strips of an originally simple plaited leaf, such as occurs permanently in a very few species, and is always found in the seedling. The palms have the parts of the flower in threes, as in the higher Monocotyledons, and they may be either perfect or diclinous, *i.e.* bearing only carpels or stamens. In the latter case both sorts of flowers may be upon the same plant, or upon different individuals as in the common date-palm. Just what relation the palms bear to the aroids is doubtful, but there is a peculiar group of plants, the Cyclantheræ, natives of the American

tropics, which seem to be to a certain extent intermediate between the two.

Another very sharply defined order of Monocotyledons is the Gramineæ, or Grasses. These are cosmopolitan in their distribution, and in the temperate regions they form one of the most important elements of the vegetation, especially over open, exposed areas. Economically they are the most important of all plants, as they include all the cereals, as well as sugar-cane and bamboo, and are the most important food plants for herbivorous animals. The number of grasses exceeds that of any other group of Monocotyledons except the orchids. They are, however, very uniform in the structure of the stem and leaves as well as of the flowers. The stems are jointed and usually hollow, sometimes of gigantic size, 30–40 metres in some of the bamboos. The narrow, two-ranked leaves, with their sheathing bases, and the chaffy scales about the simple flowers, are constant characters of this very natural family.

Certain peculiarities of the ovule and the gametophyte indicate that the grasses belong near the bottom of the series of Monocotyledons, but their great numbers and wide distribution show that they have become sufficiently modified to adapt them very perfectly to existing conditions.

Owing to the absence of any forms intermediate between the grasses and the other Monocotyledons, their exact position in the system is still very uncertain.

Closely resembling the grasses externally, but differing from them in many important particulars, are the Sedges (Cyperaceæ), which are usually associated with the grasses in a single order, Glumaceæ. It seems proba-

ble, however, that the two families are not closely related, and the sedges are probably more nearly related to some other group of Monocotyledons, possibly the Rushes (Juncaceæ) than to the grasses. Whether the simple type of flower found in the grasses and sedges
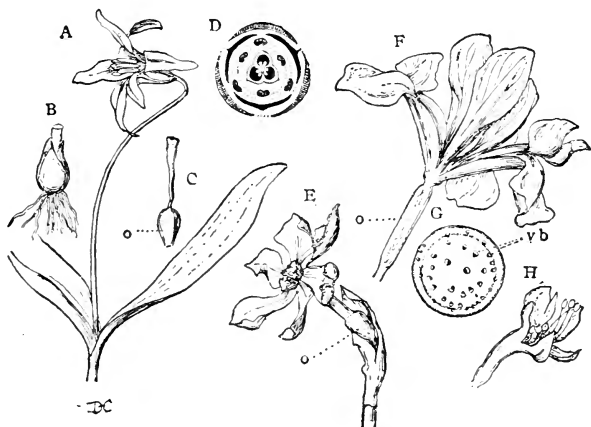
FIG. 46 (Monocotyledons — Liliifloræ). — A, a plant of yellow adder-tongue (Erythronium), a typical liliaceous plant; B, the underground thickened stem or bulb, with the simple roots growing from it; C, the pistil, composed of three united carpels; D, diagram showing the arrangement of the parts of the flower; E, flower of Narcissus, differing from the true lilies in having an "inferior" ovary, o; F, flower of an Iris, a highly specialized flower adapted to insect pollination; G, cross-section of the stem of Iris, showing the arrangement of the tissues in a typical monocotyledonous stem; vb, the vascular bundles; H, a flower of the pickerel-weed (Pontederia); the flower is strongly "zygomorphic," i.e. bilaterally symmetrical, and the stamens are in two sets.

is primitive, or whether it is the result of reduction from a more complex one, must remain for the present undecided.

All of the higher Monocotyledons are distinguished by much more specialized flowers than those found in the forms just considered. This specialization mani-

fests itself first in the development of a colored peri-
anth or floral envelope, hence they are known as the
"petaloideous" Monocotyledons. Most of these have
the carpels more or less perfectly grown together into
a compound pistil.

In the great majority of the petaloideous forms the
parts of the flower are in whorls of three, the typical
arrangement being shown in the accompanying dia-
gram (Fig. 46, D). The two sets of leaves constituting
the perianth are usually alike in color and texture, but
occasionally, e.g. Trillium, the outer leaves are green,
and form a calyx like that found in most Dicotyledons.
The six stamens are in two alternating whorls, and the
three carpels completely coherent.

Probably the lowest of the petaloideous series with
coherent carpels are the lilies, with their regular flowers
showing perfect radial symmetry. Here are found
many of the most magnificent of all flowers, and the
brilliant colors and fragrance of many of them show
their adaptation to insect aid in their pollination.

Starting from the type exhibited by the simpler mem-
bers of the lily family, it is easy to see how specializa-
tion has progressed in different directions. This is first
seen in the coherence of the leaves of the perianth, so
that the flower becomes tubular, as in the hyacinth or
tuberose. This is sometimes accompanied by a slight
inequality in the size of the perianth lobes, especially
if the flower is nodding, and in such cases the stamens
and pistil are declined so that the flower is more or less
markedly two-lipped (Fig. 46, H). Carried further, the
cohesion of the perianth extends to the pistil, and the
result is a tubular flower with a so-called "inferior"

ovary (Fig. 46, E). In such flowers the base of the
perianth is completely adherent to the ovary, so that
the outer part of the latter is completely fused with the
base of the perianth-tube, and the perianth appears to
be attached to the top of the ovary. Familiar examples
of this are seen in the various species of Narcissus (Fig.
46, E), Amaryllis, and other members of the Amaryllis
family.

Much more profound modifications of the lily type
are met with in the Iris family. Here the cohesion of
the parts of the flower is accompanied by a suppression
of one set of stamens, and in some of them the flowers
are strongly zygomorphic, *i.e.* bilaterally symmetrical,
as in Gladiolus. The genus Iris (Fig. 46, F) is per-
haps the most specialized of the family, the peculiar
arrangement of the floral parts, especially the stamens
and pistil, being such as to render insect aid abso-
lutely necessary in order that pollination may be
effected.

Some of the lily family reach the dimensions of trees,
showing a secondary increase in the thickness of the
stems, a rare occurrence among the Monocotyledons.
This is brought about, however, not by the contin-
ued growth of the primary vascular bundles as in the
Gymnosperms, but by a zone of growing tissue in the
ground-tissue, within which new vascular bundles of
limited growth develop, so that a section of the stem
of one of these arborescent Liliaceæ does not show
definite growth-rings, but appears as a mass of nearly
uniform parenchyma, in which are imbedded the
numerous isolated vascular bundles. The Yuccas of
the southern United States, and the Dracænas and

allied forms of the Old World, are the best-known examples of these arborescent lilies.

Various other adaptations of the vegetative parts are shown by many Liliiflorae. Most of them are herbaceous forms, which develop underground stems capable of resisting extremes of both cold and dryness. These are either bulbs, tubers, or similar shortened and thickened subterranean stems in whose cells, or those of thick scale-leaves growing from them, are stored up starch and other food-materials. These bulbs and tubers can endure complete drying up without injury, and remain dormant during the long periods of cold or extreme drought to which the plant may be subjected, and start into growth very quickly on the advent of favorable growing conditions, drawing upon the stored reserve food until the new leaves and roots are developed.

These bulbous liliaceous plants are especially developed in those countries which have a marked wet and dry season. California and the Cape district of Africa illustrate this, both of these regions being notably rich in liliaceous plants, many of them having flowers of great beauty.

The tendency to form zygomorphic flowers, found occasionally in the Liliiflorae, becomes the rule in the two most specialized orders of the Monocotyledons, the Scitamineae, and the Gynandrae. The former comprises the Ginger and Banana families, as well as the familiar Cannas of the gardens. The Gynandrae include two families, of which the Orchid family is by far the more important, and includes a very large majority of the forms. Both Scitamineae and Gynandrae are character-

ized by an inferior ovary and strongly zygomorphic flowers, with a reduction in the number of stamens often to a single one. These two orders represent undoubtedly the highest degree of specialization among the Monocotyledons.

THE SCITAMINEÆ

The Scitamineæ are, with very few exceptions, tropical plants of very striking and characteristic appearance. They are mostly plants of large size with very large leaves and often showy flowers. Many of them are cultivated for the beauty of their foliage and flowers, like the species and varieties of Canna (Fig. 47, A), while others, like the ginger, and especially the banana and plantain, are important food plants. They usually have a thick underground rhizome from which are sent up the strong shoots, whose large leaves when young are usually rolled up like a cornucopia. Each shoot in most of them terminates in a large inflorescence, and after the fruit is ripe the shoot dies. Occasionally the growth of the stem is not checked by the formation of flowers, and it may assume almost tree-like proportions, as in the curious "traveller's tree," Ravenala. The flowers of some genera, like Canna, are themselves very showy, but quite as often the showy inflorescence owes its attractiveness to the bright-colored bracts in whose axils the inconspicuous flowers are borne. This is well illustrated by the gaudy yellow or scarlet bracts of Heliconia and the pink or crimson ones of many species of Zingiber.

Another peculiar order of Monocotyledons confined to

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the New World, is the Bromeliaceæ. These are characterized by modifications of the vegetative parts rather than by the flowers, which are rather simple in structure. Most of the order are epiphytes, and they form one of the most striking features of the tropical American flora. The best known of these are the so-called "Spanish
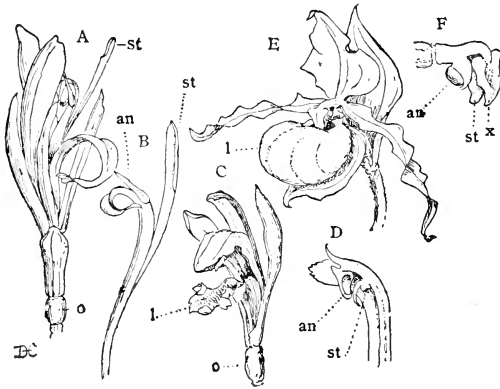
FIG. 47 (Monocotyledons, Scitamineæ, Orchidaceæ). — A, flower of Canna: the flower is strongly zygomorphic, with inferior ovary, *o*, and the stamens reduced to a single one; B, the single stamen, *an*, and the upper part of the pistil, *st*, of A; C, flower of an orchid (Arethusa), showing the marked zygomorphy, inferior ovary, *o*, and the "lip," *l*; D, a section through the "column," or coherent stamen and pistil of Arethusa, showing the single anther, *an*, and the stigma, *st*: the relative positions of the anther and the stigma are such that insect-pollination is absolutely necessary; E, flower of the wild yellow lady's-slipper (*Cypripedium pubescens*), one of the orchids; *l*, the sac-shaped lip; F, the column of the lady's-slipper, showing one of the two fertile stamens, *an*, the stigma, *st*, and the third, sterile stamen, *x*.

moss," of the southeastern United States (*Tillandsia usneoides*), and the cultivated pineapple. Several species occur in Florida, but it is further south that they reach their greatest development. In the West Indies they are abundant and varied, and form a very conspicuous feature of the vegetation, covering the branches of

the trees with great masses of their spiky leaves, with here and there clusters of showy crimson bracts, or in some cases gayly colored flowers. The broad, overlapping leaf-bases, and the scales upon them, form efficient reservoirs both for water and the accumulation of vegetable mould, which these "air-plants" need for their subsistence, as they are in no sense parasites upon the trees to which they are attached.

Probably to be regarded as the most specialized of all the Monocotyledons are the Orchids. In these the flower is strongly zygomorphic (Fig. 47, C, E), and usually one petal is decidedly different from the others and forms the "lip" (*l*). In much the greater number of them the stamens are reduced to a single one, which is coherent with the upper part of the pistil and forms with it the "column" (Fig. 47, D, F), but sometimes two stamens are present. Usually the pollen-spores are held together in masses (pollinia) by a viscid substance, and the position of the pollinia is such that insect aid is necessary to dislodge them and transfer the pollen to the stigma. We find, consequently, among the orchids a wonderful variety of ingenious devices by which cross fertilization is effected. Sometimes the flower is adapted to pollination by a single species of insect upon which it is absolutely dependent.

In spite of these perfect adaptations for cross-fertilization, the orchids seem for some reason to be less perfectly suited to their environment than many other plants. They seldom occur in such great numbers together as to make much of an impression upon the aspect of the vegetation as a whole, although individually they are often among the showiest of flowers. Compared

with the Compositæ among the Dicotyledons, or with the grasses, which they far outnumber in species, they give the impression of a group of plants in a formative condition, which has not yet reached a stage which fits them to compete successfully with their hardier rivals.

Among the interesting modifications shown by the orchids and not found elsewhere among the Monocotyledons (except in the nearly related Burmanniaceæ), is the adoption of the saprophytic habit by some of them. Such forms, *e.g.* Corallorhiza, are characterized by a partial or complete loss of chlorophyll, with a corresponding reduction of the leaves, which are small and scale-like.

Summary

Considering the Monocotyledons as a whole, they are much less numerous than the Dicotyledons as well as simpler in structure, and these points together with certain structural resemblances between them and the ferns seem to indicate that they are the more primitive of the two great divisions of the Angiosperms, and it is not improbable that they have originated directly from pteridophytic ancestors, or possibly through forms related to the Cycads.

It seems likely that the lowest of the Monocotyledons are the simple aquatic forms like Naias, where the flower consists of a single stamen or carpel, and from these the higher types with hermaphrodite flowers, and later those with a showy perianth, have been derived. It is true that many botanists consider the extreme simplicity of the flowers of the aquatic Monocotyledons to be a reduced

condition, but there is no evidence of such reduction shown by a study of their development, and they cannot readily be referred to any of the higher types of flowers.

From the apocarpous type, *i.e.* that in which the carpels are all distinct, the next step in the evolution of the flower is the development of a flower like that of the lilies, with the carpels united to form a compound pistil, usually composed of three parts. In this type, which is usually considered the central type of the Monocotyledons, the prevailing number of the different organs is three.

From the lily type may be readily derived all the higher petaloideous forms, the Iridaceæ, the Scitamineæ and the Orchidaceæ. In these there is a cohesion of certain parts of the flower and usually a reduction in the number of stamens. On the whole, the orchids represent the most highly specialized types.

The affinities of certain other groups are not so obvious. The grasses, palms, and aroids cannot readily be referred to the same series as the lilies, and it is likely that each of these groups has been derived directly from apocarpous ancestors. The palms and aroids show certain points in common, while the latter group resembles in certain respects the aquatic forms, like some of the pond-weeds and their allies, and is probably related to them.

The grasses must remain for the present very much by themselves. Perhaps a thorough study of their embryology may throw some light upon their affinities, which at present, it must be admitted, are very obscure.
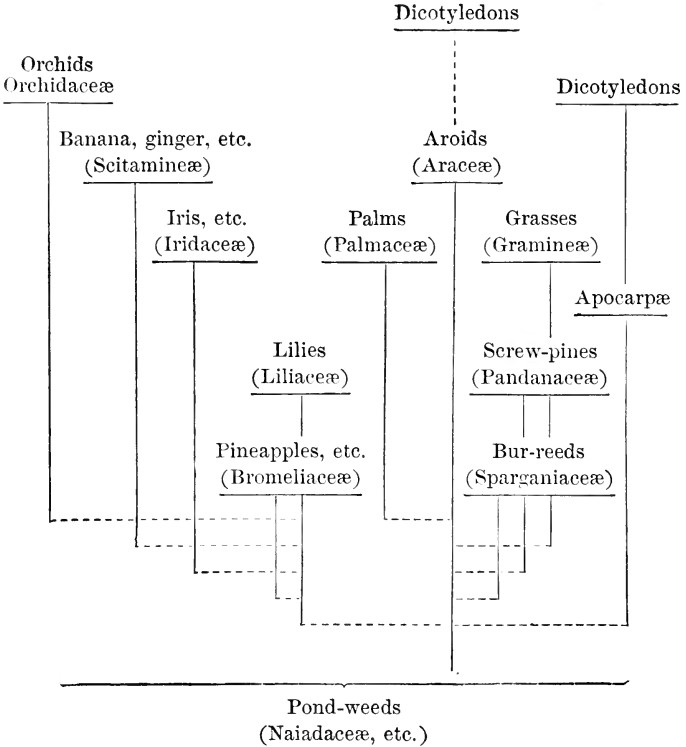
Diagram to illustrate the relationships of the principal orders of
Monocotyledons.

CHAPTER XI

DICOTYLEDONS

THE Dicotyledons, the second great division of the Angiosperms, comprise the major part of existing plant forms, and it is among these that the vegetable organism reaches its most complete expression. Compared with the Monocotyledons they are both more numerous and more varied. With the exception of the grasses and a few aquatic types, the Monocotyledons are seldom abundant enough, at least in temperate regions, to give a prevailing character to the vegetation of any district; the Dicotyledons, on the other hand, are often gregarious and better able to hold their own in the struggle for existence. All the forest trees of temperate regions, except Conifers, are Dicotyledons, and except for the grasses, hardly any of the aggressive plants we call weeds are Monocotyledons, and, as we have seen, very few types of the Monocotyledons attain the size of trees.

The most constant character shown by the Dicotyledons is the presence of two cotyledons or primary leaves in the embryo (Fig. 48). A few cases where only a single cotyledon is present can usually be accounted for by the abortion of one of the cotyledons, but it is possible that there may be forms which are intermediate in this respect between the two great

groups of Angiosperms, although at present no such forms are certainly known.

The Dicotyledons exhibit great variety in the form of the stem and leaves, and this is correlated with a much more perfect development of the tissues than is found elsewhere in the vegetable kingdom. This is shown especially in the highly developed vascular bundles, which in the stems of the woody forms show a secondary thickening like that in the coniferous stem, but the tissues of the bundle are much more specialized than in the latter. From the continued growth of the cambium or active tissue in the bundles of the stem, annual growth-rings result, and soon the greater part of the stem is made up of the secondary wood derived from the activity of the cambium. This results in the development of the massive woody stems characteristic of dicotyledonous shrubs and trees.
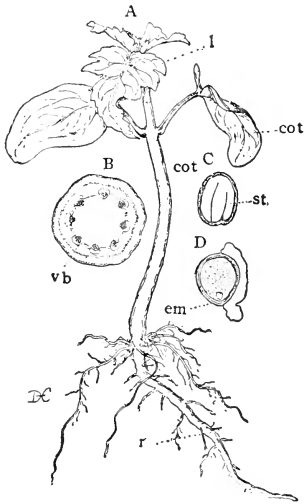
FIG. 48. — A, a seedling of the castor-bean (Ricinus), showing the difference in appearance between the two cotyledons, cot, and the second leaves, l; r, the main or tap-root, a continuation of the stem; B, cross-section of the stem, showing the arrangement of the tissues; vb, the vascular bundles; C, section of the seed of the shepherd's purse (Capsella), the embryo occupying the whole seed-cavity; cot, cotyledons; st, stem; D, section of the seed of blood-root (Sanguinaria), showing the small embryo, em.

In this secondary thickening of the stems and roots, the Dicotyledons differ from the Monocotyledons and ap-

proach the Conifers, where a similar method of second-
ary thickening seems to have been developed quite
independently.

While the leaves of the Monocotyledons are usually
linear, with parallel venation, those of the Dicotyledons
exhibit great variety in outline and venation. They
may occasionally have simple leaves much like those
of the typical Monocotyledons, but much oftener the
leaves are broadly expanded, with a clearly defined
petiole or stalk, and a broad lamina with reticulate
venation. The base of the petiole is often provided
with small leaf-like appendages, stipules. The ar-
rangement of the veins varies with the shape of the
lamina, but is always more or less clearly reticulated.
There may be only one main vein or midrib, or there
may be several large veins of nearly equal size radiat-
ing from the junction of the lamina and petiole. While
the margin of the leaf may be smooth as in most Mono-
cotyledons, it is oftener variously indented or lobed,
and this may be carried so far as to result in a complete
division of the lamina into separate leaflets, and thus
compound leaves like those of the ferns arise. The
size of the leaves is largely dependent upon the condi-
tions of growth, and in plants of very dry regions, or
in some parasites and saprophytes, the leaves may be
entirely wanting. Where leaves are entirely absent
their place may be taken by portions of the stem, whose
outer cells develop chlorophyll.

The variation in the stem is quite as marked as that
of the leaves. The stems may be herbaceous or woody;
extremely short, even bulbous, like many Monocotyle-
dons; or they may be enormously lengthened, slender

twining, or creeping ones; or again, branches may be modified into thorns or tendrils. Underground portions of the stem frequently develop stolons or tubers which serve to propagate the plant. These are but a few of the manifold forms which the dicotyledonous stems may assume.

The flowers of the Dicotyledons show much the same general structure as those of the Monocotyledons, and there is much the same difference between the highest and the lowest types, the latter hardly surpassing the simplest ones found among the Monocotyledons. While there is much variation in the number of parts in the flowers, it may be said that in the higher types the parts — at least sepals and petals, and frequently the stamens — are most commonly in fives. The number of carpels is usually smaller.

As might be expected from the great diversity shown in the flowers, there is also great variety in the character of the fruit and seeds, much more so than is the case among Monocotyledons. A further discussion of this point, however, will be left for a later chapter.

The carpels and stamens of the typical Dicotyledons resemble closely those of the Monocotyledons. The ovule has the same structure, but in many types has but a single integument, this being especially the case in the highest group, the Sympetalæ. The macrospore (embryo-sac) originates in the same way, and the fully developed gametophyte shows the egg-apparatus at the upper end of the sac, with the three antipodals at the lower end. The latter, however, may in exceptional cases be considerably increased in number.

The development of the stamen and the pollen-sacs

shows nothing peculiar. The pollen-spores are generally of the same tetrahedral type found in the lowest Archegoniates, and we see that even in these highest of all plants the microspores have hardly departed from the primitive type found in the lowest liverworts, the division of the spore mother-cell and the structure of the ripe spores being identical in both. The germination of the microspores and fertilization are as in Monocotyledons.

The development of the embryo follows at first much the same course as in Monocotyledons, but very early there is in most cases a marked difference manifested. In the Monocotyledons, as a rule, the apex of the embryo becomes transformed into the single cotyledon, the stem-apex being formed laterally; but in typical Dicotyledons the apex of the embryo forms the stem-apex, while the two opposite cotyledons are developed secondarily as lateral appendages of it. It may be stated, however, that Monocotyledons are known in which the stem is derived from a portion of the apex of the young embryo, and it is possible that a similar condition may obtain in some of the lower Dicotyledons. At present our knowledge of the embryogeny of the lower members of both of the great divisions of Angiosperms is far from complete.

The degree of development attained by the embryo before the seed ripens, varies a good deal in different Dicotyledons. In some forms, especially saprophytes and parasites with minute seeds, e.g. the Indian pipe (Monotropa), the embryo in the ripe seed is completely undifferentiated and consists of a few cells only. Usually, however, it is well developed, and the primary

organs, stem, root, and cotyledons, are readily made out.
The embryo may be imbedded in the endosperm and
not occupy the whole of the seed-cavity (Fig. 48,
D), but more often, perhaps, the endosperm is com-
pletely absorbed before the seed ripens, and the large
embryo fills the seed completely, as we see in all legu-
minous plants. In such embryos the cotyledons are
very large and thick, and their cells are filled with
starch and other food-substances which are used up in
the early stages of germination (Fig. 48, C).

The cotyledons usually differ a good deal in shape
from the later leaves (Fig. 48, A), which gradually
acquire their perfect form. The cotyledons, where the
embryo fills the seed, are, as we have seen, thick and
fleshy, with obscure veins; but where the embryo does
not fill the seed, and endosperm is present, they are
usually more like the later leaves, being thin with
prominent veins, as in the morning-glory.

None of the Dicotyledons occur as submersed marine
plants, but otherwise they are found in nearly every
situation where plants can grow at all. They may be
completely immersed in fresh water, *e.g.* bladder-weed
(Utricularia), or the leaves may float as in the water-
lilies, while many of them are inhabitants of swamps,
where they are more or less completely submerged.
Many of them live in the sand of the seashore, while
others are desert plants. The various forms of sage-
brush and cacti of our own Western arid regions are
excellent types of these "xerophytic" Dicotyledons.
In these the evaporating surface is greatly reduced by
the minute size of the leaves, and loss of water is further
retarded by excessive thickening of the outer tissues of

the stem and leaves. These thick protective tissues also serve to shield the underlying green cells from the too strong rays of the sun. The latter result is also brought about in many desert plants by the development of a thick covering of hairs to which the peculiar gray color of many of these is due.

Dicotyledons are among the last plants to disappear upon high mountains, and some of them have been encountered as far toward the poles as explorations have extended.

Among the Dicotyledons are found the most extraordinary modifications known among plants, such as the remarkable contrivances developed in some of the insectivorous plants like the pitcher-plants and the Venus's fly-trap. It is among these also that the most perfect types of climbing plants are found, especially those with tendrils of various patterns. Parasites and saprophytes are common in certain families of Dicotyledons, while among the Monocotyledons they are rare. The mistletoe and dodder are familiar examples of parasites, while the Indian pipe of the eastern United States, and its near relative the curious "snow-plant" (Sarcodes) of the Sierra Nevada, may be cited as typical saprophytes. Everywhere, except in the sea, where any vegetation exists at all, we encounter the ubiquitous Dicotyledons.

Classification of Dicotyledons: Choripetalæ

The Dicotyledons may be divided into two pretty well-defined great divisions, each of which contains numerous orders. In the lower series (Choripetalæ), the petals are quite separate, and this may be true of other parts

of the flower as well; but in a larger number the carpels are more or less completely coherent, and the sepals are also frequently united into a cup-shaped or tubular calyx.

The lowest of the Choripetalæ are the Amentaceæ, so named from usually having the simple flowers in elongated catkins or aments. The willows (Fig. 49, A–D), poplars, and various nut-trees are familiar examples of this group. A second order allied to these includes the
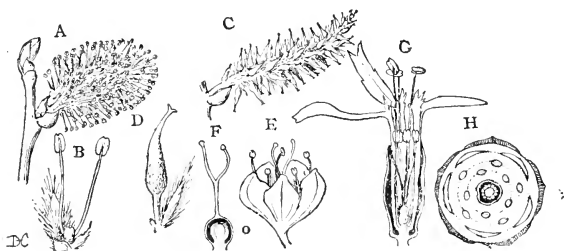
Fig. 49 (Lower Dicotyledons — Amentaceæ, Centrospermæ). — A, male inflorescence of a willow; B, an individual staminate flower consisting of two stamens surrounded by inconspicuous bracts; C, a female inflorescence of a willow, each flower (D) consisting of a single pistil made up of two coherent carpels; E, flower of a knot-grass (Polygonum) : the perianth consists of five colored sepals; F, the pistil of E, with the side of the ovary cut away to show the single ovule borne at the apex of the floral axis; G, section of the flower of a scarlet catchfly (Silene) ; the sepals are united into a tube enclosing the free petals and stamens; the petals are showy, and the flower is pollinated by insects; H, diagram of the flower of Silene; the pistil is composed of three carpels; the central axial placenta bears numerous ovules.

pepper family, a tropical group which superficially, at least, shows a curious similarity to the aroids, and may prove to comprise connecting forms between Monocotyledons and Dicotyledons. In these low types the flowers are often diclinous, *i.e.* stamens and carpels are in separate flowers and no perianth is present, or the perianth is reduced to inconspicuous scales. It is generally supposed that these amentaceous Dicotyledons

are reduced forms, but this cannot be taken for granted, and further investigation is needed before definite conclusions can be reached as to their systematic position.

The Amentaceæ are largely inhabitants of the cooler parts of the world, some of them, like the willows and
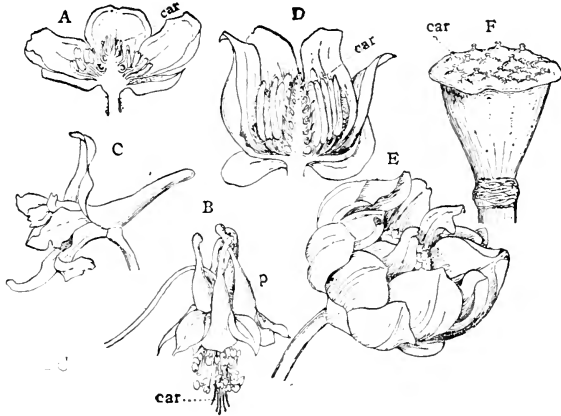
FIG. 50 (Polycarpicæ). — A, section of the flower of a buttercup (Ranunculus): the numerous carpels are entirely separate; B, flower of wild columbine (Aquilegia); the petals, p, are modified into tubular nectaries; C, flower of a larkspur (Delphinium); the flower is strongly zygomorphic, and the two upper sepals form the spur, or nectary; D, flower of the tulip-tree (Liriodendron), one of the Magnolia family; the flower is divided lengthwise to show the numerous stamens, and the separate carpels grouped together upon the elongated central receptacle; E, flower of the wild lotus (Nelumbo), one of the water-lily family; F, young fruit of the lotus, consisting of the enlarged conical receptacle, with the separate carpels, car, embedded in cavities in its upper surface.

birches, being among the most northerly of all trees and shrubs.

A second primitive group of Choripetalæ is the Polycarpicæ represented by the buttercup family and its allies. Some of these also recall one group of the Monocotyledons, the Apocarpæ, e.g. Alisma, Sagitta-

ria, etc., in the character of the flowers. The parts of the flower are all separate, and in the lower members of the group, of indefinite number. This is well shown in the various species of buttercups (Ranunculus). The Ranunculus family also offers some interesting examples of specialization within a group which nevertheless retains a very primitive type in the arrangement of the floral parts. In Anemone (Fig. 55, A) and in Clematis, as well as other genera, the petals are quite suppressed or inconspicuous, while their place is taken by the large petaloid sepals. Some other genera, like the columbines (Aquilegia), larkspurs (Delphinium), and monkshood (Aconitum), have the parts of the flower extraordinarily modified in form, and yet retain the primitive completely separated carpels and numerous stamens (Fig. 50, B, C). These modifications of the flower are all intimately connected with insect-pollination, and many of the more specialized forms like Delphinium and Aquilegia are probably entirely dependent upon insects or humming-birds for pollination. On the other hand, some species of Ranunculus with inconspicuous flowers are always self-fertilized. Other Polycarpicæ are the water-lilies (Nymphæaceæ, Fig. 50, E), magnolias, and several other less familiar families.

Another probably primitive group of the Choripetalæ is the order known as the Centrospermæ. The lowest members of the series, the buckwheat family (Polygonaceæ, Fig. 49, E), the pig-weeds (Chenopodiaceæ), etc., have flowers which recall the peppers and some of the simple Monocotyledons in having the single ovule formed directly from the apex of the floral axis (Fig. 49, F, *o*). The higher ones have numerous ovules,

which also arise from the apex of the axis, which here forms the placenta (Fig. 49, H). The lower Centrospermæ have small, inconspicuous flowers which are principally self-fertilized; but some of the higher ones, *e.g.* the pink family, often exhibit very showy flowers which depend upon insect aid. In these more specialized types the calyx is usually cup-shaped or tubular instead of being composed of completely separate sepals (Fig. 49, G). Somewhat higher is a second order (Crucifloræ), including the Cruciferæ (mustard family) and poppies (Papaveraceæ). In these the carpels are usually of definite number and united into a compound pistil. The former family is one of the most clearly defined of all the Angiosperms, having always the same number of parts in the flower, *i.e.* four sepals and petals, six stamens, and two carpels (Fig. 51, A, B). The poppies are more variable in the number of parts in the flower, and must be considered as a more generalized family than the Cruciferæ, and more nearly related to the Polycarpicæ.

The sundews and pitcher-plants (Fig. 58) represent the order Cistifloræ, and are distinguished by perfectly symmetrical flowers, but are of most interest on account of their extraordinarily modified leaves, which form very efficient insect-traps. The violets, which also belong to the Cistifloræ, are characterized by their showy, strongly zygomorphic flowers.

Under the name Eucyclæ have been included a large number of families grouped into four orders, characterized by usually symmetrical flowers whose parts are in fives. Among these may be mentioned the vines (Vitaceæ), maples (Aceraceæ), geraniums (Gerania-

P

ceæ), as well as many others more or less familiar.
(Fig. 51, C, D.)

The order Tricoccæ, of somewhat doubtful affinity, in-
cludes the single family Euphorbiaceæ with the various
species of Euphorbia as types. A few are cultivated,
like the familiar castor-bean (Ricinus), and the showy
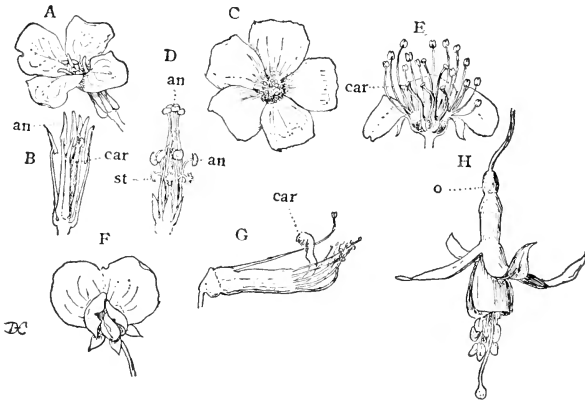
Fig. 51 (Higher Choripetalæ). — A, wall-flower (Cheiranthus): the parts
of the flower are definite in number; B, the six stamens, the two outer
ones shorter than the others, and the pistil, *car*, made up of two cohe-
rent carpels; C, flower of Oxalis, the parts perfectly symmetrical, and
in fives; D, the ten stamens, *an*, in two sets of five each, and the five
carpels, *st*; E, flower of a Spiræa, one side removed to show the five
free carpels, *car*, and the numerous stamens inserted upon the calyx
margin; F, flower of the common pea (Pisum), showing marked zygo-
morphy; G, the ten stamens, one of them free, and the single carpel, *car*,
of the pea; H, a flower of Fuchsia, with "inferior" ovary, *o*, and showy
colored sepals.

Crotons and Poinsettia of the greenhouses. The
flowers in all Euphorbiaceæ are inconspicuous, but it
is common for them to develop showy bracts about the
clusters of flowers, and these serve the same purpose as
the showy petals of other Choripetalæ.

The most specialized as well as the most numerous

of the Choripetalæ are the Calycifloræ, so called from the fact that the sepals are united into a tubular or cup-shaped calyx upon whose margin are inserted the petals and stamens. Very commonly the floral axis is prolonged into a tube which may be completely grown to the ovary at its base, so that the ovary becomes "inferior," as we have seen to be the case in the higher Monocotyledons. Much the commonest number for the sepals and petals is five, although some families show regularly four, e.g. the Onagraceæ (fuchsia, evening-primrose, etc.), and occasionally the number is indefinite (Cactaceæ). The number of stamens in the Calyciflora is occasionally the same as the petals, but usually either double the number, or still more numerous.

The order Rosifloræ, which is subdivided into several families, is one of the largest and most familiar groups of the Calyciflorae. In some of these, e.g. the strawberry, the carpels are quite separate, while in others, e.g. apple and pear, they are more or less completely united, and there is an approach to an inferior ovary.

The myrtle family (Myrtaceæ) is mainly tropical. The petals are often wanting, but the numerous stamens, which are white or red, are very conspicuous and serve to attract insects just as showy petals would do. The ovary is here inferior, and the tissues of the calyx may become fleshy and edible in the ripe fruit, as in the pomegranate or guava.

The Aralia family and the parsley family (Umbelliferæ) are two related families of the Calyciflorae, which are not, however, very clearly related to the others. Of the former the common ivy (Hedera) and the sev-

eral native species of Aralia, including the ginseng, may be mentioned. The Umbelliferæ are mainly inhabitants of the northern hemisphere and are all closely related. Both of these families are distinguished by the arrangement of their usually inconspicuous flowers in umbels — hence they are united with the allied family Cornaceæ (dogwoods) into a common order Umbellifloræ.

Two of the most specialized orders are the Passiflorinæ (passion-flowers and their allies) and the Cactaceæ. The latter is a very peculiar group of American desert plants; the former are also largely American, but belong principally to the moist tropical regions.

The last order of the Calycifloræ is a very important one, the Leguminosæ, including the beans, peas (Fig. 51, F, G), and other leguminous plants. Of the three families, two, the Mimoseæ, of which various species of Acacia and Mimosa are cultivated, and the Cæsalpineæ, of which the honey-locust (Gleditschia) and the red-bud (Cercis) may be mentioned as native, are mainly tropical, while the other and much larger family, Papilionaceæ, includes most of the numerous Leguminosæ of temperate regions. The characteristic butterfly-shaped flowers of these plants, and their pod-shaped fruits, are too familiar to need further description.

THE SYMPETALÆ

The Dicotyledons which have just been considered either have the petals entirely separate or quite absent. There is a second division, including the most specialized as well as the larger number of the Dicotyledons, in which with very few exceptions the petals are more or

less completely united, and the corolla is "sympetalous," or "gamopetalous." The greater number of these, in addition to their being more highly specialized, indicate that they are, as a whole, a later and more differentiated group than the Choripetalæ, although it must be remembered that certain families of the latter are highly specialized. The highest of the Sympetalæ, however, are probably the most recent and highly developed of all plants.

FIG. 52 (Sympetalæ). — A, flower of wild Azalea (*A. viscosa*), one of the isocarpous Sympetalæ : all the parts of the flower in fives ; B, a section of the ovary of Azalea, showing the five divisions ; C, flower of the pine-sap (Monotropa), the petals and sepals quite separate ; D, flower of the sorrel-tree (Oxydendrum), the petals coherent almost to the tips ; E, flower of the shooting-star (Dodecatheon), one of the primrose family : F, flower of Petunia, one of the anisocarpous Sympetalæ ; parts of the flower in fives, except the two carpels, shown in the cross-section of the ovary, G.

The Sympetalæ fall readily into two main divisions, the Isocarpæ, which have the carpels equal in number to the petals, and the Anisocarpæ, in which they are fewer. None of the Sympetalæ ever have the carpels separate, but they are always completely united into a compound pistil. The Isocarpæ are supposed to be the more primitive of the two divisions, and a few of them have the petals almost free (Fig. 52, C), and to some extent connect the Choripetalæ and Sympetalæ. Of these isocarpous forms the

beautiful Rhododendrons and Azaleas (Fig. 52, A) are familiar, as well as the various species of cranberries, huckleberries, wintergreen, etc.   The trailing arbutus of the Atlantic States, and the manzanita and madroño (Arbutus) of the Pacific coast are also characteristic types.   The other two orders of the Isocarpæ are represented by the primroses (Primulinæ) and the persimmons (Diosporinæ).

The great majority of the Sympetalæ belong to the second division, Anisocarpæ.   These are especially abundant in the tropics, where they form the predominant constituents of the vegetation.   The less specialized types are included in the order Tubifloræ, with regular tubular or funnel-shaped flowers.   Here belong the morning-glories, the phloxes, and nightshades, all of them including familiar wild or garden plants (Fig. 52, F).

The second order of the Anisocarpæ, the Labiatifloræ, as the name indicates, has flowers which are usually strongly bilabiate, *i.e.* are markedly zygomorphic. This, together with a reduction in the number of stamens, indicates a more specialized type than the Tubifloræ.   The two most important families of the temperate regions are the figworts (Scrophulariaceæ) and mints (Labiatæ), both of which include numerous familiar wild and cultivated plants (Fig. 53, A–D).   In both of them the stamens are reduced to two or four, and they often exhibit very perfect adaptation to cross-fertilization. Allied to these, and represented in the warmer parts of the United States by a few examples, is the Bignonia family, much more abundant, however, in tropical regions.   Catalpa and Tecoma (the trumpet-creeper) are the genera occurring within our limits.

The third order of the Anisocarpæ, the Contortæ, includes several characteristic families, among them the milkweeds (Asclepiadaceæ) and dogbanes (Apocynaceæ). To the latter belong the oleander and periwinkle, while the gentians, and the olive family
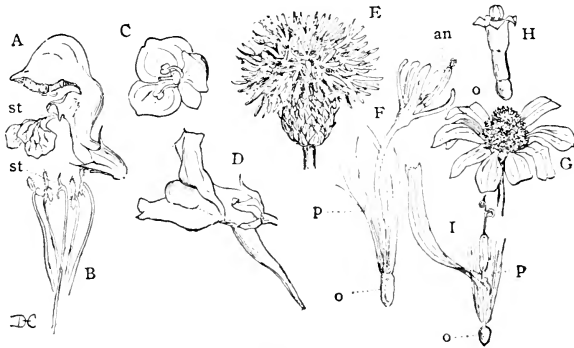
FIG. 53 (Sympetalæ, Labiatifloræ, Compositæ). — A, flower of dead-nettle (Lamium), the flower strongly zygomorphic; B, stamens and pistil of Lamium; C, flower of speedwell (Veronica), the stamens reduced to two; D, flower of toad-flax (Linaria), the flower zygomorphic, and the base of the corolla prolonged into a spur; E, inflorescence of the Canada thistle (Cirsium), the small flowers aggregated into a head which looks like a single flower; F, an individual flower of E; *o*, the inferior ovary; *p*, the hairs which form the "pappus," or calyx; *an*, the coherent anthers; G, inflorescence of the may-weed (Maruta), the outer flowers sterile and petal-like, serving merely as organs for attracting insects; H, one of the tubular perfect flowers from the central part, or disk, of the inflorescence of Maruta; I, a single flower from the inflorescence of the dandelion; all the flowers are alike and have the corolla split open and strap-shaped; *p*, the feathery pappus; *o*, the ovary.

(Oleaceæ), with the lilac and ash as familiar representatives, also belong to the Contortæ.

The highest of all the Anisocarpæ, and therefore at the head of the whole vegetable kingdom, are the Aggregatæ, including several families. Of the lower families, the honeysuckles (Caprifoliaceæ) and the madder family (Rubiaceæ) are the best known, while

the great family of Compositæ is the highest of all.
The latter is the largest family of plants and shows
extreme specialization of the floral structures in the ex-
tensive cohesion of the parts, which extends to the sta-
mens as well as the other parts of the flower. The
flowers, as is well known, are aggregated in dense heads
surrounded by bracts which give the whole inflorescence
the appearance of a single flower (Fig. 53, E, G). This
is especially so in such forms as the asters and daisies,
where the outer flowers have the corolla large and flat-
tened, so that each of these "ray-florets" looks like a
single petal. In many genera these outer flowers are
destitute of stamens and sometimes the pistil is also
abortive, and the ray-florets serve simply to make the
inflorescence conspicuous. There are many interesting
transitions between the lower Compositæ, where all the
flowers of the inflorescence are alike, and those in which
the ray-florets are entirely sterile.

The type of inflorescence developed in the Compositæ
seems to have been particularly effective, as these plants
are notoriously prolific. The actual number of seeds is
not excessively large as compared with many other
plants ; but each individual flower almost always suc-
ceeds in ripening its seed, and the one-seeded fruits are
usually provided with most efficient means of transpor-
tation. One has but to think of the legions of common
Composites, — daisies, sunflowers, thistles, burdocks,
dandelions, and many others of our commonest and
most troublesome weeds, — to realize how well fitted
these plants are to hold their own in the struggle for
existence.

Summary

Owing to the enormous number of Dicotyledons the task of arranging them systematically is a formidable one, and it is unlikely that any arrangement yet proposed can be considered final. Very much more information is needed in regard to the development of both floral and vegetative parts, as well as in regard to the embryology, especially in the obscure and doubtful types, before we shall have the data necessary for a satisfactory classification. Their relation to the Monocotyledons is also very uncertain, and a thorough comparison of the lower types of Dicotyledons with these is very much needed.

It is generally admitted that the apocarpous Choripetalæ, *i.e.* those with entirely distinct carpels, are the most primitive. The simpler Ranunculaceæ offer many resemblances to the apocarpous Monocotyledons, and it is possible that here we have a point of contact between the two groups. It is, however, not at all impossible that the Dicotyledons have had a multiple origin, and the possibility of the derivation of the Piperineæ, and possibly the lower Centrospermæ from monocotyledonous types like the aroids, is not improbable. This would imply that some, at least, of the apetalous Dicotyledons are primitive types, and not reduced from petaloideous forms. The occurrence of numerous apetalous types among the oldest fossil remains of Dicotyledons also strongly suggests their primitive character. If this view is correct, it is quite possible that the Amentaceæ and some other Apetalæ constitute a line of development entirely distinct from that of the petaloideous forms.

In passing from the lower to the higher types there is a reduction in the number of parts, accompanied by their cohesion. The carpels are first affected, and then the sepals, and finally the corolla. Reduction in the number of stamens is common in certain groups, especially the Labiatifloræ, and the cohesion of the stamens among themselves occurs regularly in the Compositæ, but is much less perfect than that of the other floral parts. Most of the more specialized types, both of Choripetalæ and Sympetalæ, have inferior ovaries.

The Sympetalæ are unquestionably the highest of the Angiosperms. Whether the group is a homogeneous one, or, as seems more likely, sympetaly has originated more than once, must be determined by further researches. The radially symmetrical (actinomorphic) Isocarpæ are probably nearer the Choripetalæ, as shown by the occurrence of forms like Monotropa, which have sepals and petals quite distinct. It has recently been suggested that the Isocarpæ have perhaps been derived from the Centrospermæ among Choripetalæ and have given rise to the Tubifloræ and Labiatifloræ, whose highest members are the mints and figworts. Another line, originating from the Calycifloræ, has through the Umbelliferæ developed the Rubiaceæ (madder family), and through these the Compositæ. There are several less important lines of development which cannot be taken up here, and it must be remembered that the suggestions given here as to the origin of the different groups of Dicotyledons are likely to be essentially modified when we are in possession of data more complete than we now possess. The accompanying diagram illustrates graphically the arrangement of the principal groups of Dicotyledons adopted here.
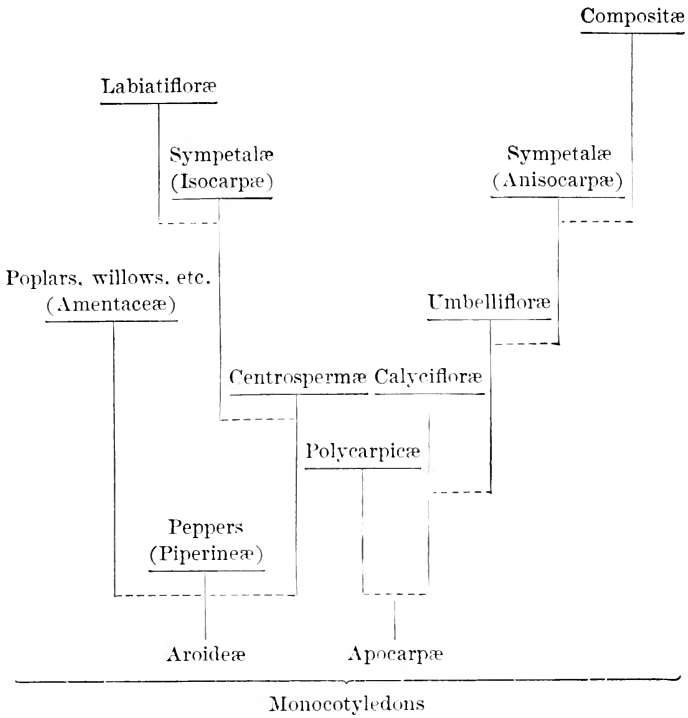
Diagram to show the relationships of the principal groups of Dicotyledons.

CHAPTER XII

GEOLOGICAL AND GEOGRAPHICAL DISTRIBUTION

THE history of the Plant Kingdom as revealed by the geological record is necessarily very fragmentary, but nevertheless the study of fossil plant remains has yielded most important evidence for tracing the succession of plant forms. The record is most unsatisfactory with reference to the lower plants, whose delicate tissues are poorly fitted to leave recognizable remains in the rocks. Long before there is any absolute evidence of the existence of plants, it must be assumed that these lower plants were present upon the earth, but naturally their delicate and extremely perishable structures have left no fossil traces. Indeed, throughout the Thallophytes, with few exceptions, the fossil remains are so imperfect that a satisfactory estimate of their real nature is often quite impossible.

The ferns and their allies have been preserved in many cases with remarkable perfection, and the same is true of many flowering plants, especially in the later formations, and among the Algæ a few groups possessing silicious or calcareous cell-walls, have been preserved in a recognizable form, but these nearly all belong to the later formations and throw no light upon the character of the earliest forms. Among the vascular plants, however, the tissues are sometimes preserved with such

remarkable perfection, that thin sections of them may be examined with the microscope and reveal the minutest details of their cellular structure. A careful study of such remains has thrown much light upon the real nature and affinities of many fossil types. Very rarely, it is true, have the reproductive parts, so essential in classification, been preserved; but occasionally this occurs, and a study of these has been of the greatest value in determining the relationship of these fossil forms.

Unfortunately, too much of the work upon fossil plants has been done by men who were not botanists and who were not sufficiently acquainted with the existing plants allied to the fossil ones. Consequently great confusion has arisen in the attempts to name and classify these fossils.

In general it may be said that the geological record bears out the conclusions reached from a study of comparative morphology, although as regards the Thallophytes the record is too imperfect to have much value.

The earliest recognizable plant remains occur in the lower Silurian rocks, where there have been found impressions which have been referred to algæ, perhaps related to the coarser red or brown forms existing at present, but not readily assignable to any existing types, so that the real nature of these plant remains, if such they really are, is exceedingly doubtful.

Of the existing types of algæ, a number are known in a fossil state, but seldom from the earlier rocks. Of the green algæ, certain Siphoneæ occur fossil in large numbers from the Permian rocks upward. These plants, like many existing ones, were heavily encrusted with

lime and seem to have played an important rôle in rock-building. That anomalous group, the Characeæ, is also represented in the later formations by a considerable number of unmistakable forms. These too, owe their preservation to the calcareous deposit in their cell-walls. The Characeæ are represented not only by fragments of stems, but also by the curious spore-fruits, which are exactly like those of the living types. The earliest of these Characeæ occur in the Miocene rocks. Certain red algæ, Corallineæ, are abundant in the Mesozoic rocks, and probably occurred in the later Palæozoic formations. Many of these are referable to existing genera, and closely resemble forms which are still living.[1]

Among the Algæ, one group, the Diatoms, have left very abundant remains, but as yet these have been found only in the more recent strata. As the silicious shells of these plants are very permanent, their complete absence from Palæozoic rocks seems to indicate that the group is, comparatively speaking, a recent one. The deposits of diatoms are extraordinarily abundant in the later formations, the first ones occurring in the Mesozoic rocks, where, however, they are much less abundant than in the Tertiary formations. The flinty valves or shells are perfectly preserved, and make their identification an easy matter. Many of the genera and even species are identical with living ones. The diatomaceous deposits are often of astonishing thickness, showing that these plants, as at present, occurred in enormous masses together.

The fossil fungi are too few and imperfect to

[1] The most recent investigations point to the existence of Coralline algæ and Siphoneæ in the early Silurian deposits.

throw any light upon the origin of these puzzling organisms.

While it is reasonable to suppose that both liverworts and mosses existed at a very early period, their great delicacy has prevented their preservation as fossils except in a few cases, and these are all in the later formations. No certain remains of Bryophytes are known from the Palæozoic rocks.

With the Pteridophytes the case is very different. From the Devonian, and possibly still lower, their remains occur in great profusion, especially in the Carboniferous rocks, where they form the predominant type of vegetation, and their remains are often preserved in a most perfect manner, even the inner structure often being so clear as to make a comparison with the tissues of the living forms an easy matter.

The earliest remains attributed to the ferns occur in the lower Silurian rocks, where a fossil named Eopteris has been found. It is doubtful, however, whether this really is a fern. In the Devonian, undoubted ferns occur. Some of these, e.g. Palæopteris, are admirably preserved so far as the leaves are concerned, and some traces of sporangia have been detected, but these are too imperfect to make clear the affinity of the plant with modern types.

It is in the coal measures that the most numerous remains of ferns are found, and many of these are in a remarkably perfect state of preservation. The most recent study of these Carboniferous ferns shows that most of them are eusporangiate, and evidently related to the living Marattiaceæ, an order which at present is represented by a small number of tropical species which are

evidently the remnants of a disappearing type. As we have endeavored to show in a previous chapter, the primitive nature of the Marattiaceæ is also shown by the structure both of gametophyte and sporophyte. The Leptosporangiatæ, which at present are the predominant types of ferns, are absent from the older formations, and first appear with certainty in the early Mesozoic rocks. The earliest ones belong to the families which are nearest the Eusporangiatæ, while the more specialized forms appear later.

While the ferns — at least the Leptosporangiates — are still important factors in the present vegetation of the earth, the other two orders are very much less prominent, and many of the types related to them are now quite extinct. Of the Equisetineæ, or horsetails, only the genus Equisetum survives. This same genus can be traced·back to the Mesozoic, and possibly even to the later Palæozoic rocks, where it is associated with many peculiar genera which disappear completely in the later formations. Among the largest and best known of these ancient forms are the species of Calamites, which were like gigantic horsetails, and whose stems exhibit a secondary thickening of the vascular bundles, so that the stem continued to increase in size until the plant assumed tree-like proportions. Another characteristic group was the Annulariæ, a peculiar family mainly restricted to the Carboniferous and sometimes associated with Calamites. In the few cases where the cones of these fossil Equisetineæ have been preserved, they show an arrangement of the tissues and sporangia much like those of the existing species of Equisetum. It is evident that some of these ancient Equisetineæ were hete-

rosporous, but the difference between the macrospores and microspores was less than in the other groups of heterosporous Pteridophytes.

The oldest fossils which can be referred to the Equisetineæ, occur in the Devonian rocks. They increase in numbers in the overlying formations, reaching their maximum development in the Carboniferous, after which they rapidly diminish in numbers, until the sole survivors of this once important group are reduced to the members of a single genus.

A very characteristic order of fossil Pteridophytes is the Sphenophylleæ, sometimes associated with the Calamiteæ, but probably better separated from the other Pteridophytes as a special class now totally extinct. They had slender stems with the leaves arranged in whorls. The leaves were narrowly spatulate, with more or less conspicuous dichotomous divisions and dichotomous venation. The stem was traversed by a single axial vascular bundle not unlike that of Lycopodium. The sporangial spikes have been preserved, and it is evident that the plants were sometimes heterosporous. Their exact relation to the other Pteridophytes is still uncertain, and further investigations are necessary to determine this.

The Lycopods also reached their greatest development during the Carboniferous, and like the Equisetineæ these ancient forms far surpassed, both in size and complexity, their modern descendants, none of which are plants of large size, the largest being slender creeping or half-climbing forms, reaching occasionally a length of four to five metres. The living genera, Lycopodium and Selaginella, both occur fossil, the former extending

back to the Devonian, thus being one of the oldest genera known in the whole class. During the Carboniferous there appeared numerous arborescent forms, the principal genera being Lepidodendron and Sigillaria. These trees exhibited a secondary growth of the stem, like that of Conifers, and the appearance of these was probably not unlike that of the modern coniferous trees, suggesting that the latter may be really related to forms like Lepidodendron. These were heterosporous like Selaginella, but apparently heterospory was not so pronounced.

Both of the lowest existing types of seed-bearing plants, the Cycads and Gingko, are found fossil. They probably originated in the later Palæozoic formations, perhaps in the later Carboniferous. After the Carboniferous they increase rapidly in numbers, reaching their maximum in the Mesozoic, after which they diminish in numbers, giving way before the more specialized Conifers and Angiosperms. Many of the fossil cycadean remains are very complete, and often are obviously much like the existing genera, several of which, including the genus Cycas, undoubtedly occur fossil.

The peculiar genus Gingko, now reduced to a single species, is represented by numerous fossil species, the oldest dating back to the Permian.

The Cordaiteæ comprise a group of entirely extinct plants which have been considered to be, in many ways, intermediate between the Cycads and Conifers. They are most abundant in the coal measures, but occur as early as the Devonian. They have been so perfectly preserved, in some instances, that the structure of the

flowers can be made out, even to the inner structure of the large pollen-spores, in which the gametophytic structure is more complicated than in any existing Gymnosperms. The pollen-spores have even been detected in the receptacle above the opening of the ovule.

It is doubtful whether any true Conifers existed prior to the Permian formations, where forms allied to living genera occur, but no existing genera, except Gingko, which probably should be removed from the Coniferæ, occur until the Mesozoic, when a number of the living types are encountered. In the later Mesozoic, especially the Cretaceous, and in the early Tertiary formations, they become abundant and characteristic fossils, some of which are scarcely distinguishable from living forms. Most of the existing genera are represented in the Cretaceous rocks, and in some cases even living species can be recognized. Thus the bald cypress of the southern United States, *Taxodium distichum*, is represented by an apparently identical form, *T. distichum miocenum*, which is a common and widespread fossil of the later Miocene and early Pliocene rocks, having been evidently far more widely distributed than at present, as is also the case with the related genera Glyptostrobus and Sequoia. The latter genus is at present reduced to two species, the coast redwood and the giant tree, confined to the mountains of California, but during early Tertiary times both of these, as well as many others, were common trees of nearly the whole northern hemisphere.

The pines and firs appear first in the middle of the Mesozoic, becoming later more abundant, and holding

their own in modern times better than any other Conifers. At present, these are decidedly the prevailing types of coniferous trees, but even these, in most regions, show signs of yielding to the encroachment of the angiospermous trees.

While various fossils from the Carboniferous and early Mesozoic formations have been assigned to the Angiosperms, it is not until the later Cretaceous is reached that undoubted remains of these plants occur. Here are found unmistakable traces of both Monocotyledons and Dicotyledons, but most of the earliest remains are of such character as to throw little light upon the relation which these two groups bear to one another. Among the earliest forms of which recognizable remains are found, are palms and screw-pines among the Monocotyledons, and birches, willows, and poplars among the Dicotyledons. It need not necessarily follow that these are the most primitive of the Angiosperms, although they are doubtless among the more primitive types. Their preservation is simply due to the fact that their tissues were firm and resisted decay long enough to leave clear impressions. Most of the living Angiosperms which are considered as probably the most primitive, especially among the Monocotyledons, have extremely delicate and perishable tissues, which, as in the case of algæ, could hardly be expected to leave recognizable fossil remains.

In the later Tertiary rocks, remains of Angiosperms became very abundant, and most of the existing groups, especially of Dicotyledons, can be distinguished. It is evident that at last a type of plants has been evolved which is rapidly crowding out the less perfect types

which had preceded it. While the comparative scarcity
of Monocotyledons has been explained by the assump-
tion that they are a later development than the Dicoty-
ledons, a more plausible explanation is probably that the
small number of types in which the tissues were firm
enough to have been preserved, accounts for their
scarcity in a fossil state.

The geological history of the Dicotyledons shows, as
might have been expected, that the earlier types are all
Choripetalæ—largely the primitive Amentaceæ, willows,
poplars, etc. These may have been preceded by herba-
ceous forms like the living Piperineæ, but of these no
traces have been found. The Sympetalæ, which are
the most specialized and numerous group at present,
do not appear until much later, and the fossil record,
so far as it goes, is quite in accord with the conclu-
sions based upon comparative morphology.

GEOGRAPHICAL DISTRIBUTION

In considering the distribution of terrestrial plants, as
they at present exist, many factors must be taken into
account. First of all, we must examine the original
distribution of the ancestors of the existing flora, as
revealed to us by the study of fossil forms. There are
next to be considered the factors affecting the distri-
bution of these forms as they are found at the present
time. The most obvious of these factors are climate,
i.e. temperature and rainfall ; direction of mountains
and distribution of arid districts ; currents of air and
water ; animals, including man.

The distribution of plants during the Tertiary period,

as revealed by their fossil remains, was evidently very different from that of the present time. The most striking point about these Tertiary fossils is the wide distribution of many types now extremely limited in their range, and a careful study of the question leads inevitably to the conclusion that at this period in the earth's history a very uniform climate must have prevailed over a large part of the northern hemisphere, and corresponding to this there was a very similar flora throughout its whole extent. It is also evident that a very much warmer and more even temperature must have prevailed in the higher latitudes which at present are incapable of supporting any but the hardiest plants. In early Tertiary times palms, sequoias, magnolias, sassafras, tulip-trees, and many other types, now quite absent from these regions, were abundant in northern Europe, and even in Greenland and Siberia, showing conclusively that at that time a very much milder climate must have prevailed there than at present. These same types occur fossil in the arid western United States, from which they have completely disappeared, owing, no doubt to the unfavorable conditions now existing.

In the higher latitudes at the present day, there exists a zone extending round the earth, where the climatic conditions are very uniform, and where the plants are very similar throughout, much as was the case over a much wider zone in Tertiary times; but instead of laurels and magnolias, palms and sequoias, we find firs and willows, birches and aspen-poplars. Many northern plants, like the beautiful little Linnæa and white birch, are equally at home in Norway and Canada, and the reasons are the same which governed

the distribution of the Tertiary flora of the same regions, *i.e.* similar climate and nearly continuous land communication.

The conditions in the Antarctic regions are very different from those in the northern hemisphere. The southern extensions of Africa and South America are widely separated, and the little explored land area surrounding the pole is totally shut off from both continents, and so far as known possesses a very scanty flora, both on account of its isolation and the excessive severity of the climate.

While, as we have seen, the flora of the high northern latitudes is very similar in both the eastern and western hemispheres, as we go south, more and more new types appear, and as a rule these are quite different in the Old and New Worlds. These differences become more pronounced as the tropics are approached, when whole orders of plants, like the Cacti and Bromeliaceæ of the New World, or the Proteaceæ of the Old World occur, which have no representatives in the other hemisphere. On the other hand, some orders, like the Compositæ and Leguminosæ, are cosmopolitan, as are certain genera, but very few species are thus widespread except as they may have been distributed through human agencies, so that, in the tropics especially, it is exceedingly rare to find identical species in the Old and New Worlds, except as they have thus been introduced.

The alpine flora of high mountains usually contains a number of plants often identical with, or closely related to, species growing much further north, but not occurring at all in the adjacent lowlands. This is es-

pecially noticeable upon lofty mountains in the tropics. Thus in Jamaica the writer has collected upon the highest peaks of the island such northern plants as strawberries and brambles, buttercups and northern species of club-mosses, none of which occur elsewhere in the island nor on the adjacent mainland.   A similar occurrence of northern plants upon high tropical mountains has been repeatedly observed.   The presence of these northern plants on the summit of tropical mountains has been explained by the supposition that their ancestors were driven south by the advance of the glacial ice-sheet, and with the retreat of the latter, and the corresponding increase in the temperature in the lowlands, they retreated up to the cooler regions of the mountain summits, not being able to live in the hot lowlands.

Where an extensive chain of mountains occurs, running north and south, it is possible to see how the northern plants follow them, ascending higher and higher as they proceed southward, seeking in this way the same climatic conditions they have left behind them. In the United States the Appalachian Mountains, the Rockies, and the ranges of the Pacific slope, are all beautiful illustrations of this method of distribution of northern plants.

Comparing the north temperate regions of the eastern and western hemispheres, we find that eastern North America much more nearly resembles eastern Asia than it does the much nearer regions of western Europe. The latter region lies, for the most part, much further north than any part of the United States, and being cut off from the south by high mountains, its whole

flora is characteristically northern. The regions bordering on the Mediterranean, of course, show many forms related to the adjacent regions of northern Africa and western Asia.

In eastern Asia the conditions are very similar to those in eastern North America. In both regions the main trend of the mountains is north and south, so that there is direct communication with the tropics, and in both the climatic conditions are remarkably similar, showing great extremes of heat and cold in the northern portions, the characteristics of a continental climate. In both regions a very large area lies much further south than Europe, and the flora is much richer, this being especially noticeable in the much larger number of forest trees. While in Europe the trees are few in number, probably not more than a third or fourth as many as in the United States or eastern Asia, in the two latter regions there is a remarkably large number of types, both of trees and herbaceous and shrubby plants, which are absent from Europe, and what is perhaps most unexpected, absent also from the Pacific coast of North America. In both eastern Asia and North America, the number of tropical types is very much larger than in Europe, where very few of these exist.

The interior of all the great continents except Europe is more or less arid, and in some cases extensive deserts occur with a very peculiar flora adapted to the desert conditions. Similar arid conditions prevail in the warmer parts of western Asia and America, but western Europe, owing to the invasion of the land by branches of the sea, and the influence of the Gulf Stream, has an insular

rather than a continental climate, and the same is true
of the northern parts of the Pacific coast of North
America.

Within the tropics there are few genera common to
the Old and New Worlds, although many families, *e.g.*
palms, orchids, aroids, and others, are abundantly repre-
sented in both regions, but usually by distinct genera.
Where a genus is common to both regions, it is usually
one which has a wide range through the north tem-
perate regions as well; *e.g.* the orchidaceous genus
Cypripedium and many genera of ferns, *e.g.* Polypodium,
Adiantum.

The flora of isolated regions, seen in its most extreme
form in such oceanic islands as the Hawaiian Islands
and St. Helena, is always exceedingly peculiar, owing to
the long intervals at which new forms are introduced and
the modifications which most of these subsequently have
undergone on account of their changed environment.
Such regions always contain a large proportion of en-
demic or peculiar species. While wide expanses of
ocean offer the most effective barriers to the distri-
bution of most plants, high mountains and deserts also
act as efficient checks to the migration of plants, and
a very different flora may exist upon opposite slopes
of high mountain ranges separated by only a few miles
of actual distance. A marked instance of this is seen
in the character of the plants upon the eastern and
western slopes of the Andes. In the United States
the almost totally different character of the plants
of the Atlantic and Pacific coasts, except in the north-
ern regions where occur a number of the sub-polar
types common to the whole northern zone, illustrates

very graphically the effect of the great central arid region and lofty mountains in preventing the migration of plants from one side of the continent to the other.

As we have already intimated, it is evident from the geological record that in Tertiary times the northern regions enjoyed a much milder climate than at present, this being shown by the character of the fossil remains of both animals and plants. Many of the common Tertiary types of plants are now represented by a small number of their descendants restricted to a much smaller range, like the species of Torreya and Sequoia. In Europe we find these forms associated with many others, like the magnolias, tulip-trees, hickories, and many more, still existing in eastern Asia and America, but elsewhere extinct. In short, the Tertiary flora of the subpolar zone was made up mainly of types still existing in regions much further south. The modern descendants of these Tertiary plants have many of them persisted unchanged in some regions, but have been quite crowded out or very much modified in others. The retreat of these plants from their northern habitat was mainly due, no doubt, to great climatic changes, and the principal of these was the severe glaciation to which the whole northern part of the globe was subjected in post-tertiary times.

As the ice-sheet advanced southward, the plants were driven before it, and many forms were doubtless completely destroyed. The fate of these progenitors of the existing flora of the northern hemisphere was very different in different parts of the earth. In America and eastern Asia the trend of the main mountain ranges is north and south, and offered no barrier to the south-

ward retreat of vegetation before the advancing ice-sheet, and as the latter retired again the plants were enabled to return northward.

In Europe, owing to the position of the great mountain chains, as well as its higher latitude, the whole region north of the Alps was subjected to the action of the glaciers, and the southward retreat of the plants being cut off, very many forms perished, while the same plants have survived in the more favored regions of Asia and America, in both of which a far larger number of survivors of the primordial Tertiary flora occur than in Europe. The occurrence of nearly related isolated types in widely separated regions can almost always be explained as a survival from once widely distributed ancestors. In the case of herbaceous plants, such as Podophyllum, Stylophorum, and other peculiar types common to eastern Asia and Atlantic North America, we can only reason from analogy, but in the case of many woody plants, especially trees, *e.g.* the tulip-tree (Liriodendron), Torreya, etc., this is abundantly proved by the fossil remains.

Perhaps the most striking instance known of close correspondence in the flora of widely separated regions, is the one already spoken of, *i.e.* the great number of identical or closely related plants found in the temperate regions of Pacific Asia, northern China, Mantchuria, and Japan — and Atlantic North America. Much of our knowledge of these extraordinary similarities we owe to the labors of Asa Gray.

The writer recalls vividly the strangely familiar aspect of the vegetation of Japan, especially in the northern part, where nearly all of the more noticeable plants

are either identical with or closely related to eastern American species. Such characteristic plants as the fox-grape, poison ivy, and other sumachs, bitter-sweet (Celastrus), the sensitive fern (*Onoclea sensibilis*), elms, maples, beeches, oaks, and magnolias, very close to their American relatives, as well as others familiar to the botanist, were the predominant features of the vegetation. Were these forms also common to Pacific North America and continuous across the continent, there would be nothing remarkable in their occurrence in Japan; but most of them are entirely absent from our Pacific coast, and from all the intermediate country.

The list of forms common to the Mantchurian-Japanese region and Atlantic North America is very large, and at first seems impossible to explain; but when we consider them, as they doubtless are, remnants of a once continuous northern flora, which have survived in these two widely separated areas owing to very similar climatic conditions, the wonder ceases.

The southern United States illustrate very clearly the very different character of plants in the same latitude, and over a continuous area, due to different conditions of topography and rainfall. The southwestern United States — southern California and Arizona — show genuine desert conditions with an extremely characteristic flora, of which cacti, agaves, yuccas, sage-brush, etc., are the conspicuous features. This flora is closely related to that of Mexico, and to some extent to that of Pacific South America. As we pass eastward, the lofty ridge of the Rocky Mountains forms an effective barrier against the passage of some forms, and the heavier rainfall on the eastern slopes of the mountains, increasing

as the Gulf of Mexico is approached, is unfavorable for
the growth of the strictly desert plants. With the
increase in the rainfall, the desert gives place to a prairie
formation, with coarse grasses and many showy flowers,
phloxes, evening primroses, and gay Compositæ. Still
further east the amount of moisture is sufficient for the
growth of a few low-spreading trees like the "mesquit"
of the Texan plains, and in eastern Texas open forests
of pines appear, which presently give way to the dense
forests and swamps of the Gulf region of Louisiana.
Here the conditions are almost tropical. An extremely
heavy rainfall and high temperature combine to produce
a rank vegetation, forming deep swamps and jungle-like
forests. Very few of the plants occurring in these wet
forests and swamps are at all related to the desert plants
of the same latitude, but have their nearest allies among
the plants of the Atlantic side of the continent. The
eastern forests, unlike those of the Pacific slope, contain
few Conifers, but there is a remarkable variety of
angiospermous trees, most of which are deciduous.
Hickories, gums, magnolias, tulip-trees, elms, beeches,
and many other trees, quite absent from the Pacific
coast, are important constituents of this magnificent
forest flora, while the herbaceous plants associated with
them are quite as diverse in character. Among the
plants of the Gulf region are a number of genuine tropi-
cal types, like the "Spanish moss," the most northerly
representative of the pineapple family, and the palmet-
toes, the most northerly palms of the United States.

California, owing to its peculiar topography, has the
most varied flora of any region within the United States,
and is extremely interesting in respect to the origin of

its flora. The longitudinal ranges of mountains traversing the state form part of a continuous series of lofty mountains extending from Alaska to Mexico, and serve as a highway for the migration of many northern types, which are thus enabled to extend their range far beyond their usual southern limit. Thus in the mountains of northern California are found northern genera like Linnæa, and violets and trilliums like those of the northeastern states. With these occur also some northern Asiatic genera, like Fritillaria, which are entirely absent from eastern North America. In the northern part of the state, and in Oregon and Washington, many of the plants common to the sub-polar zone occur in the valleys, but further south they ascend the mountains and finally disappear entirely.

The most remarkable feature of the Californian flora is the extraordinary number and immense size of the coniferous trees. Evidently the conditions upon the mountain slopes of the Pacific coast are especially favorable for the growth of these ancient trees. A very even temperature, with heavy precipitation. has apparently been the reason for the survival of the last of the great Sequoias, as well as other Conifers not found elsewhere.

Southward, the rainfall in California diminishes very rapidly, and the conditions are unsuited to plants requiring much moisture. Consequently we find the northern plants giving way to immigrants from the dry regions south, *i.e.* from Mexico and South America. To the European or eastern American, the aspect of the great valleys of central and southern California is very unfamiliar, and entirely different from that of the moun-

tainous districts of the north. Instead of dense forests, with an undergrowth of dogwoods, rhododendrons, brambles, roses, and with the ground carpeted with mosses and ferns, we find the floor of the valleys and the rolling foot-hills covered with annual grasses, with which, in the spring, are mingled numberless showy flowers, unfamiliar to the eastern botanist except in gardens. Fiery Eschscholtzias, blue Nemophilas, pink and yellow Mariposa lilies, and numberless other flowers, make masses of brilliant color of unrivalled beauty. Here and there are scattered spreading evergreen oaks, and on the hillsides are thickets of low-growing shrubs, "chaparral," made up of Manzanita, Ceanothus, and other western types, while the streams are bordered with beautiful madroños (Arbutus), bay-trees, and big-leaved maples, as well as the more familiar alders and cottonwoods. The central part of the state is the meeting-ground for the two diverse floras, the northern types often following the cañons down to the valleys, where they mingle with the southern flora.

While the natural conditions of topography and climate have, of course, been the most potent factors in the present distribution of plants, animals have also played an important part, and especially man. The advent of man into many regions has quite transformed them, so far as the flora is concerned. In the tropics many of the most characteristic plants, such as the banana, breadfruit, cocoa-palm, and mango, as well as many weeds, like the sensitive plant, have become naturalized everywhere. So in temperate regions many introduced weeds have taken possession of the soil to the

complete exclusion of the native plants. Originally the whole of Atlantic North America was an unbroken forest, with an undergrowth of delicate shade-loving plants. With the clearing away of the primeval forest these plants quickly perished, and a host of foreign weeds, grasses, thistles, dandelions, docks, plantains, rushed in to occupy the waste room. As civilization pushed westward, the hordes of these European immigrants were met by the prairie plants, which were able to cope with them successfully, so that now the farmer has to contend with two sets of enemies, the European weeds on the one hand, and the prairie weeds, rag-weed, bur-marigold, Rudbeckia, sunflowers, etc., on the other These weeds are transported with grain in railway cars, or cling to the coats of animals or the clothes of human beings, and in these days of rapid transit, plants have also taken advantage of the improved means of travel.

In most parts of California, owing to the long dry season, most of the weeds from northern Europe do not thrive, and instead we find weeds whose home is upon the shores of the Mediterranean. Probably introduced by the original Spanish settlers, wild oats, alfilaria, bur-clover, and other south European plants have established themselves in the sunny valleys of California, where they grow side by side with the poppies and lupines, which, however, are quite able to hold their own.

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CHAPTER XIII

ANIMALS AND PLANTS

ANIMALS, being incapable of manufacturing organic food themselves, are necessarily dependent, directly or indirectly, upon plants for their supply of food; but, on the other hand, many plants depend, more or less completely, upon animals for their existence. While these are usually flowering plants, still among the lower forms of plant life many instances might be cited, especially among the parasitic fungi, like the insect-fungi, and some water-moulds. The same may be said of many of the pathogenic bacteria, or disease germs.

Occasionally insects appear to be useful to certain fungi by scattering their spores. Such fungi offer certain means of attracting insects, either in the form of a honey-like secretion, or their odor. Thus the evil odor given off by some fungi, especially the Phalloideæ, attracts carrion-loving insects, which carry away with them the spores which are imbedded in a slimy substance exuded by the fungus.

It is among the seed-plants, however, that we meet with the most obvious adaptations connected with animal organisms. The development of edible seeds and fruits in so many plants is, in most cases, directly referable to such adaptation. Where the seeds themselves are edible, of course a large proportion are destroyed by the ani-

mals which devour them, but a certain number of the seeds carried away are not eaten, and these are thus distributed more widely than would be the case were they to fall to the ground directly. Where the seed itself is not the edible part of the fruit, but is enclosed in an edible pulp, there is no question that we have to do with a case of special adaptation. In such cases, *e.g.* most of the ordinary cultivated fruits, the fleshy edible portion is eaten and the seeds rejected. Or, if the fruits are small, the whole fruit is eaten and the seeds pass uninjured through the body of the animal. Birds are especially important agents in the distribution of seeds, on account of the long distances over which they travel.

FIG. 54. — A, spikelet of a grass (*Hordeum murinum*), the long awn furnished with recurved barbs; B, part of the awn enlarged to show the barbs; C, fruit of bur-clover (Medicago); D, four spiny fruits of the common hound's-tongue (Cynoglossum).

Another method of distribution of seeds and fruits through the agency of animals is seen in the development of organs of attachment, such as the awns of grasses, the hooks and barbs developed by the fruits of many Compositæ, Borraginaceæ, etc. (Fig. 54). The pedestrian who returns from a ramble through the fields, covered with a varied assortment of "burs," is but acting as Nature's unwilling agent in the distribution of her plant children. Those plants which we call weeds — burdocks, beggar's-ticks, hound's-tongue, bur-clover — owe their success in the

struggle for existence largely to the perfect provision
for the distribution of their seeds which they have de-
veloped. Every animal which brushes against one of
these plants covered with its ripe fruits, carries away its
quota of seeds, to dislodge them far away from the place
where they grew. In this way many plants have been
carried from their European home to all quarters of the
globe, and where the conditions are favorable, have
quickly taken possession of the new territory.

The extraordinary variety shown by the flowers of
Angiosperms is intimately associated with the question
of cross-fertilization through the agency of animals,
mostly insects; and the extraordinary development of
certain groups of insects is the result of a reciprocal
adaptation.

There is little doubt that the first flowers were very
simple, probably not unlike those of certain low types
still existing, and consisted of a single carpel or sta-
men, or perhaps a group of sporophylls, without any
trace of the showy corolla found in the higher forms.
The simple flowers of the aroids, pond-weeds, peppers,
willows, and others (Figs. 43, 45, 49), are examples of
such flowers, and whether this simplicity is primitive or
secondary, some such forms must have been the starting-
point from which proceeded the development of the
specialized flowers of the higher groups of Angiosperms.
Such simple flowers are usually quite dependent upon
chance for the transfer of the pollen-spores to the stigma,
and with the exception of a few aquatic forms, the agency
by which this is effected is the wind; hence these flow-
ers are called "anemophilous," or wind-fertilized. These
anemophilous flowers are always inconspicuous and odor-

less. In such plants a large amount of pollen is necessary in order that fertilization may be insured, as a very large part of it fails to reach the carpels. An extreme case of this is seen in the pines and firs, where the amount of pollen is enormously in excess of what is actually needed for fertilization.

The development of contrivances by which the transfer of pollen to the pistil is facilitated, results in an obvious saving of pollen, and is in itself an advantage; but experiment has demonstrated that cross-fertilization, *i.e.* pollination of one flower by pollen from another one, is generally of advantage to the plant, as seed so produced is usually more vigorous than when the ovule is fertilized by pollen developed in the same flower.

The simpler flowers have no enveloping leaves, and the first step toward the development of a floral envelope or perianth was probably the production of small scale-like leaves, either green or membranaceous in texture. The change from these inconspicuous, purely protective floral leaves, to those which are more or less conspicuously colored, marks the next advance in the evolution of the flower. This bright-colored corolla would no doubt make the flower more conspicuous, and attract insects in search of pollen. Such an insect visiting the flower would be pretty sure to carry some of the pollen to other flowers of the same kind, insuring cross-fertilization. As a result of natural selection, it is easy to conceive how flowers having the showiest corollas would stand a better chance of attracting insects and thus being cross-fertilized. These plants would produce a greater amount of seed, and in

time, by further modifications of their descendants, other adaptations for cross-pollination would arise.

There are many genera, especially among the lower Dicotyledons, which exhibit in a most interesting way all gradations between inconspicuous self-pollinated flowers, and showy ones dependent upon insects. This is shown, for example, in the genus Ranunculus, which includes the various species of buttercup. The inconspicuous *R. abortivus* is entirely independent of insect aid, while such showy species as *R. acris* or *R. Californicus* are visited freely by insects, although they are probably not entirely dependent upon them to insure fertilization. Similar variation is found in the genus Geranium.

Fig. 55.—A, flower of *Anemone coronaria*, the petals absent, but replaced by the showy sepals, *s*; B, inflorescence of the dogwood (*Cornus florida*), the inconspicuous flowers, *fl*, surrounded by four showy bracts, *b*; C, the "calla-lily" (Richardia), with the central spike of small flowers enclosed by the large white "spathe," *sp*.

In the simplest of these "entomophilous" or insect-fertilized flowers, such as the buttercup or anemone (Fig. 55, A), the flower is wide open, with the entirely separate parts arranged radially, and often indefinite in number. We find in such generalized flowers that the variety of insects visiting them is large, and they are seldom incapable of self-pollination in case insect

visits are prevented.   In more highly specialized flow-
ers the parts are usually so modified as to restrict the
insect visitors to a smaller number; in extreme cases
often a single species, or a few species belonging to a
single genus.   Thus in the buttercup family we find not
only the generalized type of flower of Ranunculus, or
Anemone, but the highly specialized ones of the colum-
bine (Aquilegia) (Fig. 50), larkspur (Delphinium), and
monk's-hood (Aconitum).   In these the parts of the
flower are very much changed, and in the columbine
and larkspur deep nectaries are developed which are
accessible only to insects with long tongues, like
bumblebees or butterflies; or in the case of the scar-
let-flowered columbines, they are visited by humming-
birds.   It is interesting to note that in these extremely
specialized Ranunculaceæ there has been little depart-
ure in the number of parts from the primitive buttercup,
and all the parts remain quite separate.

It sometimes happens that the flowers themselves
remain inconspicuous, but are grouped together with
showy colored bracts about the inflorescence, and these
showy leaves serve to attract insects just as the petals of
other flowers do.   Familiar examples of this are seen in
the common "calla-lily," (Fig. 55), where the large white
spathe surrounding the small flowers is very conspicu-
ous, and many other aroids, such as species of Anthu-
rium, possess these showy spathes.   Another similar
case is that of certain species of Cornus, like the beau-
tiful dogwood (*C. florida*, Fig. 55, B), where the group
of small flowers is surrounded by four large white
bracts, the whole looking like a large four-parted flower,
and the tree when in bloom is exceedingly showy,

although the flowers themselves are inconspicuous. Many such cases occur in the Euphorbia family, one of the most familiar being that of Poinsettia, a common greenhouse shrub, having the flowers surrounded by numerous large, brilliant red bracts.

We have already seen that in the more specialized types of flowers there is usually a reduction in the number of parts, accompanied by a tendency to a coalescence of the members of each series of floral leaves, and this often results in the production of a funnel-shaped or tubular corolla which has the nectar secreted at the bottom of the flower, where it can be reached only by insects having a tongue long enough to probe to the bottom of the corolla. Much less frequently this tubular form of the flower is due to the cohesion of the sepals alone, the petals remaining quite distinct, as we see in some of the pink family, *e.g.* the carnation and catchfly. A study of such tubular flowers shows that they are, for the most part, pollinated through the agency of butterflies and moths, although some smaller insects may visit them for the pollen.

The characteristic odors of so many flowers are also lures for insects, and sometimes, as in the mignonette, this is the only means of attracting attention, as the flowers are very inconspicuous in color. Many white flowers have a peculiarly strong scent, which is usually most marked at night; indeed, some flowers are odorous only at night. An examination of these pale, night-scented flowers soon reveals the fact that they are especially adapted to attract night-flying insects, the white or pale yellow color, and strong odor, making them more readily found in the twilight, or even after it is quite

dark. A flowering vine of white honeysuckle, or a bush of the pale yellow evening primrose, may often be seen at dusk to be swarming with great sphinx moths, which, poised before the flowers like humming-birds, probe the deep, narrow trumpets with their long tongues. Passing from flower to flower in their search for honey, cross-pollination is almost certain to be effected.

While the chief agents in the pollination of flowers are insects, especially butterflies and bees, other animals also may be of importance in this connection. It is said that snails have been observed to convey pollen from the flowers of some aroids, but next to insects it is birds which play the most important rôle, especially the peculiar American group of humming-birds, which are preëminently flower visitors. Although in northeastern America there is but a single humming-bird, the little ruby-throat, several of the native flowers seem to have adapted themselves especially to its visits. Among the most striking of these humming-bird flowers, are the coral honeysuckle, cardinal flower, trumpet-creeper, crimson balm (Monarda), and wild columbine. All of these have deep, narrow nectaries, and scarlet is the predominant color. Of the garden flowers, which are especial favorites of the humming-birds, may be mentioned the various species of Canna, fuchsia, nasturtium (Tropœolum), and the scarlet Mexican sage. In California the fuchsia-like Zauschneria and the crimson-flowered currant (*Ribes speciosum*), as well as a number of other bright red flowers, are eagerly sought by the native humming-birds. It will be noted that nearly all these flowers are vivid red, a color which appears to be especially attractive to these little birds.

While at first sight it would seem that flowers having
stamens and pistil together would usually be self-pol-
linated, such is rarely the case, at least in showy flowers.
An examination of these reveals many effective arrange-
ments by which this is prevented and cross-fertilization
made necessary.   One of the commonest and simplest
means is the maturing of the stamens and pistil at dif-
ferent times.   Usually it is the stamens which are ripe
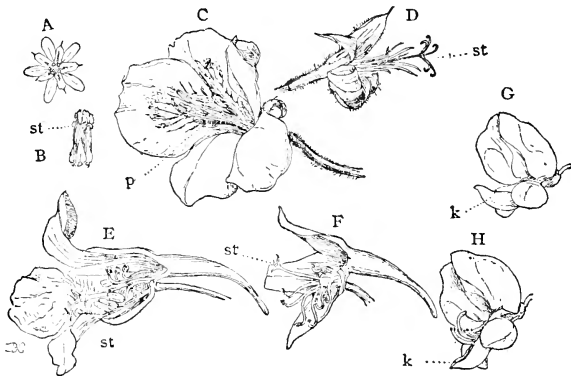
FIG. 56 (Cross-fertilization). — A, flower of Erodium, one of the Geranium
family; the flower is inconspicuous and capable of self-pollination; B,
stamens and carpels of Erodium; the stigmas, *st*, are mature when the
pollen is shed; C, young flower of Pelargonium; the pistil, *p*, is im-
mature; D, the pistil of an older flower which has shed the anthers;
the stigmatic lobes, *st*, are now ready for pollination; E, young flower
of a nasturtium (Tropœolum); three of the stamens are shedding their
pollen and occupy the space in front of the opening of the spur; the
other stamens are still closed, and with the immature pistil, *st*, are
bent down; F, stamens and pistil of an old flower; the stamens have
all shed their pollen, and the receptive stigma, *st*, now occupies the
position in front of the opening of the spur; G, flower of broom
(Sarothamnus); the stamens and pistil are included within the keel,
k; H, a flower which has had the keel forced down, liberating the
stamens and pistil.

first (proterandry), but proterogyry, or the earlier
maturing of the pistil, may also occur, *e.g.* the common

plantain. A familiar case of proterandry is seen in the common scarlet geranium and other species of Pelargonium (Fig. 56, C, D). The stamens are ripe at the time the flower first opens, and the pollen is shed almost at once, but at this time the stigma is quite closed, and the stigmatic surface cannot receive pollen. In the older flowers, after the pollen is shed, the five lobes of the stigma spread out widely and the stigmatic surfaces are exposed, but pollen must necessarily be brought from a younger flower.

A similar but more complicated arrangement is seen in the nasturtium (Fig. 56, E, F). Like Pelargonium there are seven stamens, which discharge their pollen before the stigma is in a receptive condition. The flower here is strongly zygomorphic, and the two lower petals are so placed as to form a resting-place for the bumblebees which are the commonest visitors to the flowers. In addition to this, two of the sepals are joined to form the long spur or nectary which the bee must probe for the honey contained at its apex. The seven stamens in a young flower are all bent downward (Fig. 56, E), but as they mature they rise, one by one, so that the open anther stands directly before the opening of the spur, and any insect seeking for honey must infallibly rub off some of the pollen. After all the stamens have discharged their pollen they turn down again, and their place is taken by the pistil, which has in the meantime elongated, and the three stigmatic lobes have opened and are ready to receive the pollen. The open stigma now occupies exactly the same position as did the open anthers, and any insect which has visited a younger flower is sure to deposit upon the

stigma the pollen brought from it. In both **Pelargo-nium** and Tropœolum self-fertilization is impossible.

The pea family offers many striking examples of flowers which are entirely dependent upon insects for pollination. The peculiar butterfly-shaped flowers of most of these have the stamens and pistil enclosed in the " keel " formed by the union of the two lower petals (Fig. 56, G, k). The pollen is discharged and forms a loose, powdery mass within the keel, but cannot reach the stigma owing to the presence of a brush of hairs between it and the stigma. If a bee alights upon the flower, in searching for the honey the sides of the keel are forced downward, and the apex of the pistil is exposed, usually springing out with some force and brushing out the pollen, which is thus dusted upon the visitor, which carries it to the next flower, where it is deposited upon the stigma. In some Leguminosæ, like the species of broom (Sarothamnus) (Fig. 56, G, H), the stamens and pistil are set free with a good deal of violence, and there is a small explosion when the keel is depressed, and the pollen is ejected with considerable force.

Certain parts of the flower may be sensitive to touch, and this is almost always connected with pollination. Thus in the common barberry the stamens are extremely sensitive and on being touched near the base, as happens when an insect is seeking for nectar, they spring inward with a quick motion and deposit the pollen upon the visitor. The trumpet-creeper (Tecoma), and other related plants have the stigma sensitive, the two lobes of which it is composed closing slowly after they are touched. This is possibly a provision for holding the pollen-grains deposited upon it, and perhaps hasten-

ing the germination. The mountain laurel (Kalmia) of eastern America has the stamens in the freshly opened flower bent outward, and the anther fitted into a little pocket from which it is set free by an insect visiting the flower; the suddenly released stamens spring inward much as in the barberry and scatter their pollen in the same way.

Among the sympetalous Dicotyledons the devices for effecting cross-pollination are often exceedingly perfect. Most of these have tubular and often two-lipped flowers which are very generally incapable of self-fertilization. The labiate flowers are usually horizontal or pendulous, and often adapted to special insects. Thus the common foxglove (Digitalis) is mainly visited by large bees, which creep into the bell-shaped corolla, where the back comes in contact with the open anthers which lie against the upper part of the corolla. Here the stamens mature first, so that ordinarily the pistil is pollinated by pollen from a younger flower, but it is said that in case insects are prevented from visiting the flower, self-fertilization is possible.

In various Labiatæ, or Mints, *e.g.* Lamium, Salvia (Fig. 57, A, B), the arrangements for cross-fertilization are very complete, and probably in both of these genera self-fertilization is impossible. In the former, while stamens and pistil mature about the same time, the stigma hangs below the stamens, and its receptive surface is turned away from them so that no pollen can fall on it from above, and a bee entering the flower, with pollen taken from another one, will touch the stigma and deposit the pollen upon it, before it comes in contact with the stamens. In the various species

of sage (Salvia) the flower is shaped much as in La-
mium, but the stamens are reduced to two, and the
pistil does not mature until after the pollen is shed, so
that self-pollination is quite impossible.   The anther
is very peculiar in form and balanced upon the short
filament, so that an insect striking against the lower
end of the elongated anther pushes the upper end,
with the pollen, down upon its back (Fig. 57, A).   At
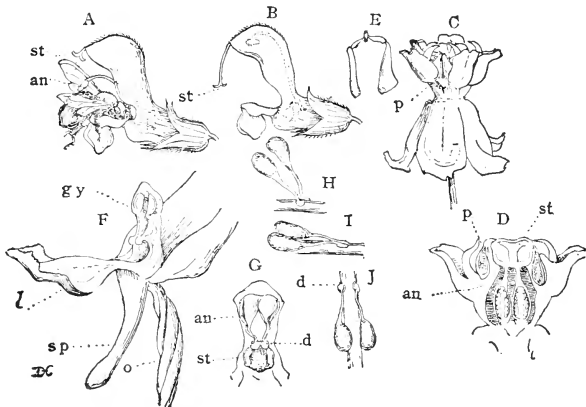
FIG. 57 (Cross-fertilization).—A, a flower of a sage, *Salvia pratensis*,
   showing the way in which a bee, visiting the flower, forces down the
   stamens so that the anthers, *an*, strike its body; the stigma, *st*, is not
   in a position to be hit by the insect; B, an older flower of the same;
   the style has elongated so that the stigma will be pollinated by a bee
   which has already visited another flower; the position of the undis-
   turbed stamens is indicated by the dotted lines; C, flower of a milk-
   weed (Asclepias); *p*, the cleft through which the pollinia are extracted;
   D, median section of the milkweed flower; *st*, stigma; *p*, pollen-mass,
   or pollinium; *an*, the base of the stamen; E, a pair of pollinia with-
   drawn from the anther; F, the flower of an orchid (*Orchis spectabilis*);
   the upper perianth leaves are bent back to expose the column, or gyno-
   stemium, *gy*; *l*, the lip prolonged backward into the spur, *sp*; *o*, the
   ovary; G, the column of F, seen from in front; *an*, the anther, con-
   sisting of the two receptacles, each containing a pollinium terminating
   in the disk, *d*; *st*, one of the stigmatic surfaces on each side of the
   opening of the spur; H–J, the pollinia removed from the anther, show-
   ing the change of position on exposure to the air.   (Figs. A, B after
   Noll.)

this time the style is still short, but in older flowers
(B) the style elongates and bends down, so that the
receptive stigma (*st*) occupies the same position as
did the anther in the younger flower; and when a bee
enters, with its back dusted with pollen, some of this
is certain to adhere to the stigma.

The milkweed family exhibits another peculiar method
of cross-fertilization. In the common milkweed (As-
clepias) the very peculiar flowers (Fig. 56, C) are
characterized by having the pollen in little packets
(pollinia) (Fig. 57, E), which are contained in closed
receptacles and can be dislodged only through insect
agency and by using considerable force. Indeed, it is
not unusual for the butterflies, which are the common
agents in pollination here, to have their tongues or legs
caught so firmly in the clefts through which the pollen-
masses are ordinarily extracted, that they are held fast,
and perish. The pollinia are provided with adhesive
disks by which they become firmly attached to the head
or legs of the insect, and are carried thus to other
flowers.

Most remarkable of all flowers, however, are some
of the orchids, among which, perhaps, are found the
most specialized of all floral structures. The flowers of
some orchids are of great size and wonderful beauty,
and some of them exhibit most marvellous contrivances
for insuring cross-fertilization. One of the simpler
types is shown in the figure (Fig. 57, F–J), and will
illustrate the character of these mechanical arrange-
ments. As in all orchids, one of the petals is modified
into the "lip" (*l*), which is prolonged backward into
a long hollow spur (*sp*), which forms the nectary.

The stamens (here reduced to a single one) and pistil are grown together into a "column" or "gyno-stemium." Like the milkweed, this orchid has the pollen-spores in two pollinia, club-shaped masses con-verging toward the base, where each terminates in a sticky disk covered over with a delicate membrane just above the opening of the spur (G, *d*). Each pol-linium lies in a little pocket from which it can be dis-lodged only through some external agency. An insect alighting upon the lip and probing the spur for nectar, must hit against the membrane which covers the base of the pollinia, and this is ruptured, and the adhesive disks are thus brought into contact with the head or tongue of the insect, to which they become firmly at-tached by the "setting" of the cement-like substance composing the disk. As the insect backs out of the flower, the two pollinia are dragged out of their recep-tacles and carried away. The action of the insect is easily imitated by inserting into the flower a slender stalk of grass, or the fine point of a pencil, which on being withdrawn will drag away the pollinia. The latter at first stand nearly vertical and diverge widely (H); but very quickly they change position, bending downward and forward until they lie nearly parallel and point almost directly forward (I, J). Thrusting the pencil-point with the pollinia in this position, into another flower, it will be found that the pollinia come into immediate contact with the two stigmatic surfaces on either side of the opening of the spur (Fig. 57, G, *st*), lower down than the anther.

Many other even more remarkable instances might be cited, but space forbids a further discussion of this

most interesting topic here. The works of Darwin, Müller, and others may be consulted by those who desire to become further acquainted with the really astonishing contrivances found among the orchids.

In most instances, flowers are visited by insects either for nectar or for pollen, but there are some exceptions to this. One of the most remarkable cases is that of various species of Yucca, which are most abundant in the arid regions of southwestern America. In the species which have been investigated, the agent in pollination is a small moth of the genus Pronuba, whose larvæ feed upon the young seeds. The moth deposits its eggs in the young ovary of the flower, and then deliberately crowds a mass of pollen into the canal of the stigma, thus insuring the fertilization of the ovules. The larvæ hatch and feed upon the growing seeds, some of which, however, are left uninjured, and ripen after the rest have been eaten by the larvæ.

A very remarkable group of plants are those known as " carnivorous " or " insectivorous " plants, which instead of being eaten by animals, themselves capture and devour insects and other small animals. In some instances, like the common sundew (Drosera) (Fig. 58, C, D) and Venus's flytrap (Dionæa), the insects are captured alive, and actually digested. In these plants the leaves are sensitive, and an insect alighting upon a leaf is either held fast by means of a sticky secretion, which increases in amount as the leaf is stimulated by the movements of the insect, and then slowly folds up about it; or, in Dionæa, the blade of the leaf is arranged much like the jaws of a spring-trap, and closes up quickly when the insect touches certain sensitive hairs upon

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its upper surface. The peculiar digestive fluid which is present in both cases is probably a direct product of the plant itself, although it has been claimed that it is due to the presence of certain bacteria, which are present in large numbers. Whether the digestive process is due to the secretions of the plant itself, or to the activity of the bacteria, the products of digestion undoubtedly serve to supply the plant with nitrogenous food.

FIG. 58 (Carnivorous plants). — A, leaf of the common pitcher-plant (*Sarracenia purpurea*) ; B, pitcher of a tropical pitcher-plant (Nepenthes) borne upon the end of a tendril, the opening protected by a lid ; C, leaf of a sundew (*Drosera longifolia*) ; D, leaf of Drosera which has captured a mosquito, showing the way in which the tentacles, *ten*, clasp the insect ; E, part of a leaf of bladder-weed (Utricularia), with the bladder-like trap, *v* ; F, a single vesicle of Utricularia more enlarged. (Figs. A, B after Goebel.)

The pitcher-plants, Nepenthes (Fig. 58, B), Sarracenia (Fig. 58, A), and Darlingtonia, are also striking examples of these carnivorous plants. All of these have the leaves modified into pitcher-shaped receptacles, into which insects are lured by the bright colors of the leaves as well as an abundant secretion of a honey-like substance. In most of them the upper part of the interior of the pitcher is lined with stiff, downward pointing hairs, below which the wall is very smooth, so that an insect which has fallen in cannot escape. A fluid is secreted by the pitcher, which partially fills it,

and acts, to some extent at least, as a digestive fluid.

The bladder-weeds (Utricularia) (Fig. 58, E, F) and the butterworts (Pinguicula) are also well-known examples of carnivorous plants. The former are aquatics, whose finely dissected leaves are provided with little bladder-like vesicles, which form perfect traps for small crustacea, and, it is said, in some cases for young fish. In all of these carnivorous plants, this peculiar habit is evidently a provision for providing them with nitrogen. They are always either bog-plants, or actually aquatic, and the roots are poorly developed or quite wanting, so that they are inadequate to provide the plants with the amount of nitrogen necessary for their growth, especially as the medium in which they grow is apt to be deficient in nitrogenous matter.

We find, among the higher plants especially, many devices for protecting them against the attacks of animals which seek them for food. These protective devices are of very different character in different forms. Thus many plants, such as the majority of perennial grasses, have creeping underground stems which send up leaves at a great many points, and these leaves are capable of continued basal growth, and may be eaten down close to the ground, growing up again promptly, so that the destruction of the plant is almost impossible. It is this tenacity of life which makes many of the grasses such troublesome weeds. It is extremely probable that the development of acrid or poisonous substances, or ill-scented essential oils, in the leaves of many plants, is primarily protective, and makes the plants offensive to animals. That these secretions do

not render the plants entirely immune, is shown, however, by the attacks of certain animals, especially insects, which have apparently adapted themselves to these peculiar conditions. Nevertheless, there is no question that such plants suffer very much less from animals than they would if these means of protection were absent. It has been thought that the sharp needle-like crystals or rhaphides, which occur so abundantly in many Monocotyledons, may deter animals from eating them, as many of them, especially the aroids, have an excessively acrid taste, which is supposed to be due to the mechanical irritation produced by these sharp crystals.

The presence of spines, thorns, and prickles, as well as rough hairs upon the stems and leaves, is doubtless mainly protective. They are usually most noticeable in plants of dry regions, where the scanty vegetation is peculiarly exposed to the attacks of herbivorous animals. The cacti are very perfect instances of this peculiarity. The terribly sharp thorns of these plants render them perfectly safe against the attacks of hungry animals, which eat them greedily if care is taken to remove their thorny armor. Where desert plants are not thorny, they are usually ill-scented and thus distasteful to herbivorous animals.

But one more of the most remarkable cases of reciprocal relations between plants and animals will be cited, namely, the peculiar arrangement known as myrmecophily, where ants inhabit certain parts of trees, to which, in return for shelter, and sometimes food in the form of honey-like secretions or peculiar albuminous fatty bodies, they protect the plants from the ravages of other

insects or larger animals. One of the best known cases of this kind is that of the tropical American genus Cecropia, trees with large palmate leaves, some species of which have the stems enlarged and hollow, serving as the abode of certain ants which keep away the leaf-cutting ants, which otherwise do great damage to the tree by eating the foliage. The leaf-cutting ants, in their turn, utilize the leaves for the formation of miniature hotbeds upon which they are said actually to cultivate a certain fungus which they use as food. Some species of Acacia develop large hollow thorns, which serve as shelters for ants which are also furnished with food-bodies like those of Cecropia, and in return protect their host against its animal foes. There are a number of other more or less well-authenticated cases of myr-mecophily.

CHAPTER XIV

INFLUENCE OF ENVIRONMENT

THE conditions for normal plant-growth are light, heat, moisture, and certain food constituents, including carbon dioxide, oxygen, and some nitrogen compounds. As these conditions necessarily are not constant in all cases, we find, as might be expected, a corresponding variation in different plants by which they have accommodated themselves to these varying conditions.

Most of the lower green plants are aquatic and all their cells are equally exposed to the medium in which they live. These plants being unicellular or composed of simple cell-aggregates made up of similar cells, each cell is capable of performing the different plant functions, which in more highly specialized plants are relegated to special cells. Each cell of these simple plants absorbs water containing the necessary food constituents in solution, and as all the cells contain chlorophyll, all are able to decompose the carbon dioxide dissolved in the imbibed water. The free oxygen needed by the plant is also taken in with the water. Associated with the aquatic habit of these plants is the power of active locomotion so often seen in their reproductive cells.

The marine forms allied to these simple algæ have become much changed in some respects, and notably in

the color of those which grow in deeper water. Most of the red algæ belong to this category, and the development of a special red pigment allied to chlorophyll seems to be a provision for increasing the absorption of certain of the light rays which pass through the water, and is doubtless concerned in some way, more or less directly, with the question of carbon assimilation. The brown and yellow pigments of the Phæophyceæ are probably purely protective, acting as screens for the chlorophyll when the plants are exposed at low tide.

Living in a medium which is of approximately equal density with the plant itself, most algæ develop no supporting or mechanical tissues, being buoyed up by the water in which they float; such forms on being removed from the water collapse completely. They also have no protection against the loss of water by evaporation, and this, when they are exposed to the air, is very rapid and complete. Where, however, water plants are exposed to the beating of the surf, as is the case in many of the large kelps and some red algæ, like the common Irish moss (*Chondrus crispus*), the cell-walls of the outer tissues become firm and cartilaginous in consistence, so that the plant is very tough and flexible and can endure the buffeting of the heavy surf without injury, and the mucilaginous nature of their inner tissues prevents too rapid loss of water when they are exposed to the air. These surf plants develop root-like holdfasts, which anchor them firmly, so that they can be torn away from their moorings only by the exercise of considerable force. In the largest of these kelps, as we have seen, the leaves are provided with floats

which bring them near the surface of the water where they may be exposed to the light.

One of the most important differences between fresh-water and marine algæ, resulting from the nature of their environment, is the different character of some of the reproductive parts. Owing to the constant level of the ocean, aside from the periodic fluctuation of the tides, marine plants are never exposed to the complete desiccation to which nearly all fresh-water plants are at times liable; nor is there nearly so much difference of temperature in the water at different seasons, as in the shallower and usually variable body of water in most lakes and rivers. We find, therefore, that the marine algæ do not develop resting-spores except in rare instances, but the spores are thin-walled or naked cells which germinate as soon as they are mature. Where the plants show a definite periodicity in their growth, as not infrequently occurs in the colder northern waters, the plant is usually perennial by means of a sort of root-stock, or rhizome, from which the annual shoots are produced.

Most fresh-water algæ, however, are plants of very limited growth, and are usually destroyed either by freezing or drying up at the end of their growing season. In the great majority of these are produced special reproductive bodies, usually resting-spores, which are capable of resisting extremes of temperature and dryness which would quickly destroy the actively vegetating plant. These resting-spores are commonly the result of fertilization, but not infrequently they may form non-sexually, as we find in various of the fission algæ, like Nostoc or Anabæna.

These resting-spores are usually produced, as in Œdogonium or Spirogyra, at the end of the plant's existence, after which the vegetative cells die, leaving the thick-walled resting-spores to carry the plant over to the next growing season.

These fresh-water plants are, as a rule, far more resistant to changes of temperature than their marine relatives, which frequently are killed very quickly by a slight rise in temperature in the water, this being especially marked in the deep-water red algæ, which are only adapted to an environment where the temperature remains almost constant and where they are protected from strong illumination. This great sensitiveness makes the cultivation in aquaria of most marine algæ exceedingly difficult.

The origin of the first terrestrial plants was due, probably, to the survival of some algal form, which, instead of dying as soon as the spores were ripe, continued to vegetate upon the mud after the subsidence of the water, as is still the case in a few algæ. Some of the lower liverworts, which probably resemble more nearly than any existing forms these primitive terrestrial plants, still show this amphibious habit, floating in the water during most of their life, but finally completing their development upon the mud left by the evaporation of the water. The capability of growing with a diminished water supply is an obvious advantage, and this is shown by the rapid evolution of these land plants which has resulted in an immense number of most diverse types.

The mosses, which are doubtless descended from aquatic ancestors, in adapting themselves to their new

terrestrial environment have become greatly modified. Thus there are developed various provisions against injury from loss of water, either by the plants as a whole acquiring the power of becoming completely dried up without being killed, or the outer tissues of the plant becoming more or less impervious to water; or the more delicate portions may be protected in various ways from the injurious effects of drouth. The tissues are always firmer than those of water plants, as the plant no longer is supported by the medium in which it is growing, but must depend upon the rigidity of its own tissues.

The spores in the mosses and all the higher plants have lost the power of locomotion possessed by the zoöspores of the aquatic algæ, and this loss of motion, as well as the thick walls with which they are furnished, are adaptations to the changed environment, where the spores depend for their distribution, not upon water, but upon air currents. It is interesting to recall that even in these terrestrial plants there is a reversion to the primitive aquatic condition when fertilization is effected.

The abandonment of the aquatic habit in the higher plants is associated with marked increase in the importance of the sporophyte, or non-sexual spore-bearing generation. This first results in the very marked alternation of generations in the Archegoniates, — mosses and ferns, — and finally has produced the seed plants, where the gametophyte is greatly reduced and is never capable of independent existence. The independence of the sporophyte, first found in the ferns, is associated with the development of special organs, stem,

leaves, and roots, and as soon as this stage was fully evolved, an entirely new type of plant structure had come into existence, which was destined to become the predominant type of the future, finally culminating in the great group of seed-bearing plants.

It is among the latter that there are found the most remarkable and perfect adaptations to special conditions. Being mostly terrestrial plants, they show, when compared with the lower plants, which are for the most part aquatic, a much greater development of mechanical tissues, by which the stem and leaves may be supported. The most highly developed of these mechanical tissues is the wood of the vascular bundles, which forms the great part of the skeleton of the stems of trees and shrubs, and also the framework of the leaves. The vascular bundles are first met with in the ferns, but occur in all the higher plants. In some vascular plants, like most Monocotyledons, the wood is poorly developed and of little use as a supporting tissue, and in these, as well as in many herbaceous Dicotyledons, the mechanical tissues of the stem belong principally to the outer part of the ground-tissue, especially the layers of cells just below the epidermis. These are frequently provided with thickened walls so that the mechanical tissue forms a cylinder just below the epidermis, which is itself often furnished with thickened cell-walls.

The woody tissue reaches its greatest development in the stems of those Conifers and Dicotyledons which increase in diameter from year to year owing to the presence of the so-called "open" vascular bundles, *i.e.* those in which there is a permanent zone of growing

tissue or cambium.   It is interesting to note that this
peculiar type of growth has developed quite indepen-
dently in several widely separated groups of plants,
apparently in response to similar conditions of growth.
Not only do we find it in the unrelated Conifers and
Dicotyledons, but also in certain Pteridophytes, both
fossil and recent.   In the Monocotyledons, when the
plant reaches tree-like proportions, the rigidity of
the trunk is brought about in part by a large develop-
ment of strengthening tissue in the outer part or cor-
tical region of the stem, and partly by the presence
of a great many separate vascular bundles, each of
which is usually surrounded by a sheath of supporting
cells.

The great mass of stems and foliage in the larger
flowering plants necessitates a very perfect system of
roots, both for anchoring the plant firmly in the earth,
and for supplying it with water and various food
elements.   In Gymnosperms and Dicotyledons, which
have woody trunks, there is very often a main or
tap-root which is a direct continuation of the stem,
and, like it, continues to increase in diameter
through the permanent growth by its vascular bundles.
In the comparatively small number of arborescent
Monocotyledons, like the palms and screw-pines, the
necessary support is given by a great many stout ad-
ventitious or secondary roots, which, however, are
usually incapable of secondary growth in thickness.
The screw-pines (*Pandanus*) are especially remarkable
in the development of these roots from points far above
the ground, and the trunk is often supported by a great
number of these, which form a conical mass of buttress-

like supports. The base of the stem of the common Indian corn shows the same thing on a small scale.

While the mechanical tissues are of course best developed in the stem and roots, the leaves, too, as we have intimated, may also be used to illustrate the formation of such tissues, and in Dicotyledons especially, the framework for supporting in the air the widely expanded leaves is very perfect. In Monocotyledons the leaves stand, as a rule, more nearly upright, and are commonly linear in form with a much less perfect skeleton than that found in most Dicotyledons.

Aquatic Plants

The contrast between the development of the mechanical tissues in closely related forms of aquatic and terrestrial plants is very instructive. Aquatic plants are of two kinds, those which are entirely submerged, and those with floating leaves. These two differ greatly in the character of the leaves, which in the former class are either narrowly linear or very much dissected so as to expose a maximum surface for the absorption of carbon dioxide. This is taken in directly by the superficial cells which, unlike those of most land plants, contain chlorophyll and have thin outer walls which allow of free interchange of fluids and gases. No cuticle is developed upon the epidermis, and the result of this is seen when these submersed aquatics are exposed to the air, where they wither up almost instantly, owing to the rapid evaporation of the water from them. Where the leaves float upon the surface, as in the various water-lilies, they are always broadly expanded and

usually almost circular in outline. Stomata are developed upon the exposed surface whose outer cell-walls are also cutinized, but are absent from below.

Many submersed aquatics have the roots imperfectly developed, serving merely as organs of attachment, or they may be quite absent, as in the common bladder-weed, Utricularia.   As these plants absorb most of their food from the substances dissolved in the surrounding water, the roots are much less important than in plants whose upper members are exposed to the air.   However, the development in rootless forms of special contrivances for procuring nitrogenous food, such as the traps of Utricularia (Fig. 58), would indicate that the roots, even of these submersed forms, are still of importance in absorbing nitrogenous compounds from the mud in which they are fastened.   Where plants float upon the surface, like the duckweed (Lemna), or Salvinia, there may be either true roots developed, or root-like organs which replace them.
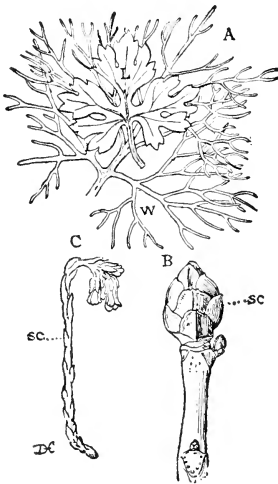
Fig. 59. — A, two leaves of an aquatic buttercup (*Ranunculus Purshii*); L, aerial leaf; *w*, submersed leaf; B, twig of horse-chestnut, showing a winter-bud protected by thick scales, *sc*; C, plant of pine-sap (Monotropa), a colorless saprophyte with rudimentary leaves, *sc*.

Most aquatic plants are entirely free from hairs or scales, so that the surface is smooth.   Exceptions to

this, however, occur in a few floating forms, *e.g.* Salvinia, Pistia, which are covered with hairs, but what the significance of this is, is hard to see.

XEROPHYTES

Very different from the plants we have been considering are the "Xerophytes," or dry-region plants, in which are developed all manner of devices for preventing loss of water, and thus resisting the effects of excessive dryness. This has been so successful that very few regions are so dry as to be absolutely destitute of vegetation.

The surface exposed to the air in these xerophytes is much reduced, the leaves being either extremely small or entirely absent, and the green assimilating tissue is confined mainly to the stem and branches, which may in some cases become flattened and leaf-like, as in many Acacias. Where the leaves are present they are either provided with very thick outer cells, so that they are hard and leathery in texture, like the oleander or manzanita, or they are covered with a dense felt of hairs, which forms a most efficient preventive against loss of water, and also acts as a shield against the too powerful rays of the sun. Many desert plants show this covering of hairs, which gives them their characteristic gray color.

The xerophytes are of course most perfectly developed in hot deserts such as those of the southwestern United States and northern Mexico, the Sahara, and many parts of Australia. The traveller passing through Arizona and New Mexico will find the vegeta-

tion thoroughly xerophytic in character. The giant cacti, Yuccas, sage-brush, and century plants give the scattered desert vegetation a peculiar aspect, which is not soon forgotten. The cacti are probably as perfect examples of adaptation to extreme desert conditions as can be found. In these the leaves have entirely disappeared and the plant in some forms is reduced to a single, enormously enlarged, often nearly globular stem, thus presenting the least possible surface, and reducing the loss of water to a minimum. The green tissues are protected by several overlying layers of cells with thick walls, the outer ones strongly cutinized so as to be waterproof. Nearly the whole inner mass of tissue is made up of thin-walled cells gorged with water, and forming a reservoir from which the slight loss of water at the surface, due to transpiration, is made good. Branches cut off and thrown upon the ground will remain alive for weeks before the water stored up in them is finally exhausted.

The Yuccas and the century plants (Agave) present a type somewhat different from that of the cacti. This is best seen in the century plant, where the leaves, instead of being absent, are very large; but like the stem of the cactus they are enormously thickened, and efficiently protected from loss of water by the heavily cutinized walls of the superficial cells.

Most of these desert plants, as we have indicated in a former chapter, are very efficiently protected against the attacks of herbivorous animals by their thorny armor. The terrible spines developed upon the cacti, and the dagger-like leaves of the Yuccas and Agaves, are quite sufficient to keep the hungriest animals at

bay. The protective character of the strong odors found in many plants of the same regions has also been referred to.

Where a region is subjected to well-marked wet and dry seasons, there are always a great many plants which pass the dry season in a dormant condition, very much as similar plants hibernate during the cold season of more northern regions. These plants generally develop bulbs or tubers, which may be completely dried up without injury. Bulbous plants are especially abundant in such semi-arid regions as central and southern California, the Cape of Good Hope, and the shores of the Mediterranean, where many bulbous Monocotyledons occur, among them some of the choicest garden flowers, like the various species of Narcissus, Iris, Gladiolus, etc.

While these special adaptations to resisting dryness are particularly well developed in the flowering plants, there are also many striking examples among the lower plants, especially among Pteridophytes and Bryophytes. In California many ferns become completely dried up during the long rainless summer, but some of them, like the gold-back fern (*Gymnogramme triangularis*), on being placed in water will revive immediately, the dried-up leaves unfolding and becoming fresh and green. The curious "resurrection plant," from the southern part of the state, is one of the club-mosses (*Selaginella lepidophylla*), and this has the same power of rapid resuscitation. Many mosses and liverworts show the same thing, the whole plant drying up completely and reviving almost instantaneously on being moistened. Less commonly in these plants

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special tubers are formed, somewhat as in so many flowering plants.

Sometimes instead of having the leaves much reduced in size, the trees and shrubs of dry, hot regions may have the position of the leaves such as to neutralize, to some extent, the power of the sun's rays. Instead of being placed horizontally, as most leaves are, in this class of xerophytes the leaf hangs vertically and both sides are alike. The various species of Eucalyptus, or Australian gum trees, show this in a very perfect way, and in western America there are a few examples, one of the best being the manzanita (Arctostaphylos) of the Californian mountains.

Many tropical trees, whose leaves at maturity show the normal position, have the young leaves pendent, so that they are protected from the full force of the sun's rays; these are also very commonly colored pink or crimson owing to the presence of red cell-sap in the outer cells, and this probably serves as a screen to protect the young chloroplasts.

It is interesting to trace the development of some of these modifications as they take place in the growth of the young plant. Thus the seedling Eucalyptus has broad, horizontal leaves, which also often occur in young shoots of the older trees, and these are gradually replaced by the pendent leaves with their vertically set lamina. In many of the Australian Acacias, where the lamina of the leaf is completely suppressed in the older plant, and replaced by the vertically flattened leaf-stalks, or phyllodia, the young plant has the feathery pinnate leaves characteristic of so many Leguminosæ, and the transition from these to the phyllodia is very

gradual.   As in Eucalyptus it is not uncommon to find
a reversion to the original leaf-form on young shoots of
the older trees.

Similar in their behavior to desert plants are the
"Halophytes," those growing along the seashore or in
salt marshes.   Thus the sea-rocket (Cakile), samphire
(Salicornia), ice-plant (Mesembryanthemum), and other
maritime plants show these peculiarities.   These plants
have fleshy stems and leaves and can live with very
little water.   The explanation of this peculiarity in
plants growing where there seems to be an abun-
dance of water, has been thought to be the fact that
the separation of the water from the salt solution is
difficult, and, moreover, the accumulation of salt within
the tissues of the plants, if free transpiration of water
from the surface took place, would be injurious to the
plant.

EPIPHYTES

Under the name Epiphytes are included those plants
which grow attached to others, but are not parasites.
While these epiphytes usually grow upon trees or other
plants, not infrequently they may attach themselves to
rocks or other inanimate objects.   Epiphytic plants are
most abundant in the moist, hot regions of the tropics,
but are by no means confined to these, since many
mosses, lichens, and liverworts which occur plentifully
in the temperate or even arctic regions, may be prop-
erly classed as epiphytes.   Of the ferns and flower-
ing plants, however, very few epiphytic types occur
outside the tropics, though there they form a most
characteristic feature of the vegetation.

These tropical epiphytes represent many families of flowering plants and also include a large number of ferns. One family of the latter, the exquisite filmy-ferns (Hymenophyllaceæ), are mainly epiphytic, and one of the most charming sights of the tropical mountain forests is exhibited by the trunks and branches of the trees, covered with the dark-green, finely cut fronds of these dainty ferns. In these dark forests, reeking with moisture, everything is covered with a mass of epiphytic growths, even the leaves near the ground being overgrown with lichens and creeping liverworts.

Of epiphytic flowering plants there may be recognized two categories — the lianas, or creepers, which, at first at least, are rooted in the earth, but may later, by developing aerial roots, become truly epiphytic; secondly, the true epiphytes, or "air plants," such as many orchids and Bromeliaceæ, like the "Spanish moss," which never are connected with the earth. These air plants abound everywhere in the tropical forests, and some of the epiphytic orchids are among the most beautiful of all plants. These showy species are, however, in a minority, as most of the tropical orchids are by no means conspicuous. The peculiarly American family, the Bromeliaceæ, includes a large number of curious epiphytes, some of which are showy plants with spiky leaves and large clusters of brilliantly colored bracts or flowers. The best known of these is the "Spanish moss," of the southern United States, but most of them are strictly tropical in their range.

Many species of Ficus, or fig, are epiphytic, while still others begin as epiphytes, germinating upon the

branches of trees, and sending down roots which finally reach the ground. These roots as they increase in number and size finally entirely envelop the trunk of the tree on which the fig is growing, and at last actually strangle it, so that the fig is left mounted on a hollow trunk composed of the more or less completely joined roots.

As true epiphytes have no root system to supply them with water, and are not connected with the earth, various devices have been developed for supplying them with the necessary moisture and soil-constituents. Many epiphytic orchids develop bulb-like enlargements of the leaf-bases, which serve at once for storing food and water, and may be almost completely dried up during their dormant season without injury. These orchids frequently have long, fleshy, aerial roots, which doubtless are important agents in absorbing moisture from the air. Most of the Tillandsias and many epiphytic ferns accumulate vegetable mould in their enlarged leaf-bases, which serve as reservoirs of moisture, and the scurfy scales with which the leaves of many species of Tillandsia are covered are also useful in holding moisture.

The various types of climbing plants may be considered in connection with epiphytes. Like these they reach their greatest development in the moist forests of the tropics, where the struggle for existence is the fiercest. The development of the climbing habit is doubtless associated with the competition of plants for the light. In more northern regions, where vegetation is less rank and the crowding not so great, fewer plants show this habit, but in the dense tropical forests climb-

ing plants are very numerous, and the tall trees are
loaded down with giant creepers which are striving to
reach the light overhead.   The means by which this is
accomplished are various.   Some plants climb by twin-
ing their slender stems about the support (Fig. 60, A),
like the morning-glory or hop; others develop special
climbing organs, ten-
drils (B, C), which
are either modified
branches or parts of
leaves.   The climb-
ing rattan palms, and
some other tropical
lianas, simply recline
over the branches of
trees, holding on by
stout hooked prickles.
A smaller number of
creepers, like the ivy
and various tropical
aroids, climb by
means of short root
tendrils.
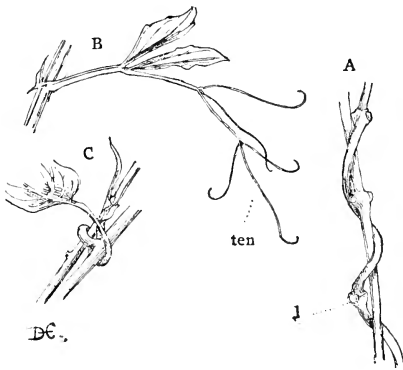
FIG. 60 (Climbing plants). — A, twining
stems of *Mandevillea suaveolens*; *l*, leaf-
scar; B, leaf of sweet-pea with the ter-
minal divisions transformed into tendrils,
ten; C, twining leaf-stalk of *Solanum
jasminoides*.

PARASITES AND SAPROPHYTES

Not to be confounded with the epiphytic plants are
the true parasites, such as the mistletoe and dodder.
Some, like the mistletoe and its numerous tropical re-
lations, species of Loranthus, are only partially para-
sitic, being provided with more or less chlorophyll, so
that they are capable of carbon assimilation.   In the

case of such complete parasites as the dodder (Cuscuta) or the gigantic Rafflesia of Sumatra, the plants are quite destitute of chlorophyll and completely dependent upon the host for their nourishment. In these the leaves are reduced to scales, and the plant sends root-like suckers into the host, or, in the case of Rafflesia and some related plants, the whole vegetative part of the parasite lives within the host, like a fungus, and only the monstrous flowers are borne upon the outside.

Similar in appearance to these parasites are a number of saprophytic plants which get their nourishment mainly from the decaying organic matter in vegetable mould or humus. Both leaves and roots in these plants are imperfectly developed (Fig. 59, C), and in some cases, at least, in common with many other plants, they are intimately associated with a fungus in the soil which seems to supply them with the food elements derived from the organic matter in the earth. The curious Indian pipe (Monotropa) and its more showy relation, the crimson snow plant (Sarcodes) of the Sierra Nevada, are examples of these humus plants. In all these parasites and saprophytes there is a marked degeneration of the assimilating organs, and this often extends to other parts of the plant, including the ovules and embryo.

SYMBIOSIS

A curious association of two plants together, or less often of a plant and animal, is a not uncommon occurrence, this "symbiosis" being apparently mutually beneficial, although sometimes it looks more like a case of parasitism. A number of liverworts, *e.g.* Blasia,

Anthoceros, and others, always have within the thallus colonies of a low blue-green alga, Nostoc, and the little water fern, Azolla, has in each leaf a cavity containing a colony of a similar alga, Anabæna. Just what are the mutual relations of the plants in these cases has not been clearly made out.

Somewhat different is the case of the lichens, where various low algæ, such as Protococcus or Nostoc, are included in a thallus whose principal constituent is a sac-fungus, whose hyphæ are closely united with the green cells of the algæ, and which is incapable of development if the algal cells are absent. The latter, however, grow perfectly well when removed from the lichen thallus, and it is doubtful whether they benefit, to any great extent, from their association with the fungus, except as they are sheltered and perhaps protected from excessive drying. Somewhat similar is the association of minute unicellular algæ with some of the lower animals, *e.g.* Paramœcium, Spongilla, Hydra, etc.

Among the most important cases of symbiosis are those existing between various organisms in the soil and the roots of flowering plants. The most noteworthy of these organisms are the nitrifying bacteria which are the principal agents in the preparation of nitrogenous matter in the soil, so that it is available for the higher plants. These peculiar organisms sometimes associate themselves directly with the plants, this being especially noticeable in the Leguminosæ, which are notably rich in nitrogen. In these, *e.g.* pea, clover, lupine, etc., there are developed upon the roots little tubercles within which are great numbers of minute bacteria, to whose activity is due the assimilation of nitrogenous

matter, to a certain extent the free nitrogen of the atmosphere, which otherwise is quite unavailable for plant food.

Finally, there is always found in connection with the roots of many trees, especially the Cupuliferæ (oaks, beeches, etc.), certain fungus filaments, or "mycorrhiza," which appear to take the place of root-hairs, and while parasitic to some extent upon the roots, nevertheless are of great importance to their host in supplying it with food from the soil.

PROTECTION AGAINST COLD

So far as can be judged from the geological evidence, the temperature of the earth was formerly more uniform than at present, and consequently the flora was also more uniform and composed of types which now belong to the temperate or sub-tropical zones. It is likely that a large part of these plants were evergreen, as is now the case in the warmer parts of the world. As the climate grew more severe with the oncoming of the glacial epoch, it is probable that the deciduous habit was developed in response to this, the only evergreen trees of high latitudes at present being the Conifers, most of which have retained their primitive evergreen habit.

Where there is each year a long period of cold weather, during which growth ceases entirely, it is clear that trees with broad leaves, exposed to the severe cold, and to loss of water by evaporation, are at a great disadvantage compared to those which shed their leaves at the end of the growing period and whose dormant buds are thoroughly protected by the thick scales developed about the winter buds of all deciduous woody

plants (Fig. 59, B). These trees and shrubs, with all their delicate tissues carefully protected against the effects of severe cold, can endure without harm a temperature which would quickly destroy any plant with broad evergreen leaves.

Most perennial herbaceous plants of cold climates also have special provision against the cold in the development of underground parts, bulbs, tubers or rootstocks, which remain dormant during the winter and send up their shoots, which grow very rapidly at the expense of the reserve food stored in these subterranean reservoirs, so soon as the first warm weather of spring starts them into growth.

MOVEMENTS OF PLANTS

We have seen that the lowest plants are actively motile and how this motility has been retained by the reproductive cells in all but the highest ones. The power of spontaneous movement is common, however, to the protoplasm of all plants, and in the higher plants movements of various organs are sufficiently familiar phenomena. These movements are, to a considerable extent, responses to external stimuli. The bending of growing parts of plants to the light, and the effect of light and temperature upon the opening and closing of many flowers are everyday occurrences. Not so familiar, except to the botanist, are the revolving movements of growing tips, especially in twining plants, which are among the most important factors in the twining. Many tendrils are exceedingly sensitive to contact, curving quickly in response to this pressure,

and no doubt this extreme sensitiveness is an advantage to the plant.

We have already spoken of the development of sensitiveness resulting in the movements of various parts of the flower, in connection with the subject of pollination.

The movements of leaves in response to stimuli of various kinds are especially developed in several groups of plants, of which the Leguminosæ are perhaps the most notable. The well-known sensitive plant (Mimosa) is the best known of these, but many common leguminous plants, like the species of clover, locust, beans, and many others, exhibit marked movements of the leaves, being especially sensitive to changes in the intensity of the light to which they are exposed. Thus most of these plants have the leaves folded up at night, exhibiting the so-called "sleep movements."

Movements of a purely mechanical kind occur in many plants, both among the lower ones and the flowering plants. The hygroscopic movements of the elaters of liverworts, or the peristome-teeth of the moss capsule, the opening of the sporangia of the ferns and of the anthers of flowers, are all good examples of this. These movements are entirely due to the unequal absorption of water by the cell-walls of the motile organ, or to unequal loss of water from them. Similar hygroscopic movements are exhibited by the awns of grasses and those attached to the fruits of other plants, *e.g.* the spirally twisted awn of the fruit in alfilaria (Erodium). The opening of most seed-vessels, such as those of the violet or balsam, are of much the same nature. All of these movements are connected with the dispersal of the spores or seeds.

CHAPTER XV

SUMMARY AND CONCLUSION

ALL plants agree closely in their essential cell structure, the typical cell having a cellulose membrane and a single nucleus. This simple type of cell constitutes the whole plant in many low forms and makes up the young parts of the higher plants. From it are derived the variously modified cell forms constituting the specialized tissues of these higher plants. In the lowest of all plants, the Bacteria and their blue-green allies the Schizophyceæ, the cell does not always show a cellulose membrane and the nucleus is imperfectly developed.

The lowest plants are mainly aquatic, and it is exceedingly probable that this is the primitive condition for plant life. Leaving aside the Schizophytes, whose affinities are somewhat doubtful, the peculiar group of motile green algæ, the Volvocineæ, probably represents more nearly than any existing forms the ancestral type of all the higher green plants. These ciliated algæ are also probably related to certain colorless flagellate Infusoria, which in turn may represent the starting-point for the whole group of Metazoa among the animals. It is not unlikely that the separation of the two great branches of organisms, plants and animals, took place among the Flagellata.

One important reason for considering the ciliated Volvocineæ as primitive forms in the very frequent reversion to this condition exhibited at times by very many of the higher green plants, whose reproductive cells, zoöspores, and gametes very generally are extraordinarily similar in structure to the simpler Volvocineæ. The persistence of motility in the reproductive cells is very remarkable, being found in members of all the groups.   The spermatozoids of the Archegoniates — mosses and ferns — illustrate this, and the recent discovery of similar motile cells in the lowest of the seed plants extends this phenomenon to the highest sub-kingdom.

Starting with this primitive motile unicellular organism, there have evidently arisen a number of independent lines of development resulting in very divergent types of structure.   The first step in the evolution of what may be termed the typical green plants is the loss of motility in the vegetative cells through the suppression of the cilia and the development of a firm cell-wall. The latter precludes the active locomotion, so characteristic of most animal forms, and makes the plant assume the more stable condition typical of the vegetable organism.

In these lowly organisms there is no clearly marked line between vegetative and reproductive cells.   An individual by simple fission gives rise to two new individuals like itself.   Many of these, however, show two kinds of cell-division, a purely vegetative one by fission into two equal parts, and a modification of this, internal cell-division, by which a number of individuals may arise by simultaneous division of the protoplasm of

the mother-cell after a preliminary division of the
nucleus into as many secondary nuclei. In the latter
case, the resulting cells may be non-sexual, or they
may exhibit the simplest form of sexual reproduction,
i.e. the cells may be similar gametes which unite in
pairs preliminary to the formation of new individuals.
These reproductive cells are usually motile and closely
resemble the ancestral Volvox cell.

If the two cells resulting from the fission of a uni-
cellular organism remain together, and this is re-
peated, there results a cell-complex, the simplest type
being the cell-row found in so many of the green
algæ, like Spirogyra or Conferva. The next step in
advance is the formation of filaments, like those of
Œdogonium, with definite base and apex, the filament
usually being attached by a simple holdfast. Next by
division in two planes is formed such a simple flat
thallus as that of Coleochæte. So far as is known at
present, this is the highest type the plant body assumes
among the Chlorophyceæ or green algæ except in the
case of the Characeæ, whose affinities with the other
algæ are doubtful. From some forms probably not
unlike Coleochæte, the lowest of the mosses were
derived.

The increasing complexity of the plant body has
been accompanied by a corresponding specialization of
the reproductive parts. Most of the green algæ have
both sexual and non-sexual reproductive cells, the latter
most commonly being motile zoöspores. The lower
members of the series have the gametes, or sexual cells,
alike, but in the higher ones the female gamete, or
egg, loses the power of movement and is retained within

a special cell, or oögonium, where it is fertilized by the much smaller motile spermatozoid.

Besides this line of Chlorophyceæ, which may be assumed to have given rise to the Bryophytes, there are several other groups which have branched off from the primitive stock. The most important of these are the Siphoneæ, characterized by the complete suppression of division walls in the often large thallus; and the two very important groups of marine algæ, the red and the brown sea-weeds, characterized by the special pigments developed, as well as other important peculiarities. It is among these marine algæ that there are found the largest and most complex of the Thallophytes, but this is not always associated with a corresponding perfection of the reproductive parts, which may be exceedingly primitive. Thus in the giant kelps, often hundreds of feet in length, so far as is known only non-sexual zoöspores of the simplest description are developed.

These great sea-weeds have been profoundly modified by their environment and have diverged widely in their structure from the primitive fresh-water forms which, in another direction, have given rise to the higher plants. It is exceedingly unlikely that either the red or the brown algæ have produced any higher types, but they themselves represent the highest expression of their respective lines of development.

The evolution of the sexual cells, *i.e.* the transition from the non-sexual zoöspores, first to similar gametes, and later to the separate male and female cells, has evidently been accomplished quite independently in several widely separated groups of plants,— *e.g.* Volvocineæ,

Confervaceæ, Siphoneæ, and Phæophyceæ, — so that the possession of sexual cells showing a similar grade of development does not by any means necessarily imply relationship.

The origin of the Phæophyceæ, or brown algæ, from free-swimming brown flagellate organisms, is by no means unlikely, and if this is shown to be the case, they must be considered as a line of development parallel with the Chlorophyceæ rather than an offshoot from these. It may also be said of the red algæ, that they may possibly constitute an entirely independent developmental line, but this is less likely than in the case of the Phæophyceæ.

The relationships of the Fungi is still an open question. Certain forms, the Phycomycetes or alga-fungi, especially the water-moulds and their allies, so closely resemble such siphoneous algæ as Vaucheria, both in the structure of the thallus and in the character of the reproductive cells, as to leave little doubt of their probable derivation from some such green ancestral forms. These Phycomycetes may be said to bear much the same relation to these green algæ that such parasites and saprophytes as the dodder and Indian pipe do to their green relatives among flowering plants.

The question of the relation of the true Fungi, or Mycomycetes, to these alga-fungi, is by no means so clear, although it is generally supposed that they have been derived from some such forms. Some authorities claim, however, that the two groups are quite independent of each other, and that the line of Mycomycetes has originated from chlorophyll-less plants of extremely simple structure.

The ancestors of the higher green plants must be sought among the simple fresh-water green algæ. The genus Coleochæte, the most specialized of the Confervaceæ, is the form which shows the nearest analogy with the lower Bryophytes, which it closely resembles in the development of a rudimentary sporophyte as the result of fertilization, and thus shows a very simple case of the alternation of generations so characteristic of all Archegoniates. In the mosses this becomes well marked, but there is a good deal of difference between the simplest of these and the highest green algæ, although the persistence of the motile spermatozoids indicates the derivation of the Archegoniates from aquatic ancestors.

The mosses, being mainly terrestrial plants, have developed much more perfect tissues than the Algæ, and in the ferns, which undoubtedly are related to them, this is still more marked. In both groups of Archegoniates, the reproductive organs, archegonia and antheridia, agree closely in structure, and the sporophyte always gives rise to spores which are formed in tetrads from a common mother-cell.

The Mosses (Bryophytes) show two well-marked series, or classes, Hepaticæ, or liverworts, and Musci, or true mosses. The former are the more primitive and show many points of resemblance to the Chlorophyceæ, and they are especially important as being the primitive stock from which the several series of archegoniate plants have diverged, bearing much the same relation to these higher Archegoniates that the green algæ do to the Thallophytes.

In the lower liverworts, the sporophyte, which arises

from the fertilized egg-cell, is very simple in structure, and is devoted almost exclusively to spore-production, having no power of independent growth, but living as a parasite upon the tissues of the gametophyte. Within the Hepaticæ, however, are forms in which the sporophyte becomes much more important, and in the genus Anthoceros, especially, it reaches a large size and becomes almost independent of the gametophyte owing to the development of several layers of green tissue communicating with the atmosphere by means of stomata, exactly as in the higher plants. Here, too, only a small part of the tissue is devoted to spore-formation, and the growth of the sporophyte does not cease as soon as the first spores are ripe. No root, however, is developed, and the sporophyte remains dependent upon the gametophyte for its supply of water and for such food elements as it cannot obtain from the air. The duration of its growth is therefore determined by that of the gametophyte.

The gametophyte in the Bryophytes may reach a very considerable size, and is sometimes quite complicated in its structure, but this does not necessarily correspond to the development of the sporophyte, which reaches its highest expression in forms with a very simple gametophyte.

It is in the Pteridophytes, or ferns, that the sporophyte first becomes entirely self-supporting. Here the embryo-sporophyte closely resembles that of the mosses, but soon develops the special organs, stem, root, and leaf, which distinguish the fern-sporophyte and render it independent of the gametophyte, which now withers away as soon as the young sporophyte is established.

The sporophyte here is a much more highly organized structure than the gametophyte, reversing the relation of these as found in the mosses. In the ferns it is the sporophyte which is had in mind when a fern is spoken of. The gametophyte (prothallium) is inconspicuous and usually of brief duration, but it must be borne in mind that the leafy fern plant, even the gigantic tree fern, is morphologically the equivalent of the moss capsule, or the still simpler sporogonium of the lower liverworts.

It is quite possible that the development of an independent sporophyte has taken place at more than one point, and that the different series of Pteridophytes have not all originated from a common stock. The biciliate spermatozoids of the club-mosses and the multiciliate ones of the other Pteridophytes favor this view, although all of the existing Pteridophytes closely resemble each other in the character of their reproductive parts.

Corresponding to the external differentiation of the sporophyte, there is a much greater diversity in the tissues of the Pteridophytes than is found in any of the lower plants, this being especially shown in the development of the complicated vascular bundles. The spores, too, are here restricted to a special organ, the sporangium.

The Pteridophytes, also, show traces of an aquatic ancestry in the development of spermatozoids, which require water in order that they may reach the archegonium, so that it is necessary for the gametophyte to be covered with water in order to insure fertilization.

With the increasing importance of the sporophyte,

there is a gradual reduction of the gametophyte. This in the lower forms is long lived and much like the simpler liverworts in its structure, and bears both archegonia and antheridia. Other forms develop male and female gametophytes from similar spores, and, finally, heterospory has arisen in several groups of Pteridophytes. In these, two sorts of spores are produced which on germination give rise respectively to exceedingly reduced male or female plants. Heterospory is found in several groups of living ferns, and in one genus, Selaginella, among the club-mosses. It is evident from a study of fossil Pteridophytes that it was also developed in the Equisetineæ. In Selaginella the germination of the spores begins within the sporangium, which sometimes falls away with the contained spores.

The permanent retention of the spores within the sporangium until the germination is complete, and the thickening of the sporangium-wall as a protection to the included gametophyte and embryo, the whole finally becoming detached from the sporophyte, is the origin of the seed of the higher plants, which is therefore only a further development of the macrosporangium of the heterosporous Pteridophytes.

In the seed plants, or flowering plants, the reduction of the gametophyte reaches its extreme, but there is no absolute break between Pteridophytes and Spermatophytes. The retention of the germinating macrospore within the sporangium has necessitated a different method of fertilization, hence the development of the pollen-tube. The lower Spermatophytes, especially the Cycads, while developing a pollen-tube from the germinating microspore, nevertheless produce spermato-

zoids within this, which are discharged, with the contained water, into the cavity above the archegonium, and fertilize the latter in the same way as among the Pteridophytes.

Comparing the homologies of the higher Pteridophytes and the flowering plants, we find that both produce two sorts of sporangia, macrosporangia and microsporangia, known usually among the latter group as ovules and pollen-sacs. In the latter, spores develop precisely as in all the Archegoniates from the lowest to the highest, *i.e.* by the division of each sporogenous cell into four spores. The macrosporangium, or ovule, of the Spermatophytes generally contains but a single macrospore, or embryo-sac, although there are some exceptions to this rule. Very often one or both of the preliminary divisions in the sporogenous cell are suppressed. The sporangia of the Spermatophytes are usually borne upon sporophylls — carpels or stamens — which are the homologues of the sporophylls of the Pteridophytes.

Of the Spermatophytes, the Gymnosperms are obviously the lowest types, *i.e.* they show more clearly their derivation from the Pteridophytes. Their more primitive character is borne out both by a study of their structure and by their geological history. It is not likely that all the Gymnosperms constitute a homogeneous class. It is much more probable that they represent the remnants of two, and possibly more, quite distinct developmental lines. The Cycads show close affinity with the true ferns, while the Conifers recall more strongly the Lycopods. Both of these groups, especially the Cycads, are much less abundant at the present time than in earlier periods of the earth's history.

The Angiosperms are preëminently the modern plant type. These have largely crowded out the other earlier types of vegetation, and at present comprise a large majority of existing species. In the earlier geological formations, Pteridophytes and Gymnosperms predominated; but as the later formations are examined, the Angiosperms become more and more important, probably first appearing in the Mesozoic age and rapidly increasing in number and variety in the more recent formations.

It is among the Angiosperms that the plant body reaches its highest expression. In the keen struggle for existence among the manifold forms of plants, the Angiosperms have shown themselves to be extraordinarily plastic, and have developed every possible device to enable them to survive this fierce competition. This is especially shown in the extraordinary variety of the floral structures to which they have given rise. The primitive flowers were doubtless very inconspicuous and, as in the case of many existing flowers of similar character, were dependent upon the wind or upon currents of water for conveying the pollen to the stigma. This uncertain mode of pollination involves a great waste of pollen, and evidently any device which insures a saving of pollen is advantageous. This has been accomplished by the adoption of insect aid in pollination. This probably began by the casual visits of insects to flowers for their pollen, some of which was transferred to the pistil of the next flower visited. Any flower which, by reason of its brighter color or stronger odor, made itself more noticeable to insects searching for pollen, would naturally stand a better chance of being vis-

ited by insects, and thus of insuring cross-fertilization, which appears to be distinctly advantageous to the plant. From these probably accidental variations have been developed the mechanical devices for insuring cross-fertilization, as well as infinite varieties of color and form, and the production of nectar and odors, serving as lures to attract insects. The extraordinary development of the Angiosperms and Insects, the two largest divisions of the vegetable and animal kingdoms respectively, is to a very great degree correlated, the two groups being largely dependent upon each other for their existence.

While provision for the development of seed is one of the most important functions of the plant, their distribution is also necessary, and many arrangements for this have been evolved. The development of edible seeds and fruits, and of the numerous organs like the wings of such fruits as those of the maple and ash, or the down in the thistle or milkweed, the hooks and prickles upon the fruits of many Compositæ and Borragineæ, are all devices for facilitating the distribution of the seeds through the agency of the wind or by animals.

Extensive modifications have arisen in the plant by which it adapts itself to a changed environment or protects itself against the attacks of animal enemies. The earliest plants were probably aquatic, and their descendants, but little changed, still exist in the low green algæ. The change from fresh to salt water has no doubt changed the marine forms profoundly, this being especially marked in the red and the brown algæ, which differ widely from their probably more primitive

green relatives of fresh water; but the modifications found in the Algæ are slight when compared with the profound structural changes exhibited by the Archegoniates and Spermatophytes, which have become adapted to terrestrial life.

With the change from the aquatic to the terrestrial environment the tissues have become very much better developed, especially the mechanical tissues which give rigidity and strength to the plant. The difference in the degree to which these are developed in closely related land and water plants is very noticeable, and is of course directly associated with the changed environment.

The degree of moisture varies extremely over land areas, and those plants which inhabit dry regions have become much changed, so that they are enabled to endure extreme dryness, either by having the surface exposed to the dry atmosphere much reduced through the partial or complete suppression of the leaves, or by having these very perfectly protected against loss of water by means of extremely thick impervious cells upon the outside, or by a thick covering of hairs or scales. Other xerophytes, or dry-region plants, are characterized by thickened underground stems which serve as reservoirs of water, or remain dormant during the dry period, starting quickly into growth with the advent of the brief rainy season.

Plants which are subject to extreme cold have developed protective structures similar to those of plants whose growth is checked by drought. These plants, too, often develop underground resting stems, which send up the annual shoots when spring arrives. The

deciduous leaves and winter buds of the woody plants of cold regions are, with little question, adaptations of a similar nature.

Normal green plants alone are capable of utilizing the carbon dioxide of the atmosphere, and those plants which have no chlorophyll must depend upon either living or dead organic matter for their carbonaceous food. Among the flowering plants, at least, these parasites, or saprophytes, are always evidently related to normal green forms, and are unquestionably secondary forms which are descended from chlorophyll-bearing plants. These parasites always show evidences of more or less profound degeneration, the leaves and roots usually being rudimentary, and the floral parts often sharing in this degeneration. This degradation of the reproductive parts in parasitic and saprophytic plants is especially noticeable in fungi, where in many instances all traces of the sexual reproductive parts are apparently lost. Among the flowering plants, the seeds of such forms are often very small and the embryo rudimentary.

Since light is of the first importance to all plants possessing chlorophyll, many adaptations are associated with this. Epiphytes and climbing plants of various kinds have developed their special habits of growth in response to the need of light. So also the development of special pigments associated with the chlorophyll is, in most cases, to be explained as being concerned with the question of light.

In short, we find that plants have succeeded in adapting themselves to almost every environment. From the open ocean to arid deserts and lofty mountain tops

some plants have succeeded in establishing themselves, and from the equator to the poles no district is completely wanting in some types of vegetable life.

Starting from indifferent unicellular organisms, intermediate in character between plants and animals, we have seen how there has been a steady progression in the direction of the more specialized plants. This progression consists in specialization of both vegetative and reproductive parts, which do not, however, necessarily advance equally. In the lower forms there is no clear distinction between the sexual and non-sexual plants, but in the highest green algæ this becomes recognizable, but is most clearly seen in the Archegoniates, where the alternation of generations is very conspicuous. In the lower Archegoniates the sexual phase, or gametophyte, is the more important, but in the higher ones the sporophyte becomes more and more prominent until, in the seed-bearing plants, the gametophyte is exceedingly rudimentary and may be reduced to a very few cells and is never capable of independent growth.

The angiospermous flowering plants are the most modern and specialized members of the vegetable kingdom, and have largely superseded the earlier plant types, although remnants of the latter persist, especially among aquatic forms, which have been subjected to less marked changes of environment and less keen competition in the struggle for existence.

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LESSONS WITH PLANTS.

SUGGESTIONS FOR SEEING AND INTERPRETING SOME OF THE
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